

RESEARCH ARTICLE

Context-dependent biosonar adjustments during active target approaches in echolocating harbour porpoises

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ABSTRACT

Echolocating mammals generally target individual prey items by transitioning through the biosonar phases of search (slow-rate, high-amplitude outputs), approach (gradually increasing rate and decreasing output amplitude) and buzzing (high-rate, low-amplitude outputs). The range to the main target of interest is often considered the key or sole driver of such biosonar adjustments of acoustic gaze. However, the actively generated auditory scene of an echolocator invariably comprises a large number of other reflectors and noise sources that likely also impact the biosonar strategies and source parameters implemented by an echolocating animal in time and space. In toothed whales, the importance of context on biosonar adjustments is largely unknown. To address this, we trained two harbour porpoises to actively approach the same sound recording target over the same approach distance in two highly different environments: a PVC-lined pool and a semi-natural net pen in a harbour, while blind-folded and wearing a sound recording tag (DTAG-4). We show that the approaching porpoises used considerably shorter interclick intervals (ICIs) in the pool than in the net pen, except during the buzz phase, where slightly longer ICIs were used in the pool. We further show that average click source levels were 4–7 dB higher in the net pen. Because of the very low-level in-band ambient noise in both environments, we posit that the porpoises adapted their echolocation strategy to the different reverberation levels between the two settings. We demonstrate that harbour porpoises use different echolocation strategies and biosonar parameters in two different environments for solving an otherwise identical target approach task and thus highlight that biosonar adjustments are both range and context dependent.

KEY WORDS: Echolocation, Interclick interval, *Phocoena phocoena*, Source level, Target range, Toothed whale

INTRODUCTION

Toothed whales use echolocation for foraging and navigation in a wide range of habitats, from shallow riverine and coastal waters to deep oceans. Between and within these habitats, the ambient noise, clutter and reverberation levels may differ significantly, and toothed whales must therefore dynamically operate their biosonar in light of these variations to facilitate extraction of relevant echo information for navigation and foraging.

Efficient biosonar operation requires that the source level (SL) of outgoing sonar pulses is high enough to return echoes from


ensonified targets at levels exceeding hearing thresholds as well as masking levels of noise, clutter or reverberation (Au, 1993). Under noise-limited conditions, higher SLs are needed to detect the same target at higher noise levels or at longer ranges, whereas in reverberation-limited situations, higher SLs fail to improve performance because SL adjustments do not alter the echo-to-reverberation ratio (Au, 1993). Although the SL of toothed whale echolocation clicks as such is a key parameter to measure and quantify to understand the performance, dynamics and capabilities of toothed whale biosonar, it is implied that SL estimates may also be contingent on the reverberant properties of the context in which the biosonar is being employed (Au, 1993). A second important parameter that is often used as a proxy for the biosonar inspection range (Penner, 1988; Thomas and Turl, 1990; Akamatsu et al., 2005) is the interclick interval (ICI), which toothed whales generally keep long enough so that echoes of interest return before a new click is produced (Morozov et al., 1972; Au et al., 1974; Au, 1993). This strategy, in combination with gradual ICI variation, presumably combats range ambiguity (Kadane and Penner, 1983), making the target echo delay measured from the most recent outgoing click directly proportional to target range (Morozov et al., 1972; Murchison, 1980).

There is considerable evidence that small toothed whales generally decrease both SL and ICI when approaching targets (Au and Benoit-Bird, 2003; Jensen et al., 2009; Wisniewska et al., 2012). Ultra-short target ranges may therefore explain why trained toothed whales in small tanks use much lower SLs and shorter ICIs (Evans, 1973; Brill and Harder, 1991) than toothed whales engaged in long-range echolocation (Au et al., 1974; Finneran et al., 2013; Ladegaard et al., 2019) or when echolocating in the wild (Villadsgaard et al., 2007; Wahlberg et al., 2011). However, it is not understood whether such biosonar adjustments are only driven by the often short spatial and hence temporal relationship with the target of interest in captive settings or whether the invoked biosonar dynamics are also affected by the environmental context of the biosonar task.

The only toothed whale study that we are aware of that, for the same animal and task, has shown environment-dependent biosonar adjustments is that of Au et al. (1985), who demonstrated that the same beluga on average raised the click SL by ~9 dB when solving the same detection task from a fixed target range in two open-water environments where the background noise level differed by 12 to 17 dB. Thus, two environments with different masking noise resulted in the same animal using higher SLs to solve the same echolocation task, which is also the prediction for biosonar operating under noise-limited conditions (Au, 1993). In other studies where different levels of artificial noise were projected during target detection tasks, the toothed whales did not respond by increasing SL with increasing noise (Au and Penner, 1981; Turl et al., 1987); however, the experiments were conducted in a naturally noisy environment and the animals might, as a

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consequence, have been operating close to their maximum output levels at all times (Au and Penner, 1981).

To our knowledge, the contextual effects on solving the same echolocation task by the same animals under different reverberant conditions has not been addressed with the same rigor, nor have any of these mechanisms been studied in animals actively approaching a target while echolocating. To address this, we designed an experiment in which we could quantify the range-dependent biosonar adjustments made by two harbour porpoises (*Phocoena phocoena*) as they actively approached the same target over the same ranges in a shallow-water pool and in a semi-natural net pen. Preliminary data have indicated that a porpoise capturing dead fish may decrease the ICI during the approach and increase the ICI during the buzz phase, when a clutter screen is introduced behind the fish (Miller, 2010). We hypothesised that the pool environment would induce similar ICI adjustments in this experiment because of the confined, reverberant environment compared with the larger net pen. We further hypothesised that the porpoises would use lower SL during target approaches in the pool than the net pen to reduce the time that reverberations persisted above the hearing threshold or background noise level following each outgoing click. Here, we report data to support these hypotheses by showing that porpoises employ context-dependent adjustments to their acoustic gaze while approaching the same target over the same range. This is likely an adaptation for using echolocation-guided navigation and foraging in a wide range of acoustic scenes in the natural environments of toothed whales.

MATERIALS AND METHODS

Animals and study sites

Two harbour porpoises [*Phocoena phocoena* (Linnaeus 1758)], Freja (22-year-old female, 60 kg) and Sif (14-year-old female, 56 kg), were temporarily moved to an oval pool (1000×550×132 cm, 56,000 litres, KITPROV 10288, Manufacturas Gre S.A., Mungia, Bizkaia, Spain) during a 2-week renovation of the porpoise net pen at Fjord&Bælt, Kerteminde, Denmark, in October 2017. The net pen (approximately 34×17 m, sandy bottom, 2.2–2.8 m depth during this study) was constructed from a concrete wall alongshore with net openings at both ends allowing a natural tidal flow. The oval pool was constructed of steel walls and blue PVC liner, erected on a layer of sand having a carpet with rubber backing, and felt cloth on top. The pool was filled with seawater (13°C) to a depth of 1.1 m using a pump system that replaced the water volume daily. The porpoises were maintained by Fjord&Bælt, Kerteminde, Denmark, under permit numbers SN 343/FY-0014 and 1996-3446-0021 from the Danish Nature Agency under the Ministry of Environment and Food of Denmark.

Experimental procedure

In both enclosures, the porpoises were given the same task of approaching a target over a range of ~8 m before touching the target with their rostra. The porpoises were trained to accept opaque suction cups over their eyes while wearing a DTAG-4 (576 kHz sampling rate, 16 bit, 170 dB re. 1 µPa clipping level, www.soundtags.org, Scottish Oceans Institute, University of St Andrews, Scotland) on their back with the hydrophone element located 3–5 cm behind the blowhole. The target consisted of a SoundTrap 202 HF (576 kHz sampling rate, 16 bit, 174 dB re. 1 µPa clipping level, Ocean Instruments, New Zealand) encased in a cylindrical aluminium cover (height 13 cm, wall thickness 0.5 cm). The target had a measured target strength based on energy of –28 dB using a 10-cycle, 130 kHz calibration pulse similar to a porpoise click. The

target depth was 0.5 m measured at the centre of the aluminium cover and 0.6 m depth at the SoundTrap hydrophone element. In the net pen, the swim path was parallel to and ~4 m from the concrete wall. In the pool, the swim path followed the longest dimension of the pool with the target deployed 1 m from the pool wall. A water outflow was located on the pool wall at a distance of 2.3 m from the target and may have acted as a low-frequency noise source. A GoPro Hero5 camera (GoPro, San Mateo, CA, USA) was mounted underwater on a PVC tube approximately 2 m from the target and filmed all target approaches. During trials, the non-participating porpoise was handled by a trainer and stationed ~2 m from the starting position of the participating porpoise with the head oriented away from both the target and the participating porpoise.

Click detection and target range estimation

Data analysis was carried out using custom scripts (MATLAB 2017a or higher versions, MathWorks, Natick, MA, USA) and scripts from the DTAG toolbox (www.soundtags.org/). Echolocation clicks were detected in the DTAG-4 recordings based on the –6 dB point relative to the peak of the amplitude envelope, after applying a 180 kHz Butterworth high-pass filter (six poles). The filter was used because clicks recorded directly behind the blowhole on the tagged porpoise contain more high-frequency energy than surface reflections and clicks from other porpoises (Madsen et al., 2010). The DTAG-4 click detection was done using an automated detector with a 1 ms blanking time following each detection and an adaptive threshold above a minimum of –50 dB relative to the clipping level. This was followed by manual inspection of all click detections in each trial using plots of intensity and power spectrum to add missed clicks and remove false detections.

Click detection in the SoundTrap recordings was done following Ladegaard et al. (2019) by creating a visual representation of incoming clicks on the target/SoundTrap. For this purpose, the DTAG-4 and SoundTrap recordings were aligned in time for each trial using ICI comparison in order to extract a series of 100 ms windows in the SoundTrap recordings that each started at a DTAG-4 click detection time. The 100 ms windows were then aligned in stack plots and colour-coded for amplitude, similar to how echograms are created (Johnson et al., 2004). The incoming clicks on the target were identified in the stack plots as distinct lines at gradually decreasing delays relative to the DTAG-4 detection times, and were then manually selected and saved with information of time-of-arrival difference (TOAD) between the two recorders. The TOAD estimates were corrected for a measured sampling rate difference of $187 \pm 0.14 \mu\text{s s}^{-1}$ between the DTAG-4 and SoundTrap recordings by accounting for the difference in number of recorded samples between clicks. The TOADs were converted to target range estimates by multiplying by a sound speed of 1482 m s^{-1} based on a measured sea temperature of 13°C, 1 m depth estimate and 20 ppm salinity (sea forecast by the Danish Meteorological Institute), following Medwin (1975). To account for occasional outlier distance estimates that were physically unrealistic, the estimates were filtered using a two-state (speed and range) Kalman filter followed by a Rauch smoother (Bar-Shalom et al., 2004). Given that the porpoises touched the target in each trial, as confirmed by the video recordings, the filtered range estimates for each trial were shifted so that the shortest range was set to 0 m target range.

Selection of on-axis clicks

The porpoises repeatedly used head scanning as they approached the target. A substantial number of clicks were therefore produced while the target was more or less off-axis relative to the biosonar beam

axis. To select likely on-axis clicks, plots were made of pressure and time recorded on the SoundTrap to visualise fluctuations in received click level. In each possible scan sequence, a presumed on-axis click was then manually selected as the click with the highest received level, following Wisniewska et al. (2012).

Biosonar parameter estimation

The raw biosonar signals were first extracted in a 1 s window centred on each detection time and filtered using a 50 kHz Butterworth high-pass filter (four poles). The filtered signals were then extracted in a 1 ms (576-sample) window centred on the detection times and the 1 ms window preceding each signal window was saved for subsequent signal-to-noise ratio (SNR) estimation. A 576-point Tukey window (taper ratio 0.2) was applied to the signal windows to de-emphasise noise, such as reflections, at the ends of the analysis window. The signal duration was then computed as the -10 dB end points of the amplitude envelope, following Madsen and Wahlberg (2007). To estimate SNR, we first computed the RMS level of the filtered amplitudes within the signal duration, then subtracted the RMS level computed within the 1 ms noise windows and divided by the noise RMS level and converted to decibels. The back-calculated SL was estimated as the peak-to-peak received level plus the transmission loss, which was assumed to follow spherical spreading, i.e. $20\log_{10}(R)$, where R is range. SL was only estimated for clicks where the target range exceeded 1 m. ICI was measured for each click as the duration between the detection time and the following click detection. An ICI threshold for buzzing was defined similarly to Telson et al. (2008) by visualising ICIs in a histogram and identifying a marked dip in the bimodal distribution. Because the buzz clicks would fall into very few bins compared with the approach clicks if spacing the bins linearly, we used a histogram with 51 bins spaced logarithmically from $\log_{10}(1 \text{ ms})$ to $\log_{10}(100 \text{ ms})$.

Background noise, reverberation and self-noise

Background noise in the two environments was estimated as the third octave levels (TOLs) calculated in non-overlapping 1 ms windows over the trial durations from approach start until, but not including, the buzz phase. The TOLs for the pooled trials in each environment were then quantified as the 5th, 50th (i.e. median) and 95th percentiles. The 1 ms window length ensured that several TOL estimates were obtained between successive approach clicks. TOL estimates were only calculated for frequencies where energy could be summed in at least 10 bins in the frequency domain, and hence third octave bands centred below 43.5 kHz were not computed (a 1 ms window and 576 kHz sampling rate produce a 1 kHz frequency resolution, i.e. for a 10 bin criterion, the minimum third octave bandwidth should exceed 10 kHz, and each third octave bandwidth equals 0.23 times the centre frequency).

Self-noise measurements of the SoundTrap and DTAG-4 were conducted in an anechoic chamber (for frequencies above 1 kHz) that also functioned as a Faraday cage at Zoophysiology, Department of Bioscience, Aarhus University, Denmark, and the self-noise was estimated similarly as the background noise.

Statistical analysis of ICI and SL adjustments

Statistical analysis was only performed for clicks classified as on-axis, given the assumption that these clicks would best represent biosonar adjustments made relative to the target. The ICIs were expected to follow a linear model if adjusted to target range given that the acoustic two-way travel time (TWTT), i.e. echo delay following click emission, scales linearly with target range.

However, the data suggested that linear dependence between approach ICIs and target range shifted approximately 2 m from the target. Separate ICI adjustment models were therefore computed for approach clicks grouped using a 2 m target range threshold. To account for possible adjustment variation between trials, the ICI adjustments were analysed using a generalised linear mixed-effects model (GLMM, MATLAB function `fitglm`). Model selection involved comparisons using theoretical likelihood ratio tests (5% significance level, MATLAB function `compare`) of increasingly complex models with the possible fixed effects being target range, enclosure type (pool and net pen), porpoise (Freja and Sif) and interactions thereof. As random effects, the models had intercepts for trial as well as by-trial random slopes for the effect of target range. Similar GLMM analysis was performed on SL adjustments for on-axis approach clicks localised to target ranges exceeding 1 m, with the difference that target range was \log_{10} transformed to reflect that geometric spreading loss changes logarithmically with range. Residual plots for all selected models were visually inspected and did not reveal any obvious deviations from homoscedasticity or normality.

RESULTS

The porpoises Freja and Sif completed 32 and 33 trials in the pool and 34 and 36 trials in the net pen, respectively. A target approach example from the net pen is shown in Fig. 1, where the on-animal recording illustrates how the porpoise continuously echolocates towards the target. Biosonar scanning across the target can be inferred from the alternating received click amplitudes on the target that differ markedly from the on-animal received levels (Fig. 1).

Out of the 161,312 total click detections in the DTAG-4 recordings, an instantaneous target range could be estimated for 156,015 clicks that were also detected on the SoundTrap. Implementing a 10 dB SNR criterion, exclusion of clicks with ICIs exceeding 100 ms ($N=145$), and classifying clicks as approach or buzz clicks after having determined a 10 ms ICI threshold for buzzing (Fig. 2) left 16,013 approach clicks and 92,069 buzz clicks for analysis. From the approach clicks, a subset of 869 presumed on-axis clicks were selected. The approach click SLs plotted against target range together with a range-adjusted clipping level showed that signal clipping was not a concern in this study (Fig. 3, Fig. S1). An overview of the approach and buzz durations, localisation ranges and click emissions for the different porpoises and environments is given in Table 1.

The two porpoises clicked at consistently shorter ICIs during approaches in the pool compared with the net pen (Fig. 4A,B). The ICI adjustments made during approaches were highly similar between the two porpoises, and no significant improvement was found during GLMM comparison by including porpoise as a fixed effect (comparisons of models with and without this fixed effect yielded P -values of 0.66 for approach clicks produced beyond the 2 m target range and 0.65 for the approach clicks within the 2 m target range). The GLMM comparison (results not shown) further indicated that the best model for both ICI groups included the fixed effects of range and enclosure type and an interaction term of range and enclosure type (see Tables S1 and S2 for confidence intervals and standard errors of model estimates). For approach clicks produced beyond the 2 m target range, the ICI model showed a 2.3 ms m^{-1} slope and 23 ms intercept in the pool and a 0.1 ms m^{-1} slope and 55 ms intercept in the net pen (Table S1). The ICI model for approach clicks produced closer than the 2 m target range showed an 8.4 ms m^{-1} slope and 10 ms intercept in the pool and a 24 ms m^{-1} slope and -4 ms intercept in the net pen (Table S2).

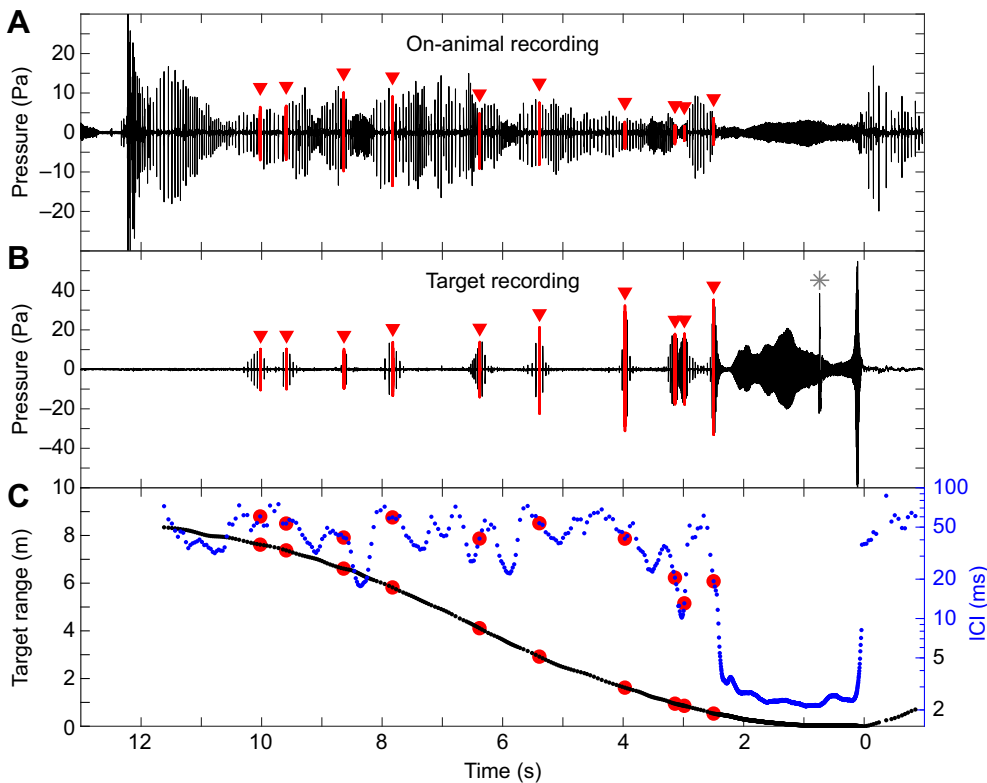


Fig. 1. Target approach example in the net pen for the harbour porpoise Freja. (A) Continuous click production recorded with the animal-worn DTAG-4 (unfiltered except for DC offset correction). The on-axis approach clicks have been highlighted in red with red triangles above. The x-axis shows time to the 0 m interpolated target range. (B) SoundTrap target recording (unfiltered except for DC offset correction), where the continuous echolocation of Freja is less obvious because Freja scanned the biosonar beam across the target to produce the alternating received click intensity pattern. On-axis clicks are marked as in A. The asterisk highlights the low-frequency impulse of when the porpoise first made physical contact with the target, and then shortly pushed away the target before the porpoise resumed contact and was bridged by the trainer. (C) Target range (black points, left y-axis) and interclick interval (ICI; blue points, right y-axis) with red circles centred on the on-axis approach clicks.

The buzz ICIs were also adjusted differently between the two environments with slightly longer ICIs being used in the pool (Fig. 4C,D). Overall, there seemed to be some adjustment of buzz ICIs with target range, especially in the net pen, although with variation in the beginning and near the end of buzzes. For the 0.1 to 0.3 m target range, where the correlation between ICI and range seemed most pronounced (Fig. 4CD), the time between click emission and echo return, i.e. lag time (Au, 1993), showed a mode (for buzz ICIs rounded to nearest 0.1 ms) for Freja of 2.4 ms in the

pool ($N=7193$) and 2.1 ms in the net pen ($N=9988$), and for Sif of 2.6 ms in the pool ($N=5430$) and 2.1 ms in the net pen ($N=12,147$).

The porpoises echolocated using higher SLs in the net pen compared with the pool (Fig. 5). The SL adjustments were best explained using a model with the fixed effects of $\log_{10}(R)$, porpoise, enclosure type, an interaction term between $\log_{10}(R)$ and enclosure type, and an interaction term between $\log_{10}(R)$ and porpoise (see Table S3 for confidence intervals and standard errors of model estimates, model comparison results not shown). The SL model showed for the pool environment that the porpoises Freja and Sif on average adjusted SL by $12\log_{10}(R)$ and $15\log_{10}(R)$, respectively (Table S3, Fig. 5). In the net pen, the $\log_{10}(R)$ slopes for both porpoises were lower by -3 relative to their adjustments in the pool. For both porpoises, the intercepts were 7 dB higher in the net pen compared with the pool, with the average SL difference being 4–7 dB over the approach distance (Fig. 5). Despite the fact that the relative increase in SL for the net pen compared with the pool was similar for both porpoises, the SL model showed that intercepts for Sif were 9 dB higher than for Freja (Table S3), thus resulting in a 9–11 dB average difference over the target approach distance (Fig. 5).

The background noise at high frequencies above 100 kHz that are relevant for porpoise echolocation could not be measured because of self-noise limitations in both the pool and the net pen. This is shown from the 5th percentiles of the estimated noise in the SoundTrap recordings in the two environments that are practically identical to the self-noise for all third octave bands (Fig. 6B). The SoundTrap 128 kHz TOL estimates suggested that the pool was a more reverberant environment compared with the net pen given that the 95th percentile was 14 dB higher in the pool (Fig. 6A), despite the fact that the two porpoises echolocated using SLs that were 4–7 dB lower in the pool (Fig. 5). Further, the 128 kHz TOL 50th percentile for the pool was practically identical to the 95th percentile for the net pen, whereas the 50th percentile for the net pen was

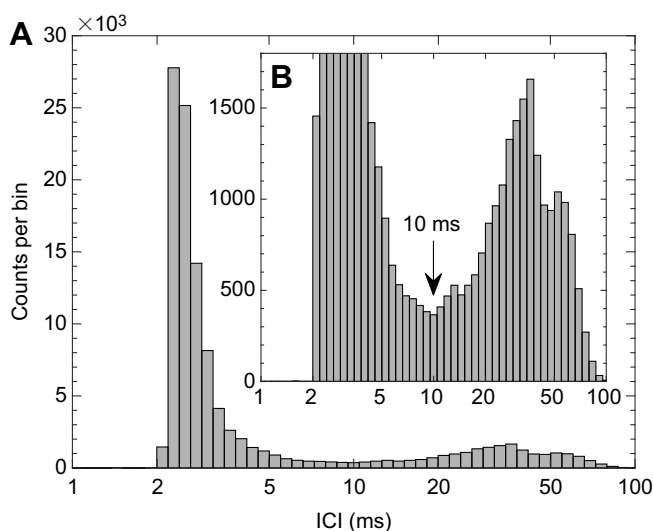


Fig. 2. ICI usage and ICI threshold for buzzing. (A) Histogram of ICI distribution for all clicks detected at the target at a signal-to-noise ratio (SNR) exceeding 10 dB [$N=111,751$; 51 logarithmically spaced bins from $\log_{10}(1 \text{ ms})$ to $\log_{10}(100 \text{ ms})$]. (B) Zoomed-in view of the same histogram as in A, highlighting the dip in the bimodal distribution at 10 ms.

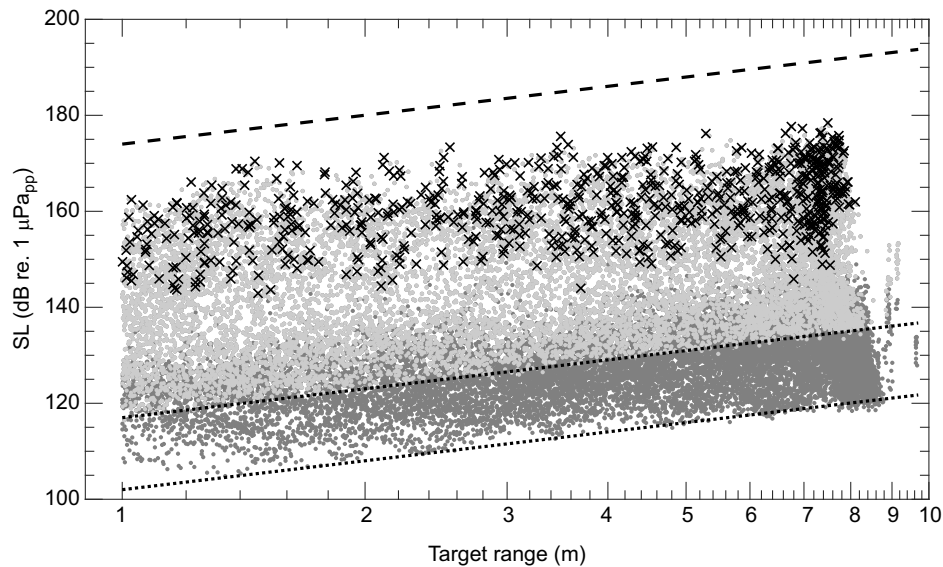


Fig. 3. Back-calculated source levels (SLs) and inclusion thresholds for approach clicks. The clicks exceeding the 10 ms ICI buzz threshold and exceeding 1 m localisation range are shown as dark grey circles ($N=27,264$). The subset of clicks that also exceed an SNR of 10 dB are plotted on top in light grey ($N=12,283$). On-axis clicks are marked by black crosses ($N=727$). The dashed line shows the SoundTrap peak clipping level plus a transmission loss estimate of $20\log_{10}(R)$, where R is range, which is a conservative estimate of the maximum source level that the recording system was capable of accurately measuring at a given animal-to-target range. The lower dotted line illustrates an approximate click detection threshold of 102 dB re. $1 \mu\text{Pa}$ plus $20\log_{10}(R)$. The upper dotted line shows that the 10 dB SNR criterion raised the inclusion threshold to approximately 117 dB re. $1 \mu\text{Pa}$ plus $20\log_{10}(R)$. Note that all SLs are below the line, indicating signal clipping by the recording system, and that the lowermost on-axis SLs recorded at the furthestmost target ranges are comparable to the lowest short-range on-axis SLs. Together, this indicates that undesirable $20\log_{10}(R)$ filtering of the on-axis SLs did not constitute a problem in this study.

barely above the estimated self-noise (Fig. 6A). When comparing the mean click amplitude with the average sum of reflections and reverberation that followed the clicks in each environment, the reverberation is seen to build up faster and to a higher level relative to the click amplitude in the pool compared with the net pen (Fig. 6B).

DISCUSSION

Toothed whales approaching targets of interest can dynamically adjust their biosonar outputs through changes in ICI (Morozov et al., 1972; DeRuiter et al., 2009), SL (Au and Benoit-Bird, 2003; Jensen et al., 2009) and beamwidth (Moore et al., 2008; Jensen et al., 2015; Wisniewska et al., 2015). Target range is likely a strong driver of such acoustic gaze changes for many species, despite the fact that

echolocating animals invariably also have to perceptually organize auditory streams from other features and objects in the environment (Murchison, 1980; Moss and Surlykke, 2001; Verfuß et al., 2005). The ability to accommodate context in concert with range-dependent adjustments to the main target(s) of interest is likely of high ecological importance for wild animals that go through the biosonar phases associated with finding and capturing prey, while simultaneously being exposed to rapidly changing acoustic scenes when navigating through their natural environments (Schnitzler et al., 2003; Moss and Surlykke, 2010; Madsen et al., 2013). However, most studies of acoustic gaze changes in biosonars tend to ignore such confounding variables by assuming that the echolocating animal mainly adjusts to the target of experimental interest. To disentangle potential context-dependent biosonar adjustments from target-range-dependent adjustments, we designed a study in which two porpoises solved the same target approach task in two different echoic environments, and we show that biosonar adjustments differed markedly between those two environments.

Interclick interval adjustments and acoustic gaze

Toothed whales generally use ICIs that are longer than the TWTT to targets of interest (Au, 1993), i.e. target echoes are received prior to a subsequent click emission, which presumably serves to avoid range ambiguity problems (Kadane and Penner, 1983; Surlykke et al., 2014). The two porpoises in this study always clicked at longer ICIs than the TWTT in both environments (Fig. 4). In the pool, the porpoises clicked at relatively high rates and decreased ICIs slowly from approach start until ~ 2 m target range, whereas much longer ICIs and practically no adjustments were used over the same distance in the net pen (Fig. 4A,B). Therefore, the transition into the buzz phase that occurred when porpoises were closer than ~ 2 m from the target involved a three times steeper range-dependent ICI adjustment in the net pen (Fig. 4A,B, Table S2). The observed behaviour suggests that in the net pen, the porpoises were

Table 1. Summary of harbour porpoise approaches in the pool and net pen

	Freja		Sif	
	Pool	Net pen	Pool	Net pen
First localisation range (m)	7.5 \pm 0.5	8.0 \pm 0.3	7.6 \pm 0.3	8.0 \pm 0.2
Approach duration (s)	7.3 \pm 1.3	8.2 \pm 1.0	12.1 \pm 1.7	8.0 \pm 0.7
Approach clicks	193 \pm 41	189 \pm 31	378 \pm 58	197 \pm 31
Approach clicks, 10 dB SNR	89 \pm 24	82 \pm 26	175 \pm 35	128 \pm 30
Buzz clicks	854 \pm 162	1002 \pm 173	767 \pm 181	865 \pm 142
Buzz clicks, 10 dB SNR	648 \pm 265	965 \pm 191	418 \pm 223	687 \pm 163
Buzz duration (s)	2.7 \pm 0.5	2.6 \pm 0.5	2.9 \pm 0.9	2.4 \pm 0.4
Buzz onset range (m)	0.8 \pm 0.2	0.6 \pm 0.1	0.4 \pm 0.1	0.5 \pm 0.2
Number of trials	32	34	33	36

Values are reported as trial means \pm s.d. for each porpoise in each environment. Click counts are reported for all approach and buzz clicks detected at the target and as the number of those clicks exceeding a signal-to-noise ratio (SNR) of 10 dB.

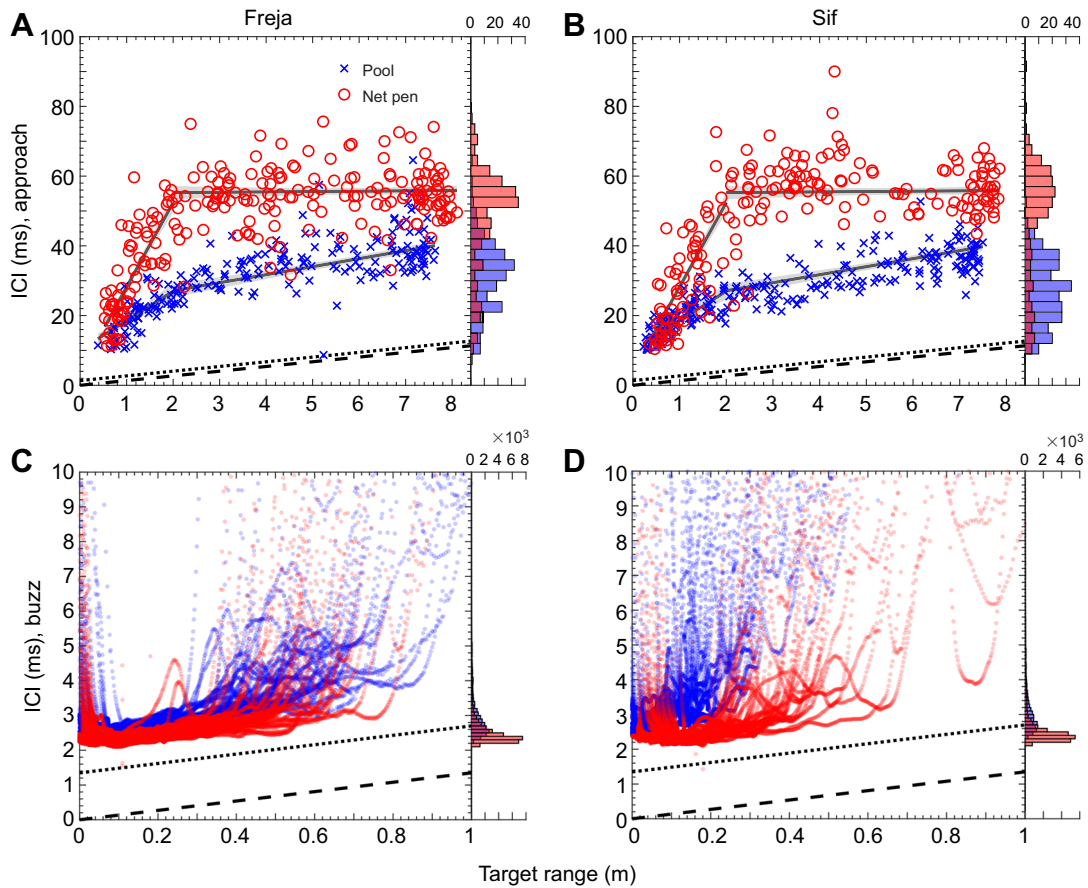


Fig. 4. Range-dependent ICI adjustments during approach and buzz phase. (A) ICIs for on-axis approach clicks for Freja in the pool ($N=212$) and net pen ($N=217$). The predicted mean ICIs are shown as solid lines (95% CI in grey) for the ICI models for on-axis clicks localised beyond and within the 2 m target range (Tables S1 and S2). The two-way travel time (TWTT) to the target is shown by the dashed line and the TWTT to the wall 1 m behind the target in the pool is indicated by the dotted line. Histogram (3 ms bin width) on the right side shows ICI distributions for on-axis clicks in the pool (blue) and net pen (red). (B) ICIs for on-axis approach clicks for Sif in the pool ($N=252$) and net pen ($N=188$) with illustrations as in A. (C) ICIs for all buzz clicks produced up to the time of target contact for Freja in the pool (blue, $N=22,227$) and net pen (red, $N=31,532$) with TWTT lines as in A. Histogram bin width is 0.3 ms. (D) ICIs for all buzz clicks produced up to the time of target contact for Sif in the pool (blue, $N=12,712$) and net pen (red, $N=24,709$). Overlapping data in all histograms are dark red.

echolocating using an acoustic gaze that could also accommodate the returning echo streams from objects more distant than the target to avoid ambiguous range estimates from those objects (Verfuß

et al., 2005). For ICIs between 40 and 70 ms and assuming a sound speed of 1500 m s^{-1} , an echo will return for objects out to 30–53 m range before the next click is produced and hence for target ranges

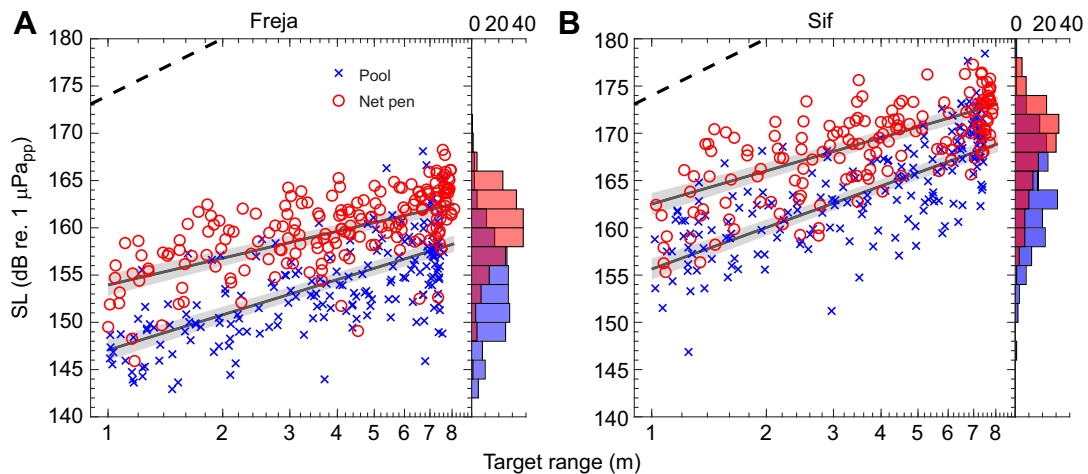


Fig. 5. Range-dependent SL adjustments of on-axis clicks. (A) On-axis SL for Freja during approaches in the pool (blue, $N=193$) and net pen (red, $N=190$). The predicted mean SL in each environment is shown as a solid line (95% CI in grey, Table S3). Histogram bin width is 2 dB. The peak clipping level plus $20\log_{10}(R)$ is indicated by the dashed line as in Fig. 3. (B) On-axis SL for Sif in the pool ($N=192$) and net pen (156) with illustrations as in A. Overlapping data in all histograms are dark red.

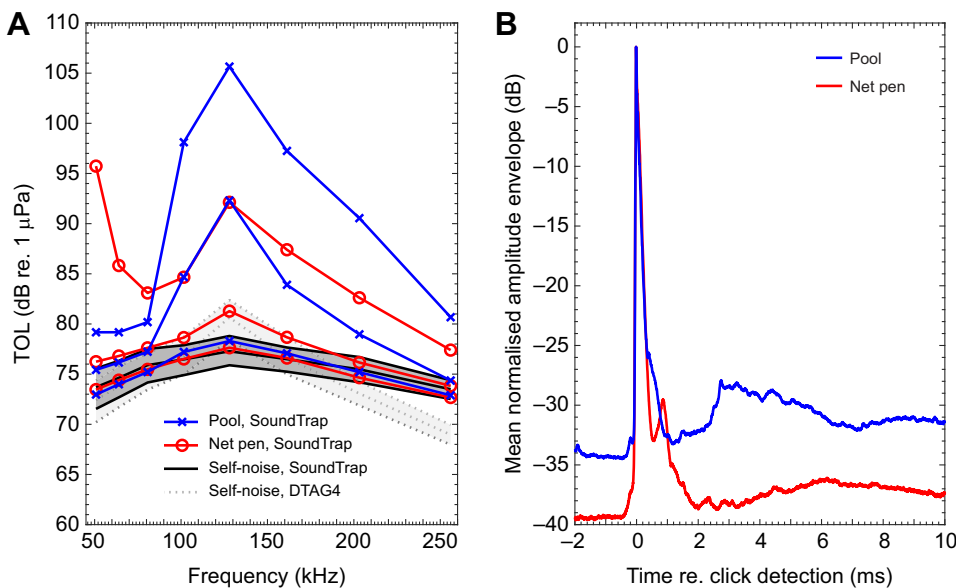


Fig. 6. Background noise, self-noise and reverberation. (A) Third octave level (TOL) estimates from the target recordings during target approaches in the pool (blue lines) and net pen (red lines) shown together with the estimated self-noise profile for the SoundTrap (black lines, dark grey area) and DTAG-4 (grey dotted lines, light grey area). For each category, the lower, middle and upper trace correspond to the 5th, 50th and 95th percentiles of the TOL noise estimates. (B) Average differences in reverberation following approach clicks (ICI > 10 ms), as recorded from the porpoise perspective on the DTAG-4, illustrated here as the mean normalised amplitude envelope around the time of click production in the pool and net pen. The click amplitude peak is set to 0 dB for both pool and net pen. A 50 kHz Butterworth high-pass filter (four poles) was applied to each signal waveform before envelope computation and averaging.

above ~2 m the porpoises used ICIs long enough to receive the direct echoes from all objects ensonified within the net pen prior to emitting a new click. In the pool, there were few other objects to focus on apart from the target and the pool wall, and the distances to other objects were all short relative to the target range, which likely explain the stronger relationship between ICI and target range in this environment. It seems that porpoises have considerable flexibility in the way that click rates can be adjusted when homing in on just a single target, which has also been seen in prey capture studies of porpoises (DeRuiter et al., 2009) and other toothed whale species (Wisniewska et al., 2014). The approach phase results of this study (Fig. 4A,B) does therefore not support the concept of a somewhat fixed average lag time (Au, 1993), i.e. a fixed delay from target echo reception to next click emission. Biosonar inspection ranges have previously been estimated for toothed whales based on the ICI (Penner, 1988; Thomas and Turl, 1990) or ICI minus an assumed fixed lag time (Akamatsu et al., 2005). However, there is increasing evidence that lag time may not be fixed to target range (Wisniewska et al., 2012; Madsen et al., 2013; Ladegaard et al., 2019) and also observations of little to no range-dependent ICI adjustment over large parts of target approaches (DeRuiter et al., 2009; Verfuß et al., 2009) (Fig. 4A,B). Therefore, ICIs do not lend themselves to straightforward range estimation of main targets, although they might still serve as a useful proxy for the maximum biosonar inspection range. Further, the fact that biosonar clicking rates may change depending on the environment for the same species (Simard et al., 2010; Madsen et al., 2013) (Fig. 4) suggests that ICI distributions may be a weak parameter for species discrimination in passive acoustic monitoring studies (Baumann-Pickering et al., 2010).

Buzzing behaviour modified by context

Close-up inspection and interception of targets involves a buzz phase of ultra-high clicking rates with ICI adjustments closely related to target range (Wisniewska et al., 2014), although the relationship may depend on echoic features of inspected targets (Johnson et al., 2008). Here, we show that for the same target, the porpoises clicked at ICIs that were longer in the pool than the net pen, with a 14% difference in buzz ICI mode for Freja and 24% for Sif (Fig. 4C,D). From this, we conclude that the different settings provoked a change in the buzz phase biosonar behaviour, but

we cannot provide a definitive explanation for this change. The porpoises may have sought to accommodate the delayed echo from a strong reflector, the pool wall, in their buzz ICIs to avoid potential range ambiguity problems associated with clicking too fast to receive the wall echo between clicks. However, if the porpoises used similar buzz ICIs in the pool as they used in the net pen, the direct reflection returning from the pool wall 1 m behind the target would still have returned before a new click was produced (Fig. 4C,D). Therefore, the use of longer buzz ICIs in the pool is seemingly not explained by some need to wait for the pool wall echo before the next click is emitted. However, if there is an adjustment above a minimum lag time in the buzz phase that does not solely depend on target echo arrivals, it may be that longer buzz ICIs were used in the pool to maintain a minimum lag time above ~1 ms relative to the pool wall echoes (Fig. 4C,D).

The buzz ICIs used by Amazon river dolphins, which inhabit shallow rivers and seasonally flooded forests, are several times longer than seen in other similar-sized toothed whales, and might be an adaptation for echolocation in reverberant environments (Ladegaard et al., 2017). The combination of relatively short approach ICIs and longer buzz ICIs used by the porpoises in the pool compared with the net pen thus resembles the adjustments used by Amazon river dolphins during prey interception (Ladegaard et al., 2017) and also preliminary data from a porpoise capturing fish in the presence or absence of a clutter screen behind the fish (Miller, 2010). This suggests that the differences in ICI adjustments between the two environments were made in response to differences in clutter and reverberation levels.

Biosonar output levels

Porpoises and dolphins echolocating in open water have been shown to produce much higher click SLs compared with conspecifics in confined enclosures (Au et al., 1974; Villadsgaard et al., 2007; Wahlberg et al., 2011). However, it is unclear whether the observed SL differences are mainly the result of different ranges to targets of interest between studies, because small toothed whales often use range-dependent SL adjustments, and target ranges are generally shorter in confined environments than in open water. Here, we show that when two porpoises solved the same approach task over the same approach distance in a pool and a net pen, the two porpoises used 4–7 dB higher SLs in the pen compared with the

pool (Fig. 5, Table S3). The similar change in SL adjustment employed by the two porpoises between environments might seem surprising given the 9–11 dB difference in average SL between individuals. Sif's use of higher SLs might have been the result of poorer hearing compared with Freja, as Sif was treated with the ototoxic antibiotic amikacin ~10 years prior to this study (Wahlberg et al., 2017). It has been suggested that sensation level for porpoises is proportional to the level above the hearing threshold (Tougaard et al., 2015), so if Sif had a higher hearing threshold at high frequencies, she might have used higher SLs to achieve echo sensation levels similar to those of Freja, which would explain why they made similar relative adjustments between environments. The overall adjustments of on-axis SL with target range across animals and environments was found to be $10-15\log_{10}(R)$, which is an estimate unlikely to be biased by $20\log_{10}(R)$ filtering that can result from clipping and detection threshold limitations (Fig. 3; Ladegaard et al., 2017). This resembles previous observations of $\sim 15\log_{10}(R)$ adjustments (Beedholm and Miller, 2007), but is lower than other findings of $17-22\log_{10}(R)$ (Atem et al., 2009) and $21-23\log_{10}(R)$ (Wisniewska et al., 2012). Porpoises therefore seem to operate their biosonar using varying degrees of dynamic output adjustments as a function of range to targets.

The low background noise levels (below the self-noise of the SoundTrap; Fig. 6A) in both environments suggest that the porpoises were likely operating under reverberation-limited sonar conditions defined by their own click production rather than noise-limited conditions. If reverberation-limited conditions applied, the use of lower click SL in the pool should then bear no cost in terms of the echo-to-reverberation ratio achievable in that environment. If so, lower SLs would in fact have the benefit of decreasing the duration that reverberations lasted in the environment following each click, so if the porpoises adjusted the click rate to allow reverberation to fall below some threshold level in between clicks, then lower SLs will allow the use of higher sampling rates, as was also observed for the pool environment. Lower SLs may further lead to less forward masking of the outgoing click on the hearing side and therefore provide better hearing thresholds in the first 30 ms after click emission (Schröder et al., 2017). Whether forward masking or reverberation conditions set the detection threshold at short ranges in the pool remains an open question. Based on our results, we propose that co-dependent mechanisms involving SL, forward masking, reverberation and ICI drive the different implemented acoustic gazes in the two environments.

Conclusions

Here, we have shown that two harbour porpoises engaged in active target approaches use different dynamic biosonar adjustments when the same target approach task is performed in two different environments. In a more reverberant PVC-lined pool, the porpoises produced clicks at low SLs and clicked at shorter ICIs during the approach phase than in the semi-natural net pen, whereas the buzz ICIs in the pool were slightly longer. We posit that the different biosonar adjustments were mainly due to different reverberant properties of the two environments as they both had very low noise levels.

This study demonstrates that harbour porpoises adjust their biosonar depending on the context in which they are echolocating, implying that SL and ICI may not be a direct indicator of target range. Context-dependent biosonar adjustments add another layer of complexity to understanding how toothed whales modify their biosonar behaviour as they close in on targets in addition to the range-dependent biosonar adjustments demonstrated for several

toothed whale species. The context-dependent implementation of ICI and SL for the same target range also has implications for passive acoustic monitoring both in terms of species identification and detection ranges. Flexible biosonar operation has likely been a major evolutionary driver towards establishing toothed whales as apex predators in marine and riverine habitats across the planet.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.L., P.T.M.; Methodology: M.L., P.T.M.; Software: M.L.; Validation: M.L., P.T.M.; Formal analysis: M.L.; Investigation: M.L.; Resources: P.T.M.; Data curation: M.L.; Writing - original draft: M.L., P.T.M.; Writing - review & editing: M.L., P.T.M.; Visualization: M.L.; Supervision: P.T.M.; Project administration: M.L., P.T.M.; Funding acquisition: P.T.M.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.206169.supplemental>

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Supplementary Information

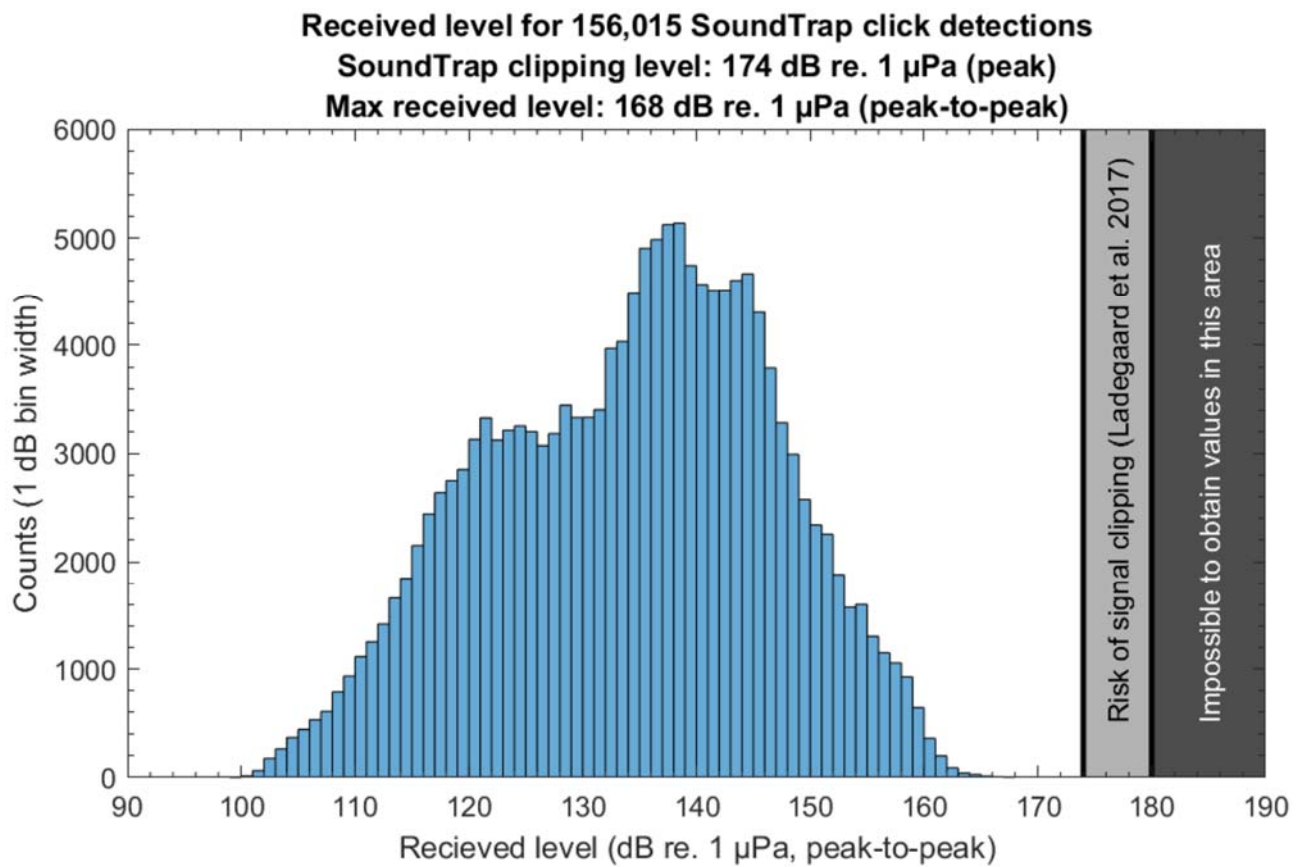


Fig. S1 Received level distribution for clicks detected at the target in relation to clipping level. Histogram showing the distribution of received levels for the 156,015 clicks detected in the recordings of the target-mounted SoundTrap. The SoundTrap's peak clipping level of 174 dB re. 1 μ Pa and the maximum peak-to-peak value of 180 dB re. 1 μ Pa that could be recorded are indicated as black vertical lines. Please see Ladegaard et al. (2017) for further discussion on signal clipping.

Table S1 Generalised linear mixed-effects model of ICI (ms) for 572 approach clicks recorded on-axis at target ranges exceeding 2 m. In this model, the standard condition for which the intercept is computed is porpoise Freja performing target approaches in the pool.

Model information:

Number of observations	572
Fixed effects coefficients	4
Random effects coefficients	270
Covariance parameters	4
Distribution	Normal
Link	Identity
FitMethod	Laplace

Model:

ICI ~ 1 + range + enclosure type + range:enclosure type + (1 + range | trial)

Model fit statistics:

AIC	LogLikelihood	Deviance
3839.7	-1911.9	3823.7

Fixed effects coefficients (95% CIs):

Name	Estimate	SE	t-statistic	df	p-value	Lower	Upper
Intercept	22.5	1.4	15.7	568	2.7*10 ⁻⁴⁶	19.7	25.4
net pen	32.6	2.0	16.5	568	3.0*10 ⁻⁵⁰	28.7	36.4
range	2.3	0.23	9.9	568	2.3*10 ⁻²¹	1.8	2.8
range:net pen	-2.2	0.32	-6.9	568	1.4 *10 ⁻¹¹	-2.8	-1.6

Random effects covariance parameters:

Name1	Name2	Type	Estimate
Intercept	Intercept	std	6.57
R	Intercept	corr	-1
R	R	std	0.75

Error

Name	Estimate
sqrt(Dispersion)	6.33

Table S2 Generalised linear mixed-effects model of ICI (ms) for 297 approach clicks recorded on-axis at target ranges less than 2 m. In this model, the standard condition for which the intercept is computed is porpoise Freja performing target approaches in the pool.

Model information:

Number of observations	297
Fixed effects coefficients	4
Random effects coefficients	260
Covariance parameters	4
Distribution	Normal
Link	Identity
FitMethod	Laplace

Model:

ICI ~ 1 + range + enclosure type + range:enclosure type + (1 + range | trial)

Model fit statistics:

AIC	LogLikelihood	Deviance
1951.3	1980.8	1935.3

Fixed effects coefficients (95% CIs):

Name	Estimate	SE	t-statistic	df	p-value	Lower	Upper
Intercept	10.1	1.1	8.9	293	4.5*10 ⁻¹⁷	7.9	12.4
net pen	-6.1	1.9	-3.3	293	1.3*10 ⁻³	-9.8	-2.4
range	8.4	1.0	8.1	293	1.3*10 ⁻¹⁴	6.4	10.5
range:net pen	15.8	1.7	9.3	293	3.5 *10 ⁻¹⁸	12.4	19.1

Random effects covariance parameters:

Name1	Name2	Type	Estimate
Intercept	Intercept	std	0.55
R	Intercept	corr	-1
R	R	std	2.65

Error

Name	Estimate
sqrt(Dispersion)	5.81

Table S3 Generalised linear mixed-effects model of SL (dB re. 1 μ Pa, pp) for 731 approach clicks recorded on-axis at target ranges, R, exceeding 1 m. In this model, the standard condition for which the intercept is computed is porpoise Freja performing target approaches in the pool. The intercept *p*-value of $<2.2 \times 10^{-308}$ means that the value is lower than the smallest positive normalised floating-point number in IEEE double precision.

Model information:							
Number of observations	731						
Fixed effects coefficients	6						
Random effects coefficients	270						
Covariance parameters	4						
Distribution	Normal						
Link	Identity						
FitMethod	Laplace						
Model:							
SL _{pp} ~ 1 + log ₁₀ (R) + enclosure type + porpoise + log ₁₀ (R):enclosure type + log ₁₀ (R):porpoise + (1 + log ₁₀ (R) trial)							
Model fit statistics:							
AIC	LogLikelihood	Deviance					
3679.7	-1829.8	3659.7					
Fixed effects coefficients (95% CIs):							
Name	Estimate	SE	t-statistic	df	p-value	Lower	Upper
Intercept	147.1	0.58	254.7	725	$<2.2 \times 10^{-308}$	145.9	148.2
log ₁₀ (R)	12.4	0.74	16.7	725	2.0×10^{-53}	10.9	13.8
porpoise Sif	8.6	0.67	12.7	725	1.0×10^{-33}	7.2	9.9
net pen	6.9	0.67	10.2	725	5.4×10^{-23}	5.6	8.2
log ₁₀ (R):net pen	-2.9	0.87	-3.4	725	8.0×10^{-4}	-4.6	-1.2
log ₁₀ (R):porpoise Sif	2.2	0.87	2.6	725	0.011	0.52	3.9
Random effects covariance parameters:							
Name1	Name2	Type	Estimate				
Intercept	Intercept	std	2.96				
R	Intercept	corr	-0.64				
R	R	std	3.03				
Error							
Name	Estimate						
sqrt(Dispersion)	2.41						