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Charlotte Cure, Saana Isojunno, Heike Vester, Fleur Visser, Machiel Oudejans, et al.. Evidence for discrimination between feeding sounds of familiar fish and unfamiliar mammal-eating killer whale ecotypes by long-finned pilot whales. *Animal Cognition*, 2019, 22, pp. 863-882. 10.1007/s10071-019-01282-1 . hal-02915511

HAL Id: hal-02915511

<https://hal.science/hal-02915511>

Submitted on 28 May 2021

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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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Acknowledgments

Animal experiments were carried out with permission from the Norwegian Animal Research Authority (Permit No. 2004/20607 and S-2007/61201). Protocols were approved by the Animal Welfare and Ethics Committee of the University of St Andrews (UK). We are grateful to the many researchers and vessel crew members who participated to conduct fieldwork and to collect data. We particularly thank our colleagues from the 3S project (Sea mammals, Sonar, Safety). We acknowledge Volker Deecke who organized fieldwork in SE Alaska during which the Dtag acoustic recordings of mammal-eating killer whale sounds were collected in collaboration with PJOM. Research funding was provided by the US Office of Naval Research, the DGA/TN (France), the UK Natural Environmental Research Council, and the Ministeries of Defence of Norway and The Netherlands. PLT acknowledges funding received from the MASTS pooling initiative (The Marine Alliance for Science and Technology for Scotland). MASTS is funded by the Scottish Funding Council (grant reference HR09011) and contributing institutions. CC acknowledges statistical support provided by the Multi-study Ocean acoustics Human effects Analysis (MOCHA) project funded by the United States Office of Naval Research (grant N00014-12-1-0204).

1 **Abstract**

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

22 **Key words** : *Globicephala melas* – acoustic playbacks – killer whale ecotypes – heterospecific
23 sound discrimination – multi-sensor tags – cetacean behavioral responses

24 **Introduction**

25 Individuals not only interact and exchange information intentionally, but they can also intercept
26 unintended signals from conspecifics and heterospecifics, which can provide an additional gain
27 of information at reduced cost for eavesdroppers (Peake et al. 2001; Blanchet et al. 2010). Such
28 information gathering can benefit a wide range of fitness-enhancing activities such as habitat
29 selection, foraging efficiency, adapted antipredator responses, or mate choice (Blanchet et al.
30 2010; Magrath et al. 2015).

31 Animal sounds play an important role for communication and species/individual
32 recognition in many animals, including anurans, birds, insects, terrestrial and aquatic mammals
33 (Bradbury and Vehrencamp 1998). Moreover, in species such as bats and toothed whales,
34 echolocation sounds can be important to find and track food or to navigate (Madsen and
35 Surlykke 2013). Detecting heterospecific sounds can be particularly relevant in the dynamics of
36 predator-prey interactions and interspecific competition (Dorado Correa et al. 2013). When prey
37 species detect acoustic signals produced by their predator, they can evaluate the level of
38 predation risk (e.g. identification of the predator species) and adopt the most appropriate anti-
39 predator strategy (Seyfarth et al. 1980; Manser 2001). For example, mule deer (*Odocoileus*
40 *hemionus*) are able acoustically to discriminate among different predator species, i.e. coyotes
41 (*Canis latrans*), mountain lions (*Puma concolor*) and wolves (*Canis lupus*) and respond
42 differently according to the perceived level of threat (Hettena et al. 2014). Breeding songbirds
43 can assess the spatial distribution of predators by listening to their vocalizations and then choose
44 the most appropriate nest site, leading to increased reproductive success (Emmering and Schmidt

45 2011). On the other hand, listening to the acoustic cues emitted by species sharing similar
46 ecological requirements (e.g. diet or habitat) can provide beneficial information such as the
47 presence of potential competitors. Competing species may directly interfere, e.g. by aggressively
48 attempting to exclude one another from particular habitats (interference competition), or
49 indirectly by exploiting similar resources, e.g. by consuming similar food (exploitation
50 competition) (Eccard et al. 2008). For instance, bats can eavesdrop on foraging echolocation
51 signals produced by conspecifics and heterospecifics to locate feeding sites, thus reducing
52 foraging costs (Balcombe and Fenton 1988; Uebernickel et al. 2012; Dorado Correa et al. 2013).
53 Lemurs are able to acoustically identify heterospecific species competing for similar food and
54 adjust their behavior accordingly in order to defend the area where they forage (Rakotonirina et
55 al. 2016). Moreover, species can cooperate rather than exclude each other (e.g. in primates,
56 (Eckardt and Zuberbühler 2004)). For instance, many bird and mammal species form mixed-
57 species feeding associations which can improve their foraging efficiency (e.g. in birds,
58 Monkkonen et al. 1996; in cetaceans, Jourdain and Vongraven 2017).

59 Cetaceans are typically social and vocal species. They rely primarily on sound to
60 communicate with their conspecifics (e.g. in breeding context or to coordinate with their group
61 members), to get information from their environment (e.g. to identify the presence of other
62 species), and in toothed whales, to orientate and acquire food through echolocation (Tyack
63 2008). Most cetacean species have the ability to hear at least part of the frequency range of
64 sounds produced by other cetacean species, enabling them to hear each other (Mooney et al.
65 2012). Cetaceans belong to a complex trophic network in which predation and competition
66 interactions occur at various trophic levels (Paine 2006). Therefore, they represent interesting
67 model species for studying heterospecific sound eavesdropping.

68 The killer whale (*Orcinus orca*) is present in all the world's oceans. As an apex marine
69 predator, it has a unique position in the food web of marine ecosystems (Reeves et al. 2006).
70 Killer whales can feed on a large diversity of prey including fish, cephalopods, birds, turtles,
71 seals, dolphins and whales (Foote et al. 2009; De Bruyn et al. 2013; Vongraven and Bisther
72 2014). From the point of view of other cetacean species, the killer whale can be thus considered
73 as both a potential predator and/or a competitor for resources (e.g. habitat, prey). A wide variety
74 of observed interactions have been reported between killer whales and other cetaceans (Jefferson
75 et al. 1991) ranging from avoidance behavior (e.g. in beluga whales, Fish & Vania 1971),
76 physical attacks (e.g. in grey whales, Ford et al. 2005), feeding associations to approach
77 responses (in humpback whales: Pitman et al. 2015, Jourdain and Vongraven 2017). To date, at
78 least 10 different forms of killer whales, also called "ecotypes", have been recognized. Ecotypes
79 can differ according to their prey preferences, distribution, social structure, foraging habits,
80 acoustic behavior, physical features and genetics (Jefferson et al. 1991; De Bruyn et al. 2013).
81 Locally, populations often specialize on specific prey species, sharing hunting strategies with
82 their group members and adapting their foraging techniques according to the type and
83 availability of prey resource. All ecotypes produce echolocation clicks, pulsed calls and whistles
84 (Ford 1989). Substantial differences in acoustic behavior have been described across the
85 different killer whale ecotypes (e.g. variation in call frequency or in vocal rate) (Foote and
86 Nystuen 2008; Deecke et al. 2011; Filatova et al. 2015). Overall, fish-eating killer whales are
87 very vocal during the whole period of foraging, relying mainly on echolocation clicks to find
88 food and producing social calls and whistles to coordinate with group members (Simon et al.,
89 2007; Holt et al. 2016). Moreover, herring-feeding killer whales stun herring using their flukes,
90 which produces an audible signal (Simon et al. 2005, 2007). By contrast, mammal-eating killer

91 whales are usually quiet at the early stage of a hunt, *i.e.* before attacking, probably to remain
92 undetectable by their prey, and increase their vocalization rate (mainly calls and whistles) once
93 the attack has been engaged, likely to coordinate group members and maintain group cohesion
94 (Ford et al. 2005; Deecke et al. 2011). The fundamental frequency of calls of mammal-eating
95 killer whales is slightly lower than those of fish-eating killer whales (Filatova et al. 2015).

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

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

113 In the North-East Atlantic Ocean, killer whales have been reported to attack cetaceans
114 including large baleen whales (humpback whales, McCordic et al. 2013). Killer whales have
115 been also observed attacking long-finned pilot whales off Iceland (Donovan and Gunnlaugsson
116 1989), Greenland and the Faroe Islands (Jefferson et al. 1991), although to our knowledge there
117 are no such reports from Norwegian waters. In Iceland (pers. obs. by author P.W.), in Norway
118 and in the Mediterranean Sea (Strait of Gibraltar) (De Stephanis et al. 2014), long-finned pilot
119 whales have been observed chasing towards fish-eating killer whales, with the killer whales
120 fleeing away from the pilot whales. These observations have been interpreted either as the anti-
121 predatory behavior of pilot whales mobbing dangerous killer whales, or pilot whales chasing
122 killer whales away from foraging areas that might be exploited by both species. In the North
123 Atlantic Ocean, long-finned pilot whales feed primarily on squid and occasionally eat small
124 schooling fish (Desportes and Mouritsen 1993). In Norway and Iceland, long-finned pilot whales
125 coexist with at least two forms of killer whales: one fish-eating ecotype that predominantly feeds
126 on Atlantic herring (Simila et al. 1996; Vester and Hammerschmidt 2013), and one more
127 generalist ecotype that feeds on both fish and marine mammals (seals, harbor porpoises) (Foote
128 et al. 2009; Jourdain et al. 2017; Samarra et al. 2017). It might be also that long-finned pilot
129 whales have experienced presence of additional ecotypes in the North-East Atlantic Ocean such
130 as the one observed feeding on large baleen whales but no such interaction has been reported in
131 our studied area off Norway. There, long-finned pilot whales may have the opportunity to learn
132 that the calls of local herring-eating killer whales represent a relatively low threat, while in
133 contrast it is expected that any other killer whale sounds, i.e. from familiar mammal-feeding
134 killer whales or unfamiliar (fish- or mammal-feeding) killer whales, should be perceived as
135 threatening as familiar mammal-feeding killer whale sounds (Deecke et al. 2002). Pilot whales

136 hear well at the frequencies of killer whale vocalizations (Pacini et al. 2010) and thus may assess
137 and respond to killer whale presence by eavesdropping on their vocalizations or other sounds
138 they produce such as tail-slaps. Curé et al. (2012) showed that long-finned pilot whales were
139 horizontally attracted to sounds of local fish-eating killer whales and that they joined with other
140 pilot whale groups to form bigger groups. Based on their results, the authors could not resolve
141 whether pilot whales perceived killer whale sounds as either a potential opportunity of feeding,
142 explaining their attraction towards an identified food patch ('dinner bell' effect, Stansbury et al.
143 2015), or as a threatening stimulus (competitor or predator) that would have resulted in a chasing
144 behavior as part of an active intimidation response.

145 To evaluate these questions, we conducted playback experiments and monitored the
146 behavioral responses of long-finned pilot whales using multi-sensor tags and surface behavioral
147 observations of the tagged whale and its group. We compared the behavioral responses of long-
148 finned pilot whales to the playback of i) familiar herring-feeding killer whale sounds simulating
149 a local sympatric species exploiting similar foraging areas, ii) unfamiliar mammal-eating killer
150 whale sounds simulating a potential high level of predation risk (Deecke et al. 2002; Curé et al.
151 2015), and iii) control sounds. We analyzed a wide range of behavioral variables typically
152 observed in predatory, competition and foraging contexts to test whether long-finned pilot
153 whales display different behavioral response strategies according to the perceived stimulus
154 playback, and particularly between sound playbacks of the two killer whale ecotypes.
155 Specifically, we predicted that if a stimulus was perceived as a potential threat, it should elicit
156 fitness-enhancing behaviors such as reduced foraging activity, avoidance reactions and social
157 defense response strategies (e.g. including approach and grouping). For perceived high-level
158 threatening stimuli, we would expect particularly biologically costly responses such as a

159 complete and prolonged cessation of feeding and/or extended avoidance responses. In contrast, a
160 ‘dinner bell effect’ would be reflected by an approach response along with potential grouping
161 behavior and initiation of search for food in non-feeding whales.

162

163 **Material and Methods**

164 **Study species and general protocol**

165 We conducted our study on free-ranging long-finned pilot whales encountered in the Norwegian
166 Sea in May/June 2008, 2009, 2010, 2013 and 2014. The protocol consisted of the following
167 phases: (1) Tagging operation in which a non-invasive multi-sensor suction-cup tag was attached
168 to the whale using a 6 m carbon fibre hand-held pole (see details of the tagging protocol in Miller
169 et al. 2012 and Visser et al. 2016); These tags are devices carrying a suite of sensors, which have
170 been specifically developed to monitor the behavior of marine mammals and their response to
171 sound continuously throughout the dive cycle (Johnson & Tyack 2003). (2) Baseline data
172 collection of the tagged animal (focal follow) following a post-tagging period of at least 30 min
173 to reduce potential effects of the tagging procedure; (3) Playback experiments (see next section);
174 and (4) End of tracking after the tag released, and tag recovery. Tagging operations and playback
175 experiments were carried out from a small motor boat (5-8m) launched from the research vessel
176 (55m). In most cases only one whale of a group was tagged, becoming the focal follow animal
177 for which visual observations were collected from a dedicated observation platform on a vessel
178 (20-27m) continuously following the focal whale at a range of 300-500 m. In two cases, another
179 whale associated with the focal group was tagged (Gm13_169b and Gm13_180b). These

180 secondary tagged whales were not focal follow animals (no visual observations) but provided
181 additional recorded tag data.

182 **Playback experiments**

183 The playback experiments used an M-Audio II microtrack player, a Cadence Z8000 amplifier,
184 and a Lubell speaker LL9642T (described in details in Curé et al. 2012; Visser et al. 2016).
185 Playback sounds were monitored using a calibrated hydrophone (Bruel & Kjaer 8105) placed 1
186 m from the speaker and connected to a charge amplifier (Bruel & Kjaer 2635) that was itself
187 connected to a M-Audio Microtrack II recorder. The playback boat from which the speaker was
188 deployed in the water was positioned with respect to the playback subjects to provide a geometry
189 designed to identify either horizontal attraction to or avoidance of the sound source.

190 We played 4 acoustic stimuli: two types of killer whale sounds produced by groups of 4-7
191 killer whales while feeding, and two types of control sounds. Control sounds were used to
192 distinguish behavioral changes elicited in response specifically to the killer whale sounds from
193 those induced unspecifically by other sounds in their environment. The two killer whale sound
194 stimuli were: i) familiar herring-eating killer whale sounds (fKW) recorded previously in the
195 study area (expected to be perceived as a local competitor for food and/or resource territory), and
196 ii) unfamiliar mammal-eating KW sounds (mKW) recorded in the North Pacific (expected to be
197 perceived as an increased potential predation risk; Deecke et al. 2002). Both types of killer whale
198 sounds were previously recorded using animal-attached Dtags (Johnson and Tyack 2003). The
199 two control stimuli were: i) a broadband noise control (CTRL-) with most energy within the 0.5-
200 10 kHz frequency band, corresponding to amplified non-calling periods taken from the
201 recordings of the killer whale sounds (see Curé et al. 2012), and ii) a synthetic hyperbolic
202 upsweep 1-2 kHz tonal signal (CTRL+) of 1 s duration repeated every 20 s, matching the

203 dominant frequency range of many killer whale calls (Ford 1989). All playbacks lasted 15 min
204 and stimuli were generated at comparable root-mean square power, each within the range of the
205 natural source levels of killer whale vocalizations (Miller 2006). The source level of the killer
206 whale stimuli ranged from 147 to 154 dB re 1 μ Pa m (mean \pm SD: 151 \pm 2 dB re 1 μ Pa m, n = 3
207 mKW and 4 fKW stimuli). The source levels of the control stimuli were adjusted to match those
208 of the killer whale sound stimuli, ranging from 145 to 151 dB re 1 μ Pa m for CTRL- (mean \pm SD:
209 148 \pm 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:
210 152 \pm 1 dB re 1 μ Pa m, n = 3 stimuli). The elapsed time separating the successive playback
211 stimuli performed on a tested whale was set at \geq 30min, in order to include a recovery period of
212 15 min of post-exposure followed by 15 min of pre-exposure before the next stimulus. In some
213 cases, this recovery period was shortened due to logistical constraints (e.g. weather conditions).
214 For these cases (7 out of 27 playback trials, see Table 1), the pre-exposure phase of a given
215 playback overlapped at least partly with the post-exposure phase of the previous playback trial.

216 For all stimulus types (except for CTRL+), 3 different versions (i.e. coming from
217 different recordings) were used to avoid excessive pseudoreplication (McGregor et al. 1992).

218 **Data collection from tags and visual observations**

219 Tag data were collected using movement and sound recording Dtags (Johnson and Tyack 2003)
220 and in one case a movement recording Little Leonardo tag (Aoki et al. 2013) (Table 1). All tags
221 were equipped with depth and three-dimensional accelerometer and magnetometer sensors,
222 sampled at 50 Hz for the Dtags and 10 Hz for the Little Leonardo tag. Additionally, Dtags
223 contained hydrophones that recorded stereo sound with 16-bit resolution at 96 or 192 kHz
224 sampling rate. Some tagged whales (gm13_149a, gm13_169a, gm13_169b) were also equipped
225 with a small Fastloc-GPS logger (Fastloc2, Sirtrack, New Zealand) attached to the Dtag. All

226 Dtags contained a VHF transmitter beacon that we used to relocate the focal whale when it
227 surfaced. Measurements of bearing and visual estimates of range during surfacing events were
228 collected to calculate the position of the tagged whale from the position of the observation
229 vessel. Simultaneously, surface behavioral data of the focal tagged whale and its group were
230 collected. The focal group was composed of all individuals in closer proximity to the focal
231 tagged individual and to each other than to other individuals in the area (Visser et al. 2014). This
232 definition is based on the relative spacing of individuals to each other. All individuals with a
233 similar distance to each other are part of a group (distance in body lengths, with categories
234 ranging from <1 body length, to >15 body lengths, see Visser et al. 2014 for details). Whale
235 positional data and visual behavior observations were recorded using the software Logger at
236 minimum 2 min intervals when the tagged whale was present at the surface (see Visser et al.
237 2014 for protocol details).

238 **Processing of the data**

239 We converted the tag's pressure data to depth and plotted vertical and horizontal movements
240 throughout the deployment period using Matlab software (version 7.8.0; www.mathworks.com).
241 We used the Dtag's acoustic recordings to identify sounds produced by the tagged whale or
242 nearby conspecifics. Specifically, we inspected spectrograms (Blackman-Harris window; FFT
243 length: 4096; time resolution: 21.3 ms) of the acoustic recordings using Adobe Audition software
244 and manually identified the production of clicks, buzzes and calls/whistles. Each annotated
245 sound was categorized according to its amplitude (see detailed method in Miller et al. 2012).
246 Sounds were classified by their perceived signal-to-noise ratio following the method of Alves et
247 al. 2014, in which loud (as perceived by the auditor) and clearly visible sounds on spectrograms
248 were considered likely to be produced by the tagged whale or nearby individuals, while faint and

249 barely detectable sounds (i.e. low signal-to-noise ratio) were considered likely to have been
250 produced by more distant whales. Only sounds likely produced by the tagged whale or nearby
251 animals were included in further analysis. Horizontal tracks of the focal whales were obtained
252 from the collected measurements of the relative bearing to the whale, visual estimates of
253 observer-whale range and the GPS location and course of the observation vessel. Where
254 available, GPS locations recorded by the GPS logger were also included in the horizontal track.
255 In one case, a non-focal tagged whale (Gm13_169b) had a GPS logger, allowing us to obtain
256 also the horizontal track of the non-focal whale. The accuracy of such Fastloc-GPS positions is
257 comparable to that of the visual position fixes and generally in the order of tens of meters, but
258 dependent upon other factors (Wensveen et al., 2015a). The tagged whale's direction of
259 movement was calculated from the horizontal track as the true bearing from the previous
260 location. Horizontal speed was calculated as the ratio between the distance and time between 2
261 successive locations of the tagged whale. To quantify the degree of aggregation, coordination
262 and surface activity of the focal group, we recorded seven metrics from surface observations
263 following Visser et al. (2014): 1) focal group size ; 2) number of individuals in the focal area (i.e.
264 within 200m of the focal animal); 3) distance to the nearest other group; 4) individual spacing 5)
265 surfacing synchrony, and 6) presence/absence of logging events in the focal group (i.e. whale
266 horizontally floating at the surface) and 7) number of spyhops (i.e. brief event for which the
267 whale positions itself vertically with head out of the water).

268 **Assessment of changes in behavior**

269 We used two different analytical approaches to detect behavioral responses of the pilot whales
270 exposed to the acoustic stimuli: 1) an expert panel scoring the severity of behavioral responses

271 by inspecting standardized plots of multivariate time series, and 2) univariate analyses of a range
272 of behavioral variables.

273 ***Severity scoring panel method***

274 Expert identification and scoring of responses was used to evaluate the severity of behavioral
275 responses on a numeric scale (Southall et al. 2007)) ranging from no effect (0), effects not likely
276 to influence vital rates (severity scores 1 to 3), effects that could affect vital rates (severity scores
277 4 to 6), to effects that are likely to affect vital rates (severity scores 7 to 9). The severity score of
278 a response depended on the type of behavioral response and its duration relative to the duration
279 of the playback (Southall et al. 2007; Miller et al. 2012; Sivle et al. 2015). The behavioral
280 responses in the 2008–2009 dataset (2 whales with Dtags) were scored by Miller et al. (2012),
281 and the 2010, 2013 and 2014 dataset (8 whales with Dtags) were scored in the present work in
282 exactly the same way. The behavioral changes were described and scored based on the
283 inspection of the geographic track plots and time series data plots generated from Dtag data and
284 visual observations; changes were scored by 2 independent scorer panels in accordance with the
285 severity scale (see Fig. S1 for example plots). One panel consisted of authors C.C., S.I., P.W. and
286 P.M., and the other of authors F.V., L.S., and two more scorers. All scorers are expert scientists
287 in this field of research. Since most of them participated to conduct fieldwork and data
288 collection, they could not be blind to the experiments. Therefore, panels were blind to each
289 other's scoring but not blind to the experimental condition. Thereafter, the 2 panels compared
290 and assimilated their results in the presence of an adjudicator (P.T) to reach a consensus scoring.
291 The adjudicator and 6 of the 8 scorers had previously scored long-finned pilot whale responses
292 using a similar scoring procedure (Miller et al. 2012); therefore, we are confident that the new
293 scoring effort is consistent with Miller et al. (2012). Overall, 80% of the attributed scores were

294 similar between both teams; among the 20% that differed and needed discussion, none of them
295 required the adjudicator for reaching a consensus. This indicates that the scoring measures of this
296 study were highly reliable across scorers.

297 For each exposure experiment, panels inspected the multivariate data plots and scored the
298 occurrence and severity of 7 behavioral metrics (see Table S1): avoidance of the sound source,
299 change in locomotion, change in orientation, change in the dive profile, impact on feeding (based
300 on alteration of the production of regular foraging clicks and buzzes), modification of vocal
301 behavior, change in group distribution. For all scored experiments, we distinguished between a
302 score of 0 (no behavioral change) and the absence of a score. The absence of a score for a
303 particular behavioral metric could have resulted from either missing data (e.g. no acoustics on
304 some tag data because of recording failure, no social behavioral data of non-focal whales) or
305 because of a particular behavioral context (e.g. cessation of feeding could only be assessed for
306 animals that were actually feeding before the start of the exposure). Then, for each experiment,
307 we quantified the proportion of scored behavioral metrics (%), expressed as the total number of
308 behavioral metrics for which a non-zero score was attributed, normalized to the maximum
309 number of potential scored behavioral metrics (i.e. excluding cases for which scores could not be
310 assessed) (Table S2).

311 ***Quantitative (univariate) analysis of behavioral metrics***

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

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

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

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

337 Regular clicks and buzzes produced during dives were attributed to foraging activity
338 whereas calls, whistles and buzzes produced near surface were attributed to social contexts (in
339 Risso's dolphins: Arranz et al. 2016; in long-finned pilot whales: Visser et al. 2016). For each

340 experimental phase, we calculated four acoustic variables: the proportion of time clicking while
341 diving (%), the occurrence of calls (#calls per min), the occurrence of buzzes (#buzzes per min)
342 produced at depth (i.e. while in a dive mode) and the occurrence of buzzes produced near
343 surface. Because the buzz rate at depth was particularly variable across animals, we inspected the
344 frequency distribution of the calculated change scores PRE_DUR and PRE_POST (see Fig. S2).
345 This analysis showed that most change scores values ranged from -0.25 to +0.25 (arbitrary unit),
346 whereas other values were spread out with values <-0.25 and $>+0.25$. Based on this, change
347 scores of buzz rate at depth were converted to -1 if <-0.25 buzz/min (reduction of buzzing), +1 if
348 >0.25 buzz/min (increase of buzzing), 0 if ranging between -0.25 and +0.25 buzz/min (very
349 weak or no change in buzz rate).

350 Horizontal approach or avoidance was quantified by calculating a movement reaction
351 score which was based on the comparison between the observed horizontal track during the
352 playback and the projected course of the whale given its direction of movement during the PRE
353 phase (method detailed in Curé et al. 2012). Positive or negative movement reaction scores
354 (arbitrary units) indicated respectively a horizontal attraction or avoidance response to the
355 playback. We also calculated for each phase the mean horizontal speed.

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

360 ***Statistical analyses***

361 To account for repeated measures (whales were exposed to several sound playbacks) and cases in
362 which two whales of the same group were exposed to a playback, we used Generalized

363 Estimating Equation (GEE) models that allowed us to specify a blocking unit (the focal group
364 ID) within which observations can be correlated (Hardin and Hilbe 2002). Statistical analyses
365 were performed using geepack (Carey et al. 2012) in R v.3.0.2 (R Development Core Team
366 2013).

367 For the severity scoring variable, *i.e.* proportion of non-zero scored responses per stimulus type,
368 we tested whether the two covariates *Signal* (4 factor levels: CTRL+, CTRL-, fKW, mKW) and
369 playback *Order* (2 factor levels: first and later than first) had an effect on the response variable.

370 For the univariate analysis approach, we tested whether the three covariates *Signal*, *Order* and
371 *Period* (2 factor levels: PRE_DUR and PRE_POST), as well as the 2-way interaction term
372 *Signal:Period*, had an effect on the change scores calculated for each of the behavioral response

373 variables. All explanatory variables (*i.e.* *Signal* and *Order* for the proportion of scored responses;
374 *Signal*, *Order*, *Period* and *Signal:Period* for the other variables) were included in the full GEE
375 models of all variables except for the horizontal movement reaction score for which there was no

376 *Period* covariate (because only the change score PRE_DUR was assessed). The change score
377 values of the univariate analysis variables and the severity scoring variable were modeled as
378 Gaussian response variables, and the blocking unit was the tagged whale group ID (accounting

379 for possible dependencies in the two cases for which the data included the focal tagged whale
380 and a secondary tagged non-focal whale of its group). As the Sandwich variance estimator can be
381 biased for small sample sizes, a Jackknife variance estimator was applied. For all GEE models,

382 we first ran the full model with all candidate explanatory variables. We conducted hypothesis-
383 based model selection using p-values given by an ANOVA (sequential Wald test) and backwards
384 selection (detailed method in Curé et al. (2015)). After fitting each model, an ANOVA was

385 conducted and the covariate or interaction term with the highest p-value was removed and the

386 GEE model refitted. This was repeated until all terms retained in the ANOVA were significant at
387 5% level.

388 **Results**

389 We tested 9 groups of long-finned pilot whales of which seven groups had one tagged whale, and
390 two groups had two tagged whales. Out of the 11 tagged whales, 8 were exposed to CTRL-, 5 to
391 CTRL+, 7 to fKW, and 6 to mKW playbacks (see Table 1). CTRL+ and Mammal-eating KW
392 playbacks were conducted in 2013 and 2014. CTRL- and fish eating KW playbacks were
393 conducted in 2008, 2009, 2010. Part of data of individuals tested in 2008, 2009 and 2010 were
394 used in previous work to describe responses to the fish-eating killer whale sound playback
395 (Miller et al. 2012; Curé et al. 2012) and/or to contrast them to responses to naval sonar as part
396 of a parallel project (Visser et al. 2016, Isojunno et al. 2017).

397

398 The total number of playback trials conducted per group tested ranged from 1 to 4 with an
399 average (\pm sem) recovery period between two successive playbacks of 37 ± 11 min ($n=14$
400 recovery periods). Nine of those playbacks were played before any other stimuli (at first order
401 #1) and 17 were played as 2nd, 3rd or 4th order (different than #1). We excluded three playback
402 trials (2 playbacks of Gm09_138a and the first playback of Gm08_159a) from the dataset
403 because the tagged whales were too far from the sound source to detect sounds (see Curé et al.
404 (2012)). The first playback of Gm13_137a consisted of an unfamiliar humpback whale song
405 stimulus (HW) that was not included in the statistical analyses since $n=1$. The tagged whales
406 Gm08_159a and Gm09_156b presented in Table 1 were previously exposed to sonar sounds as
407 part of a parallel project (Kvadsheim et al. 2009).

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

415 Regarding the univariate analysis, for most behavioral variables, only the factor *Signal*
416 was retained in the best fitting GEE model, indicating that the playback *Signal* was the main
417 factor explaining the variance in the data (Tables 2 and 3). For mean horizontal speed and near
418 surface buzz rate, the interaction term *Signal:Period* was retained. For the number of animals
419 present in the focal area and the change in the proportion of time spent in diving at depth ranging
420 from 5 to 10m, the two main factors *Signal* and *Period* were retained in the best fitting GEE
421 model. For the occurrence of buzzing at depth and the ratio of time spent near the surface to time
422 spent diving, the factors *Signal* and *Order* were retained. For the change in the proportion of time
423 spent in diving deeper than 10m, the ANOVA did not retain any of the factors, indicating that
424 none of them explained the variance in the data for this variable.

425 **Attraction versus avoidance responses**

426 ***Horizontal movements***

427 A horizontal approach response was scored in 100% of the CTRL+, fKW and mKW playbacks
428 whereas no change in horizontal movement was ever scored in response to CTRL- (Fig. 1b;
429 Table S1). A horizontal avoidance response was never scored to any of the stimulus types. The
430 calculated movement reaction scores were highly positive in response to fKW, mKW, and

431 CTRL+, indicating a clear horizontal attraction towards the sound source (Fig. 2a; Table S4). For
432 these three stimulus types, the tested whales reduced their horizontal speed during the post-
433 exposure (Fig. 2b), once they were already near the source. All these results significantly
434 contrasted to the response to CTRL- for which whales barely changed direction and decreased
435 speed only during the exposure (Fig. 1b; Table S4).

436

437 *Vertical movements*

438 The severity scoring panel results showed that the whales changed their dive profile most
439 consistently in response to mKW and CTRL+ playbacks (Fig. 1; Table S1) and that these
440 changes varied across subjects depending on the behavioral context of the whales during the
441 period preceding the start of playback (Table S1). One consistent result was that the whales that
442 interrupted feeding behavior in response to mKW and CTRL+ playbacks switched from a clear
443 foraging dive mode to shallower dives (Table S1). Results of the quantitative analysis conducted
444 on the dive behavior metrics showed that the whales exposed to mKW playbacks spent
445 significantly less time near surface compared to the absence of such a change in response to both
446 control playbacks CTRL- and CTRL+ (Fig. 3a; Online Resource, Table S4). Moreover, whales
447 exposed to mKW spent more time diving at shallow depths (<5m) and at the depth range of the
448 speaker (between 5 and 10m) compared to the three other stimuli (Fig. 3b-c; Table S4). There
449 was no evidence of vertical avoidance responses to greater depths (Fig. 3d; Table S1). The order
450 of playbacks had an effect on dive behavior, indicated by an increased proportion of time spent
451 near surface for the first playback compared to the following exposures (effect of *Order* at level
452 of $p < 0.05$, Table S4). Moreover, the overall increased proportion of time spent in diving at the

453 depth range of the speaker observed after the end of most playbacks differed significantly from
454 the slight change occurring during playbacks (effect of *Period* at level of $p < 0.05$, Table S4).

455

456 ***Changes in social behavior and surface displays***

457 The severity scoring panel results demonstrated for all stimulus playback types except CTRL-,
458 that group distribution changed for the duration of the exposure or even longer (severity score 5
459 or 6) (Table S1). Moreover, inspection of the multivariate plots showed that changes in group
460 distribution and surface displays such as spyhops were scored more in response to CTRL+ and
461 mKW sound playbacks compared to fKW sound playbacks, whereas they barely occurred in
462 response to CTRL- (Fig. 1b). Univariate analyses showed that both the number of whales in the
463 focal group and in the focal area increased significantly in response to CTRL+ and to fKW
464 playbacks compared to the overall no change observed in response to CTRL- (Fig. 4a-b; Table
465 S4). Those changes in group distribution in response to CTRL+ and fKW significantly
466 contrasted to the lack of response to mKW sound playbacks (Fig. 4a-b; Table S4). The distance
467 between whales within the focal group clearly decreased in response to mKW sound playbacks
468 compared to the overall lack of response observed to fKW, CTRL- and CTRL+ sound playback
469 (Fig. 4c; Table S4). Whales came significantly closer to other groups present in the focal area in
470 response to fKW playback compared to the overall lack of change in response to CTRL- and
471 mKW playbacks (Fig. 4d; Table S4). Moreover, whales became less synchronized when
472 surfacing in response to CTRL+ compared to the overall level of synchrony maintained during
473 exposure to CTRL- and fKW playbacks (Fig. 4e; Table S4). Whales exhibited significantly more
474 spyhops in response to CTRL+, fKW and mKW compared to CTRL- playbacks (Fig. 5a) and
475 increased logging in response to CTRL+ only (Fig. 5b; Table S4). Moreover, they increased

476 calling activity in response to fKW compared to mKW playbacks (Fig. 6a; Table S4). There was
477 a significant decrease in buzzing recorded near surface in response to fKW sound playbacks
478 compared to CTRL- that lasted beyond the end of playback (Fig. 6b; Table S4). This
479 modification in vocal behavior in response to the fKW playback significantly contrasted to the
480 increase in near-surface buzz rate during mKW sound playbacks. Whales also increased near-
481 surface buzz rate in response to CTRL+ compared to CTRL- but only after the end of playback
482 (difference between CTRL+ and CTRL- dependent on the *Period*; Table S4).

483

484 ***Effects on foraging behavior***

485 Based on inspection of the dive profile and production of foraging sounds (regular clicks and
486 buzzes) when available, the severity scoring panel could determine whether the whales were in a
487 foraging mode. Playbacks for which whales were clearly not foraging before the start of
488 exposure (4 CTRL-, 2 CTRL+, 2 fKW and 2 mKW; excluding data without acoustics) were
489 never associated with a start of feeding. Clear cessation of feeding was only scored in response
490 to CTRL+ and mKW playbacks (Fig. 1b; Table S1). Specifically, both whales that were
491 conducting deep foraging dives (>100m depth) before the start of CTRL+ and mKW (N=2
492 playbacks each) switched to a shallower dive mode along with a cessation of buzzing and a
493 reduction of clicking rate (Table S1). The cessation of feeding extended until after the end of
494 exposure, resulting in a severity score of 7. The other whales exposed to CTRL+ (N=1) and
495 mKW (N=2) were conducting shallower dives while producing regular clicks and buzzes before
496 the start of exposure; this was considered to represent a potential foraging mode. Severity
497 scoring panels did not score cessation of feeding for those whales (score 0; Table S1). By
498 contrast, none of the fKW playbacks resulted in a scored cessation of feeding. The whale

499 Gm08_159a that was in a deep foraging mode before the start of fKW playback, switched to a
500 shallower dive mode but kept producing clicks and buzzes while diving, and therefore was
501 assumed to have continued feeding activity (score 0; Table S1). The whale Gm09_156b, which
502 was exposed twice to fKW playbacks and for which no acoustic data was recorded (failure of
503 Dtag), was in a deep dive mode before the start of playback, thus indicating likely feeding
504 behavior. This whale remained in this deep dive mode during both fKW playbacks (score 0;
505 Table S1). Quantitative analyses showed that the proportion of time spent clicking while diving
506 significantly decreased in response to CTRL+ and to mKW playbacks compared to the overall no
507 change in response to CTRL-, whereas the reduction was not statistically supported for fKW
508 sound playbacks (Fig. 6c; Table S4). Moreover, the whales significantly reduced their production
509 of buzzes while diving in response to mKW compared to both CTRL- and fKW playbacks (Fig.
510 6d; Table S4). This reduced buzzing rate was more pronounced for the first playback than for the
511 other following playbacks (effect of *Order* at level of $p < 0.05$; Table S4).

512

513 **Discussion**

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

518 The most striking outcomes reveal first, that the whales barely changed their behavior in
519 response to the broadband noise control playback (CTRL-). Whales were consistently attracted
520 to all the other three sound presentations (fKW, mKW, and CTRL+), indicating a strong

521 tendency for this species to approach, presumably to inspect the source of these sounds occurring
522 in their environment (Table 2). However, details of how their behavior changed in response to
523 each stimulus type indicate functional discrimination of these sound types. The whales stopped
524 feeding and reduced time spent near the surface in response to mKW playbacks, whereas they
525 joined other groups to form bigger groups in response to fKW playbacks. And finally, the whales
526 clearly changed behavior in response to a repeated modulated upswEEP artificial 1-2kHz
527 playback signal (CTRL+). In particular, the response to CTRL+ playbacks included a
528 combination of parts of the responses to mKW (interruption of feeding) and to fKW (joining
529 other groups), and specifically a reduced surface synchrony and an increased logging events
530 compared to CTRL- (Table 2).

531 **Contrasting response to CTRL- versus other stimuli**

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

541 The three other playback stimuli had tonal modulated frequency components (CTRL+,
542 fKW and mKW) and induced a clear horizontal approach towards the sound source along with
543 an increase in spyhopping. The same approach response was also elicited to playback of

544 unfamiliar humpback whale sounds (data not shown). The shared behavioral response towards
545 playbacks which contained tonal sounds could be a way to probe information about the location
546 and/or characteristics of the sound source by getting closer and gathering visual cues from the
547 surface.

548 **Response to killer whale sound playbacks**

549 Previous work with parts of this data set (whales tested in 2008, 2009 and 2010) showed that
550 pilot whales approached a fKW sound source and aggregated with other whales (Curé et al.
551 2012). Beside the possibility that an approach response might be a way to investigate the sound
552 source and to assess level of disturbance risk, we had hypothesized other, not mutually exclusive,
553 potential functions. One hypothesis was that pilot whales learn to associate fKW presence with
554 an opportunity to feed and they may eavesdrop on fKW sounds to locate a food patch and
555 increase their foraging efficiency ('dinner bell' effect, Stansbury et al. 2015). If so, one would
556 expect pilot whales to approach the source and initiate exploratory or foraging dives to search for
557 a potential prey patch, the aggregation being a consequence of the food appeal triggered by the
558 source and available to other animals present in the area. In the present study, by investigating
559 the foraging (diving and echolocation) behavior of the whales, we showed that none of the
560 playbacks, including fKW sounds, appeared to induce an initiation of foraging behavior.
561 Moreover, visual observations conducted in Norway reported that killer whales actively feeding
562 on herring were chased away by pilot whales that did not seem themselves interested in preying
563 upon herring (De Stephanis et al. 2014). Altogether, these results do not support the 'dinner bell'
564 hypothesis, indicating that pilot whales might not have perceived fKW sounds as indicating an
565 opportunity to feed.

566 A second hypothesis was that pilot whales display an active intimidation behavior in
567 response to fKW sounds, either to mob a potential predator (e.g. in mammals: Tamura 1989; in
568 birds: Francis et al. 1989, Preisser et al. 2005) or to chase away an intruder perceived as a
569 potential competitor exploiting the same foraging areas (e.g. in birds: Boyden 1978 ; in fish:
570 Kohda 1991; Lehtonen et al. 2010). This behavior usually involves a pursuit along with the
571 production of sounds and additional intimidation behaviors (e.g. grouping with other individuals,
572 physical defense behavior) (reviewed in Alcock 2009). “Fight” strategies involving intimidation
573 behaviors have been observed in other cetaceans in response to killer whale attacks, such as the
574 sea-surface rolling and tail fluke splashing of grey whales defending their calves (Ford & Reeves
575 2008). Here, the clear horizontal attraction towards fKW sound source along with joining of
576 different subgroups and increased production rate of social calls in response to fKW playbacks
577 compared to mKW playbacks support an active intimidation behavior rather than the dinner bell
578 effect, which is in line with the chasing behavior observations described by De Stephanis et al.
579 (2014).

580 In order to investigate whether such active intimidation behavior is driven by a perceived
581 competition for the habitat/foraging areas (since competition for the same prey is unlikely) or an
582 increased predation risk in pilot whales, we detailed the differences in behavioral responses to
583 both fKW and mKW sounds. Though pilot whales approached the source in response to both
584 fKW and mKW, the exact response strategy appeared different in response to mKW. Indeed,
585 there was a tightening of animals within their group in response to mKW playbacks, indicating
586 potential increased group cohesion, which contrasted with the joining to other groups observed in
587 response to fKW playbacks. Moreover, during the mKW playbacks, whales spent less time near
588 surface and more time in shallow dives and dives within the depth range of the speaker. The fact

589 that mKW sounds are unfamiliar to the pilot whales could explain a need for additional efforts
590 (e.g. spending more time within depth range of sound source) to probe for acoustic information
591 specifically in response to this stimulus.

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

611 more discrete way (i.e. more directional or short-range distance) than calls that can travel longer
612 distances (Norris and Dohl 1979 ; Perrin et al. 2009).

613 Since only the behavioral response to the fKW contained the typical combination of
614 behavioral indicators of an active intimidation behavior (joining with other groups while
615 approaching), we conclude that this response was specifically exhibited to fKW but not to mKW.
616 In Norway, long-finned pilot whales may be able to learn that the sounds produced by local
617 herring-eating killer whales represent a relatively low-risk stimulus. The active intimidation
618 behavior in response to fKW playbacks could be driven by a perceived low predator risk or
619 alternatively by perceived competition with the fKW. Indeed, although pilot whales in Norway
620 likely do not feed on the same prey as local herring-eating killer whales (De Stephanis et al.
621 2014), they target demersal prey (cod, *Todarodes*) that do eat herring, which could explain the
622 correlation between occurrence of pilot whales and herring (Nottestad et al. 2015), and possible
623 indirect competition with local killer whales for the exploitation of common foraging areas.

624 Another striking difference between responses to both KW sound types was the clear
625 cessation of feeding induced by mKW playbacks that contrasted with no case of such an effect in
626 response to fKW. An animal's decision to respond to a threat is based upon a trade-off between
627 the costs and benefits of behavioral change and the perceived risks evaluated by the animal
628 (Lima and Dill 1990; Frid and Dill 2002; Sih 2013). Thus, animals must make a choice between
629 avoiding the perceived risk from the threat versus continuing fitness-enhancing activities such as
630 feeding. Encountering a predator is probably the maximum level of natural threat an animal can
631 meet, since it may lead to death. One can thus expect the adaptive response of the prey to a
632 perceived increased predation risk to be particularly costly (e.g. by interrupting fitness-enhancing
633 activities such as feeding) compared to other natural disturbance types (Curé et al. 2016).

634 Cessation of feeding is typically observed in perceived high-risk predatory contexts in terrestrial
635 taxa (e.g. in mule deer, Altendorf et al. 2001; in birds, Turney and Godin 2014) as well as in
636 other cetacean species (e.g. in sperm whales, Curé et al. 2013; in humpback whales, Curé et al.
637 2015). Here, we found clear cessation of feeding in response to mKW playbacks that lasted for
638 longer than the duration of the exposure (severity score 7), which if persistent, could potentially
639 lead to impact on vital rates (Southall et al. 2007). The specifically costly response (cessation of
640 feeding) to mKW playbacks supports the hypothesis that pilot whales perceived the unfamiliar
641 mKW sounds as a particularly threatening stimulus, possibly a predator-signaling cue. Although
642 the subject individuals could not have experienced predatory interactions with the Pacific
643 mammal-eating killer whales from which we collected sounds to prepare our stimuli, and given
644 that it seems unlikely that the Atlantic mammal-eating killer whales would predate on pilot
645 whales, pilot whales may have conserved past historical antipredator strategies (Sih et al. 2013;
646 De Stephanis et al. 2014; Hettena et al. 2014).

647 The more cryptic and more cohesive approach response strategy to mKW playbacks (no
648 grouping behavior, individuals tightening within group, less time near surface, promoting surface
649 buzzing vocal activity) compared to fKW playbacks could be a way to ‘inspect’ the situation in
650 order to evaluate the level of threat (e.g. inspecting the level of predator threat, Pitcher et al.
651 1986) before engaging in a further response, for instance either a social defense strategy or a
652 flight response (Curé et al. 2015).

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

657 stimulus, i.e. a low predation risk or a known heterospecific species exploiting the same habitat,
658 and an anti-predator behavior directed towards a perceived high-level of predation risk.

659 One could argue that the difference between the behavioral responses to both killer whale
660 sound types is due to perceived familiar fKW versus unfamiliar mKW sound stimuli (Deecke et
661 al. 2002). Indeed, by having experienced that the local fish-eating killer whales (fKW) are
662 harmless, pilot whales might have shaped their response strategy to the detected presence of this
663 killer whale ecotype. By contrast, they would react differently to any other unfamiliar KW
664 sounds such as mKW. Moreover, it might be possible that the missing upper frequency spectrum
665 part of the KW sound playback (since the speaker played sounds only up to 20kHz) had an effect
666 of the behavioral response of pilot whales, particularly once they got close to the source where
667 higher frequencies should be detectable if the whale is pointing towards the subject (Miller
668 2002).

669

670 **Response to CTRL+**

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

679 One of the analytical approaches to improve our ability to assess potential behavioral
680 disturbance effects of a non-natural stimulus such as anthropogenic noise is to compare
681 responses to this stimulus with responses to known or novel signals from predators as a reference
682 pattern of disturbance expressed in relevant natural context (Frid and Dill 2002; Curé et al.
683 2016). Our results indicate that in addition to the anti-predator responses to known predators or
684 to unfamiliar signals that could indicate an unknown level of predation risk, the responses to
685 novel signals (here the CTRL+ signal) can be also valuable high level-disturbance reference
686 models to help in the interpretation of the biological significance of the responses to other
687 stimuli. Indeed, such models could be used to extend the risk-disturbance hypothesis to species
688 without natural predators, such as the killer whale whose apparent sensitivity to anthropogenic
689 noise could not be explained by the predation risk template (Harris et al. 2017).

690 Second, CTRL+ playbacks specifically induced a reduction in surface synchrony and an
691 increase in the number of logging events. The decrease in synchrony could reflect a social
692 reorganization within the group or a difficulty for the individuals of the group to maintain
693 cohesion (Visser et al. 2016). Logging more might be a way for whales to reduce the risk of
694 masking and to use visual cues to supplement acoustics in relocating group members and
695 maintaining group cohesion, as also observed for pilot whales in this area in response to naval
696 sonar exposure (Wensveen et al. 2015b; Visser et al. 2016).

697 Interestingly, our findings match partly those of previous research that showed a
698 cessation of foraging and increased logging behavior (at received levels of 145-170dB) in
699 response to a controlled CTRL+ exposure generated at much higher SPLs, used to simulate a
700 naval sonar exercise (LFAS 1-2kHz signals in: Miller et al. 2012; Sivle et al. 2012; Wensveen et
701 al. 2015b; Visser et al. 2016). However, the responses did not match entirely. There was no

702 horizontal approach but some horizontal avoidance recorded in response to the powerful sonar
703 CTRL+ source (Miller et al. 2012) compared to the CTRL+ playbacks we conducted in the
704 present study, indicating whales perceive different levels of disturbance between these two
705 presentations.

706

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

725 playback approach should be investigated to gain insight in the use of eavesdropping and other
726 processes that might explain the range of inter-specific interactions with killer whales and other
727 species.

728

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1015 **Figure Captions**

1016 **Fig. 1.** Severity scoring panel results. a) Proportion of scored behavioral responses (all 7
1017 behavioral response types combined) for each of the 4 stimulus types (in %, shown as mean \pm
1018 sem). This proportion is expressed as the number of behavioral metrics for which a non-zero
1019 score was attributed, normalized to the maximum number of potential scorable behavioral
1020 metrics. As an example, CTRL+ playbacks induced 75.6% (\pm 10.4) of scored behavioral
1021 responses among the potential maximum 100%. *P*-values are from GEE results of the paired-
1022 comparisons across the 4 stimulus types (Table S4) and are given as **P*<0.05, ***P*<0.01 and
1023 ****P*<0.001. b) Cumulated proportions of scored responses for each of the 7 behavioral response
1024 categories of the scoring panel across the 4 stimulus playback types (%). As an example,
1025 avoidance responses never occurred during any playbacks (0% whatever the stimulus playback
1026 type), whereas change in locomotion (horizontal approach towards the source) was the most
1027 common response type (100% of the CTRL+, fKW and mKW playbacks). CTRL- = broadband
1028 noise control playback; CTRL+= 1-2kHz tonal sound control playback; fKW= fish-eating killer

1029 whale sound playback; mKW= mammal-eating killer whale sound playback. N: number of tested
1030 individuals; n: number of playback trials.

1031

1032 **Fig. 2.** Quantitative analysis of the effects of sound playbacks on the direction of horizontal
1033 movement: a) mean movement reaction score (arbitrary units, a.u) showing avoidance (if
1034 negative) versus approach response (if positive), and b) change in mean horizontal speed ($\text{m}\cdot\text{s}^{-1}$)
1035 showing increase (if positive) versus decrease (if negative) of speed. The mean movement
1036 reaction score is a PRE_DUR change score, whereas for speed, both change scores (PRE_DUR
1037 and PRE_POST) are shown. For speed, the factors *Signal*, *Period* and *Signal:Period* were
1038 retained in the ANOVA (Table S3). *P*-values of the GEE results are given as * $P < 0.05$, ** $P < 0.01$
1039 and *** $P < 0.001$ for paired differences between stimuli independent of *Period* (interpretation of
1040 the factor *Signal*; Table S4), and as ⁺ $P < 0.05$, ⁺⁺ $P < 0.01$ and ⁺⁺⁺ $P < 0.001$ for cases where the
1041 factor *Signal:Period* was significant (Table S4). PRE_DUR = difference between the DUR
1042 (sound playback) and PRE phases reflecting the behavioral change induced during the sound
1043 exposure; PRE_POST = difference between the POST and PRE phases indicating whether the
1044 behavioral change lasted (or eventually started) after the end of exposure. CTRL- = broadband
1045 noise control playback; CTRL+= 1-2kHz tonal sound control playback; fKW= fish-eating killer
1046 whale sound playback; mKW= mammal-eating killer whale sound playback. N: number of tested
1047 individuals; n: number of playback trials.

1048

1049 **Fig. 3.** Quantitative analysis of the effects of sound playbacks on dive behavior : a) Ratio of
1050 time spent near surface over diving time, b) change in the proportion (%) of time spent in
1051 shallow diving (i.e. maximum depth <5m), c) change in the proportion (%) of time spent in

1052 diving within the depth range of the speaker (i.e. $5\text{m} \leq \text{maximum depth} < 10\text{m}$), d) changes in the
1053 proportion (%) of time spent in deeper diving (i.e. $\text{maximum depth} \geq 10\text{m}$). For the change in %
1054 of time spent in diving at depth deeper than 10m (d), the ANOVA did not retain any factors,
1055 indicating that the variance in the data was not explained by any of those covariates. For the
1056 three other parameters (a, b, c), the factor *Signal* explained the differences between the paired-
1057 comparisons (Tables 3 and 4). For (a), the factor *Order* (not illustrated on the figure) also
1058 explained the variance in the data (Tables 4 and 5). For (c), the factor *Period* was also retained in
1059 the ANOVA but the interaction term *Signal:Period* was not significant, indicating that the effects
1060 of *Signal* and *Period* were independent to each other. *P*-values from GEE results are given as
1061 $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$. PRE_DUR = difference between the DUR (sound
1062 playback) and PRE phases reflecting the behavioral change induced during the sound exposure;
1063 PRE_POST = difference between the POST and PRE phases indicating whether the behavioral
1064 change lasted (or eventually started) after the end of exposure. CTRL- = broadband noise control
1065 playback; CTRL+= 1-2kHz tonal sound control playback; fKW= fish-eating killer whale sound
1066 playback; mKW= mammal-eating killer whale sound playback. N: number of tested individuals;
1067 n: number of playback trials.

1068

1069 **Fig. 4.** Quantitative analysis of the effects of sound playbacks on the group distribution
1070 parameters : a) change in group size (in number of animals), b) change in the number of animals
1071 in the focal area (in number of animals), c) change in individual spacing (a.u.) representing
1072 positive values as spreading and negative values as tightening of whales within the group, d)
1073 change in the distance to nearest other subgroup (a.u.), e) change in surface synchrony (a.u.). For
1074 each of those 5 parameters (a-e), only the factor *Signal* explained the differences between the

1075 paired-comparisons, independently of the *Period* (Tables 3 and 4). *P*-values from GEE results
1076 are given as **P*<0.05, ***P*<0.01 and ****P*<0.001. PRE_DUR = difference between the DUR
1077 (sound playback) and PRE phases reflecting the behavioral change induced during the sound
1078 exposure; PRE_POST = difference between the POST and PRE phases indicating whether the
1079 behavioral change lasted (or eventually started) after the end of exposure. CTRL- = broadband
1080 noise control playback; CTRL+= 1-2kHz tonal sound control playback; fKW= fish-eating killer
1081 whale sound playback; mKW= mammal-eating killer whale sound playback. N: number of tested
1082 individuals; n: number of playback trials.

1083

1084 **Fig. 5.** Quantitative analysis of the effects of sound playbacks on behavioral surface displays: a)
1085 change in occurrence of spyhops (in number of spyhops per min), b) changes in occurrence of
1086 logging (number of logging events per min). For these 2 parameters (a-b), only the factor *Signal*
1087 explained the differences between the paired-comparisons, independently of the *Period* (Tables 3
1088 and 4). *P*-values from GEE results are given as **P*<0.05, ***P*<0.01 and ****P*<0.001. PRE_DUR
1089 = difference between the DUR (sound playback) and PRE phases reflecting the behavioral
1090 change induced during the sound exposure; PRE_POST = difference between the POST and
1091 PRE phases indicating whether the behavioral change lasted (or eventually started) after the end
1092 of exposure. CTRL- = broadband noise control playback; CTRL+= 1-2kHz tonal sound control
1093 playback; fKW= fish-eating killer whale sound playback; mKW= mammal-eating killer whale
1094 sound playback. N: number of tested individuals; n: number of playback trials.

1095

1096 **Fig. 6.** Quantitative analysis of the effects of sound playbacks on vocal behavior: a) changes in
1097 occurrence of social calls (#calling per min), b) change in occurrence of near surface buzzes

1098 (#buzzing event per min), c) change in the proportion of time spent clicking while diving (%),
1099 and d) changes in occurrence of buzzes at depth (a.u). The differences of the occurrence of near
1100 surface buzzing across the stimulus types depend on the *Period* (Table S3). For the other 3
1101 parameters (a, c, d), the paired differences observed between the stimulus types were
1102 independent of the *Period* (Tables 3 and 4). For the occurrence of buzzes produced at depth (d),
1103 the factor *Order* (not illustrated on the figure) also explained the variance in the data (see Tables
1104 3 and 4). *P*-values from GEE results are given as **P*<0.05, ***P*<0.01 and ****P*<0.001 for paired
1105 differences between stimuli independent of *Period* (interpretation of the factor *Signal*, Table S4),
1106 and as +*P*<0.05, ++*P*<0.01 and +++*P*<0.001 for cases where the factor *Signal:Period* was
1107 significant (Table S4). PRE_DUR = difference between the DUR (sound playback) and PRE
1108 phases reflecting the behavioral change induced during the sound exposure; PRE_POST =
1109 difference between the POST and PRE phases indicating whether the behavioral change lasted
1110 (or eventually started) after the end of exposure. CTRL- = broadband noise control playback;
1111 CTRL+= 1-2kHz tonal sound control playback; fKW= fish-eating killer whale sound playback;
1112 mKW= mammal-eating killer whale sound playback. N: number of tested individuals; n: number
1113 of playback trials.

1114

FIGURES

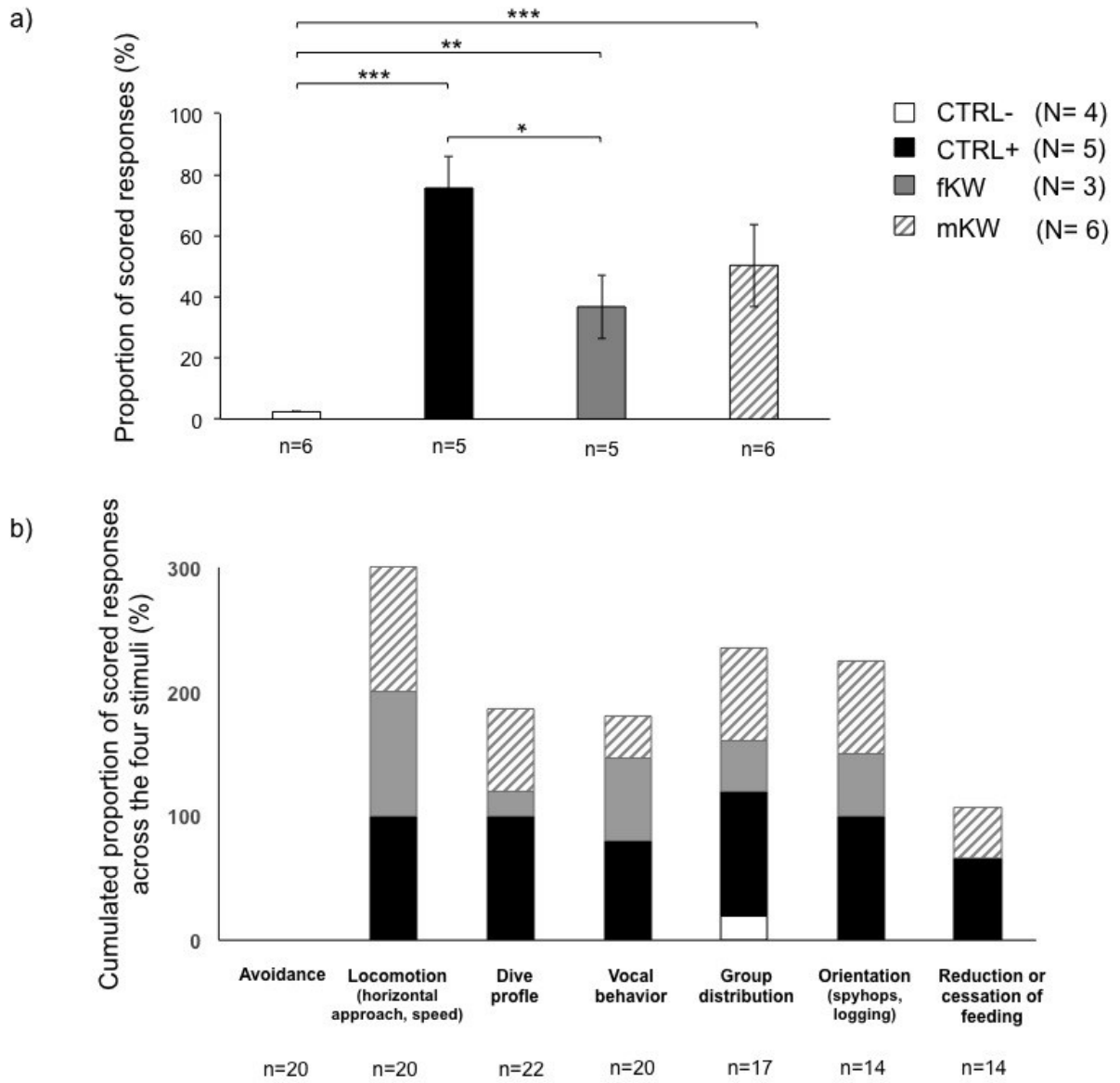


Figure 1.

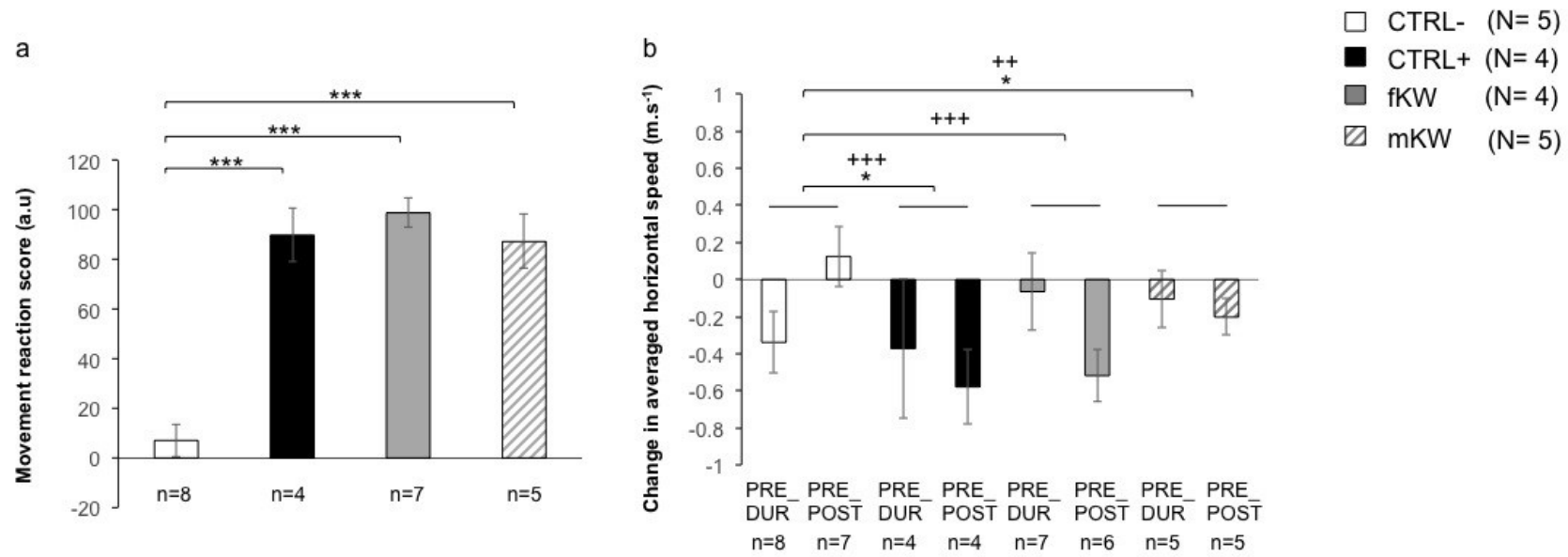


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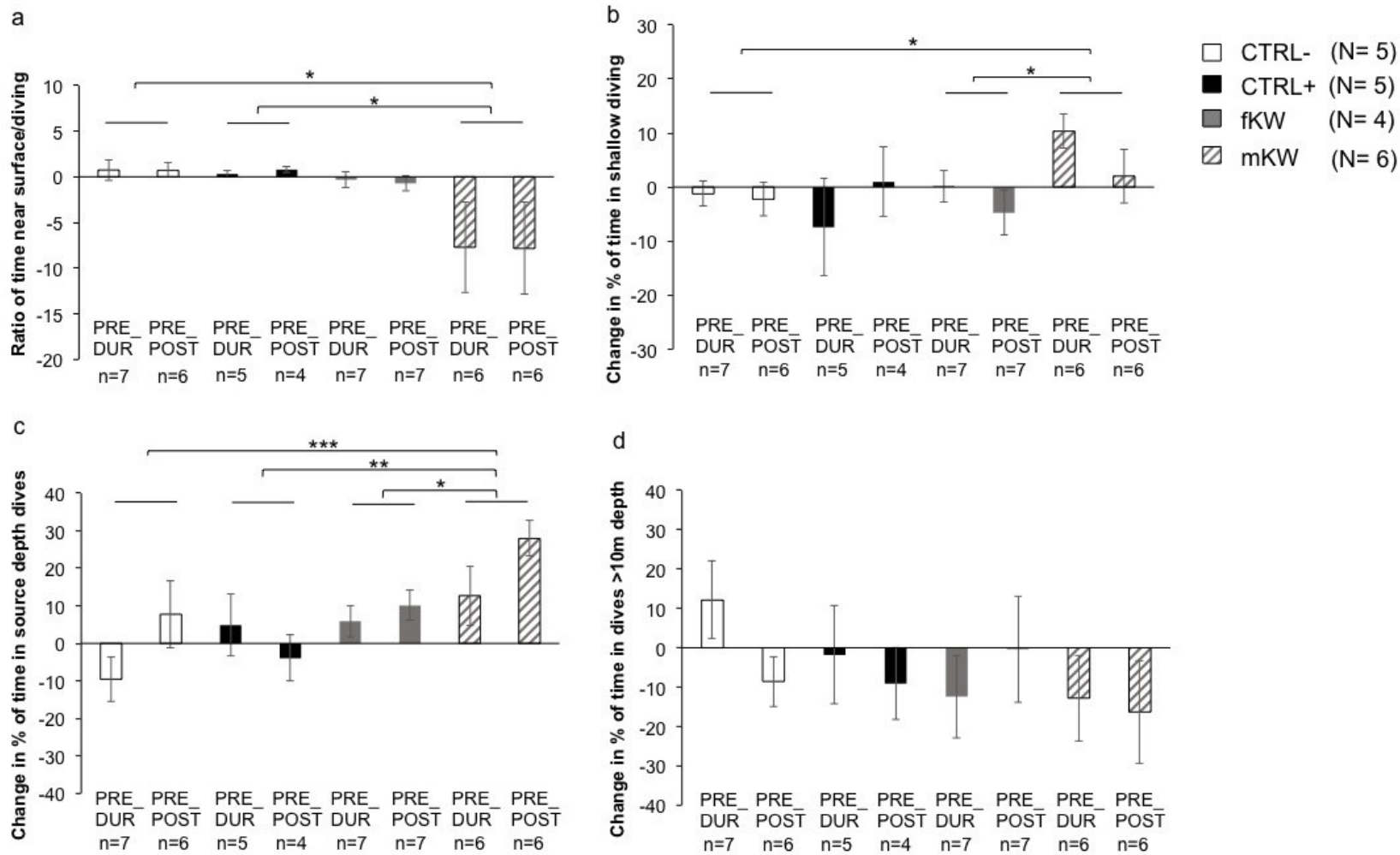


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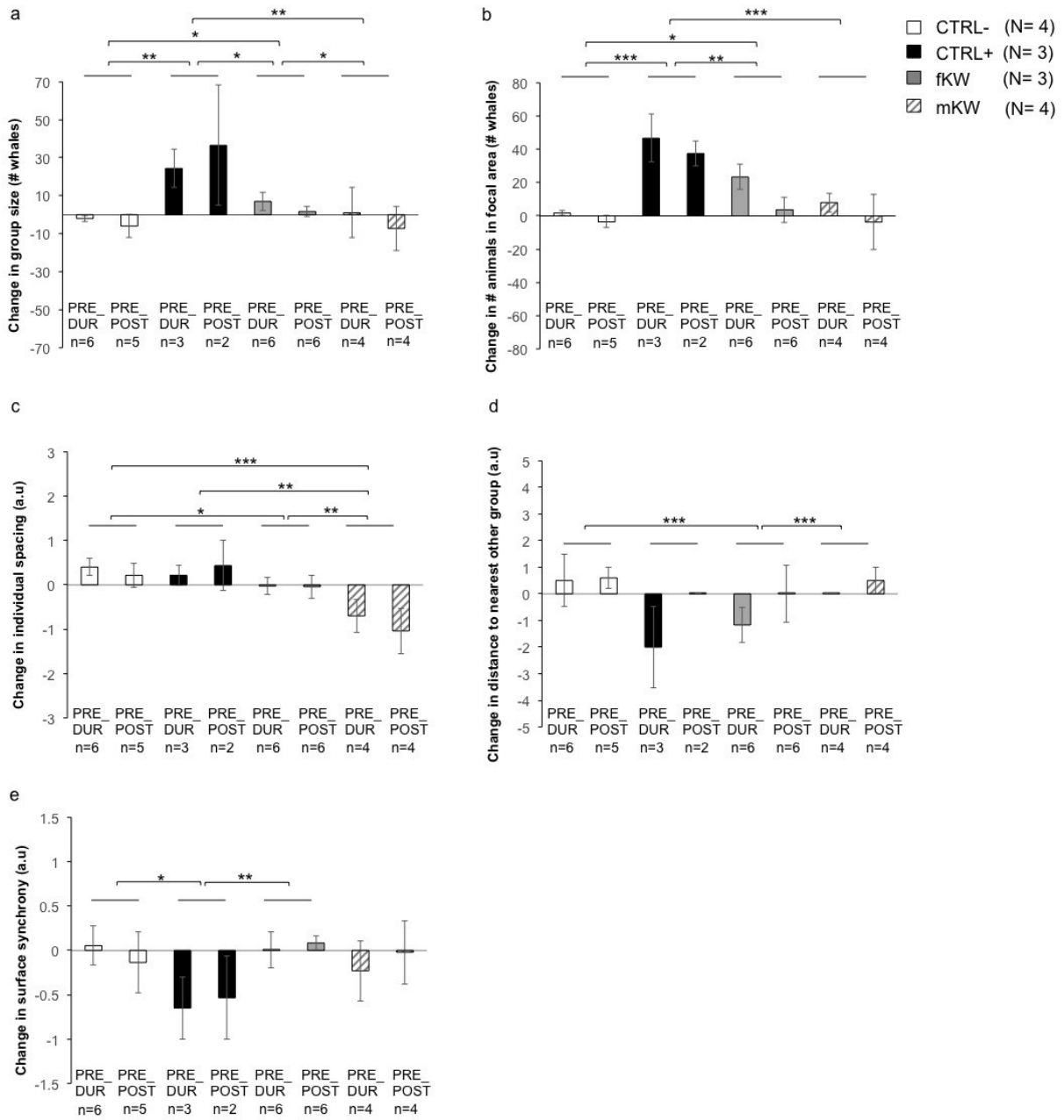


Figure 4.

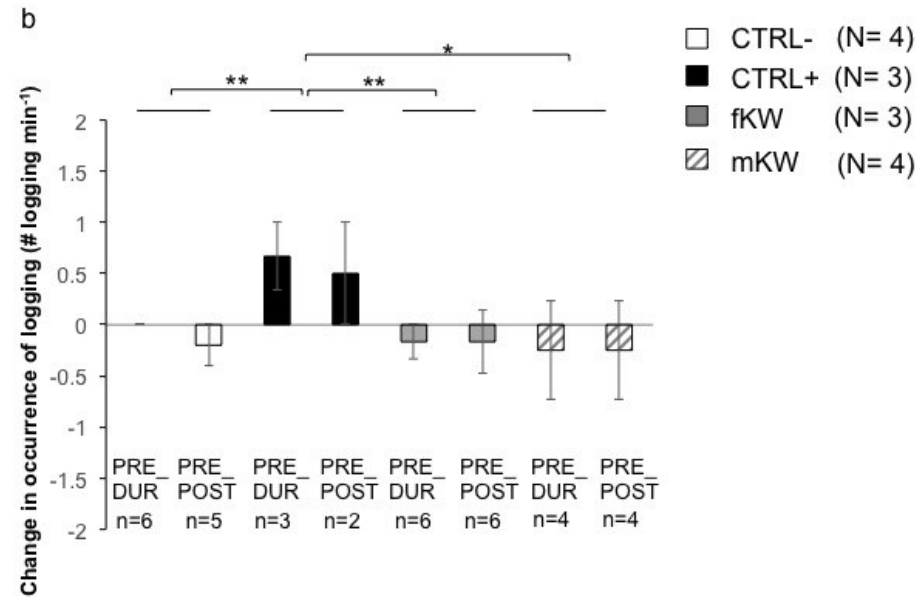
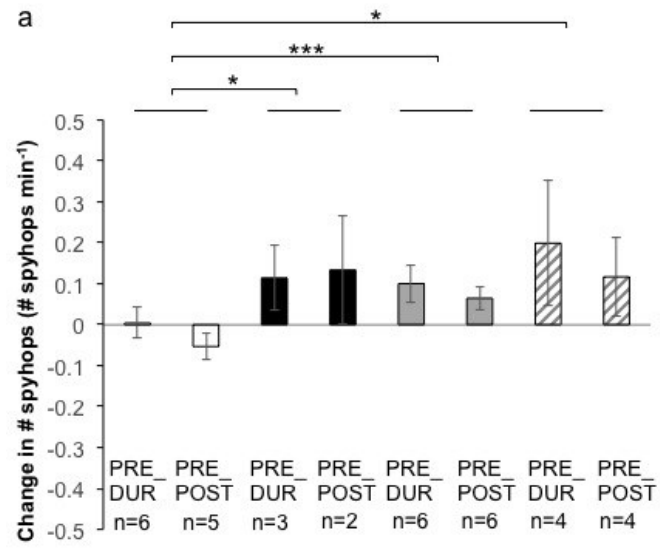


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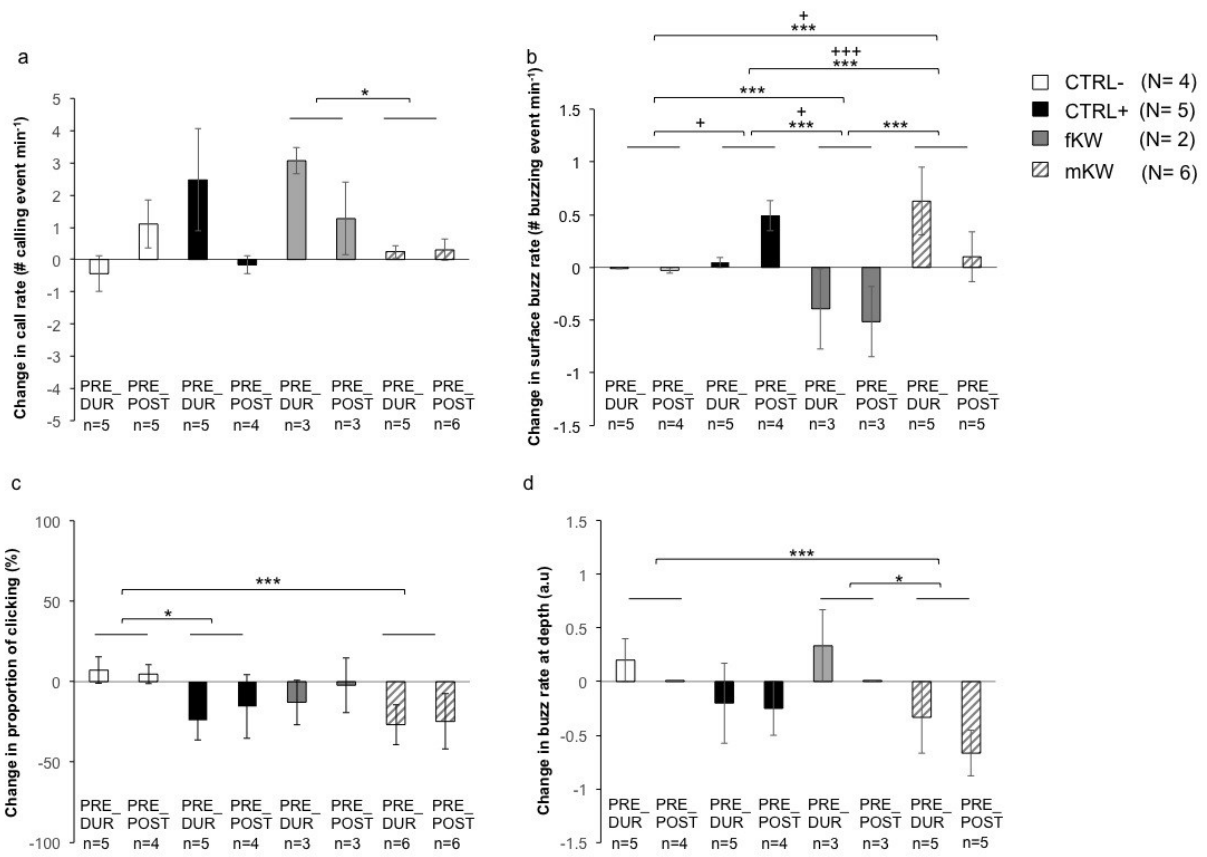


Figure 6.

TABLES

Table 1. Overview of collected data. 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. Absence of a change score is due to missing data for one or more of the three phases PRE, DUR and POST. Italic lines 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. Whale tag ID = identification number of tagged whale for each experiment. The code for the whales ID tagged with a D-tag 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 code ID (LpW_10pm1N). 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 to the focal follow group. Playback stimuli: CTRL- = broadband noise control playback; CTRL+= 1-2kHz 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.

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	(1 ;1)	(0;0)	(1*;1*)	(1 ;1)
LpW_10pm1N	CTRL-	1	(1 ;1)	(0;0)	(1 ;1)	(1 ;1)
<i>LpW_10pm1N</i>	<i>fKW</i>	2	(1 ;1)	(0 ;0)	(1 ;1)	(1 ;1)
<i>LpW_10pm1N</i>	<i>CTRL-</i>	3	(1 ;1)	(0 ;0)	(1 ;1)	(1 ;1)
<i>LpW_10pm1N</i>	<i>fKW</i>	4	(1 ;1)	(0 ;0)	(1 ;1)	(1 ;1)
Gm10_157b	CTRL-	1	(1 ;1)	(1 ;1)	(1 ;1)	(1 ;1)
<i>Gm10_157b</i>	<i>CTRL-</i>	2	(1 ;1)	(1 ;1)	(1 ;0)	(1 ;0)
Gm10_158d	CTRL-	1	(1 ;1)	(1 ;1)	(1 ;1)	(1 ;1)
<i>Gm10_158d</i>	<i>fKW</i>	2	(1 ;1)	(1 ;1)	(1 ;1)	(1 ;1)
Gm10_158d	CTRL-	3	(1 ;1)	(1 ;1)	(1 ;1)	(1 ;1)
<i>Gm10_158d</i>	<i>fKW</i>	4	(1 ;1)	(1 ;1)	(1 ;1)	(1 ;1)
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)

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-). For each stimulus type, filled boxes indicate the occurrence of the associated described behavioral changes whereas empty boxes mean 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 4 stimuli were obtained, resulting in a total of 6 tested paired comparisons (i.e. differences between the 4 factor levels of Signal). To account for potential effect of multiple testing, we highlighted results supported at Bonferoni-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+= 1-2kHz tonal sound control playback; fKW= fish-eating killer whale sound playback; mKW= mammal-eating killer whale sound playback.

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	*	**	*