



Evidence for discrimination between feeding sounds of familiar fish and unfamiliar mammal-eating killer whale ecotypes by long-finned pilot whales

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Abstract

Killer whales (KW) may be predators or competitors of other cetaceans. Since their foraging behavior and acoustics differ among populations ('ecotypes'), we hypothesized that other cetaceans can eavesdrop on KW sounds and adjust their behavior according to the KW ecotype. We performed playback experiments on long-finned pilot whales (*Globicephala melas*) in Norway using familiar fish-eating KW sounds (fKW) simulating a sympatric population that might compete for foraging areas, unfamiliar mammal-eating KW sounds (mKW) simulating a potential predator threat, and two control sounds. We assessed behavioral responses using animal-borne multi-sensor tags and surface visual observations. Pilot whales barely changed behavior to a broadband noise (CTRL-), whereas they were attracted and exhibited spyhops to fKW, mKW, and to a repeated-tonal upsweep signal (CTRL+). Whales never stopped nor started feeding in response to fKW, whereas they reduced or stopped foraging to mKW and CTRL+. Moreover, pilot whales joined other subgroups in response to fKW and CTRL+, whereas they tightened individual spacing within group and reduced time at surface in response to mKW. Typical active intimidation behavior displayed to fKW might be an antipredator strategy to a known low-risk ecotype or alternatively a way of securing the habitat exploited by a heterospecific sympatric population. Cessation of feeding and more cohesive approach to mKW playbacks might reflect an antipredator behavior towards an unknown KW ecotype of potentially higher risk. We conclude that pilot whales are able to acoustically discriminate between familiar and unfamiliar KW ecotypes, enabling them to adjust their behavior according to the perceived disturbance type.

Keywords *Globicephala melas* · Acoustic playbacks · Killer whale ecotypes · Heterospecific sound discrimination · Multi-sensor tags · Cetacean behavioral responses

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Introduction

Individuals not only interact and exchange information intentionally, but they can also intercept unintended signals from conspecifics and heterospecifics, which can provide an additional gain of information at reduced cost for eavesdroppers (Peake et al. 2001; Blanchet et al. 2010). Such information gathering can benefit a wide range of fitness-enhancing activities such as habitat selection, foraging efficiency, adapted antipredator responses, or mate choice (Blanchet et al. 2010; Magrath et al. 2015).

Animal sounds play an important role for communication and species/individual recognition in many animals, including anurans, birds, insects, and terrestrial and aquatic mammals (Bradbury and Vehrencamp 1998). Moreover, in species such as bats and toothed whales, echolocation sounds can be important to find and track food or to navigate (Madsen and Surlykke 2013). Detecting heterospecific sounds can be particularly relevant in the dynamics of predator–prey interactions and interspecific competition (Dorado Correa et al. 2013). When prey species detect acoustic signals produced by their predator, they can evaluate the level of predation risk (e.g., identification of the predator species) and adopt the most appropriate antipredator strategy (Seyfarth et al. 1980; Manser 2001). For example, mule deer (*Odocoileus hemionus*) are able to acoustically discriminate among different predator species, i.e., coyotes (*Canis latrans*), mountain lions (*Puma concolor*), and wolves (*Canis lupus*), and respond differently according to the perceived level of threat (Hettena et al. 2014). Breeding songbirds can assess the spatial distribution of predators by listening to their vocalizations and then choose the most appropriate nest site, leading to increased reproductive success (Emmering and Schmidt 2011). On the other hand, listening to the acoustic cues emitted by species sharing similar ecological requirements (e.g., diet or habitat) can provide beneficial information such as the presence of potential competitors. Competing species may directly interfere, e.g., by aggressively attempting to exclude one another from particular habitats (interference competition), or indirectly by exploiting similar resources, e.g., by consuming similar food (exploitation competition) (Eccard et al. 2008). For instance, bats can eavesdrop on foraging echolocation signals produced by conspecifics and heterospecifics to locate feeding sites, thus reducing foraging costs (Balcombe and Fenton 1988; Uebernickel et al. 2012; Dorado Correa et al. 2013). Lemurs are able to acoustically identify heterospecific species competing for similar food and adjust their behavior accordingly to defend the area where they forage (Rakotonirina et al. 2016). Moreover, species can cooperate rather than exclude each other [e.g., in primates,

(Eckardt and Zuberbühler 2004)]. For instance, many bird and mammal species form mixed-species feeding associations which can improve their foraging efficiency (e.g., in birds, Monkkonen et al. 1996; in cetaceans, Jourdain and Vongraven 2017).

Cetaceans are typically social and vocal species. They rely primarily on sound to communicate with their conspecifics (e.g., in breeding context or to coordinate with their group members), to get information from their environment (e.g., to identify the presence of other species), and in toothed whales, to orientate and acquire food through echolocation (Tyack 2008). Most cetacean species have the ability to hear at least part of the frequency range of sounds produced by other cetacean species, enabling them to hear each other (Mooney et al. 2012). Cetaceans belong to a complex trophic network in which predation and competition interactions occur at various trophic levels (Paine 2006). Therefore, they represent interesting model species for studying heterospecific sound eavesdropping.

The killer whale (*Orcinus orca*) is present in all the world's oceans. As an apex marine predator, it has a unique position in the food web of marine ecosystems (Reeves et al. 2006). Killer whales can feed on a large diversity of prey including fish, cephalopods, birds, turtles, seals, dolphins, and whales (Foote et al. 2009; De Bruyn et al. 2013; Vongraven and Bisther 2014). From the point of view of other cetacean species, the killer whale can be, thus, considered as both a potential predator and/or a competitor for resources (e.g., habitat and prey). A wide variety of observed interactions have been reported between killer whales and other cetaceans (Jefferson et al. 1991) ranging from avoidance behavior (e.g., in beluga whales, Fish and Vania 1971), physical attacks (e.g., in gray whales, Ford et al. 2005), and feeding associations with approach responses (in humpback whales: Pitman et al. 2015; Jourdain and Vongraven 2017). To date, at least ten different forms of killer whales, also called “ecotypes”, have been recognized. Ecotypes can differ according to their prey preferences, distribution, social structure, foraging habits, acoustic behavior, physical features, and genetics (Jefferson et al. 1991; De Bruyn et al. 2013). Locally, populations often specialize on specific prey species, sharing hunting strategies with their group members and adapting their foraging techniques according to the type and availability of prey resource. All ecotypes produce echolocation clicks, pulsed calls, and whistles (Ford 1989). Substantial differences in acoustic behavior have been described across the different killer whale ecotypes (e.g., variation in call frequency or in vocal rate) (Foote and Nystuen 2008; Deecke et al. 2011; Filatova et al. 2015). Overall, fish-eating killer whales are very vocal during the whole period of foraging, relying mainly on echolocation clicks to find food and producing social calls and whistles to coordinate with group members (Simon et al. 2007; Holt et al.

2016). Moreover, herring-feeding killer whales stun herring using their flukes, which produces an audible signal (Simon et al. 2005, 2007). By contrast, mammal-eating killer whales are usually quiet at the early stage of a hunt, i.e., before attacking, probably to remain undetectable by their prey, and increase their vocalization rate (mainly calls and whistles) once the attack has been engaged, likely to coordinate group members and maintain group cohesion (Ford et al. 2005; Deecke et al. 2011). The fundamental frequency of calls of mammal-eating killer whales is slightly lower than those of fish-eating killer whales (Filatova et al. 2015).

Given the recognized importance of the use of sound in cetaceans and the particular trophic position of the killer whale, representing a potential predator or competitor for food and/or foraging areas to other cetacean species, we hypothesized that cetaceans are able to discriminate different familiar and unfamiliar killer whale ecotypes by listening to the sounds they produce. Such an ability to acoustically discriminate ecotypes might give other cetacean species the opportunity to evaluate whether they are at risk of increased competition or predation and to adjust their behavior accordingly at an early stage of potential encounters with killer whales.

We conducted our research on the northern Norway population of long-finned pilot whales (*Globicephala melas*), which live in sympatry with killer whales (Eskesen et al. 2011), although both species are rarely sighted together (Simila et al. 1996; Vester 2017). Long-finned pilot whales are social toothed whales that live in stable matrilineal groups and can temporarily form large aggregations with different groups (Visser et al. 2014). Their vocal repertoire includes clicks and buzzes used for echolocation and a variety of pulsed calls and whistles used for communication (Weilgart and Whitehead 1990; Vester et al. 2017). Long-finned pilot whales spend most of their time close to the surface and typically conduct bouts of foraging dives that can reach several hundred meters in depth (Sivle et al. 2012; Isojunno et al. 2017).

In the North-East Atlantic Ocean, killer whales have been reported to attack cetaceans including large baleen whales (humpback whales, McCordic et al. 2013). Killer whales have been also observed attacking long-finned pilot whales off Iceland (Donovan and Gunnlaugsson 1989), Greenland, and the Faroe Islands (Jefferson et al. 1991), although, to our knowledge, there are no such reports from Norwegian waters. In Iceland (pers. obs. by author P.W.), in Norway, and in the Mediterranean Sea (Strait of Gibraltar) (De Stephanis et al. 2014), long-finned pilot whales have been observed chasing towards fish-eating killer whales, with the killer whales fleeing away from the pilot whales. These observations have been interpreted either as the antipredatory behavior of pilot whales mobbing dangerous killer whales, or pilot whales chasing killer whales away from foraging areas that

might be exploited by both species. In the North Atlantic Ocean, long-finned pilot whales feed primarily on squid and occasionally eat small schooling fish (Desportes and Mouritsen 1993). In Norway and Iceland, long-finned pilot whales coexist with at least two forms of killer whales: one fish-eating ecotype that predominantly feeds on Atlantic herring (Simila et al. 1996; Vester and Hammerschmidt 2013), and one more generalist ecotype that feeds on both fish and marine mammals (seals and harbor porpoises) (Foote et al. 2009; Jourdain et al. 2017; Samarra et al. 2017). It might be also that long-finned pilot whales have experienced the presence of additional ecotypes in the North-East Atlantic Ocean such as the one observed feeding on large baleen whales, but no such interaction has been reported in our studied area off Norway. There, long-finned pilot whales may have the opportunity to learn that the calls of local herring-eating killer whales represent a relatively low threat, while, in contrast, it is expected that any other killer whale sounds, i.e., from familiar mammal-feeding killer whales or unfamiliar (fish- or mammal-feeding) killer whales, should be perceived as threatening as familiar mammal-feeding killer whale sounds (Deecke et al. 2002). Pilot whales hear well at the frequencies of killer whale vocalizations (Pacini et al. 2010) and, thus, may assess and respond to killer whale presence by eavesdropping on their vocalizations or other sounds which they produce such as tail slaps. Curé et al. (2012) showed that long-finned pilot whales were horizontally attracted to sounds of local fish-eating killer whales and that they joined with other pilot whale groups to form bigger groups. Based on their results, the authors could not resolve whether pilot whales perceived killer whale sounds as either a potential opportunity of feeding, explaining their attraction towards an identified food patch ('dinner bell' effect, Stansbury et al. 2015), or as a threatening stimulus (competitor or predator) that would have resulted in a chasing behavior as part of an active intimidation response.

To evaluate these questions, we conducted playback experiments and monitored the behavioral responses of long-finned pilot whales using multi-sensor tags and surface behavioral observations of the tagged whale and its group. We compared the behavioral responses of long-finned pilot whales to the playback of (i) familiar herring-feeding killer whale sounds simulating a local sympatric species exploiting similar foraging areas, (ii) unfamiliar mammal-eating killer whale sounds simulating a potential high level of predation risk (Deecke et al. 2002; Curé et al. 2015), and (iii) control sounds. We analyzed a wide range of behavioral variables typically observed in predatory, competition, and foraging contexts to test whether long-finned pilot whales display different behavioral response strategies according to the perceived stimulus playback, and particularly between sound playbacks of the two killer whale ecotypes. Specifically, we predicted that if a stimulus was perceived as a potential

threat, it should elicit fitness-enhancing behaviors such as reduced foraging activity, avoidance reactions, and social defense response strategies (e.g., approach, grouping). For perceived high-level threatening stimuli, we would expect particularly biologically costly responses such as a complete and prolonged cessation of feeding and/or extended avoidance responses. In contrast, a ‘dinner bell effect’ would be reflected by an approach response along with potential grouping behavior and initiation of search for food in non-feeding whales.

Materials and methods

Study species and general protocol

We conducted our study on free-ranging long-finned pilot whales encountered in the Norwegian Sea in May/June 2008, 2009, 2010, 2013, and 2014. The protocol consisted of the following phases: (1) Tagging operation in which a non-invasive multi-sensor suction-cup tag was attached to the whale using a 6 m carbon fiber hand-held pole (see details of the tagging protocol in Miller et al. 2012 and Visser et al. 2016); These tags are devices carrying a suite of sensors, which have been specifically developed to monitor the behavior of marine mammals and their response to sound continuously throughout the dive cycle (Johnson and Tyack 2003). (2) Baseline data collection of the tagged animal (focal follow) following a post-tagging period of at least 30 min to reduce potential effects of the tagging procedure; (3) Playback experiments (see next section); and (4) End of tracking after the tag released, and tag recovery. Tagging operations and playback experiments were carried out from a small motor boat (5–8 m) launched from the research vessel (55 m). In most cases, only one whale of a group was tagged, becoming the focal follow animal for which visual observations were collected from a dedicated observation platform on a vessel (20–27 m) continuously following the focal whale at a range of 300–500 m. In two cases, another whale associated with the focal group was tagged (Gm13_169b and Gm13_180b). These secondary tagged whales were not focal follow animals (no visual observations), but provided additional recorded tag data.

Playback experiments

The playback experiments used an M-Audio II microtrack player, a Cadence Z8000 amplifier, and a Lubell speaker LL9642T (described in details in Curé et al. 2012; Visser et al. 2016). Playback sounds were monitored using a calibrated hydrophone (Bruel & Kjaer 8105) placed 1 m from the speaker and connected to a charge amplifier (Bruel & Kjaer 2635) that was itself connected to an

M-Audio Microtrack II recorder. The playback boat from which the speaker was deployed in the water was positioned with respect to the playback subjects to provide a geometry designed to identify either horizontal attraction to or avoidance of the sound source.

We played four acoustic stimuli: two types of killer whale sounds produced by groups of 4–7 killer whales while feeding, and two types of control sounds. Control sounds were used to distinguish behavioral changes elicited in response specifically to the killer whale sounds from those induced unspecifically by other sounds in their environment. The two killer whale sound stimuli were: (i) familiar herring-eating killer whale sounds (fKW) recorded previously in the study area (expected to be perceived as a local competitor for food and/or resource territory), and (ii) unfamiliar mammal-eating KW sounds (mKW) recorded in the North Pacific (expected to be perceived as an increased potential predation risk; Deecke et al. 2002). Both types of killer whale sounds were previously recorded using animal-attached Dtags (Johnson and Tyack 2003). The two control stimuli were: (i) a broadband noise control (CTRL–) with most energy within the 0.5–10 kHz frequency band, corresponding to amplified non-calling periods taken from the recordings of the killer whale sounds (see Curé et al. 2012), and ii) a synthetic hyperbolic upsweep 1–2 kHz tonal signal (CTRL+) of 1 s duration repeated every 20 s, matching the dominant frequency range of many killer whale calls (Ford 1989). All playbacks lasted 15 min and stimuli were generated at comparable root-mean-square power, each within the range of the natural source levels of killer whale vocalizations (Miller 2006). The source level of the killer whale stimuli ranged from 147 to 154 dB re 1 μ Pa m (mean \pm SD: 151 ± 2 dB re 1 μ Pa m, $n = 3$ mKW, and 4 fKW stimuli). The source levels of the control stimuli were adjusted to match those of the killer whale sound stimuli, ranging from 145 to 151 dB re 1 μ Pa m for CTRL– (mean \pm SD: 148 ± 2 dB re 1 μ Pa m, $n = 6$ stimuli) and from 149 to 155 dB re 1 μ Pa m for CTRL+ (mean \pm SD: 152 ± 1 dB re 1 μ Pa m, $n = 3$ stimuli). The elapsed time separating the successive playback stimuli performed on a tested whale was set at ≥ 30 min, to include a recovery period of 15 min of post-exposure followed by 15 min of pre-exposure before the next stimulus. In some cases, this recovery period was shortened due to logistical constraints (e.g., weather conditions). For these cases (7 out of 27 playback trials, see Table 1), the pre-exposure phase of a given playback overlapped at least partly with the post-exposure phase of the previous playback trial.

For all stimulus types (except for CTRL+), three different versions (i.e., coming from different recordings) were used to avoid excessive pseudoreplication (McGregor et al. 1992).

Table 1 Overview of collected data

Whale tag ID	Playback signal	Playback order	Horizontal movement	Acoustics	Surface behavior	Dive data
Gm08_159a	fKW	2	(1;1)	(1;1)	(0*;0*)	(1;1)
Gm09_156b	fKW	1	(1;1)	(0;0)	(1*;0*)	(1;1)
<i>Gm09_156b</i>	<i>fKW</i>	2	<i>(1;1)</i>	<i>(0;0)</i>	<i>(1*;1*)</i>	<i>(1;1)</i>
LpW_10pm1 N	CTRL-	1	(1;1)	(0;0)	(1;1)	(1;1)
<i>LpW_10pm1 N</i>	<i>fKW</i>	2	<i>(1;1)</i>	<i>(0;0)</i>	<i>(1;1)</i>	<i>(1;1)</i>
<i>LpW_10pm1 N</i>	<i>CTRL-</i>	3	<i>(1;1)</i>	<i>(0;0)</i>	<i>(1;1)</i>	<i>(1;1)</i>
<i>LpW_10pm1 N</i>	<i>fKW</i>	4	<i>(1;1)</i>	<i>(0;0)</i>	<i>(1;1)</i>	<i>(1;1)</i>
Gm10_157b	CTRL-	1	(1;1)	(1;1)	(1;1)	(1;1)
<i>Gm10_157b</i>	<i>CTRL-</i>	2	<i>(1;1)</i>	<i>(1;1)</i>	<i>(1;0)</i>	<i>(1;0)</i>
Gm10_158d	CTRL-	1	(1;1)	(1;1)	(1;1)	(1;1)
<i>Gm10_158d</i>	<i>fKW</i>	2	<i>(1;1)</i>	<i>(1;1)</i>	<i>(1;1)</i>	<i>(1;1)</i>
Gm10_158d	CTRL-	3	(1;1)	(1;1)	(1;1)	(1;1)
<i>Gm10_158d</i>	<i>fKW</i>	4	<i>(1;1)</i>	<i>(1;1)</i>	<i>(1;1)</i>	<i>(1;1)</i>
Gm13_137a	HW	1	(1;1)	(1;1)	(1;1)	(1;1)
Gm13_137a	mKW	2	(1;1)	(1;1)	(1;1)	(1;1)
Gm13_149a	CTRL+	1	(1;0)	(1;0)	(1;0)	(1;0)
Gm13_149a	mKW	2	(1;1)	(1;1)	(1;1)	(1;1)
Gm13_169a	mKW	1	(1;1)	(1;1)	(1;1)	(1;1)
Gm13_169a	CTRL+	2	(1;1)	(1;1)	(1;1)	(1;1)
Gm13_169a	CTRL-	3	(1;1)	(1;1)	(1;1)	(1;1)
Gm13_169b	mKW	1	(1;1)	(1;1)	(0;0)	(1;1)
Gm13_169b	CTRL+	2	(1;1)	(1;1)	(0;0)	(1;1)
Gm13_169b	CTRL-	3	(1;1)	(1;1)	(0;0)	(1;1)
Gm14_180a	CTRL+	1	(1;1)	(1;1)	(1;1)	(1;1)
Gm14_180a	mKW	2	(1;1)	(1;1)	(1;1)	(1;1)
Gm14_180b	CTRL+	1	(0;0)	(1;1)	(0;0)	(1;1)
Gm14_180b	mKW	2	(0;0)	(1;1)	(0;0)	(1;1)

The presence or absence of a change score is indicated, respectively, by 1 or 0 for both change scores (PRE_DUR; PRE_POST). Horizontal movement indicates horizontal track collected by visual observations and/or by GPS logger attached to the tag. Surface behavior indicates collection of social parameters and surface behavioral events of the focal follow group. Acoustics and dive data indicate, respectively, sound recording and depth data collected from tags. The absence of a change score is due to missing data for one or more of the three phases PRE, DUR, and POST. Italic indicate cases for which the PRE period overlapped at least partly with the POST period of the previous signal playback. Numbers with * indicate cases with not fully recorded surface behavioral parameters. The code for the whales ID tagged with a Dtag are identified as Gm (for the species abbreviation, i.e., *Globicephala melas*), followed by the two last numbers of the year of conducted field work (08, 09, 10, 13, or 14), the day number of the year and a letter (e.g., 'a', for identifying the deployment of the day). Only one whale which was tagged with a Little Leonardo tag in 2010 has a different tag ID (LpW_10pm1 N). All tagged whales except two are focal follow animals. The other two non-focal whales (Gm13_169b and Gm13_180b) are secondary tagged whales associated with the focal follow group. Playback stimuli: CTRL- = broadband noise control playback; CTRL+ = 1–2 kHz tonal sound control playback; fKW = fish-eating killer whale sound playback; mKW = mammal-eating killer whale sound playback. Playback order indicates the order of stimuli presentation, since whales could be exposed from 1 to 4 playbacks

Data collection from tags and visual observations

Tag data were collected using movement and sound recording Dtags (Johnson and Tyack 2003) and in one case a movement recording Little Leonardo tag (Aoki et al. 2013) (Table 1). All tags were equipped with depth and three-dimensional accelerometer and magnetometer sensors,

sampled at 50 Hz for the Dtags and 10 Hz for the Little Leonardo tag. In addition, Dtags contained hydrophones that recorded stereo sound with 16-bit resolution at 96 or 192 kHz sampling rate. Some tagged whales (Gm13_149a, Gm13_169a, and Gm13_169b) were also equipped with a small Fastloc-GPS logger (Fastloc2, Sirtrack, New Zealand) attached to the Dtag. All Dtags contained a VHF transmitter

beacon that we used to relocate the focal whale when it surfaced. Measurements of bearing and visual estimates of range during surfacing events were collected to calculate the position of the tagged whale from the position of the observation vessel. Simultaneously, surface behavioral data of the focal tagged whale and its group were collected. The focal group was composed of all individuals in closer proximity to the focal tagged individual and to each other than to other individuals in the area (Visser et al. 2014). This definition is based on the relative spacing of individuals to each other. All individuals with a similar distance to each other are part of a group (distance in body lengths, with categories ranging from < 1 body length, to > 15 body lengths, see Visser et al. 2014 for details). Whale positional data and visual behavior observations were recorded using the software Logger at minimum 2 min intervals when the tagged whale was present at the surface (see Visser et al. 2014 for protocol details).

Processing of the data

We converted the tag's pressure data to depth and plotted vertical and horizontal movements throughout the deployment period using Matlab software (version 7.8.0; www.mathworks.com). We used the Dtag's acoustic recordings to identify sounds produced by the tagged whale or nearby conspecifics. Specifically, we inspected spectrograms (Blackman–Harris window; FFT length: 4096; time resolution: 21.3 ms) of the acoustic recordings using Adobe Audition software and manually identified the production of clicks, buzzes, and calls/whistles. Each annotated sound was categorized according to its amplitude (see detailed method in Miller et al. 2012). Sounds were classified by their perceived signal-to-noise ratio following the method of Alves et al. 2014, in which loud (as perceived by the auditor) and clearly visible sounds on spectrograms were considered likely to be produced by the tagged whale or nearby individuals, while faint and barely detectable sounds (i.e., low signal-to-noise ratio) were considered likely to have been produced by more distant whales. Only sounds likely produced by the tagged whale or nearby animals were included in further analysis. Horizontal tracks of the focal whales were obtained from the collected measurements of the relative bearing to the whale, visual estimates of observer-whale range, and the GPS location and course of the observation vessel. Where available, GPS locations recorded by the GPS logger were also included in the horizontal track. In one case, a non-focal tagged whale (Gm13_169b) had a GPS logger, allowing us to obtain also the horizontal track of the non-focal whale. The accuracy of such Fastloc-GPS positions is comparable to that of the visual position fixes and generally in the order of tens of meters, but dependent upon other factors (Wensveen et al. 2015a). The tagged whale's direction of

movement was calculated from the horizontal track as the true bearing from the previous location. Horizontal speed was calculated as the ratio between the distance and time between two successive locations of the tagged whale. To quantify the degree of aggregation, coordination, and surface activity of the focal group, we recorded seven metrics from surface observations following Visser et al. (2014): (1) focal group size; (2) number of individuals in the focal area (i.e., within 200 m of the focal animal); (3) distance to the nearest other group; (4) individual spacing (5) surfacing synchrony, and (6) presence/absence of logging events in the focal group (i.e., whale horizontally floating at the surface), and (7) number of spyhops (i.e., brief event for which the whale positions itself vertically with head out of the water).

Assessment of changes in behavior

We used two different analytical approaches to detect behavioral responses of the pilot whales exposed to the acoustic stimuli: (1) an expert panel scoring the severity of behavioral responses by inspecting standardized plots of multivariate time series, and (2) univariate analyses of a range of behavioral variables.

Severity scoring panel method

Expert identification and scoring of responses was used to evaluate the severity of behavioral responses on a numeric scale (Southall et al. 2007) ranging from no effect (0), effects not likely to influence vital rates (severity scores 1–3), effects that could affect vital rates (severity scores 4–6), and to effects that are likely to affect vital rates (severity scores 7–9). The severity score of a response depended on the type of behavioral response and its duration relative to the duration of the playback (Southall et al. 2007; Miller et al. 2012; Sivle et al. 2015). The behavioral responses in the 2008–2009 data sets (two whales with Dtags) were scored by Miller et al. (2012), and the 2010, 2013, and 2014 data set (eight whales with Dtags) were scored in the present work in exactly the same way. The behavioral changes were described and scored based on the inspection of the geographic track plots and time-series data plots generated from Dtag data and visual observations; changes were scored by two independent scorer panels in accordance with the severity scale (see Fig. S1 for example plots). One panel consisted of authors C.C., S.I., P.W., and P.M., and the other of authors F.V., L.S., and two more scorers. All scorers are expert scientists in this field of research. Since most of them participated to conduct fieldwork and data collection, they could not be blind to the experiments. Thus, panels were blind to each other's scoring but not blind to the experimental condition. Thereafter, the two panels compared and assimilated their results in the presence of an adjudicator

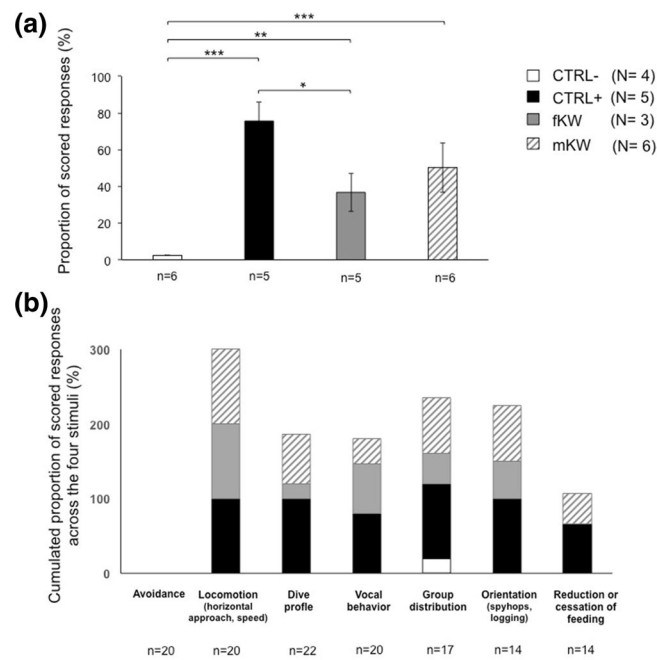


Fig. 1 Severity scoring panel results. **a** Proportion of scored behavioral responses (all 7 behavioral response types combined) for each of the four stimulus types (in %, shown as mean \pm sem). This proportion is expressed as the number of behavioral metrics for which a non-zero score was attributed, normalized to the maximum number of potential scorable behavioral metrics. As an example, CTRL+ playbacks induced 75.6% (\pm 10.4) of scored behavioral responses among the potential maximum 100%. *P* values are from GEE results of the paired comparisons across the four stimulus types (Table S4) and are given as **p* < 0.05, ***p* < 0.01 and ****p* < 0.001. **b** Cumulated proportions of scored responses for each of the seven behavioral response

categories of the scoring panel across the four stimulus playback types (%). As an example, avoidance responses never occurred during any playbacks (0% whatever the stimulus playback type), whereas change in locomotion (horizontal approach towards the source) was the most common response type (100% of the CTRL-, fKW, and mKW playbacks). CTRL- = broadband noise control playback; CTRL+ = 1–2 kHz tonal sound control playback; fKW = fish-eating killer whale sound playback, mKW = mammal-eating killer whale sound playback, *N* number of tested individuals; *n*: number of playback trials

(P.T.) to reach a consensus scoring. The adjudicator and 6 of the 8 scorers had previously scored long-finned pilot whale responses using a similar scoring procedure (Miller et al. 2012); therefore, we are confident that the new scoring effort is consistent with Miller et al. (2012). Overall, 80% of the attributed scores were similar between both teams; among the 20% that differed and needed discussion, none of them required the adjudicator for reaching a consensus. This indicates that the scoring measures of this study were highly reliable across scorers.

For each exposure experiment, panels inspected the multivariate data plots and scored the occurrence and severity of seven behavioral metrics (see Table S1): avoidance of the sound source, change in locomotion, change in orientation, change in the dive profile, impact on feeding (based on alteration of the production of regular foraging clicks and buzzes), modification of vocal behavior, and change in group distribution. For all scored experiments, we distinguished between a score of 0 (no behavioral change) and the absence of a score. The absence of a score for a particular behavioral metric could have resulted from either missing data (e.g., no acoustics on some tag data because of recording failure and

no social behavioral data of non-focal whales) or because of a particular behavioral context (e.g., cessation of feeding could only be assessed for animals that were actually feeding before the start of the exposure). Then, for each experiment, we quantified the proportion of scored behavioral metrics (%), expressed as the total number of behavioral metrics for which a non-zero score was attributed, normalized to the maximum number of potential scored behavioral metrics (i.e., excluding cases for which scores could not be assessed) (Table S2).

Quantitative (univariate) analysis of behavioral metrics

We defined three experimental phases for each sound playback: PRE (period preceding exposure), DUR (during exposure), and POST (period following end of exposure). The DUR phase always lasted the duration of the playback (i.e., ~ 15 min), the PRE and POST phases each lasted 15 min where possible, but could be shorter due to logistical constraints. For each numerical variable, we calculated two behavioral change scores (Table S2): (1) the difference

between the DUR and the PRE experimental phases, reflecting any behavioral change induced during the sound exposure (change score PRE_DUR) and (2) the difference between the POST and the PRE exposure periods, indicating whether the behavioral change lasted (or eventually started) after the end of exposure (change score PRE_POST).

For the univariate quantitative analysis, we defined and investigated behavioral metrics reflecting the three main types of pilot whale behavioral responses expected to occur in case of any perceived threatening or ‘dinner bell’ stimuli: avoidance/approach responses (both horizontal and vertical), modification of the group structure and surface behavioral displays, and changes in foraging activity.

A dive was defined as having a maximum depth > 5.3 m and/or a duration > 37.8 s (based on a mixture model of the same tag deployments, Isojunno et al. 2017). Non-dive periods were called ‘near-surface’ behavior. First, for each phase, we calculated the ratio between the total duration of the near-surface periods and of the diving periods, as a proxy for time budget spent near the surface versus diving. To investigate whether animals made dives to probe for information at the depth of the speaker or whether they attempted to avoid the source by moving deeper or shallower, we classified the dives into three categories based on their maximum depth: (1) shallow dives, at depths < 5 m (but which had a duration of 37.8 s or longer); (2) dives performed within the depth range of the speaker, ≥ 5 m and < 10 m; and (3) dives at depth ≥ 10 m, likely to include foraging dives. Then, for each phase, we assessed the proportion of time spent in each of these three dive categories (%).

Regular clicks and buzzes produced during dives were attributed to foraging activity, whereas calls, whistles, and buzzes produced near surface were attributed to social contexts (in Risso’s dolphins: Arranz et al. 2016; in long-finned pilot whales: Visser et al. 2016). For each experimental phase, we calculated four acoustic variables: the proportion of time clicking while diving (%), the occurrence of calls (#calls per min), the occurrence of buzzes (#buzzes per min) produced at depth (i.e., while in a dive mode), and the occurrence of buzzes produced near surface. Because the buzz rate at depth was particularly variable across animals, we inspected the frequency distribution of the calculated change scores PRE_DUR and PRE_POST (see Fig. S2). This analysis showed that most change scores values ranged from -0.25 to $+0.25$ (arbitrary unit), whereas the other values were spread out with values < -0.25 and $> +0.25$. Based on this, change scores of buzz rate at depth were converted to -1 if < -0.25 buzz/min (reduction of buzzing), $+1$ if > 0.25 buzz/min (increase of buzzing), and 0 if ranging between -0.25 and $+0.25$ buzz/min (very weak or no change in buzz rate).

Horizontal approach or avoidance was quantified by calculating a movement reaction score which was based on the

comparison between the observed horizontal track during the playback and the projected course of the whale given its direction of movement during the PRE phase (method detailed in Curé et al. 2012). Positive or negative movement reaction scores (arbitrary units) indicated, respectively, a horizontal attraction or avoidance response to the playback. We also calculated for each phase the mean horizontal speed.

For each phase, we recorded maximum focal group size and maximum number of animals in the focal area, minimum distance to nearest other subgroup, mean individual spacing and surfacing synchrony, presence/absence of logging events, and the rate of spyhopping (#spyhops per min) (Visser et al. 2014).

Statistical analyses

To account for repeated measures (whales were exposed to several sound playbacks) and cases in which two whales of the same group were exposed to a playback, we used Generalized Estimating Equation (GEE) models that allowed us to specify a blocking unit (the focal group ID) within which observations can be correlated (Hardin and Hilbe 2002). Statistical analyses were performed using geepack (Carey et al. 2012) in R v.3.0.2 (R Development Core Team 2013).

For the severity scoring variable, i.e., proportion of non-zero scored responses per stimulus type, we tested whether the two covariates *Signal* (four factor levels: CTRL+, CTRL-, fKW, and mKW) and playback *Order* (two factor levels: first and later than first) had an effect on the response variable. For the univariate analysis approach, we tested whether the three covariates *Signal*, *Order*, and *Period* (two factor levels: PRE_DUR and PRE_POST), as well as the two-way interaction term *Signal:Period*, had an effect on the change scores calculated for each of the behavioral response variables. All explanatory variables (i.e., *Signal* and *Order* for the proportion of scored responses; *Signal*, *Order*, *Period*, and *Signal:Period* for the other variables) were included in the full GEE models of all variables except for the horizontal movement reaction score for which there was no *Period* covariate (because only the change score PRE_DUR was assessed). The change score values of the univariate analysis variables and the severity scoring variable were modeled as Gaussian response variables, and the blocking unit was the tagged whale group ID (accounting for possible dependencies in the two cases for which the data included the focal tagged whale and a secondary tagged non-focal whale of its group). As the Sandwich variance estimator can be biased for small sample sizes, a Jackknife variance estimator was applied. For all GEE models, we first ran the full model with all candidate explanatory variables. We conducted hypothesis-based model selection using *p* values given by an ANOVA (sequential Wald test) and backward selection [detailed method in Curé et al. (2015)]. After fitting each model, an ANOVA was conducted and the covariate or interaction term with the highest *p* value was removed and the

GEE model refitted. This was repeated until all terms retained in the ANOVA were significant at 5% level.

Results

We tested nine groups of long-finned pilot whales of which seven groups had one tagged whale, and two groups had two tagged whales. Out of the 11 tagged whales, 8 were exposed to CTRL–, 5 to CTRL+, 7 to fKW, and 6 to mKW playbacks (see Table 1). CTRL+ and Mammal-eating KW playbacks were conducted in 2013 and 2014. CTRL– and fish-eating KW playbacks were conducted in 2008, 2009, and 2010. Part of data of individuals tested in 2008, 2009, and 2010 were used in the previous work to describe responses to the fish-eating killer whale sound playback (Miller et al. 2012; Curé et al. 2012) and/or to contrast them to responses to naval sonar as part of a parallel project (Visser et al. 2016; Isojunno et al. 2017).

The total number of playback trials conducted per group tested ranged from 1 to 4 with an average (\pm sem) recovery period between two successive playbacks of 37 ± 11 min ($n = 14$ recovery periods). Nine of those playbacks were played before any other stimuli (at first order #1) and 17 were played as second, third, or fourth order (different than #1). We excluded three playback trials (two playbacks of Gm09_138a and the first playback of Gm08_159a) from the data set, because the tagged whales were too far from the sound source to detect sounds (see Curé et al. (2012)). The first playback of Gm13_137a consisted of an unfamiliar humpback whale song stimulus (HW) that was not included in the statistical analyses since $n = 1$. The tagged whales Gm08_159a and Gm09_156b presented in Table 1 were previously exposed to sonar sounds as part of a parallel project (Kvadsheim et al. 2009).

Severity scoring panel results showed that CTRL– and CTRL+ playbacks were associated with the lowest (2.4%) and highest (75.6%) proportion of scored responses (i.e., % scored responses different from 0), respectively. fKW and mKW sound playbacks, respectively, resulted in 36.8% and 50.3% of scored responses (Fig. 1a). Moreover, the highest severities were scored during CTRL+ and mKW playbacks with a maximum score value of 7 (Table S1). In comparison, the maximum severity score value was 5 during fKW playback and 3 in response to the CTRL–.

Regarding the univariate analysis, for most behavioral variables, only the factor *Signal* was retained in the best fitting GEE model, indicating that the playback *Signal* was the main factor explaining the variance in the data (Tables S2, S3). For mean horizontal speed and near-surface buzz rate, the interaction term *Signal:Period* was retained. For the number of animals present in the focal

area and the change in the proportion of time spent in diving at depth ranging from 5 to 10 m, the two main factors *Signal* and *Period* were retained in the best fitting GEE model. For the occurrence of buzzing at depth and the ratio of time spent near the surface to time spent diving, the factors *Signal* and *Order* were retained. For the change in the proportion of time spent in diving deeper than 10 m, the ANOVA did not retain any of the factors, indicating that none of them explained the variance in the data for this variable.

Attraction versus avoidance responses

Horizontal movements

A horizontal approach response was scored in 100% of the CTRL+, fKW, and mKW playbacks, whereas no change in horizontal movement was ever scored in response to CTRL– (Fig. 1b; Table S1). A horizontal avoidance response was never scored to any of the stimulus types. The calculated movement reaction scores were highly positive in response to fKW, mKW, and CTRL+, indicating a clear horizontal attraction towards the sound source (Fig. 2a; Table S4). For these three stimulus types, the tested whales reduced their horizontal speed during the post-exposure (Fig. 2b), once they were already near the source. All these results significantly contrasted to the response to CTRL– for which whales barely changed direction and decreased speed only during the exposure (Fig. 1b; Table S4).

Vertical movements

The severity scoring panel results showed that the whales changed their dive profile most consistently in response to mKW and CTRL+ playbacks (Fig. 1; Table S1) and that these changes varied across subjects depending on the behavioral context of the whales during the period preceding the start of playback (Table S1). One consistent result was that the whales that interrupted feeding behavior in response to mKW and CTRL+ playbacks switched from a clear foraging dive mode to shallower dives (Table S1). Results of the quantitative analysis conducted on the dive behavior metrics showed that the whales exposed to mKW playbacks spent significantly less time near surface compared to the absence of such a change in response to both control playbacks CTRL– and CTRL+ (Fig. 3a; Table S4). Moreover, whales exposed to mKW spent more time diving at shallow depths (<5 m) and at the depth range of the speaker (between 5 and 10 m) compared to the three other stimuli (Fig. 3b, c; Table S4). There was no evidence of vertical avoidance responses to greater depths (Fig. 3d; Table S1). The order of playbacks had an effect on dive

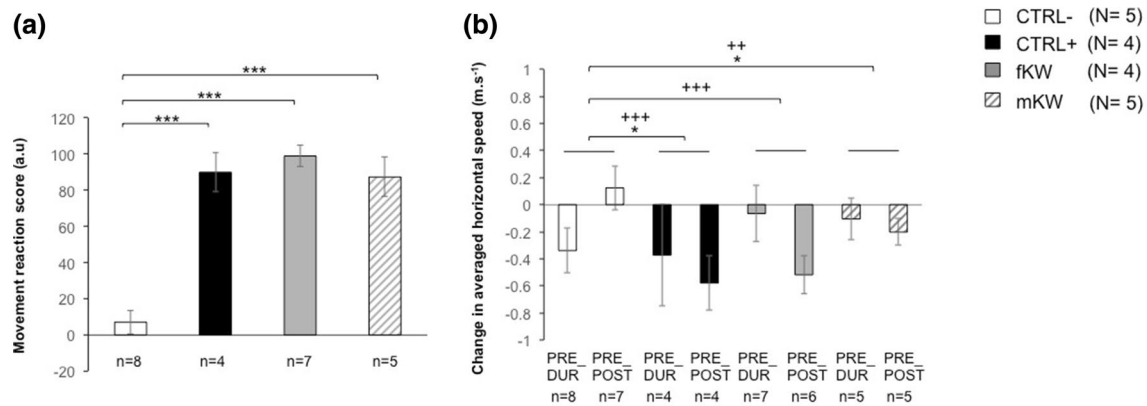


Fig. 2 Quantitative analysis of the effects of sound playbacks on the direction of horizontal movement: **a** mean movement reaction score (arbitrary units, a.u.) showing avoidance (if negative) versus approach response (if positive), and **b** change in mean horizontal speed (m s^{-1}) showing increase (if positive) versus decrease (if negative) of speed. The mean movement reaction score is a PRE_DUR change score, whereas, for speed, both change scores (PRE_DUR and PRE_POST) are shown. For speed, the factors *Signal*, *Period*, and *Signal:Period* were retained in the ANOVA (Table S3). *P* values of the GEE results are given as $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$ for paired differences between stimuli independent of *Period* (interpretation

of the factor *Signal*; Table S4), and as $+p < 0.05$, $++p < 0.01$, and $+++p < 0.001$ for cases where the factor *Signal:Period* was significant (Table S4). PRE_DUR = difference between the DUR (sound playback) and PRE phases reflecting the behavioral change induced during the sound exposure; PRE_POST = difference between the POST and PRE phases indicating whether the behavioral change lasted (or eventually started) after the end of exposure. CTRL- = broadband noise control playback; CTRL+ = 1–2 kHz tonal sound control playback; fKW = fish-eating killer whale sound playback, mKW = mammal-eating killer whale sound playback. *N* number of tested individuals, *n* number of playback trials

behavior, indicated by an increased proportion of time spent near surface for the first playback compared to the following exposures (effect of *Order* at level of $p < 0.05$, Table S4). Moreover, the overall increased proportion of time spent in diving at the depth range of the speaker observed after the end of most playbacks differed significantly from the slight change occurring during playbacks (effect of *Period* at level of $p < 0.05$, Table S4).

Changes in social behavior and surface displays

The severity scoring panel results demonstrated for all stimulus playback types except CTRL-, that group distribution changed for the duration of the exposure or even longer (severity score 5 or 6) (Table S1). Moreover, inspection of the multivariate plots showed that changes in group distribution and surface displays such as spyhops were scored more in response to CTRL+ and mKW sound playbacks compared to fKW sound playbacks, whereas they barely occurred in response to CTRL- (Fig. 1b). Univariate analyses showed that both the number of whales in the focal group and in the focal area increased significantly in response to CTRL+ and to fKW playbacks compared to the overall no change observed in response to CTRL- (Fig. 4a, b; Table S4). Those changes in group distribution in response to CTRL+ and fKW significantly contrasted to the lack of response to mKW sound playbacks (Fig. 4a, b; Table S4). The distance between whales

within the focal group clearly decreased in response to mKW sound playbacks compared to the overall lack of response observed to fKW, CTRL-, and CTRL+ sound playback (Fig. 4c; Table S4). Whales came significantly closer to other groups present in the focal area in response to fKW playback compared to the overall lack of change in response to CTRL- and mKW playbacks (Fig. 4d; Table S4). Moreover, whales became less synchronized when surfacing in response to CTRL+ compared to the overall level of synchrony maintained during exposure to CTRL- and fKW playbacks (Fig. 4e; Table S4). Whales exhibited significantly more spyhops in response to CTRL+, fKW, and mKW compared to CTRL- playbacks (Fig. 5a) and increased logging in response to CTRL+ only (Fig. 5b; Table S4). Moreover, they increased calling activity in response to fKW compared to mKW playbacks (Fig. 6a; Table S4). There was a significant decrease in buzzing recorded near surface in response to fKW sound playbacks compared to CTRL- that lasted beyond the end of playback (Fig. 6b; Table S4). This modification in vocal behavior in response to the fKW playback significantly contrasted to the increase in near-surface buzz rate during mKW sound playbacks. Whales also increased near-surface buzz rate in response to CTRL+ compared to CTRL- but only after the end of playback (difference between CTRL+ and CTRL- dependent on the *Period*; Table S4).

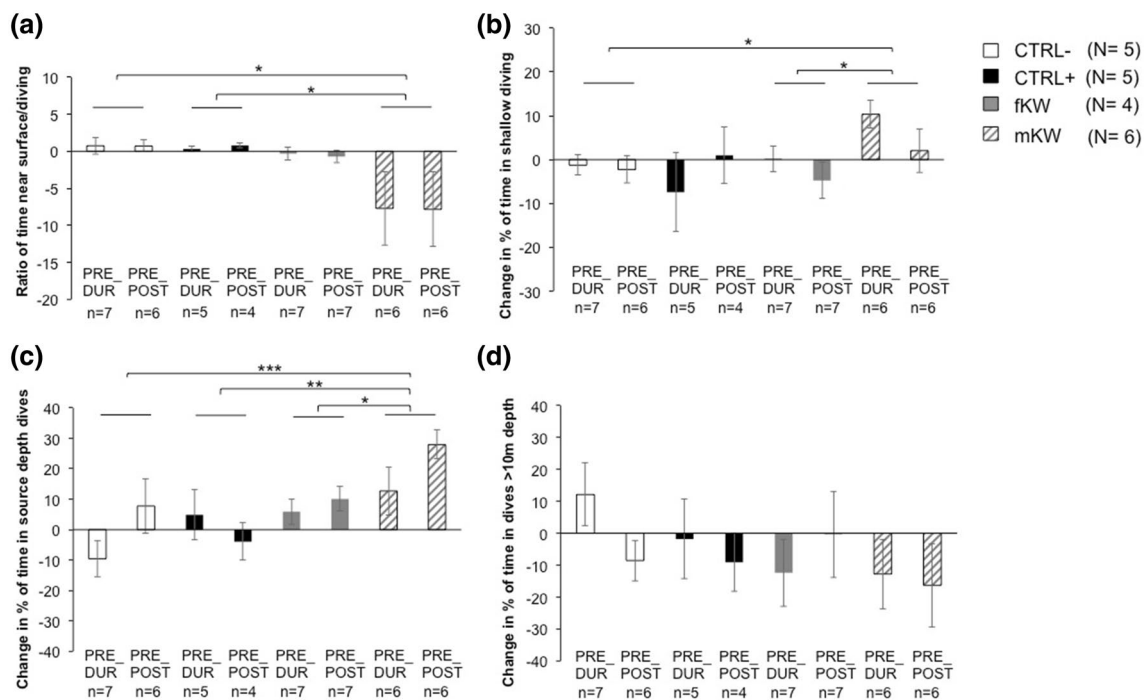


Fig. 3 Quantitative analysis of the effects of sound playbacks on dive behavior: **a** Ratio of time spent near surface over diving time, **b** change in the proportion (%) of time spent in shallow diving (i.e., maximum depth < 5 m), **c** change in the proportion (%) of time spent in diving within the depth range of the speaker (i.e., 5 m ≤ maximum depth < 10 m), and **d** changes in the proportion (%) of time spent in deeper diving (i.e., maximum depth ≥ 10 m). For the change in % of time spent in diving at depth deeper than 10 m (**d**), the ANOVA did not retain any factors, indicating that the variance in the data was not explained by any of those covariates. For the three other parameters (**a–c**), the factor *Signal* explained the differences between the paired comparisons (Tables S3, S4). For (**a**), the factor *Order* (not illustrated on the figure) also explained the variance in the data (Tables S3, S4).

For (**c**), the factor *Period* was also retained in the ANOVA, but the interaction term *Signal:Period* was not significant, indicating that the effects of *Signal* and *Period* were independent to each other. *P* values from GEE results are given as **p* < 0.05, ***p* < 0.01, and ****p* < 0.001. PRE_DUR = difference between the DUR (sound playback) and PRE phases reflecting the behavioral change induced during the sound exposure; PRE_POST = difference between the POST and PRE phases indicating whether the behavioral change lasted (or eventually started) after the end of exposure. CTRL- = broadband noise control playback; CTRL+ = 1–2 kHz tonal sound control playback; fKW = fish-eating killer whale sound playback, mKW = mammal-eating killer whale sound playback. *N*: number of tested individuals; *n*: number of playback trials

Effects on foraging behavior

Based on inspection of the dive profile and production of foraging sounds (regular clicks and buzzes) when available, the severity scoring panel could determine whether the whales were in a foraging mode. Playbacks for which whales were clearly not foraging before the start of exposure (4 CTRL-, 2 CTRL+, 2 fKW, and 2 mKW; excluding data without acoustics) were never associated with a start of feeding. Clear cessation of feeding was only scored in response to CTRL+ and mKW playbacks (Fig. 1b; Table S1). Specifically, both whales that were conducting deep foraging dives (> 100 m depth) before the start of CTRL+ and mKW (N = 2 playbacks each) switched to a shallower dive mode along with a cessation of buzzing and a reduction of clicking rate (Table S1). The cessation of feeding extended until after the end of exposure, resulting in a severity score of 7. The other whales exposed to CTRL+ (N = 1) and mKW (N = 2) were conducting shallower dives while producing

regular clicks and buzzes before the start of exposure; this was considered to represent a potential foraging mode. Severity scoring panels did not score cessation of feeding for those whales (score 0; Table S1). By contrast, none of the fKW playbacks resulted in a scored cessation of feeding. The whale Gm08_159a that was in a deep foraging mode before the start of fKW playback, switched to a shallower dive mode but kept producing clicks and buzzes while diving, and, therefore, was assumed to have continued feeding activity (score 0; Table S1). The whale Gm09_156b, which was exposed twice to fKW playbacks and for which no acoustic data were recorded (failure of Dtag), was in a deep dive mode before the start of playback, thus indicating likely feeding behavior. This whale remained in this deep dive mode during both fKW playbacks (score 0; Table S1). Quantitative analyses showed that the proportion of time spent clicking while diving significantly decreased in response to CTRL+ and to mKW playbacks compared to the overall no change in response to CTRL-, whereas the reduction was

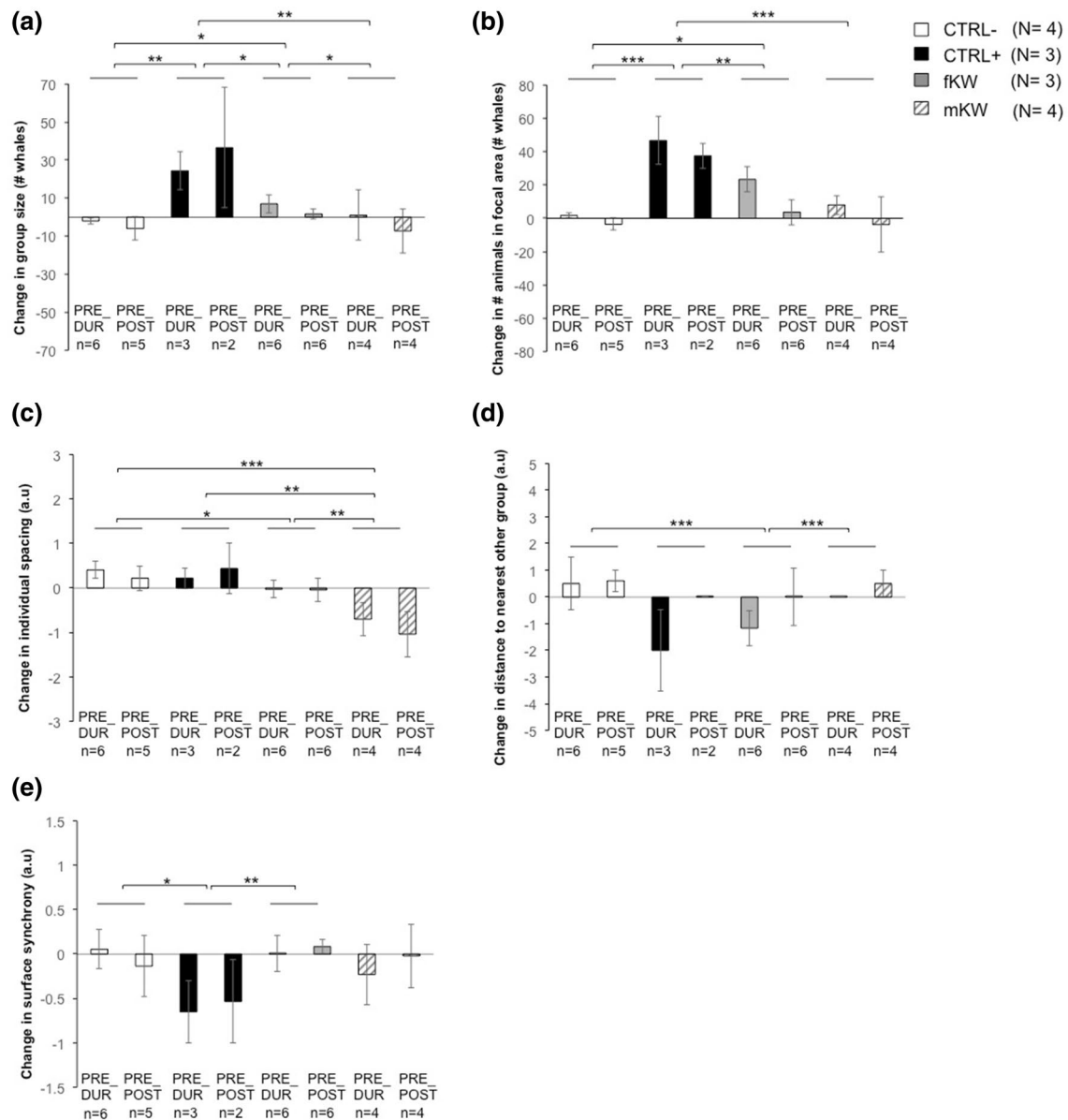


Fig. 4 Quantitative analysis of the effects of sound playbacks on the group distribution parameters: **a** change in group size (in number of animals), **b** change in the number of animals in the focal area (in number of animals), **c** change in individual spacing (a.u.) representing positive values as spreading and negative values as tightening of whales within the group, **d** change in the distance to nearest other subgroup (a.u.), and **e** change in surface synchrony (a.u.). For each of those five parameters (**a–e**), only the factor *Signal* explained the differences between the paired-comparisons, independently of the *Period* (Tables S3, S4). *P* values from GEE results are given

as $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$. PRE_DUR = difference between the DUR (sound playback) and PRE phases reflecting the behavioral change induced during the sound exposure; PRE_POST = difference between the POST and PRE phases indicating whether the behavioral change lasted (or eventually started) after the end of exposure. CTRL- = broadband noise control playback; CTRL+ = 1–2 kHz tonal sound control playback; fKW = fish-eating killer whale sound playback, mKW = mammal-eating killer whale sound playback. *N*: number of tested individuals; *n*: number of playback trials

not statistically supported for fKW sound playbacks (Fig. 6c; Table S4). Moreover, the whales significantly reduced their production of buzzes while diving in response to mKW compared to both CTRL- and fKW playbacks (Fig. 6d;

Table S4). This reduced buzzing rate was more pronounced for the first playback than for the other following playbacks (effect of *Order* at level of $p < 0.05$; Table S4).

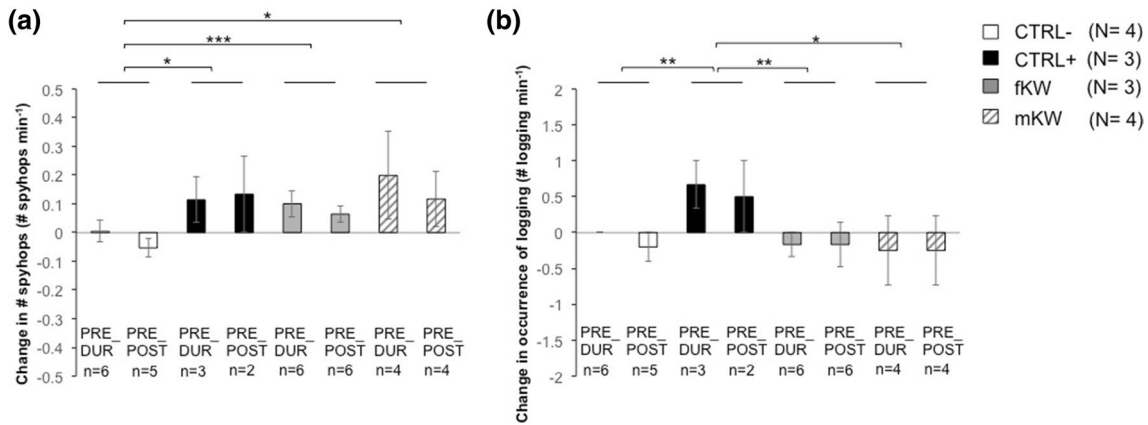


Fig. 5 Quantitative analysis of the effects of sound playbacks on behavioral surface displays: **a** change in occurrence of spyhops (in number of spyhops per min); **b** changes in occurrence of logging (number of logging events per min). For these two parameters (**a**, **b**), only the factor *Signal* explained the differences between the paired-comparisons, independently of the *Period* (Tables S3, S4). *P* values from GEE results are given as **p* < 0.05, ***p* < 0.01, and ****p* < 0.001. PRE_DUR = difference between the DUR (sound play-

back) and PRE phases reflecting the behavioral change induced during the sound exposure; PRE_POST = difference between the POST and PRE phases indicating whether the behavioral change lasted (or eventually started) after the end of exposure. CTRL- = broadband noise control playback; CTRL+ = 1–2 kHz tonal sound control playback; fKW = fish-eating killer whale sound playback, mKW = mammal-eating killer whale sound playback. *N*: number of tested individuals; *n*: number of playback trials

Discussion

We found that long-finned pilot whales modified their behavior in different ways in response to fish-eating killer whale sounds, mammal-eating killer whale sounds, and two control sounds, indicating that they were able to acoustically discriminate between these four stimulus types (Table 2).

The most striking outcomes reveal, first, that the whales barely changed their behavior in response to the broadband noise control playback (CTRL-). Whales were consistently attracted to all the other three sound presentations (fKW, mKW, and CTRL+), indicating a strong tendency for this species to approach, presumably to inspect the source of these sounds occurring in their environment (Table 2). However, details of how their behavior changed in response to each stimulus type indicate functional discrimination of these sound types. The whales stopped feeding and reduced time spent near the surface in response to mKW playbacks, whereas they joined the other groups to form bigger groups in response to fKW playbacks. And finally, the whales clearly changed behavior in response to a repeated modulated upswEEP artificial 1–2 kHz playback signal (CTRL+). In particular, the response to CTRL+ playbacks included a combination of parts of the responses to mKW (interruption of feeding) and to fKW (joining other groups), and specifically a reduced surface synchrony and an increased logging events compared to CTRL- (Table 2).

Contrasting response to CTRL- versus other stimuli

For all behavioral metrics studied, the whales either did not change or only slightly changed their behavior in response to CTRL-. This stimulus resembles a continuous broadband noise generated by the engine of a vessel and is possibly perceived as a common sound heard by the whales. Indeed, the subject pilot whale groups occupy a coastal habitat in Norway that regularly experiences a high amount of ship traffic, including large cargo vessels and fishing vessels. These ships generate broadband noises to which the whales might have habituated. In addition, the previous studies found that pilot whales in these areas hardly changed their behavior in response to an approaching ship, indicating that vessel noise might have a limited effect on their behavior (Miller et al. 2012; Sivle et al. 2012; Isojunno et al. 2017).

The three other playback stimuli had tonal modulated frequency components (CTRL+, fKW, and mKW) and induced a clear horizontal approach towards the sound source along with an increase in spyhopping. The same approach response was also elicited to playback of unfamiliar humpback whale sounds (data not shown). The shared behavioral response towards playbacks which contained tonal sounds could be a way to probe information about the location and/or characteristics of the sound source by getting closer and gathering visual cues from the surface.

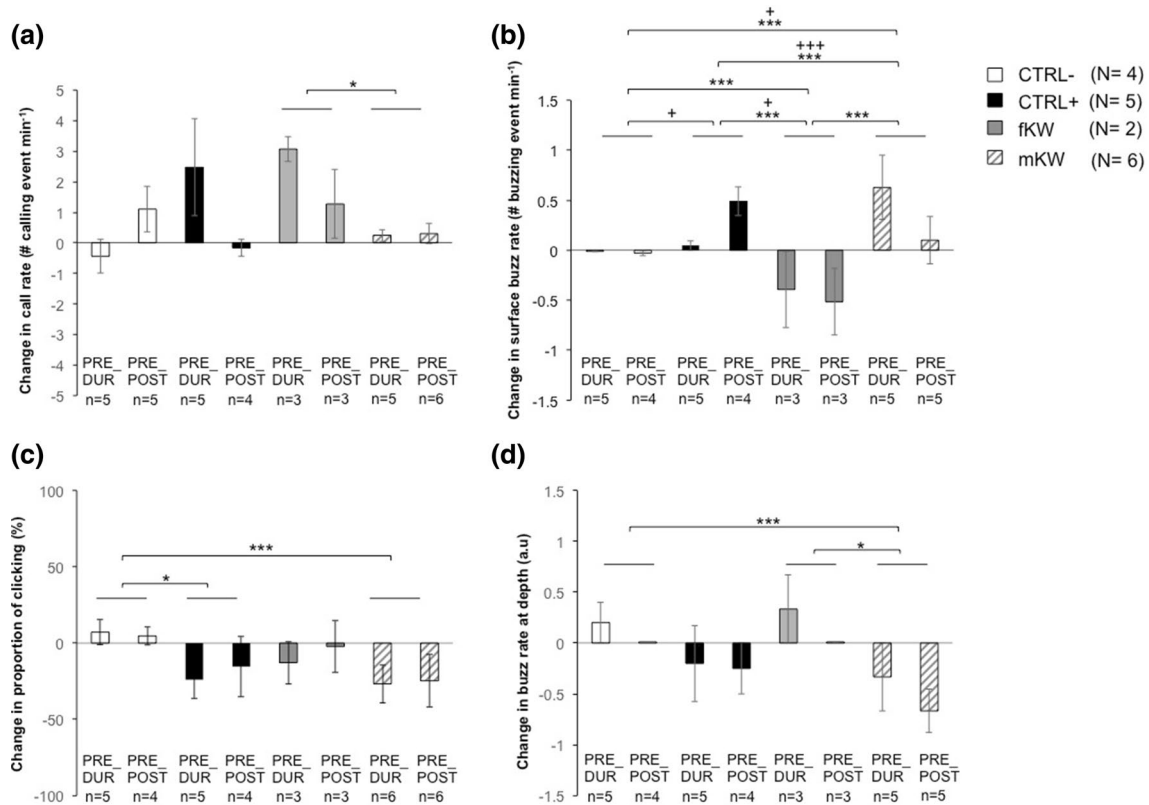


Fig. 6 Quantitative analysis of the effects of sound playbacks on vocal behavior: **a** changes in occurrence of social calls (#calling per min), **b** change in occurrence of near-surface buzzes (#buzzing event per min), **c** change in the proportion of time spent clicking while diving (%), and **d** changes in occurrence of buzzes at depth (a.u.). The differences of the occurrence of near-surface buzzing across the stimulus types depend on the *Period* (Table S3). For the other three parameters (**a**, **c**, **d**), the paired differences observed between the stimulus types were independent of the *Period* (Tables S3, S4). For the occurrence of buzzes produced at depth (d), the factor *Order* (not illustrated on the figure) also explained the variance in the data (see Tables S3, S4). *P* values from GEE results are given as * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$ for paired differences between stimuli

independent of *Period* (interpretation of the factor *Signal*, Table S4), and as + $p < 0.05$, ++ $p < 0.01$, and +++ $p < 0.001$ for cases where the factor *Signal:Period* was significant (Table S4). PRE_DUR = difference between the DUR (sound playback) and PRE phases reflecting the behavioral change induced during the sound exposure; PRE_POST = difference between the POST and PRE phases indicating whether the behavioral change lasted (or eventually started) after the end of exposure. CTRL- = broadband noise control playback; CTRL+ = 1–2 kHz tonal sound control playback; fKW = fish-eating killer whale sound playback; mKW = mammal-eating killer whale sound playback. *N* number of tested individuals; *n* number of playback trials

Response to killer whale sound playbacks

The previous work with parts of this data set (whales tested in 2008, 2009, and 2010) showed that pilot whales approached an fKW sound source and aggregated with other whales (Curé et al. 2012). Beside the possibility that an approach response might be a way to investigate the sound source and to assess level of disturbance risk, we had hypothesized other, not mutually exclusive, potential functions. One hypothesis was that pilot whales learn to associate fKW presence with an opportunity to feed and they may eavesdrop on fKW sounds to locate a food patch and increase their foraging efficiency ('dinner bell' effect, Stansbury et al. 2015). If so, one would expect pilot whales to approach the source and initiate exploratory or foraging

dives to search for a potential prey patch, the aggregation being a consequence of the food appeal triggered by the source and available to other animals present in the area. In the present study, by investigating the foraging (diving and echolocation) behavior of the whales, we showed that none of the playbacks, including fKW sounds, appeared to induce an initiation of foraging behavior. Moreover, visual observations conducted in Norway reported that killer whales actively feeding on herring were chased away by pilot whales that did not seem themselves interested in preying upon herring (De Stephanis et al. 2014). Altogether, these results do not support the 'dinner bell' hypothesis, indicating that pilot whales might not have perceived fKW sounds as indicating an opportunity to feed.

Table 2 Summary table of results indicating the most relevant behavioral changes exhibited in response to playbacks of the three acoustic stimuli CTRL+, fKW, and mKW compared to the broadband noise control playback (CTRL–)

Behavioral changes in response to playback sounds	CTRL+	fKW	mKW
Horizontal and vertical movements			
Horizontal approach towards sound source (Fig. 2a)	**	**	**
Reduced horizontal speed after end of playback (Fig. 2b)	**	**	*
Reduced time spent near surface compared to diving, and increased time spent in shallow diving (Fig. 3a, b)			*
Increased time spent within depth range of speaker (Fig. 3c)			**
Foraging behavior			
Clear cessation of feeding (interruption of foraging dives) (Fig. 1b)	Yes		Yes
Reduced clicking and/or buzzing while diving (Fig. 6c, d)	*		**
Social response			
Increased group size and/or number of animals within focal area (Fig. 4a, b)	**	*	
Reduced distance to nearest other group (Fig. 4d)	*	**	
Decreased surface synchrony (Fig. 4e)	*		
Decreased individual spacing (Fig. 4c)			**
Reduced near-surface buzzing (Fig. 6b)		**	
Increased near-surface buzzing (Fig. 6b)	*(after end of playback)		** (during playback)
Behavioral surface displays			
Increased logging events	**		
Exhibition of spyhops	*	**	*

For each stimulus type, filled boxes indicate the occurrence of the associated described behavioral changes, whereas empty boxes mean that there was no significant change compared to CTRL–. Only ‘Clear cessation of feeding’ events (interruption of foraging dives) are presented as ‘Yes’ when they did happen (based from severity scoring panel results). There was never a cessation of feeding in response to CTRL–. For each quantitative behavioral parameter, the GEE results of the paired comparisons across the four stimuli were obtained, resulting in a total of six tested paired comparisons (i.e., differences between the four factor levels of Signal). To account for potential effect of multiple testing, we highlighted results supported at Bonferroni-corrected levels ($\alpha=0.05/6=0.008$). Results supported by $p<0.05$ and $p<0.008$ (after Bonferroni correction) are, respectively, represented as * and ** CTRL+ = 1–2 kHz tonal sound control playback; fKW = fish-eating killer whale sound playback; mKW = mammal-eating killer whale sound playback

A second hypothesis was that pilot whales display an active intimidation behavior in response to fKW sounds, either to mob a potential predator (e.g., in mammals: Tamura 1989; in birds: Francis et al. 1989; Preisser et al. 2005) or to chase away an intruder perceived as a potential competitor exploiting the same foraging areas (e.g., in birds: Boyden 1978; in fish: Kohda 1991; Lehtonen et al. 2010). This behavior usually involves a pursuit along with the production of sounds and additional intimidation behaviors (e.g., grouping with other individuals and physical defense behavior) (reviewed in Alcock 2009). ‘‘Fight’’ strategies involving intimidation behaviors have been observed in other cetaceans in response to killer whale attacks, such as the sea-surface rolling and tail fluke splashing of gray whales defending their calves (Ford and Reeves 2008). Here, the clear horizontal attraction towards fKW sound source along with joining of different subgroups and increased production rate of social calls in response to fKW playbacks compared to mKW playbacks support an active intimidation behavior rather than the

dinner bell effect, which is in line with the chasing behavior observations described by De Stephanis et al. (2014).

To investigate whether such active intimidation behavior is driven by a perceived competition for the habitat/foraging areas (since competition for the same prey is unlikely) or an increased predation risk in pilot whales, we detailed the differences in behavioral responses to both fKW and mKW sounds. Though pilot whales approached the source in response to both fKW and mKW, the exact response strategy appeared different in response to mKW. Indeed, there was a tightening of animals within their group in response to mKW playbacks, indicating potential increased group cohesion, which contrasted with the joining to other groups observed in response to fKW playbacks. Moreover, during the mKW playbacks, whales spent less time near surface and more time in shallow dives and dives within the depth range of the speaker. The fact that mKW sounds are unfamiliar to the pilot whales could explain a need for additional efforts (e.g., spending more time within depth range of sound source) to probe

for acoustic information specifically in response to this stimulus.

Production of click signals (i.e., clicks and buzzes) is usually associated with echolocation functions including the gain of information about the environment (e.g., used for orientation) and foraging behaviors (Au 1997). The ‘buzz,’ which is characterized by a fast click train, is usually associated with attempts to capture prey or to collect information about elements present in the environment (e.g., used as a proxy for feeding in deep diving pilot whales, Quick et al. 2017). However, click signals may also carry a communication function in cetaceans as, for instance, the slow clicks produced typically near surface in sperm whales (*Physeter microcephalus*) (Oliveira et al. 2013), some types of narrow-band high-frequency clicks in Commerson’s dolphins (*Cephalorhynchus commersonii*) (Yoshida et al. 2014), and “rasps” or “burst pulses” in short-finned pilot whales (*Globicephala macrorhynchus*) and Risso’s dolphins (*Grampus griseus*) (Arranz et al. 2016; Perez et al. 2016). Most studies on acoustic communication signals in pilot whales have focused on calls that would essentially function to relocate and coordinate with group members (Jensen et al. 2011; Zwamborn and Whitehead 2016). Because fast click trains are mainly emitted, while whales are diving in a foraging context (i.e. buzzes), the ones produced near the surface have received little attention and their function has remained poorly understood (Vester 2017; Vester et al. 2017). It may be that, in our study, fast click trains produced near surface (called as “near-surface buzzing”) reflect an attempt by the pilot whales to use echolocation to gain information about an unfamiliar sound source. Alternatively, near-surface buzzing may be used as a way of communicating near surface and/or in a more effective and/or more discrete way (i.e., more directional or short-range distance) than calls that can travel longer distances (Norris and Dohl 1979; Perrin et al. 2009).

Since only the behavioral response to the fKW contained the typical combination of behavioral indicators of an active intimidation behavior (joining with other groups while approaching), we conclude that this response was specifically exhibited to fKW but not to mKW.

In Norway, long-finned pilot whales may be able to learn that the sounds produced by local herring-eating killer whales represent a relatively low-risk stimulus. The active intimidation behavior in response to fKW playbacks could be driven by a perceived low predator risk or alternatively by perceived competition with the fKW. Indeed, although pilot whales in Norway likely do not feed on the same prey as local herring-eating killer whales (De Stephanis et al. 2014), they target demersal prey (cod, *Todarodes*) that do eat herring, which could explain the correlation between occurrence of pilot whales and herring (Nottestad et al. 2015), and possible indirect competition with local killer whales for the exploitation of common foraging areas.

Another striking difference between responses to both KW sound types was the clear cessation of feeding induced by mKW playbacks that contrasted with no case of such an effect in response to fKW. An animal’s decision to respond to a threat is based upon a trade-off between the costs and benefits of behavioral change and the perceived risks evaluated by the animal (Lima and Dill 1990; Frid and Dill 2002; Sih 2013). Thus, animals must make a choice between avoiding the perceived risk from the threat versus continuing fitness-enhancing activities such as feeding. Encountering a predator is probably the maximum level of natural threat an animal can meet, since it may lead to death. One can, thus, expect the adaptive response of the prey to a perceived increased predation risk to be particularly costly (e.g., by interrupting fitness-enhancing activities such as feeding) compared to other natural disturbance types (Curé et al. 2016). Cessation of feeding is typically observed in perceived high-risk predatory contexts in terrestrial taxa (e.g., in mule deer, Altendorf et al. 2001; in birds, Turney and Godin 2014) as well as in other cetacean species (e.g., in sperm whales, Curé et al. 2013; in humpback whales, Curé et al. 2015). Here, we found clear cessation of feeding in response to mKW playbacks that lasted for longer than the duration of the exposure (severity score 7), which, if persistent, could potentially lead to impact on vital rates (Southall et al. 2007). The specifically costly response (cessation of feeding) to mKW playbacks supports the hypothesis that pilot whales perceived the unfamiliar mKW sounds as a particularly threatening stimulus, possibly a predator-signaling cue. Although the subject individuals could not have experienced predatory interactions with the Pacific mammal-eating killer whales from which we collected sounds to prepare our stimuli, and given that it seems unlikely that the Atlantic mammal-eating killer whales would predate on pilot whales, pilot whales may have conserved past historical antipredator strategies (Sih et al. 2013; De Stephanis et al. 2014; Hettner et al. 2014).

The more cryptic and more cohesive approach response strategy to mKW playbacks (no grouping behavior, individuals tightening within group, and less time near surface, promoting surface buzzing vocal activity) compared to fKW playbacks could be a way to ‘inspect’ the situation to evaluate the level of threat (e.g., inspecting the level of predator threat, Pitcher et al. 1986) before engaging in a further response, for instance, either a social defense strategy or a flight response (Curé et al. 2015).

Altogether, the different behavioral approach strategies exhibited by pilot whales in response to fKW playbacks (joining other groups) and mKW playbacks (cessation of feeding, reduced time spent near surface, and tightening of individuals within group) support, respectively, an interspecific intimidation behavior associated with a perceived familiar low threatening stimulus, i.e., a low predation risk

or a known heterospecific species exploiting the same habitat, and an antipredator behavior directed towards a perceived high level of predation risk.

One could argue that the difference between the behavioral responses to both killer whale sound types is due to perceived familiar fKW versus unfamiliar mKW sound stimuli (Deecke et al. 2002). Indeed, by having experienced that the local fish-eating killer whales (fKW) are harmless, pilot whales might have shaped their response strategy to the detected presence of this killer whale ecotype. By contrast, they would react differently to any other unfamiliar KW sounds such as mKW. Moreover, it might be possible that the missing upper frequency spectrum part of the KW sound playback (since the speaker played sounds only up to 20 kHz) had an effect of the behavioral response of pilot whales, particularly once they got close to the source where higher frequencies should be detectable if the whale is pointing towards the subject (Miller 2002).

Response to CTRL+

Whales showed a mixed/intermediate response relative to responses to both killer whale sound stimuli. Indeed, they stopped feeding in response to CTRL+ playbacks, similar to their response to mKW playbacks (unfamiliar signal with a potentially high predation risk), indicating that pilot whales might have perceived a higher level of threat in those two stimuli compared to the fKW sounds. Moreover, in response to CTRL+, pilot whales exhibited both approach and grouping behavioral responses similar to the fKW playbacks. Therefore, it seems that pilot whales exhibited a strong fitness-reducing behavioral response to CTRL+, combining partly both the responses to mKW and to fKW.

One of the analytical approaches to improve our ability to assess potential behavioral disturbance effects of a non-natural stimulus such as anthropogenic noise is to compare responses to this stimulus with responses to known or novel signals from predators as a reference pattern of disturbance expressed in relevant natural context (Frid and Dill 2002; Curé et al. 2016). Our results indicate that, in addition to the antipredator responses to known predators or to unfamiliar signals that could indicate an unknown level of predation risk, the responses to novel signals (here the CTRL+ signal) can be also valuable high-level disturbance reference models to help in the interpretation of the biological significance of the responses to other stimuli. Indeed, such models could be used to extend the risk-disturbance hypothesis to species without natural predators, such as the killer whale whose apparent sensitivity to anthropogenic noise could not be explained by the predation risk template (Harris et al. 2017).

Second, CTRL+ playbacks specifically induced a reduction in surface synchrony and an increase in the number of

logging events. The decrease in synchrony could reflect a social reorganization within the group or a difficulty for the individuals of the group to maintain cohesion (Visser et al. 2016). Logging more might be a way for whales to reduce the risk of masking and to use visual cues to supplement acoustics in relocating group members and maintaining group cohesion, as also observed for pilot whales in this area in response to naval sonar exposure (Wensveen et al. 2015b; Visser et al. 2016).

Interestingly, our findings match partly those of previous research that showed a cessation of foraging and increased logging behavior (at received levels of 145–170 dB) in response to a controlled CTRL+ exposure generated at much higher SPLs, used to simulate a naval sonar exercise (LFAS 1–2 kHz signals in: Miller et al. 2012; Sivle et al. 2012; Wensveen et al. 2015b; Visser et al. 2016). However, the responses did not match entirely. There was no horizontal approach, but some horizontal avoidance recorded in response to the powerful sonar CTRL+ source (Miller et al. 2012) compared to the CTRL+ playbacks which we conducted in the present study, indicating whales perceive different levels of disturbance between these two presentations.

To conclude, our findings confirm that cetacean species can eavesdrop on heterospecific sounds (Curé et al. 2012, 2013, 2015) and demonstrate their ability to acoustically discriminate across familiar and unfamiliar sub-populations of another species, allowing them to adjust their behavioral response strategies according to the perceived level of disturbance. More experiments testing responses to familiar mKW and unfamiliar fKW sounds could be useful to identify the specific role that familiarity versus novelty might have on how long-finned pilot whales respond to sounds produced by killer whales. However, the different combination of behavioral changes exhibited in response to the two unfamiliar sound stimuli (mKW sounds and CTRL+) which indicate that the familiarity versus unfamiliar aspect should not be the only driver of the response. One strength of our approach is that we used the entire suite of natural sounds recorded from killer whales. However, without further research, we cannot be conclusive about specifically which sounds (vocalizations, tail slaps, and clicks) produced by the killer whales might be the salient cues recognized by the long-finned pilot whales. Indeed, Bowers et al. (2018) showed that, in a close related species, the short-finned pilot whale, and, in Risso's dolphins, responses to the playback of familiar transient (mammal-eaters) killer whales sounds were selectively induced only when specific call types were present in the playback stimuli. A wide range of other cetacean species have unexplained interactions with killer whales (e.g., humpback whales approaching or avoiding killer whales (Pitman et al. 2017) or with other species. Further experiments using similar playback approach

should be investigated to gain insight in the use of eavesdropping and other processes that might explain the range of interspecific interactions with killer whales and other species.

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