



Habituation to an acoustic harassment device (AHD) by killer whales depredating demersal longlines

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Acoustic harassment devices (AHDs) have been increasingly implemented in various fisheries that suffer significant losses caused by odontocete depredation. However, the efficacy of AHDs to deter odontocetes from fishing gear remains poorly investigated. To determine the effectiveness of AHDs in deterring depredation, we experimentally tested a high amplitude device (195 dB re 1 μ Pa 6.5 kHz 1 m from the source) from a Patagonian toothfish *Dissostichus eleginoides* longliner operating off the Crozet Islands, while it was subjected to heavy depredation by killer whales *Orcinus orca*. This species usually depredates longlines within a 10- to 300-m range from the vessel, as they only have access to fishing gear during hauling. We expected this distance to increase in response to the acoustic disturbance created by the AHD. The distances of 29 killer whales from the vessel ($n = 1812$ records) were collected during phases of AHD activation and phases during which the AHD was turned off. Two multiexposed killer whale social units fled over 700 m away from the vessel when first exposed to the AHD. However, they remained within a 10- to 300-m range and depredated longlines again past the third and seventh exposures, respectively, showing an insignificant behavioural response to further activations of the AHD. When tested through generalized linear mixed models, the effect of AHD activation was only significant when killer whales were first exposed to the device. However, the effect disappeared after successive exposures suggesting that killer whales became habituated to the AHD and may sustain potentially harmful hearing disturbance to access the resource made available by longliners. In addition to raising significant conservation concerns, this rapid return of initial depredation behaviour strongly suggests that AHDs are ineffective at deterring depredating killer whales, and that fisheries should favour the use of other mitigation techniques when facing repeated depredation by this species.

Keywords: acoustic harassment device AHD, depredation, killer whales, longline fisheries.

Introduction

Growing competition for natural resources between humans and wildlife in recent decades was reported to have contributed to the increase of both the number and intensity of depredation cases worldwide (Read, 2008). As depredation often results in financial losses, human responses to such conflict have initially been lethal for wildlife raising critical conservation issues for the species involved. As a consequence, research effort has recently begun to focus on various mitigation solutions with most attention directed towards management controls, visual, acoustic and chemical deterrents, and physical protection of resources (Arangio, 2012). Although physical protection of resources is primarily used in terrestrial environments (Nowell and Jackson, 1996; Boitani, 2000), this approach is harder

to implement in marine environments where efficiency is limited to some fish farms and net fisheries (Wursig and Bailey, 2002; Brotons *et al.*, 2008). In addition, a number of cases have reported marine mammals damaging protective gear to access a resource (Northridge and Hofman, 1999; Gilman *et al.*, 2006). As a consequence, stakeholders have often switched to other techniques to prevent depredation such as the use of acoustic harassment devices (AHDs).

Unlike net and pot fisheries, longlining is a technique that exposes hooked fish to marine predators; therefore, this fishery is confronted with depredation worldwide. Four odontocete species have been documented in the depredation of longlines (Hamer *et al.*, 2012). Killer whales (*Orcinus orca*) and sperm whales

(*Physeter macrocephalus*) are known to depredate demersal longlines in higher latitudes (Dahlheim, 1988; Hucke-Gaete et al., 2004; Purves et al., 2004; Roche et al., 2007; Sigler et al., 2008), while short finned pilot whales (*Globicephalus macrorhynchus*) and false killer whales (*Pseudorca crassidens*) have been documented depredating pelagic longlines in lower latitudes (e.g. Baird and Gorgone, 2005; Mooney et al., 2009; Rabearisoa et al., 2012). As the economic impact of longline depredation can be significant, effective methods for odontocete deterrence are required in some areas. As odontocetes have sensitive hearing, AHDs producing high amplitude sounds greater than 180 dB (at 1 m from the source) are designed to encourage or force them to leave the vicinity of the fishing gear (Nowacek et al., 2007). However, the short- and long-term effects that AHDs have on odontocetes are not well understood. In some cases, the use of these devices may be considered unethical or cause conservation concerns (Johnston and Woodley, 1998; Morton and Symonds, 2002). Despite this, the current increase in use of such devices with little or no regulatory policies critically urges the need for rigorous and controlled field testing.

In recent years, high levels of killer whale and sperm whale depredation have been reported on the Patagonian toothfish (*Dissostichus eleginoides*) demersal longline fishery operating off the Crozet Islands [French Exclusive Economic Zone (EEZ)—Southern Indian Ocean S 46°25'; E 51°59'] (Roche et al., 2007). The seven licenced vessels of the fishery operate all year-round in the Crozet EEZ and all have a fishery observer aboard monitoring all fishing operations. However, most activity occurs between 1st February and 15th March because of the second fishing area of the fleet, i.e. the Kerguelen EEZ, is closed to fishing during that period to limit seabird bycatch. The Crozet killer whales feed on a wide range of natural prey items such as seals, penguins, large whales, and fish (Guinet, 1992). Great variations in the level of interaction with fisheries were detected between the matriline (i.e. social units composed of on average 3–4 constantly associated individuals) composing the population (Tixier et al., 2010). Killer whales depredate longlines all year-round and across all fishing grounds of the Crozet EEZ. However, their probability of interaction with vessels varies both in time and in space. For instance, a decrease of such probability was detected from October to December, which is a period of high resource abundance as southern elephant seals (*Mirounga leonina*), i.e. the main prey of the Crozet killer whales, aggregate on land and in inshore waters during that period (Guinet, 1992; Tixier, 2012). As killer whales are responsible for depredating significantly more fish than sperm whales (Roche et al., 2007; Tixier et al., 2010), fishing vessels offered unique platforms of opportunity to test various techniques aimed at reducing killer whale depredation. The implementation of fish pots as an alternative fishing technique to longlining suppressed depredation, but did not provide economically sustainable catch per unit effort (cpue; Gasco et al., 2010). Other research into operational variables and fishing practices provided effective techniques for reducing killer whale depredation for several vessels (Tixier et al., 2010, 2014). However, one of the seven vessels operating in the Crozet EEZ still experienced high levels of depredation, likely because the skipper did not modify its fishing technique according to the fishing practices that were found to reduce depredation and/or because it mainly operates in areas of high probability of interaction with killer whales. However, as odontocetes appear to use specific acoustic cues to detect and to locate vessels (Thode et al., 2007), we may also hypothesize that the acoustic features of this vessel

may cause a higher probability of being detected by killer whales than such probabilities of the other vessels. This vessel served as a suitable platform from which to conduct studies of the efficacy of an AHD called the “Orcasaver”. Although this AHD is frequently used in various demersal longline fisheries, no experimental testing has ever been implemented to assess its efficacy in deterring odontocetes from depredating longlines. This study provides results of the efficacy of this AHD on depredating killer whales and may provide valuable insights for policy-makers as well as developers and users of AHDs around the world.

Methods

The AHD was experimentally tested from a 60-m Patagonian toothfish longliner operating within the Crozet EEZ (Figure 1) between 6 February 2011 and 24 February 2011. As the AHD was independently purchased by the fishing company owning this vessel and operated in real fishing conditions, we designed an experiment that was implemented at sea on a voluntary scheme by fishers aboard and supervised by the fishery observer. Paired with an expected limited time of operation of the vessel in the Crozet EEZ, we focused the experiment on the behavioural response of the Crozet killer whales to exposure to the AHD when already depredating a longline set. This behavioural response was examined through the analysis of the distances of individuals from the vessel during hauling paired with photo-identification data. Usually, killer whales approached vessels within 50 m when they depredated longlines and we therefore expected this distance to increase in response to the high amplitude noise produced by the AHD. However, as we also expected a habituation process to occur after successive exposures, we investigated the variations of such response after repeated activations of the system during different depredation events of specific killer whale matriline. To test such assumptions, we modelled the distance of killer whales from the vessel during: (i) activation of the AHD and (ii) successive exposures to specific identified killer whale matriline.

AHD technical features

The AHD dimensions are 90 × 45 × 35 cm. It is built with a combination of stainless steel, aluminium, ferrite, silver, electronics, rubber, plastic, and different types of Polyurethane resin with a total weight of 175 kg. The acoustic system is composed of 40 transducers divided into 10 groups of 4. Amplitude of the output signal is 195 dB re 1 μ Pa (1 m from the source) and frequency is 6.5 kHz. Three different modes of signal production are available depending on interval between pulses:

1. Two fixed groups of four transducers emit a 1-s pulse at 6.5 kHz. The mean duty cycle is 20%.
2. Two fixed groups of four transducers emit a 150- to 200-ms pulse at 6.5 kHz. The duty cycle differs per group, since the selection of groups is random, but the mean duty cycle is 1%.
3. Two randomly addressed groups of four transducers emit a 50-ms pulse at 6.5 kHz. The mean duty cycle is 10%.

The device was placed at depths of 8–10 m below the vessel during hauling and connected to a control unit on board allowing crew to turn it on and off and to switch modes of signal production.

Experimental protocol design

From 6 February to 24 February 2011, the vessel set and hauled a total of 91 longlines. However, the device was only run during

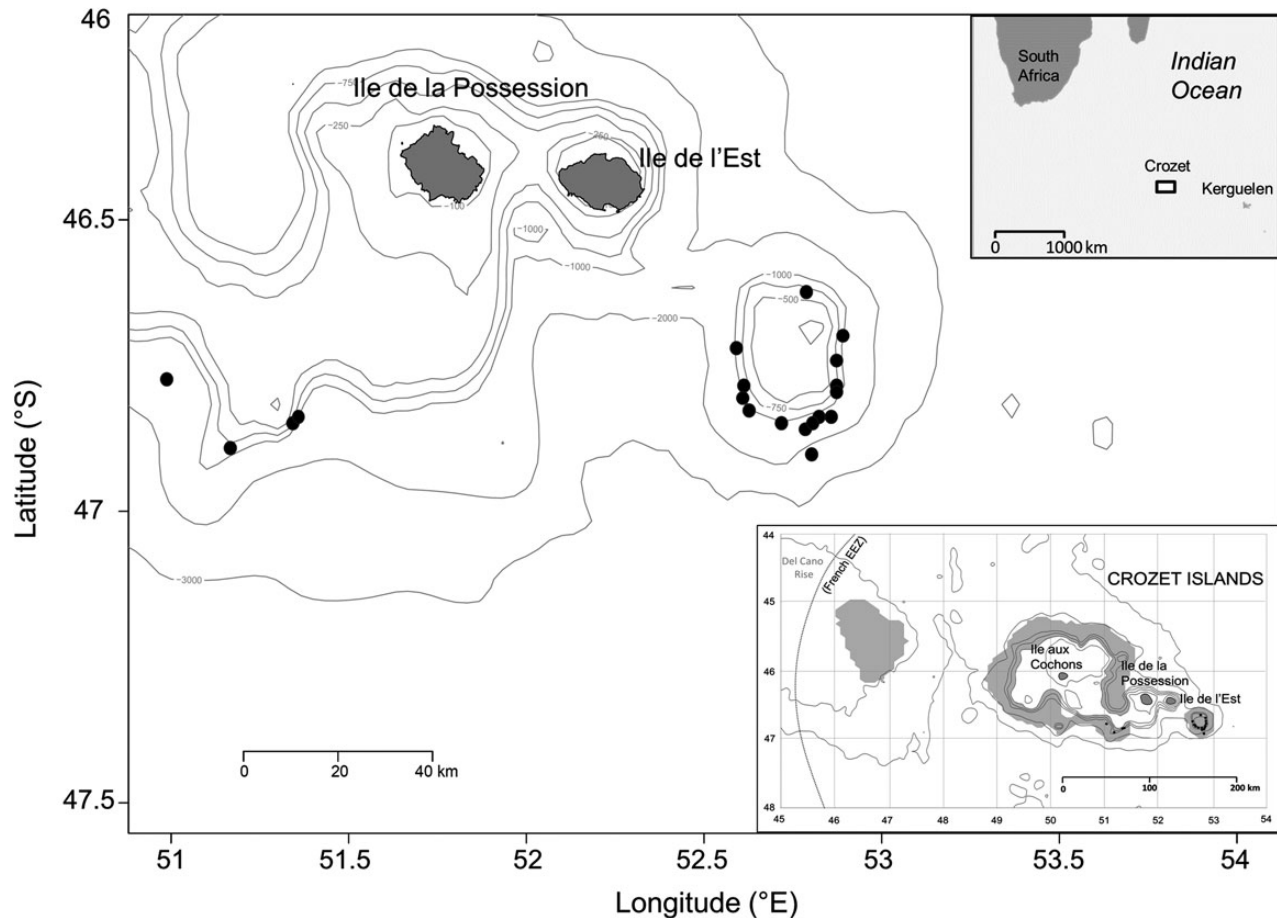


Figure 1. Study area: distribution of the 23 longline sets that were hauled from 6 February to 24 February 2011 with activation of the AHD in the presence of killer whales depredating Patagonian toothfish (black dots) off the Crozet islands. Lower right inset: Patagonian toothfish longline fishing grounds around the islands (grey background) and the Crozet EEZ western limit (dashed line). Upper right inset: position of the Crozet islands at the southern Indian Ocean scale.

daytime when visibility was >2 km and when killer whales were interacting with the longline vessel during hauling, which restricted the experiment to 23 longline sets that met both criteria. The number of these experimental sets hauled per day varied between days from 1 to 6. Test longlines had 4500 hooks each (5.4 km in length) and were set parallel from each other at a distance of 2.8 km. The number of sets that were placed parallel varied from 2 to 6. For each longline set, the initial design of the experiment was to collect data during four distinct phases:

- 15 min of hauling before turning on the AHD,
- 20 min of hauling with AHD on,
- 15 min of hauling after turning off the AHD, and
- 15 min of hauling with AHD on again.

The duration of phases was set according to the maximum observed dive duration of killer whales when depredating longlines, which never exceeds 15 min, and rarely exceeds 10 min (P. Tixier and N. Gasco, pers. comm.). The duration of phase (b) was increased of 5 min to account for a possible time-lag in the expected reaction of killer whales to move away from the AHD. The distance of killer whales to vessels in the minutes following the activation of the AHD may indeed be correlated with their distance before activation of the

AHD, and increased recording time during phase (b) may limit such bias in the data.

Another bias in the data may result from the fact that although phases (a) and (b) occurred on all experimental sets, fishers and fishery observers met some difficulties to also run phases (c) and (d) on all sets. Consequently, we were forced to consider each phase independently when analysing the data. For instance, each of the (b) and (d) phases of operational AHD were considered as two separate exposure events for killer whales. The time between two successive exposures ranged from 15 min when the AHD was activated during more than one phase during hauling of the same set to 174 h when the AHD was successively activated during hauling of two different sets. Date, time, position, longline number, sea state, and windspeed were recorded for each phase. The mode of signal production (A, B, or C) was randomly set before activating the AHD and recorded by the fishery observer.

The typical dive cycle observed for a killer whale when depredating longlines is composed of series of short dives (<30 s) followed by a longer dive (<15 min) during which it may take fish off the hooks at depths between 50 and 100 m (Nolan *et al.*, 2000). Here, the fishery observer recorded one distance value for that given individual when sighted while surfacing several times between long dives. For each phase, the distances of individual killer whales from the vessel were either recorded using a range finder

(Heinemann, 1981), either estimated visually depending on sea state conditions. To account for uncertainty of such methods of data collection, the numbers of individual distance data were assigned to 10 range classes (m): [0–10], [10–20], [20–30], [30–50], [50–100], [100–200], [200–300], [300–500], [500–1000], and [1000–2000].

Killer whales interacting with the vessel during hauling were photo-identified and compared with a previously compiled catalogue of individuals. Previous photo-identification research in the Crozet Islands has documented 21 matriline of killer whales regularly interacting with longline fisheries (Tixier et al., 2011). As these matriline are highly stable social units, the photo-identification data gathered in this study allowed us to know the exact number of individuals present during interaction events and therefore, the exact number of individuals exposed to the AHD.

Modelling distances of individual killer whales from the vessel

As raw sighting data of the distances of individual killer whales were distributed into 10 classes of different ranges, we assigned the median value of the range class in which the sighting was included to each recorded distance data. These values were first log-transformed [$\log(\text{dist})$] to allow for testing of fixed effects with random terms in a normal distribution framework. Generalized linear models (GLMs) with or without random terms (generalized linear mixed models, referred to as GLMM—function `lme` in `nlme` package in R 2.10.1 - R Development Core Team, 2010) were used.

We first tested the effect of the activation of the AHD (fixed effect: AHD) as a factor with binary values: (1) when the AHD was on and (0) when the AHD was off. This was conducted through two models using: all distance data from all four phases (a), (b), (c), and (d) [$\log(\text{dist})_{a,b,c,d}$ —model (1)], and phases (a) and (b) distance data from the first exposure of specific killer whale matriline to the AHD [$\log(\text{dist}_{(first)})_{a,b}$ —model (2)]. In both models, the iD of the killer whale matriline interacting with the longline set and for which individual distance data were recorded (*group*) was tested as a fixed effect, both as additive (+) and in interaction (*) with the activation of the AHD. The great behavioural variations observed between killer whale matriline with respect to depredation behaviour may induce variability to the recorded distance data. In model (1), three additional fixed effects were included in the full model: (i) the order of longline sets hauled during the same day and for which the AHD was tested (*set.day*). One may assume that killer whales may become satiated after depredating large amounts of toothfish on the first longline sets hauled during a given day and may therefore depredate the following sets hauled during that day to a lesser extent, which may influence their distance to the vessel. *set.day* varied from 1 to 6 longline sets hauled during the same day. (ii) The time between activation phases of the AHD (*l.lag.AHD*). We may assume that killer whales may react differently to the AHD according to the time elapsed between two exposures, which greatly varied during the experiment. (iii) The mode of activation of the device (*mode*): A, B, or C, which acoustic features may trigger different reactions from killer whales to the AHD. The full model was completed with a random term: (i) the successive trials [one trial is one phase (a)-phase (b)-phase (c)-phase (d) sequence - *seq*], from the first trial of 6 February to the last on 24 February (an iD number was assigned to each trial in a chronological order). The two complete GLMM and GLM, testing the effect of the activation of the AHD on killer whale distance to vessels during all exposures and during first exposures, respectively, were

built as such:

$$\text{Model 1 : } \log(\text{dist})_{a,b,c,d} \sim \text{set.day} + t.\text{lag.AHD} + \text{mode} + \text{group} + \text{AHD} + \text{group} * \text{AHD}, \text{random} \sim 1 | \text{seq}$$

$$\text{Model 2 : } \log(\text{dist}_{(first)})_{a,b} \sim \text{group} + \text{AHD}_{(first)} + \text{group} * \text{AHD}_{(first)}$$

Killer whale habituation to the AHD was investigated through two response variables in two separate models (3 and 4). Successive exposures of a given killer whale matriline were tested as a numeric fixed effect (*exposure*) on log-transformed raw distance data recorded during phases (b) only in model (3) and on the log-transformed absolute difference of mean killer whale distances to vessel between phases (a) and phases (b) (noted $\log(\Delta \text{dist})_{|a-b|}$) in model (4). In both models, the killer whale matriline identity was included as a fixed effect to investigate variations in response to the AHD between matriline (*group*). Both fixed effects were tested as additive and interaction terms (*exposure*group*) to also examine if the habituation rates to the AHD would vary between matriline. The three variables *set.day*, *t.lag.AHD*, and *mode* were also included in the full models as fixed effects. The random term (*seq*) was defined as the ID number of the trials including phases (b) during which killer whale matriline were exposed in model (3) and phases (a) and (b) in model (4). The complete GLMMs were built as such:

$$\text{Model 3 : } \log(\text{dist})_b \sim \text{set.day} + t.\text{lag.AHD} + \text{mode} + \text{exposure} + \text{group} + \text{exposure} * \text{group}, \text{random} \sim 1 | \text{seq}$$

$$\text{Model 4 : } \log(\Delta \text{dist})_{|a-b|} \sim \text{set.day} + t.\text{lag.AHD} + \text{mode} + \text{exposure} + \text{group} + \text{exposure} * \text{group}, \text{random} \sim 1 | \text{seq}$$

Model validation was performed using the goodness of fit as described in Magee (1990—Supplementary Appendix 1).

Results

From 6 February to 24 February 2011, the AHD was activated on 45 occasions [27 (b) phases and 18 (d) phases] during the hauling of 23 longline sets while in the presence of killer whales. The distances of killer whales from the vessel were recorded for all 45 exposure events. These were compared to distances recorded for 31 non-exposure occasions [27 (a) phases and 4 (c) phases]. In all, 1812 distances were recorded during all phases of both exposure and non-exposure events. These data were used for analyses in model (1).

Photo-identification data resulted in all 29 killer whales belonging to nine matriline that were exposed to the AHD at least once. However, we were forced to focus our analyses on two matriline only: C018 ($n = 5$ individuals in 2011) and C002 ($n = 4$ individuals in 2011). These two matriline were the most exposed to the AHD. They were successively exposed to the AHD on 5 and 22 occasions, respectively. Furthermore, these two units never associated with each other while depredating but always associated with at least one of the seven other matriline that were also exposed to the AHD. These association events occurred at second exposure for C018 with the C012 matriline and at sixth exposure for C002 with the C063 matriline and remained associated until last exposures. As observers could not distinguish between individuals from different matriline when recording distance data, all matriline associated during the same exposure event were considered as a whole.

Therefore, model (2) was run with two pairs of phase (a)–phase (b) data of first exposure for these two matriline, using 81 recorded distances. Model (3) was run using 769 recorded distances, 145 of the C018 matriline exposed on five successive phase (b) and 624 of the C002 matriline exposed on 22 successive phase (b). Model (4) was run using 27 mean estimates of changes of distance between phases (a) and (b): 5 and 22 for the C018 and C002 matriline, respectively.

The overall effect of the AHD on the distances of individual killer whales from the vessel was not significant when using all activation (1) and non-activation (0) data of all phases of trials (Table 1—model (1) and Figure 2a). The mean distances of killer whales to vessel during phases (a) and phases (b) were 179.1 ± 222.4 (SD) m ($n = 413$) and 251.8 ± 277.0 m ($n = 1290$), respectively. The effects of the time between successive exposures, the hauling order of sets during

the same day, and the mode of signal production on killer whale distance to vessel were not significant in model (1) (Table 1). However, the AHD was found to positively and significantly influence distances of killer whales from the vessel during first exposures of the two matriline, C018 and C002 [Table 1—model (2) and Figure 2b]. At first exposure, the mean distance of killer whales from the vessel was 276.6 ± 293.2 m ($n = 58$) before AHD activation [phase (a)] and was 932.6 ± 452.9 m ($n = 23$) when the AHD was turned on [phase (b)]. Also, as suggested by the significance of the group effect both as additive and in interaction with the activation of the AHD, the two matriline seem to have responded differently when first exposed to the AHD. All individuals from the C018 matriline were actually observed to flee and to move over 1000 m away from the vessel when first exposed to the AHD, whereas the C002 matriline remained in a 500- to 1200-m range from the vessel.

Table 1. Parameter estimates of the GLMM and the GLM used to test the influence of the activation of the AHD (AHD) using all data of all-trial phases (a, b, c, and d)—model (1) and the activation of the AHD at first exposure [AHD(first)] using phases (a) and (b) of first exposures of killer whale matriline—model (2), on the distance of killer whales from the vessel [$\log(dist)$].

Data	Model	Parameter	Value	SE	D.f.	t-value	p-value
All	1	Intercept	5.085	0.281	1733	18.077	<0.001
		set.day	-0.111	0.075	1733	-1.474	0.141
		t.lag.AHD	-0.001	0.003	70	-0.314	0.754
		mode_B	0.030	0.314	70	0.097	0.923
		mode_C	0.196	0.275	70	0.712	0.479
		group_C018	0.155	0.466	70	-0.333	0.740
		AHD	0.086	0.219	70	0.394	0.695
		group_C018*AHD	0.824	0.574	70	1.435	0.156
		Intercept	5.587	0.148	79	37.880	<0.001
Phases (a) and (b) of first exposures	2	group_C018	-1.943	0.249	79	-7.805	<0.001
		AHD(first)	0.830	0.263	79	3.156	0.002
		AHD*group_C018	2.435	0.494	79	4.933	<0.001

Additional fixed effects were the identity of the two matriline C002 and C018 exposed to the AHD during the experiment (group), both as additive (+) and interaction (*) terms, as well as the chronological order of sets hauled during the same day (set.day), the time between exposures (t.lag.AHD), and the sound production mode (mode—A, B, and C). In model (1), the chronological trials of the AHD were included as a random term (sequence). The significance of fixed effects in models (p -value > 0.05) are highlighted (bold).

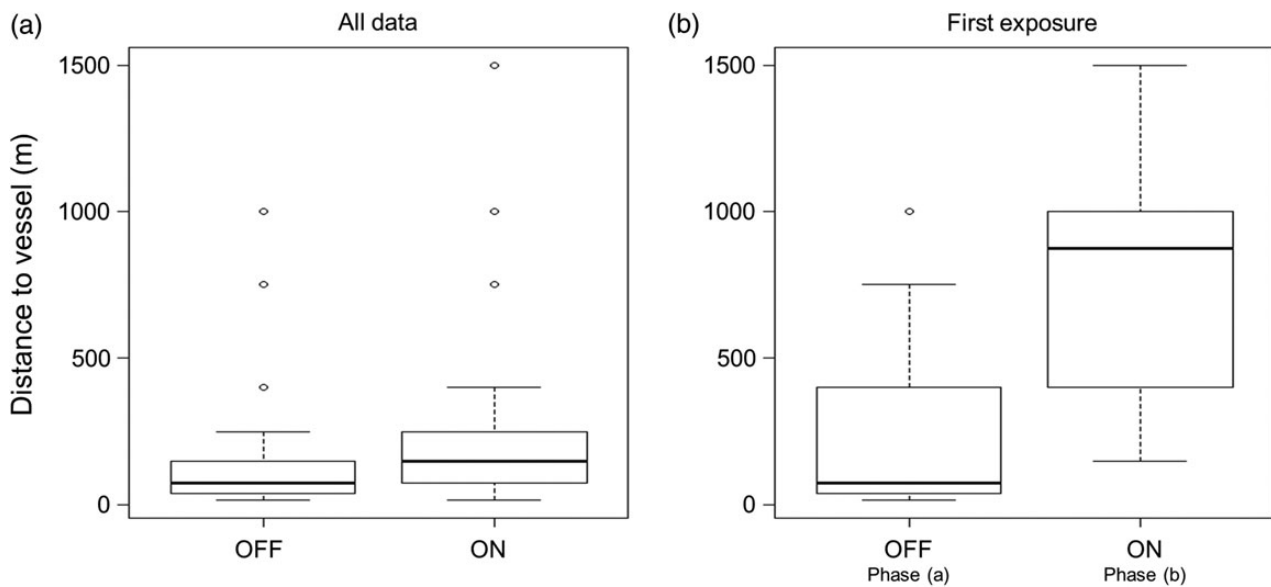


Figure 2. Influence of the AHD activation (ON) on the distances of killer whales from the vessel: (a) using all data, $n(OFF) = 1291$ and $n(ON) = 521$ individual distances, and (b) using phases (a) and (b) data at first exposure of the two killer whale matriline C002 and C018, $n(OFF) = 58$ and $n(ON) = 23$ individual distances.

Table 2. Parameter estimates of the two complete GLMMs used to test the influence of killer whale matriline's successive exposures (*exposure*) to the AHD on the distance of their individuals from the vessel [$\log(\text{dist})$] during phases of activation (b)—model (3) and on the change in such distance between phases (a) and (b)—model (4).

Data	Model	Parameter	Value	SE	d.f.	t-value	p-value
AHD ON All phases (b)	3	Intercept	5.596	0.304	1215	18.420	<0.001
		<i>set.day</i>	-0.054	0.096	1215	-0.567	0.571
		<i>t.lag.AHD</i>	-0.002	0.004	45	-0.599	0.551
		<i>mode_B</i>	-0.081	0.279	45	-0.289	0.774
		<i>mode_C</i>	0.133	0.248	45	0.536	0.594
		<i>group_C018</i>	1.942	0.778	45	2.501	0.016
		<i>Exposure</i>	-0.027	0.013	45	-2.048	0.046
		<i>exposure*group_C018</i>	-0.370	0.185	45	-1.999	0.052
AHD ON Phases (a) and (b)	4	Intercept	6.234	0.373	19	16.701	<0.001
		<i>set.day</i>	0.137	0.128	19	1.066	0.300
		<i>t.lag.AHD</i>	-0.001	0.004	19	-0.342	0.736
		<i>mode_B</i>	0.006	0.364	19	0.015	0.988
		<i>mode_C</i>	0.276	0.351	19	0.784	0.442
		<i>group_C018</i>	0.597	0.820	19	0.728	0.476
		<i>Exposure</i>	-0.180	0.027	19	-6.606	< 0.001
		<i>exposure*group_C018</i>	-0.273	0.224	19	-1.216	0.239

Additional fixed effects were the identity of the two matriline C002 and C018 exposed to the AHD during the experiment (*group*), both as additive (+) and interaction (*) terms, as well as the chronological order of sets hauled during the same day (*set.day*), the time between exposures (*t.lag.AHD*), and the sound production mode (A, B and C). In both models, the chronological trials of the AHD were included as a random term (*sequence*). The significance of fixed effects in models (*p*-value > 0.05) are highlighted (bold).

Successive AHD exposures to both killer whale matriline negatively and significantly influenced the distances of individuals from the vessel during the 27 phases (b) of hauling used in analyses [Table 2—model (3) and Figure 3a], as well as the change in distance between phases (a) and (b) [Table 2—model (4) and Figure 3b]. Mean distances from the vessel of individuals from these two matriline during exposure phases significantly dropped over consecutive trials of the AHD (Figure 3a). For instance, the C018 matriline, which fled from the vessel when first exposed to the AHD, remained in a 300-m range from the vessel past the third exposure and depredated the longline that was being hauled. This is further emphasized by Figure 3b, which presents the difference between distance from the vessel before exposure [phase (a)] and distance from the vessel during exposure [phase (b)] and thus illustrates the behavioural response of individuals to the activation of the AHD. For instance, the C002 matriline was recorded moving over 500 m away from the vessel during most of the first six exposures. Past the seventh exposure, the changes in distance between killer whales and the vessel during both phase (a) and phase (b) became insignificant during the next 16 exposures. Model (3) output parameter estimates also suggest a significant effect of the matriline (*group*), with killer whales from the C018 matriline being observed at greater average distances from the vessel than individuals from the C002 matriline. However, this may be caused by heterogeneity in the amount of available data between the two matriline. That said, the interaction term *exposure*group* was negative and close to significant, suggesting that the negative effect of successive exposures was greater for the C018 matriline. Although no test could be performed due to limited amount of data available, one should mention that first exposures of the two matriline C012 and C063, which associated with the already exposed C018 and C002 matriline respectively, did not seem to affect the observed habituation process. For instance, the C012 matriline was first exposed to the AHD at the second exposure of C018, but did not flee in reaction to the AHD activation. Instead, individuals from both matriline remained at a similar distance from the vessel. The effects of the time between

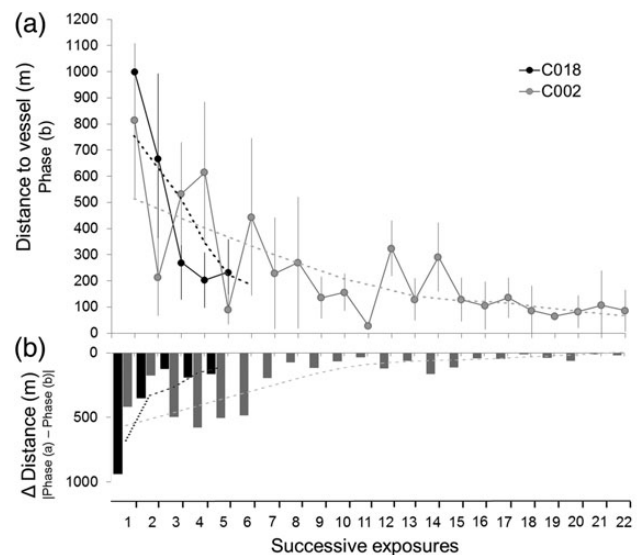


Figure 3. Influence of successive exposures of two killer whale matriline (C018—black and C002—grey) to the AHD on (a). Mean \pm SD distance from the vessel (m) during AHD activation [phase (b)] per exposure and (b) differences of mean distances from the vessel (m) between the phase preceding AHD activation [phase (a)] and during AHD activation [phase (b)] per exposure. Raw data (a—dots and solid curves and b—vertical bars) and fitted distance estimates (dashed line) from models (3) and (4) are represented.

successive exposures, the hauling order of sets during the same day, and the mode of signal production were not significant in models (3) and (4) (Table 2).

Discussion

This study showed that killer whales depredating longlines off the Crozet Islands became habituated to the use of an “Orcasaver”

AHD. Although first exposures caused killer whales to flee from the fishing vessel operating the AHD, this effect disappeared after <10 successive exposures. The initial flee reaction may have been caused by both the introduction of new acoustic signals in the killer whale habitat and the hearing disturbance caused by exposure to high amplitude sounds (197 dB re 1 μ Pa 1 m from the source). However, after a number of exposures and a possible period during which killer whales assessed this new variable, they did not alter their behaviour or distance from the vessel significantly between phases when the AHD was on and off. This finding, paired with the lack of knowledge of the potential short or long-term impacts that high amplitude sound may have on killer whales, motivated us to end the study and to recommend that the use of this AHD be abandoned for deterring this species from depredation of longlines.

Although impacts of AHDs on hearing systems of odontocetes are unknown, other studies have shown that anthropogenic noise can be highly disturbing for various species. Reported effects of high amplitude sounds produced by humans in cetacean habitat include changes of distribution of exposed populations and increase of mass stranding events (e.g. Glockner-Ferrari and Ferrari, 1990; Richardson and Wursig, 1997; Frantzis, 1998; Wursig *et al.*, 2000; Lusseau, 2007). Such impacts were also reported when AHDs were used to repel marine mammals from fish farms or fishing nets (e.g. Johnston and Woodley, 1998; Culik *et al.*, 2001; Olesiuk *et al.*, 2002). For example, AHDs used by fish farms in British Columbia to prevent seals and sea lions from depredating captive salmon cause killer whales to change their distribution in response to high acoustic pollution (Morton and Symonds, 2002). These devices were very similar to the one used in this study (amplitude 194 dB re 1 μ Pa 10 kHz vs. 197 dB re 1 μ Pa 6.5 kHz for the Orcasaver). However, the deterred killer whales reported by Morton and Symonds (2002) were not the targeted species as they were not depredating any fish resource, while the AHD used in this study was aimed specifically at deterring killer whales from depredating longlines, but it was not effective. The Crozet killer whales may sustain potentially harmful hearing disturbance to access a highly energetic resource. Patagonian toothfish made easily available by longline fisheries appears indeed to engage the Crozet killer whales to modify their natural behaviour of avoidance of such acoustic disturbance.

Depredation is a well-established behaviour within the Crozet killer whale population. Long-term monitoring of the population showed that most matriline known to currently interact with fisheries started to depredate longlines as soon as longliners started to operate in the area in 1996 (C. Guinet, pers. comm.). However, great between-matrilines heterogeneity in the level of depredation was reported, with only a few matriline from the Crozet killer whale population that were responsible for most of the interactions with longliners. Such heterogeneity may result from between-matrilines cultural differences in natural foraging habits with two combined processes: (i) different degrees of specialization to Patagonian toothfish may have existed before fisheries and engaged matriline to depredate longlines at different levels (Guinet and Tixier, 2011) and (ii) matriline-to-matriline social transfer (Ford *et al.*, 1998; Rendell and Whitehead, 2001) of the depredation behaviour may have favoured some matriline to learn depredation from already depredating matriline depending on their social relatedness. In 2011, among the 21 depredating matriline, four were involved in nearly 70% of all recorded interactions with longlines (Tixier, 2012). The C018 matriline recorded in this

study is among the four matriline documented to interact the most with fisheries. They depredate longlines within all Crozet fishing grounds and actively follow vessels over great distances. Conversely, the C002 matriline interacts with vessels in a more opportunistic way and within limited fishing areas (Tixier, 2012). Despite observations of most matriline fleeing from the vessel during their first exposure to the AHD, we expected that the most depredation-specialist matriline would quickly become habituated to the device. This assumption was confirmed by the close significance of the interaction terms of successive exposure and matriline variables in model (3), paired with differences of slope between the two matriline C018 and C002 as shown in Figure 2a, suggesting a greater habituation rate for the C018 matriline. For instance, from the observed data one can estimate that it, respectively, took three and seven exposures to the C018 and C002 matriline to drop their response to the AHD to <20% of their response at first exposure. This suggests that the level of motivation to sustain hearing disturbance to access a resource may vary between different killer whale matriline and therefore influence both the duration of their habituation process and their level of exposure to the AHD.

Furthermore, this study suggests that two matriline (C012 and C063) previously unexposed to the AHD, but that were associating with a multiexposed matriline displayed immediate habituation, which may result from a likely between-matrilines social transfer making habituation extremely rapid. Indeed, a large part of killer whale behaviours relies on cultural transmission through both vertical (intergenerational) and horizontal (intragenerational) processes (Ford *et al.*, 1998). Horizontal transmission, which primarily occurs through mimicry and can be especially effective in rapidly learning new behaviours in quickly changing environments (Whiten, 2000; Rendell and Whitehead, 2001), is likely to be a key determinant of the way killer whales may respond to an AHD when exposed to it for the first time. One may indeed expect newly exposed killer whales to benefit from experienced individuals when associating with already exposed matriline while depredating longlines, and therefore to increase their habituation rate to the AHD. The effect of such social transfer, which may require further investigation with more data, brings additional support to the limited efficacy of AHDs to deter highly social species such as the killer whale from a coveted fish resource.

The Orcasaver is a device that was designed to reduce depredation by odontocetes and thus, ultimately to increase cpue for fishers investing in this device. Although this study focused on the behavioural response of killer whales to the AHD, our findings on the rapid habituation of killer whales to this device suggest that it is not effective in reducing fish losses. Additionally, the short- or long-term use of this AHD may pose unknown risks to the viability of this killer whale population. For these reasons, and the fact that fishers usually are unable to determine if they are dealing with depredation from naive or experienced killer whales, we strongly recommend that fishers, managers, and authorities favour other more effective techniques such as those outlined by Hamer *et al.* (2012) and Tixier *et al.* (2014) for reducing depredation on longlines from killer whales.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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