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The fine-scale behavior of harbor porpoises towards pingers

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ABSTRACT

High numbers of harbor porpoises (*Phocoena phocoena*) end up as bycatch in gillnets every year. Acoustic alarms (pingers) have been demonstrated to be an efficient mitigation tool to prevent bycatch of this species; however, little is known about the behavioral reactions of wild porpoises to pingers. This knowledge is important for optimizing the design and use of pingers. We tracked 16 wild porpoises with a drone and recorded their behavior before and during exposure to pinger sounds. Range from the pinger to the porpoise was 158–797 m when the pinger was first activated. In four of the exposures, with pinger-to-porpoise ranges of 199–521 m, reaction to the pinger was strong avoidance behavior with increased swimming speed heading away from the pinger. Average number of surfacings decreased from 3.4 surfacings/min before pinging to 2.8 surfacings/min during pinging. Eight animals were lost from the drone's field of view as soon as the pinger playback started, indicating that they were either diving deep or speeding away from the area very rapidly. Four animals did not respond to pinger sounds, demonstrating a diversity in the behavioral response. Neither the behavior of porpoises (i.e., foraging, socializing and traveling) before sound exposure, the animal's initial direction in relation to the sound source, nor the porpoise-to-pinger range affected their reaction in relation to the pinger. Pingers can cause very strong aversive reactions in harbor porpoises, which explains their efficiency in reducing bycatch. The strong aversive reactions may suggest that pinger use should be limited to critical time periods and regions, or that more focus needs to be put on developing acoustic devices which cause less severe behavioral reactions. At the same time, this study shows that 25 % of animals may not react to pinger sounds, indicating a great diversity in behavioral responses.

1. Introduction

During the last decades, many harbor porpoises (*Phocoena phocoena*) were caught incidentally every year in Northern European waters, mainly in static fishing gear such as bottom-set gill nets (Bjørge et al., 2013; Kock and Benke, 1996a, 1996b; Skóra and Kuklik, 1992; Tregenza et al., 1997; Vinther, 1999; Vinther and Larsen, 2004). To reduce bycatch, several mitigation strategies have been tested or implemented, such as gear modifications (Kratzer et al., 2020; Larsen et al., 2007), fishing area closures during certain time periods (Murray et al., 2000; van Beest et al., 2017), and introduction of acoustic alarms, i.e., pingers (Dawson et al., 2013). Pingers are attached at 200–400-m intervals along fishing nets, emitting signals in the 10–150 kHz frequency range. In European gill net fisheries, use of pingers is mandatory in certain fishing areas and types of fisheries (EC, 2004, 2019).

Several studies have confirmed the effectiveness of pingers in displacing harbor porpoises and thus, reducing bycatch. Behavioral responses in harbor porpoises in human care include avoidance of pingers, increased respiration rate, and decreased echolocation activity and heart rate (Kastelein et al., 2001; Kastelein et al., 2000a, 2000b; Lockyer et al., 2001; Teilmann et al., 2006). Gillnets equipped with pingers efficiently reduce bycatch (Larsen et al., 2013, 2002; Larsen and Eigaard, 2014; Palka et al., 2008). Studies with passive acoustic monitoring have demonstrated that animals are displaced by pingers during extensive

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time periods (Cox et al., 2001; Kindt-Larsen et al., 2019; Kyhn et al., 2015; Omeyer et al., 2020), though a gradual habituation to some types of pingers has been documented (Cox et al., 2001; Kindt-Larsen et al., 2019; Königson et al., 2021; Kyhn et al., 2015).

Even though many studies have confirmed that porpoises are strongly deterred by pingers, the fine-scale reaction of wild harbor porpoises to pingers has only been described in a few studies. Culik et al. (2001) used theodolite observations and reported clear avoidance responses by porpoises to a pinger at ranges of several hundreds of meters; however, important questions are left unanswered: how is the behavior of porpoises affected by the intensity, frequency content, and duration of the emitted signals? In addition, it is not known how often and how randomly these signals should be emitted. Knowledge about how free-living porpoises react to pingers is important for optimizing conservation efforts and for designing pingers that cause less strong behavioral disturbances while remaining efficient reducing bycatch (Nabe-Nielsen et al., 2018, 2014).

Studies on how porpoises react to pingers have struggled with methodological limitations to observe the detailed behavior of porpoises over extensive range and duration during playback. Here we used drones to observe the behavior of wild harbor porpoises in response to pinger signals and obtained detailed data on their reactions.

2. Materials and methods

2.1. Study site

Field work was carried out from May 29 - June 30, 2019 at various locations around the north coast of Funen, Denmark (Fig. 1). Harbor porpoises are often encountered in this area close to the shore (Heide-Jørgensen et al., 1992).

2.2. Data collection

Video recordings of harbor porpoises were collected using a drone (DJI Phantom 4 Professional v2.0, P4Pv2, www.dji.com) equipped with a polarizing filter (Polarpro ND8-PL) to reduce reflections from the

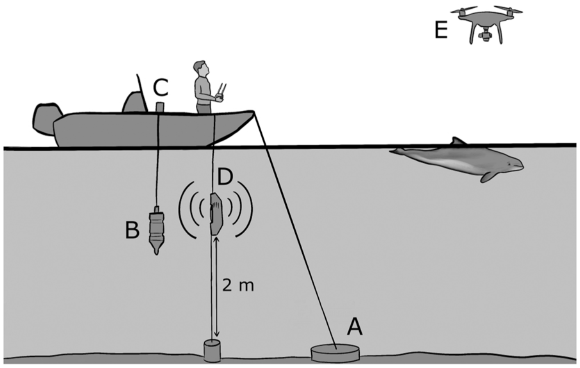


Fig. 2. Controlled exposure experimental set-up to measure behavioral response of harbor porpoises to pinger sounds. A: Anchor, B: Acoustic data logger, C: GPS connected to acoustic data logger, D: Pinger, E: Drone.

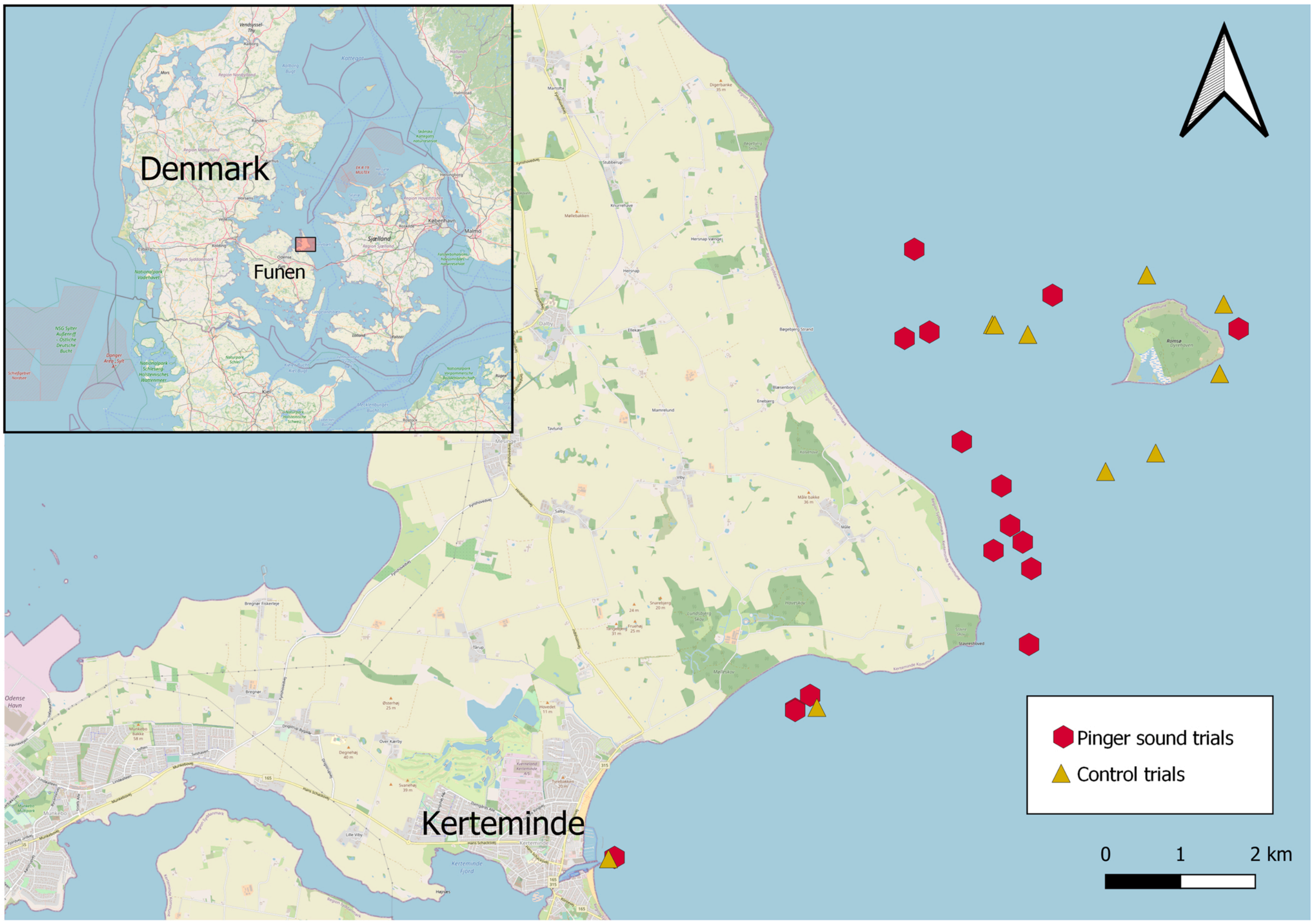


Fig. 1. Map of survey area with the position of porpoises during the start of the pinger sound (hexagons) and control trials (triangles). Coordinate system ETRS89LAEA, Pseudo Mercator WGS 84, EPSG 3857, openstreetmap.

water surface (Fig. 2). The drone carried a gimbal-stabilized DJI camera recording with an f/2.8–11, 8.8 mm/24 mm lens in 4 K and 30 fps. During flight, the DJI GO 4 app (Android DJI 4.3.14) was used to live-stream video signals to a tablet mounted on a drone remote controller allowing the pilot to follow and record porpoises throughout flights. The drone was operated under Trafik-, Bygge- og Boligstyren (Danish transport, construction and housing authority) permit numbers 5032864 and 5411169, and playback was performed under a permission by the University of Southern Denmark's Animal Ethics Committee, assigned by the Danish Animal Ethics Inspectorate, permit number 2021/1, as well as by a permit from the Ministry of Environment (permit nr. 13081).

The drone was flown during good weather conditions, i.e., sunshine, no precipitation, wind speeds < 5 m/s and calm seas (wave height less than 30 cm). During flights, every 100 ms, the drone logged parameters such as GPS location, time, altitude, pitch, and camera yaw. The drone was flown at an altitude between 6 and 95 m above the water surface to minimize disturbance during observations (Christiansen et al., 2020, 2016).

2.3. Acoustic recording equipment

The pinger used to conduct behavioral response testing was a so-called banana pinger (Fishtek), emitting signals at randomized intervals of 4–12 s. The signals varied slightly from each other but all had a duration of 0.3 s with a frequency range between 50 and 120 kHz with a source level of 144 dB re 1 μPa rms @1 m. The source level was measured prior to and at the end of the playback experiments in a 3 m deep and 3 m diameter calibration tank using a hydrophone (Reson 4014) connected to a 30 dB hydrophone amplifier (frequency response 0.010–400 kHz; ETEC, Slangerup, Denmark), 1 kHz high-pass filter (ETEC, Slangerup, Denmark) and a digitization board (USB-6351, National Instruments, sampling rate 500 kHz, 16 bits resolution).

The pinger emitted signals a few seconds after submersion. Prior to playback, the water activated pinger was kept in a water bucket on board the boat to ensure that it was immediately transmitting when deployed. Acoustic recordings confirmed that while the pinger was in the bucket, no signals penetrated the hull into the water. During playback, the pinger was attached to a line running from the boat to a weight deployed on the seabed. The pinger was fixed 2 m above the seabed and placed at 5–10 m water depth, measured using a labeled anchor line. For acoustic recordings, positioning and timing of pinger, we used a GPS synched acoustic data logger (Soundtrap v1.7 ST300HF, with a Soundtrap ST-GPS unit, Ocean Instruments). Sound was digitized at a sampling rate of 576 kHz, 16-bit resolution, preamp set to high gain with a recording clipping level of 176 dB re 1 μPa p and a flat (± 3 dB) frequency response ranging from 50 Hz to 150 kHz, including a built-in anti-aliasing filter with a cut-off frequency of 150 kHz.

2.4. Focal-animal sampling

All video-recorded behavioral observations were conducted from a 5.3 m boat (Pioner Multi). Porpoises were carefully approached, maintaining at least 200 m distance to the animals unless the animals approached the boat on their own volition. After locating a focal porpoise, the boat's engine was turned off to minimize disturbance. The vessel was anchored to remain stationary and to launch the drone. Only one animal was sampled during each flight even though this animal may have belonged to a group of animals. In an initial observation phase, we recorded lone animals or one porpoise in a group for at least 40 s and up to 6 min, enabling us to obtain baseline behavior before the pinger was deployed with a minimum distance between boat and porpoise of 158 m. The drone was right above the focal porpoise when playback was initiated. Porpoises were recorded until the drone was retrieved to exchange batteries or until we lost track of the animals. Total recording time for each porpoise after sound exposure started ranged from 2 s to 12 min. After each playback trial, we left the anchor with the pinger attached to a buoy and moved the boat to the position where the focal porpoise was observed when playback started. At this position (determined from the operator's screen of the drone path during the trial), we recorded the sound produced by the pinger with the acoustic data logger for 3 min to analyze the received pinger level experienced by the porpoise during the pinger sessions. For control trials, the same procedure was followed, except that a pinger with a disconnected battery inside was deployed and no recordings were made after the trial. Playback trials were made between 29th of May and 17th of June, 2019, and control trials were made between the 22nd and 28th of June, 2019. There was a maximum of four playback trials and nine control trials on any field day, with each trial being carried out at least 25 min after the previous one. Since either the porpoise or the boat moving around between each trial, it was extremely unlikely that we would have targeted the same individual porpoise(s) during several playback or control experiments. All playback and control trials were conducted in daylight hours between 06:00 and 21:00 local Danish (daylight saving) time.

2.5. Analysis

Drone-based videos were converted to 1280 × 720 using video analysis software (VLC player, Vetiniari). The behavioral state of the focal animal was determined during 1 min before pinger exposure from the drone videos. Three broad behavioral categories were documented: i) foraging, where porpoises were either bottom feeding or surface feeding on prey items; ii) socializing, where porpoises were interacting with a conspecific either through mother/calf movements, approaching or coordinated surface activities; and iii) traveling, where porpoises demonstrated directed movements in a consistent direction, with regular surfacing intervals. Furthermore, the reaction of porpoises to pingers was also categorized using a decision tree (Fig. 3): i) escape, where a sudden change of a porpoise's previous behavioral state, including swimming away from the pinger, was recorded for a period longer than 30 s after the pinger sound transmission started; ii) lost briefly, where porpoises would dive within a few seconds after the pinger started emitting a sound, and were not visible at or around their previous position; and iii) no reaction, where porpoises continued with their baseline behavioral state during pinger exposure. When focal animals were lost briefly after the pinger sound transmission started due to murky water conditions or high cloud coverage resulting in a more reflective water surface, we immediately increased the drone altitude to check if the porpoise was still present in the observed area. In total, we conducted 16 playbacks and ten controls. Surfacing rates were calculated for both playbacks (both during pre-exposure and playback) and controls (both before and after deploying the non-working pinger). Surfacing rates were calculated as the number of surfacings per minute. Only animals observed longer than 2 min before and after the pinger exposure were used for surfacing rate estimates. Tail strokes were averaged for every 10 s during a 1-min period before and after the pinger exposure.

The location of the focal porpoise was determined from the drone

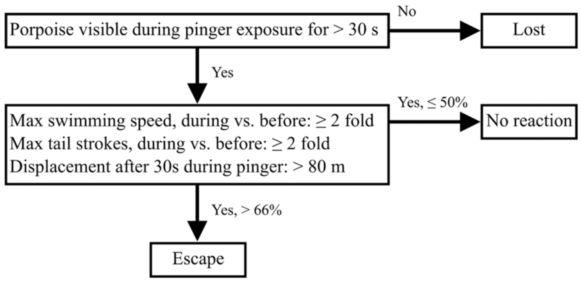


Fig. 3. Decision tree showing the categorization of porpoise reactions towards pingers: i) escape, ii) lost and iii) no reaction.

video recordings using tailored analysis software (Egemose and Midtiby, 2019). The operator indicated the location of the porpoise with the mouse, after which the program calculated the absolute coordinates of the animal using the drone log information on drone height, camera roll, pitch and yaw and drone location. Prior to running the program, the drone camera had been calibrated by filming a checkboard pattern at different heights to avoid angle-dependencies in distance measurements. Each surfacing event as well as the porpoise location every other second (whenever possible) were logged (Fig. 4). From this information, breathing rates, swimming velocity and direction of the porpoise could be calculated by a separate custom-made program in Matlab (ver. 2019, Mathworks Inc. Natick, MA, USA). In addition, the body heading relative to sound source was determined at the start time of pinger emissions using another custom-made Matlab routine.

To determine when on the drone file the porpoise was exposed to the pinger, each drone flight was started and ended by a *tap* test, where an operator was filmed by the drone while lifting the data logger out of the sea and tapping gently on the hydrophone a few times. This made it possible to determine the delay from the tap to the onset of the pinger, as recorded on the data logger, and transfer this time difference to the drone video data. For all response variables, we compared the swimming behavior of the animals: a) before and during pinger exposure, b) during the control trials and pinger trials after pinger exposure started. To test for significant differences between playback and control conditions in each response, surfacing rates and swimming speed, we used ANOVA. Statistical analyses were performed using R software, version 3.5.2 (R Core Team, 2018). Data visualization was conducted using the "ggplot2" package, version 3.2.1, in R software (Wickham 2016).

To determine how well GPS location and speed of the porpoise could be determined, we flew the drone at a height of 30 m above a boat at a speed measured with a GPS, varying from 3 to 10 m/s. When comparing the location and the speed of the boat with the one calculated when analyzing the drone data in the same way as for determining the location and speed of the individual animals, we could measure a precision both in positioning and speed measurements with 2.4 ± 1.5 m and 0.28 ± 0.2 m/s (average ± 1 SD) (see Supplementary Material for further details on these experiments).

3. Results

3.1. Signal and noise levels

For 12 of the 16 playback trials, the signals recorded at the site of the porpoises at the start of the playback was of sufficient signal-to-noise ratio (i.e., more than 6 dB) to measure their intensity, varying from 90 to 104 dB re 1 μPa rms (Fig. 5). For these trials, the range to the pinger at the start of playback varied from 173 to 380 m. With a source level of 144 dB re 1 μPa rms @1 m, the geometric spreading loss best fitting these data was very close to spherical spreading loss, namely 20.2 log10 (r) with $R^2 = 0.91$. We observed no difference in background noise levels between trials eliciting or not eliciting a response (Fig. 6).

3.2. Behavioral responses

Playback experiments are summarized in Table 1. In total, 16 playback sessions were made during seven days of field work on 11 individual porpoises, and five porpoises belonging to groups of two to three animals. The range from the pinger to the individual porpoises at the start of playback varied from 158 to 797 m. The pre-exposure behavior was foraging during ten, traveling during two and socializing during two of the trials, respectively. The type of reactions to the pinger varied between animals. For foraging animals, a clear escape reaction to the pinger sound was observed in one animal (see Supplementary Material, video 1, for an example), whereas six were lost briefly after the pinger sound transmissions started, and three animals did not show any reaction. For the two traveling animals, one escaped and the other one was lost when the pinger playback started. For the two socializing animals, one of them escaped and the other one did not show any reaction. None of the animals in the ten control trials showed a behavioral reaction when the non-functioning pinger was lowered into the sea. The four animals with a clear reaction in the active pinger transmission test (i.e. increased swimming speed and tail stroke frequency, decreased surfacing rate, change in heading away from pinger) had a distance to the pinger of 199–521 m, while the four animals without a reaction were at a distance of between 241 and 797 m to the pinger at start of playback. The highest displacement was more than 1200 m in almost 8 min (Fig. 7).

3.3. Surfacing rates and tail strokes

Prior to pinger exposure, the average surfacing rate was 3.4 (± 0.8 SD) surfacings/min, and during exposure 2.8 surfacings/min (± 0.8 SD), or an 18 % decrease. For the control trials, before and during 'exposure', the average rate was 3.2 (± 0.7 SD) and 3.0 surfacings/min (± 0.7 SD), respectively. There was no significant difference in surfacing rates when comparing before and after exposure to the pinger sounds (ANOVA, F (3, 20) = 0.67, p = 0.58), even though we observed a reduction in the surfacing rate during some exposures (Fig. 8, Table 1). There were no trials were the surfacing rate increased after playback started. The tail-stroke frequency increased from on average 4.5 tail strokes/10 s in all trials before sound exposure to 13 tail strokes in the playback trials with escape reaction (Fig. 9). The number of 10-s intervals where the animal was not visible was significantly higher after playback than before (Student's paired *t*-test, N = 16, $p < 0.02$) whereas there was no significant difference before and after the inactive pinger was deployed during control trials (Student's *t*-test, N = 10, $p > 0.7$).

3.4. Swimming speed

During the playback, a fast increase in swimming speed up to 10 m/s and vigorous fluking were observed in four animals exposed to the pinger sound, where the swimming speed was faster during pinger exposure compared to before playback (Fig. 10A and B). For the other 11 animals, no change in swimming speed could be observed after playback was initiated. Overall, no significant change in swimming speed was observed in any of the trials (ANOVA, F (3, 39) = 0.95, p = 0.43). The swimming speed data are summarized in Table 1.

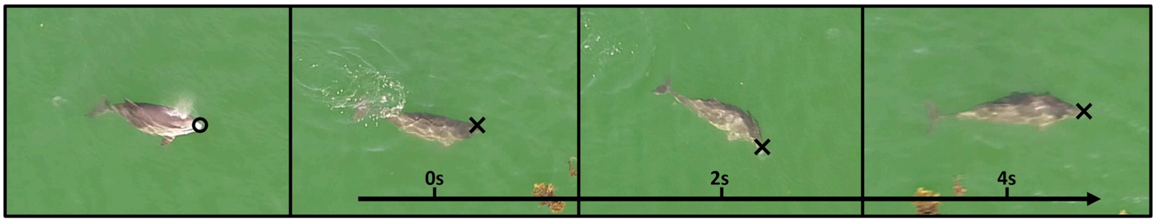


Fig. 4. Harbor porpoise position tracking every 2 s (x) and for each surfacing (o).

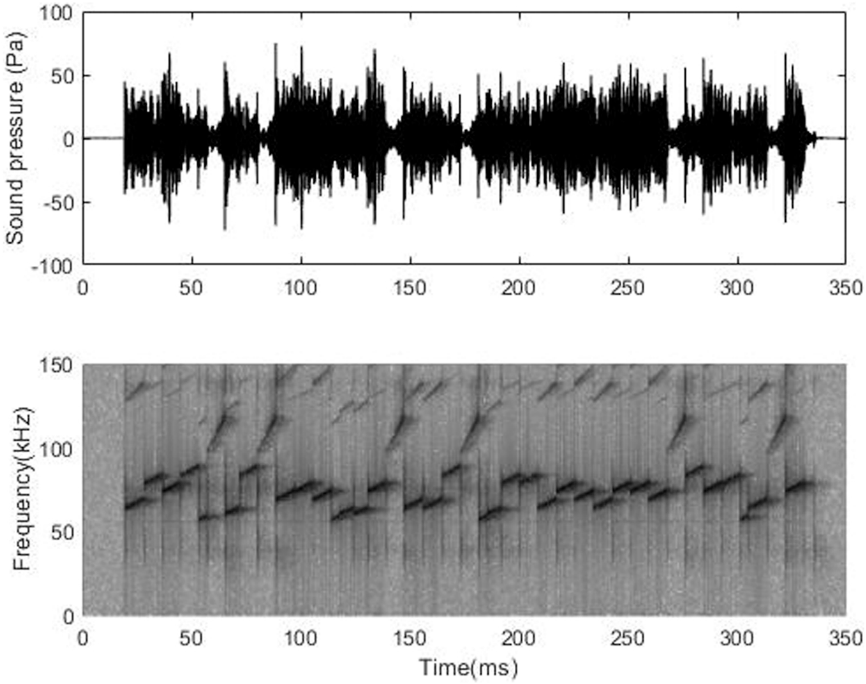


Fig. 5. (A) The oscillogram is that of the pinger signal recorded in a 3 m diameter and 3 m deep water tank (sampling rate 576 kHz). (B) Spectrogram of the same signal (FFT size 1024, Hanning window, 50 % overlap).

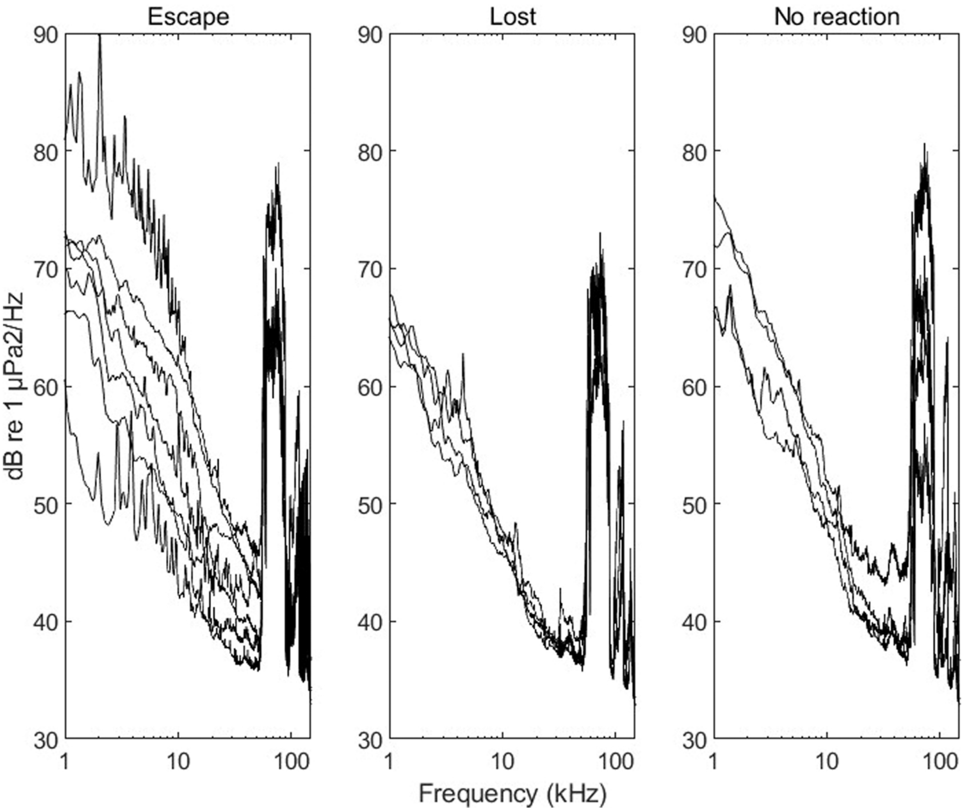


Fig. 6. Power spectral density plots of recordings made during exposure trials, sorted between those giving escape response, animal lost after exposure start and animals showing no response. The high noise levels in the 60–80 kHz band are due to the emitted playback signals. Signals were recorded with a SoundTrap with a sampling rate of 576 kHz and 16 bits, preamp setting high. The analysis was made with the Welch periodic method, FFT size 8192, Hanning window, 50 % overlap (Welch, 1967).

3.5. *Heading of the animal relative to pinger*

In control trials as well as during the observations made before playback, the animals made large changes in their swimming direction between each surfacing (Fig. 11A and B). After playback was initiated, a change in swimming direction with a reorientation away from the sound source was observed in four animals (Fig. 11A). There were no significant differences in the heading of the animal relative to the pinger at the start of playback for pinger sound and control trials, and neither between pinger sound trials where animals showed strong or no reactions

Table 1
Behavioral responses of porpoises to pinger exposure. The distance from porpoise to pinger and number of porpoises were measured at the time of playback start (1c = calf). The behavior prior to playback was evaluated during a 1-min period before pinger exposure, and the reaction to the pinger sound was evaluated for a 30-s period after pinger exposure in the cases of 'escape' reaction and 'no reaction'. C1–C10 are control trials. Maximum swimming speed was determined in a 30 s period before and after playback. Surfacing rates were calculated only in trials with an observation period longer than 2 min before and after the pinger exposure.

Trial No.	No. of porpoises	Observation period prior to playback (s)	Observation period during playback (s)	Porpoise - pinger distance (m)	Behaviour prior to playback	Reaction to pinger	Max speed prior to playback (m/s)	Max speed during playback (m/s)	Surfacing rate prior to playback (Surfacings/ min)	Surfacing rate during playback (Surfacings/ min)
1	1	224	17	158	Foraging	Lost briefly after pinger start	1.8	1.9	N.A.	N.A.
2	1	186	37	642	Foraging	No reaction	2.7	2.9	N.A.	N.A.
3	2	275	2	538	Foraging	Lost briefly after pinger start	3.2	N.A.	N.A.	N.A.
4	1	235	9	315	Foraging	Lost briefly after pinger start	2.9	0.8	N.A.	N.A.
5	1	334	18	366	Foraging	Lost briefly after pinger start	1.6	1.4	N.A.	N.A.
6	1	47	6	434	N.A.	Lost briefly after pinger start	1.2	0.4	N.A.	N.A.
7	1	175	477	201	Foraging	Escape	2.2	4.4	2.7	2.0
8	2	48	281	521	N.A.	Escape	2.9	10.1	N.A.	N.A.
9	3	154	144	380	Socializing	Escape	1.2	4	2.7	2.9
10	1 + 1c	138	131	199	Traveling	Escape	1.8	4.3	3.0	1.8
11	1	203	359	797	Foraging	No reaction	1.9	1.8	4.4	3.8
12	3	61	36	430	Socializing	No reaction	1.5	5.9	N.A.	N.A.
13	1	249	3	274	Traveling	Lost briefly after pinger start	6.1	N.A.	N.A.	N.A.
14	1	210	9	301	Foraging	Lost briefly after pinger start	1.9	2	N.A.	N.A.
15	1	189	2	190	Foraging	Lost briefly after pinger start	1.8	N.A.	N.A.	N.A.
16	1	255	241	241	Foraging	No reaction	3.1	4.9	4.0	3.2
C1	1	272	722	246	Foraging	No reaction	1.5	2.1	4.4	2.7
C2	1	41	304	407	N.A.	No reaction	1.8	5.9	N.A.	N.A.
C3	1	276	139	248	Traveling	No reaction	1.1	2.2	3.0	3.4
C4	1	222	608	143	Foraging	No reaction	3	2.8	4.1	4.2
C5	1	99	458	722	Traveling	No reaction	1.3	1.2	2.4	3.3
C6	1	382	449	341	Traveling	No reaction	8.4	8.6	3.1	2.7
C7	3+1c	307	675	169	Socializing	No reaction	3	3.1	2.9	2.4
C8	1	301	424	206	Traveling	No reaction	4.6	2.9	2.6	2.4
C9	1	36	238	231	N.A.	No reaction	1.2	4.2	N.A.	N.A.
C10	1	240	264	53	Foraging	No reaction	3	2	N.A.	N.A.

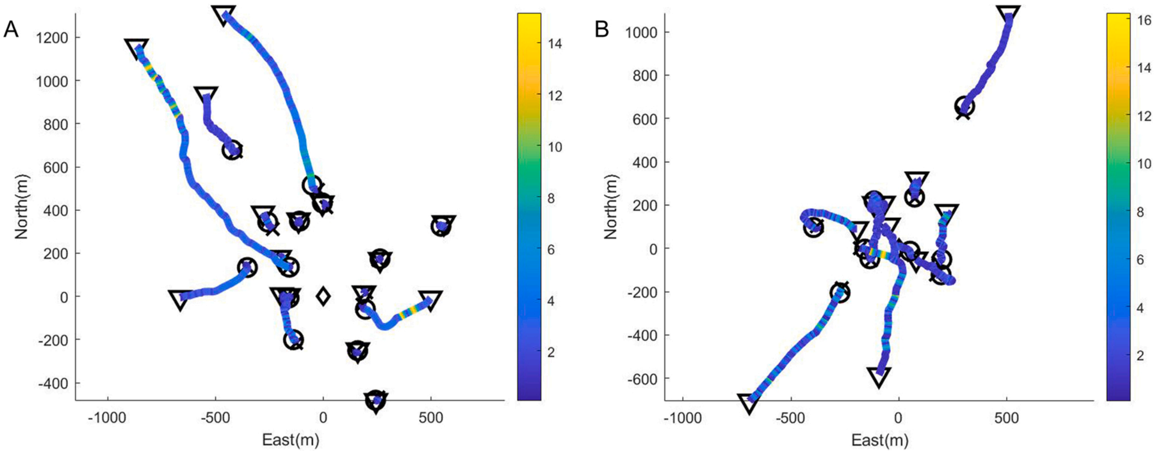


Fig. 7. Tracks from porpoises observed by drone 30 s before sound exposure until end of tracking. Positions are relative to playback-boat position (rhombus at 0.0). Crosses indicate trial start, triangles trial end; circles indicate positions when the pinger was activated. Swimming speed is colour-coded in m/s. (A) Pinger trials. (B) Controls. Where track start and stop overlaps, the porpoise was lost immediately after playback onset.

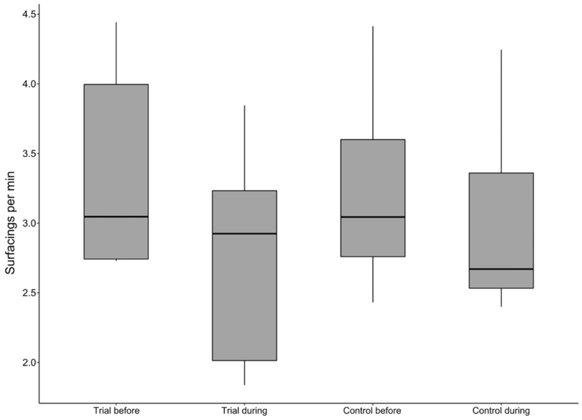


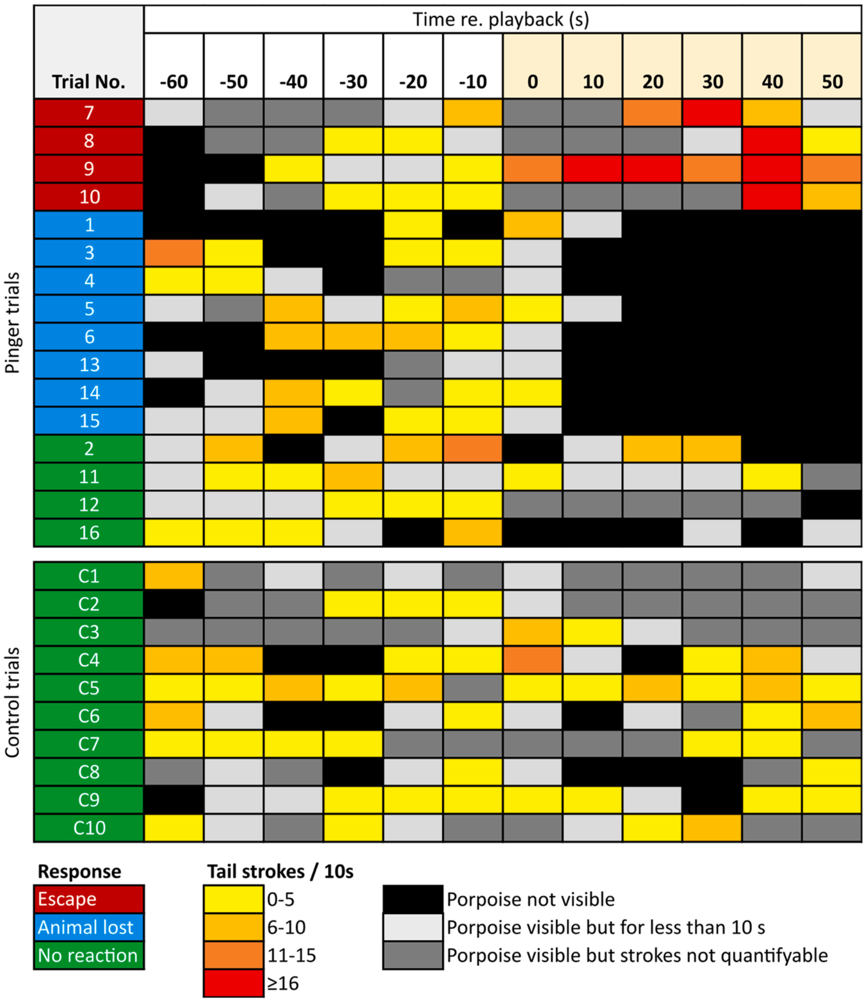
Fig. 8. Surfacing rate/min before playback and during pinger playback (trial before and trial during, n = 5) and for controls before and during 'playback' (control before and control during, n = 7) in recordings more than 2 min before and after pinger exposure. Lines indicate medians and whiskers indicate the first and third quartile.

(Fig. 12).

4. Discussion

For decades, pingers have been used to reduce incidental bycatch of harbor porpoises. Previous studies on the efficiency of pingers focused either on the behavior of individuals in human care (Kastelein et al., 2001; Lockyer et al., 2001; Teilmann et al., 2006), comparing bycatch in commercial gillnet fisheries with and without pingers (Larsen et al., 2013, 2002; Larsen and Eigaard, 2014; Palka et al., 2008), or were in the context of acoustic monitoring studies (Cox et al., 2001; Kindt-Larsen et al., 2019; Königson et al., 2021; Kyhn et al., 2015; Omeyer et al., 2020). Even though studies of captive individuals provide details on their behavioral and physiological response, captive animals may not respond in a similar manner as wild ones, as they are confined as well as usually conditioned and trained, and usually having a good health status.

Counting the actual bycatch and monitoring the porpoise echolocation activity in areas where pingers are used are important for understanding the efficiency of pingers to reduce bycatch, but also assessing the risk of pingers causing long-term exclusion of porpoises from certain habitats. However, all these approaches lack the direct observation of the animals' reaction to the pinger. In the present study, we used drone technology to observe wild porpoises in natural conditions and analyzed their behavior in response to the presence of a pinger. While maintaining an appropriate distance to the animals, we could follow the focal animal's behavior before and during the pinger exposure. We demonstrated that pingers can cause an immediate and strong escape reaction with increased tail stroke frequency and increased swimming speed directed away from the sound source and with fewer surfacings during the exposure time. However, in other cases, the pinger may not cause any response at all.



		Time re. playback (s)											
	Trial No.	-60	-50	-40	-30	-20	-10	0	10	20	30	40	50
Pinger trials	🟥 7	⬜	▩	▩	▩	⬜	🟧	▩	▩	🔶	🔴	🟧	⬜
	🟥 8	⬛	▩	▩	🟨	🟨	⬜	▩	▩	▩	⬜	🔴	🟨
	🟥 9	⬛	⬛	🟨	⬜	⬜	🟨	🔶	🔴	🔴	🔶	🔴	🔶
	🟥 10	⬛	⬜	▩	🟨	🟨	🟨	▩	▩	▩	▩	🔴	🟧
	🟦 1	⬛	⬛	⬛	⬛	🟨	⬛	🟧	⬜	⬛	⬛	⬛	⬛
	🟦 3	🔶	🟨	⬛	⬛	🟨	🟨	⬜	⬛	⬛	⬛	⬛	⬛
	🟦 4	🟨	🟨	⬜	⬛	▩	▩	⬜	⬛	⬛	⬛	⬛	⬛
	🟦 5	⬜	▩	🟧	⬜	🟨	🟧	🟨	⬜	⬛	⬛	⬛	⬛
	🟦 6	⬛	⬛	🟧	🟧	🟧	🟨	⬜	⬛	⬛	⬛	⬛	⬛
	🟦 13	⬜	⬛	⬛	⬛	▩	⬜	⬜	⬛	⬛	⬛	⬛	⬛
	🟦 14	⬛	⬜	🟧	🟨	▩	🟨	🟨	⬛	⬛	⬛	⬛	⬛
	🟦 15	⬜	⬜	🟧	⬛	🟨	🟨	⬜	⬛	⬛	⬛	⬛	⬛
	🟩 2	⬜	🟧	⬛	⬜	🟧	🔶	⬛	⬜	🟧	🟧	⬛	⬛
	🟩 11	⬜	🟨	🟨	🟧	⬜	⬜	🟨	⬜	⬜	⬜	🟨	▩
	🟩 12	⬜	⬜	⬜	🟨	🟨	🟨	▩	▩	▩	▩	▩	⬛
	🟩 16	🟨	🟨	🟨	⬜	⬛	🟧	⬛	⬛	⬛	⬜	⬛	⬜

		-60	-50	-40	-30	-20	-10	0	10	20	30	40	50
Control trials	🟩 C1	🟧	▩	⬜	▩	⬜	▩	⬜	▩	▩	▩	▩	⬜
	🟩 C2	⬛	▩	▩	🟨	🟨	🟨	⬜	▩	▩	▩	▩	▩
	🟩 C3	▩	▩	▩	▩	▩	⬜	🟧	🟨	⬜	▩	▩	▩
	🟩 C4	🟧	🟧	⬛	⬛	🟨	🟨	🔶	⬜	⬛	🟨	🟧	⬜
	🟩 C5	🟨	🟨	🟧	🟨	🟧	▩	🟨	🟨	🟧	🟨	🟧	🟨
	🟩 C6	🟧	⬜	⬛	⬛	⬜	🟨	⬜	⬛	⬜	▩	🟨	🟧
	🟩 C7	🟨	🟨	🟨	🟨	▩	▩	▩	▩	▩	🟨	🟨	▩
	🟩 C8	▩	⬜	▩	⬛	⬜	🟨	⬜	⬛	⬛	⬛	▩	🟨
	🟩 C9	⬛	⬜	⬜	🟨	🟨	🟨	🟨	🟨	⬜	⬛	🟨	🟨
	🟩 C10	🟨	⬜	▩	🟨	⬜	▩	▩	⬜	🟨	🟧	▩	▩

Response
🟥 Escape
🟦 Animal lost
🟩 No reaction

Tail strokes / 10s
🟨 0-5
🟧 6-10
🔶 11-15
🔴 ≥16

⬛ Porpoise not visible
⬜ Porpoise visible but for less than 10 s
▩ Porpoise visible but strokes not quantifyable

Fig. 9. Tail strokes/10 s 1 min before and after sound exposure for all trials. The trial numbers refer to the ones in Table 1.

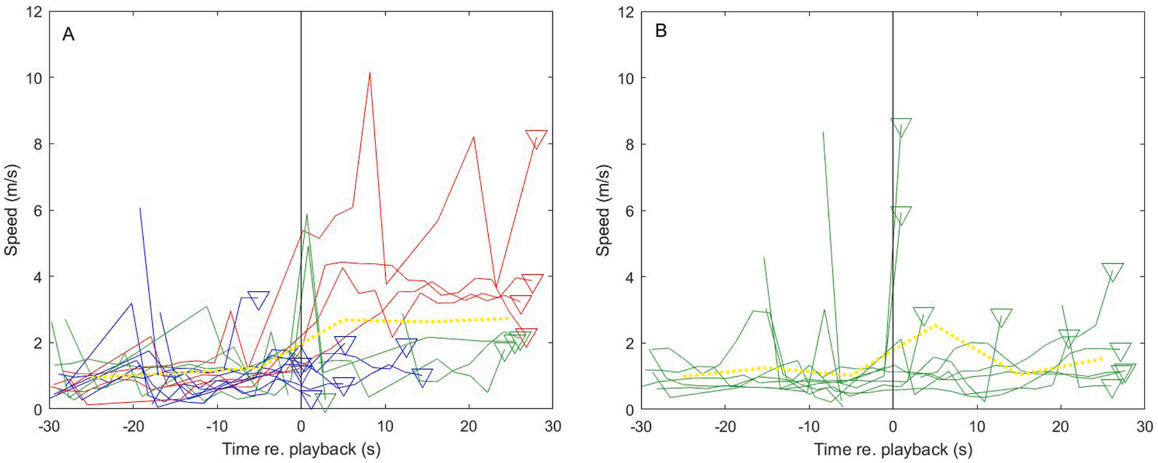


Fig. 10. Swimming speed before and during the sound exposure with moving average of ten positions. (A) Pinger trials. (B) Controls. Color coded for playback trials with escape reaction (red), no reaction (green), and animal lost at pinger start (blue), as well as the averaged velocity (yellow).

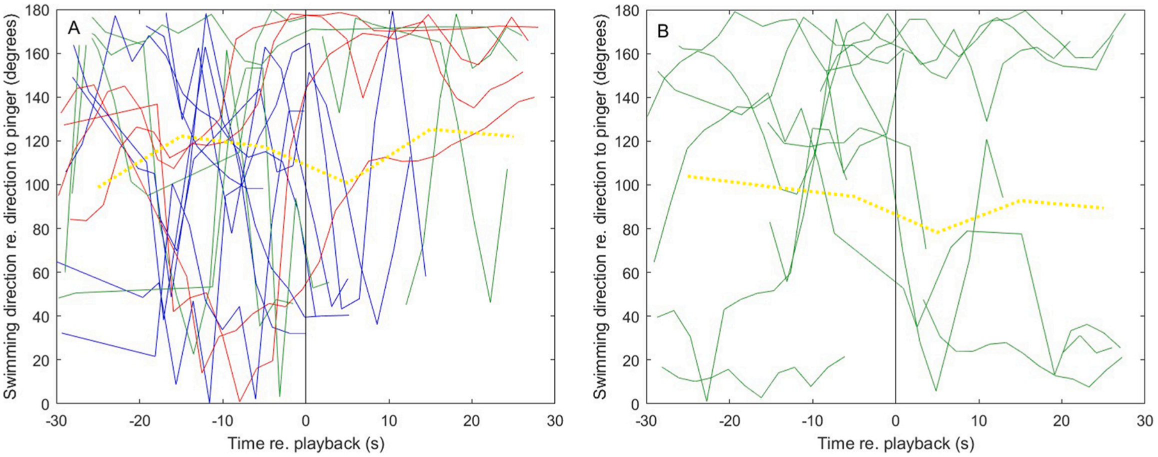


Fig. 11. Swimming direction relative to sound source; 180 degrees means swimming straight away from it, and 0 degrees towards it. (A) Pinger trials 30 s before and after sound exposure. (B) Controls 30 s before and after sound exposure. Color coded for playback trials with escape reaction (red), no reaction (green), and animal lost at pinger start (blue), as well as the averaged swimming direction (yellow).

The most parsimonious explanation for the animals being lost at pinger playback onset is that they dove to the bottom or sped up so rapidly that we were not able to be tracked within the field-of-view of the drone. Therefore, the most common behavior observed in our study was avoidance behavior of porpoises in response to pinger sounds (i.e., swimming away fast from the pinger, or swimming down to the sea floor and remaining there for an extended period of time). Two recently published studies demonstrated similar reactions to other types of sound exposure. Mikkelsen et al. (2017) documented avoidance reactions of porpoises as far as ranges of 525 m when playing back seal scarer sounds. In addition, Wisniewska et al. (2018) used acoustic tags to observe behavioral disruptions to high intensities of vessel noise levels, causing the animal to dive to the bottom of the seabed, interrupt foraging and increase fluke strike rates. Avoidance behavior and stress responses to pingers have also previously been documented in porpoises in human care (Kastelein et al., 2001; Kastelein et al., 2000a, 2000b; Lockyer et al., 2001; Teilmann et al., 2006). However, for those porpoises, pingers caused an increased surfacing rate, which is the opposite to what was found in our study and other studies on wild animals. A possible explanation for the discrepancy between studies of free-living and captive porpoises may be related to the difference between an open and a (semi-) enclosed environment. Kastelein et al. (2000b, 2001) and Teilmann et al. (2006) studied a total of four animals to test the behavior of porpoises towards pingers. Age, sex, experience of the individuals, pool size and ambient noise may have influenced the behavior of these animals. While porpoises in human care were already alert due to space limitation, several of the free-living animals tried to swim away as fast as possible.

Four porpoises did not show any reaction to pingers. We tested whether a high level of background noise, a long distance to the pinger at the time of playback, the heading of the animal relative to the pinger or a special behavioral state of the porpoises (e.g., foraging, socializing and traveling) before being exposed to the pinger might have influenced the reaction to pingers. Associated background noise levels such as boat noises may be responsible for masking the sound of pingers, resulting in a decreased pinger response rate (Hardy et al., 2012). In our study, the presence of boats (e.g., motor-boats and sailing boats) was frequently observed during fieldwork, which may have the influenced animals' reaction to pingers. However, the analysis of the background noise levels at playback did not reveal any significant difference between trials eliciting or not eliciting a response.

From acoustic monitoring studies, it is known that the effect of pinger sounds decreases with increasing distance to the sound source (e.g., Kindt-Larsen et al., 2019, Königson et al., 2021 and Omeyer et al., 2020). In our study, the longest distance between the pinger and the porpoise eliciting a reaction was 538 m. However, one animal, which

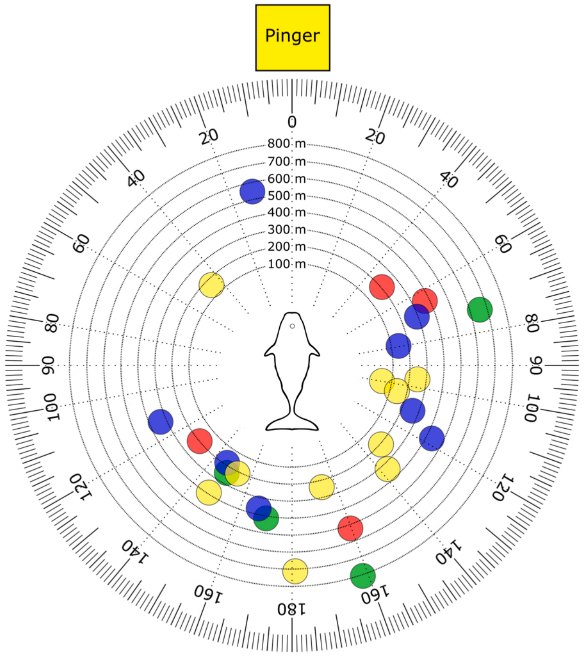


Fig. 12. Heading of animal relative to sound source at the start of the playback, color coded for playback trials with escape reaction (red), no reaction (green), and animal lost at pinger start (blue), as well as control trials (yellow). Dotted circles indicate distance to pinger in 100 m increments with the porpoises at distance zero in the center.

was only 241 m away, did not react to the pinger. Although we cannot draw generalized conclusions for one animal's behavior, further data collection is needed to determine how exactly distance to the pinger can affect porpoises. In shallow water environments, with many multipath interferences from surface and bottom reflections, the received level of the pinger can dramatically change with small spatial changes of the animal (Shapiro et al., 2009). Even though we measured the sound intensity at the site of the animal at onset of playback, small shifts in animal position may have caused large deviations in the received level that could not be detected here. Therefore, it cannot be ruled out that a low received level could in part explain the unresponsiveness of 25 % of the porpoises.

An increasing number of studies have suggested that when porpoises are distracted by conspecifics or while chasing prey, the risk of entanglement on gillnets is higher (Kastelein et al., 2000a, 2000b; Nielsen et al., 2012). In addition, Goldbogen et al. (2013) noted that the reaction of blue wales to mid-frequency sonar signals depended on whether the whales were foraging at the time of exposure. Therefore, we expected that the behavior of porpoises immediately prior to pinger exposure would have an influence on their reaction to pingers. However, none of the pre-exposure behavior seemed to have any impact on their reaction.

Additionally, we do not know if the age (e.g. possibly influencing hearing sensitivity) of the animal could determine their reaction to pingers. Age plays a large role in bycatch, as mostly juveniles end up entangled in nets (Berggren, 1994; Kinze, 1994; Kock and Benke, 1996a, 1996b; Siebert et al., 2020; Tregenza et al., 1997). Furthermore, the receiving beam of the harbor porpoise becomes narrower as the frequency of signals increases (Kastelein et al., 2005). Since we used a high frequency pinger, it could be that when porpoises are not turned towards the pinger that they can simply not hear it due to the directionality of hearing in the porpoise or the received SPL is too low to elicit a response (Kastelein et al., 2005). Directly from behind the hearing threshold at 64 and100kHz is ~15 dB above that in front of the animal (Kastelein et al., 2005). This would affect the received SPL and hence the reaction. However, our measurements of porpoise heading at pinger onset does not indicate any clear differences between neither pinger and control trials, nor for different types of responses during playback (Fig. 12). The above-mentioned causes for lack of reaction to pingers could also help in explaining why there is a low percentage of animals reported as bycatch in gill nets in previous commercial fisheries pinger studies (Larsen et al., 2013; Larsen and Eigaard, 2014; Palka et al., 2008) and in acoustic monitoring studies, where harbor porpoises could still be detected near active pingers (Kyhn et al., 2015; Königson et al., 2021; Omeyer et al., 2020).

Another possible explanation to some animals not reacting to the pingers is habituation. Previous studies have shown that some animals may at least partially habituate to pinger sounds after long-time exposure (Carlström et al., 2009; Kindt-Larsen et al., 2019; Kyhn et al., 2015). However, in the inner Danish waters only very few vessels use pingers, since only vessels longer than 12 m are obliged to use pingers as part of the European Council regulation 812/2004 (EC, 2004) and full implementation with active enforcement has been sparse in Denmark (ICES, 2020, 2018). The playback experiments reported here were thus performed in an area where banana pingers are not used, and other pinger types are only very rarely used and mainly under scientific circumstances (Kindt-Larsen et al., 2019). Also, there is limited exchange between individual porpoises in the inner Danish waters with the North Sea population, where pingers are more commonly used, especially in the UK (ICES, 2020). Therefore, habituation seems like a very unlikely explanation for the unresponsive animals observed in this study.

Therefore, the most likely explanation for the variability in pinger responses is therefore differences in behavioral reactions of individual porpoises. Some animals may be more skittish than others, being more prone to react strongly to pingers whereas others are much more conservative in their reaction patterns. Such differences may be caused by innate differences, or by previously being scared by different types of natural and man-made sounds, causing them to either be sensitized to such sounds or desensitized. The fact that several long-term pinger studies indicate a partial habituation in animals (Kyhn et al., 2015, Kindt-Larsen et al., 2019) may further corroborate the existence of such differences in the reactions between individual animals. Furthermore, porpoise clicks were also recorded in the active pinger periods meaning that porpoises do come close to active pingers (Kindt-Larsen et al., 2019; Königson et al., 2021; van Beest et al., 2017).

One drawback of this study is that in our experiments, the porpoises are not approaching the pinger under natural conditions. When pingers are normally used in fisheries, net are placed and stay in the same position. This entails that when a porpoise approach a net, the pinger sound is very low at first and only increases if it swims closer. This entails that if the porpoise approaches the net the sound is very low and only increases if the porpoise swim closer. In our case the porpoises were more rapid introduced to the sound source, as the pinger signals immediately began when the pinger is submerged. This can be the reason for the observed escape behavior which likely would be different in porpoises approaching a net. Despite this we however believe that direct recordings of porpoise responses to pingers can contribute to a better understanding of the animals' reactions and thus support future modifications of pingers sounds.

Even though the use of pingers is still rather limited in the commercial fisheries, pingers are still one of the main tools to mitigate bycatch without affecting the gillnet effort and the implementation of pingers are thus increasing, thereby contributing to the underwater ambient noise (Findlay et al., 2018; Findlay et al., 2021; Todd et al., 2021). Habitat loss (Kastelein et al., 2000a, 2000b; Kastelein et al., 2001; Laake et al., 1998; Teilmann et al., 2006) and reduced foraging efficiency due to interruption and escape reactions of porpoises potentially affecting individual survival and the total population size (van Beest et al., 2017) are some of the negative effects on harbor porpoises when introducing pingers in fisheries. On the other hand, pingers may fill a function in some areas to prevent excessive mortality in bycatch. Also, our data strongly indicate that reaction to pingers is diverse, with some animals reacting strongly and some animals not reacting, so that the impact of the porpoise population from pinger usage may not be as severe as previously assumed. Studies like the present one, offering a detailed insight into the behavior of porpoises when exposed to pingers and can be used to optimize the type of pinger sounds, source levels and duty cycling employed to best avoid bycatch by reducing any unwanted effects of these devices. Using higher frequencies in the pinger sounds reduces the range of impact, due to frequency-dependent absorption.

CRediT authorship contribution statement

Dennis Brennecke: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Ursula Siebert:** Conceptualization, Resources, Writing – review & editing, Supervision. **Lotte Kindt-Larsen:** Conceptualization, Methodology, Validation, Resources, Supervision, Project administration, Funding acquisition. **Henrik Skov Midtiby:** Software, Writing – review & editing. **Henrik Dyrberg Egemose:** Software. **Sara Torres Ortiz:** Methodology, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Katrin Knickmeier:** Resources, Supervision, Funding acquisition. **Magnus Wahlberg:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

https://doi.pangaea.de/10.1594/PANGAEA.932770.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106437.

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