

Diving apart together: Call propagation in diving long-finned pilot whales

Annebelle C.M. Kok^a, Lisette van Kolfshoten^{ab}, James A. Campbell^a, Alexander M. von Benda-Beckmann^c, Patrick J. O. Miller^d, Hans Slabbekoorn^a and Fleur Visser^{e,f,g}

a: Institute of Biology, Leiden University, the Netherlands

b: Naturalis Biodiversity Center, Leiden, the Netherlands

c: Netherlands Organisation for Applied Scientific Research (TNO), The Hague, the Netherlands

d: Sea Mammal Research Unit, School of Biology, University of St Andrews, United Kingdom

e: Department of Freshwater and Marine Ecology, IBED, University of Amsterdam, the Netherlands

f: Department of Coastal Systems, NIOZ and Utrecht University, the Netherlands

g: Kelp Marine Research, Hoorn, The Netherlands

Corresponding author: Annebelle C. M. Kok

e-mail: a.c.m.kok@biology.leidenuniv.nl

Telephone: +31 (0)71 527 5045

Postal address: IBL, Sylviusweg 72, 2333 BE Leiden, the Netherlands

Correspondence co-authors: lisette.vankolfschoten@ebc.uu.se;
jamesadamcampbell@gmail.com; sander.vonbendabeckmann@tno.nl; pm29@st-andrews.ac.uk; h.w.slabbekoorn@biology.leidenuniv.nl; fvisser@kelpmarineresearch.com

ABSTRACT

Group-living animals must communicate to stay in contact. In long-finned pilot whales, there is a trade-off between the benefits of foraging individually at depth and the formation of tight social groups at the surface. Using theoretical modelling and empirical data of tagged pairs within a group, we examined the potential of pilot whale social calls to reach dispersed group-members during foraging periods. Both theoretical predictions and empirical data of tag pairs showed a potential for communication between diving and non-diving group members over separation distances up to at least 385 m (empirical) and 1800 m (theoretical). These distances are at or exceeding pilot whale dive depths recorded across populations. Call characteristics and environmental characteristics were analysed to investigate determinants of call detectability. Longer calls with a higher sound pressure level (SPL) that were received in a quieter environment were more often detected than their shorter, lower SPL counterparts within a noisier environment. In a noisier environment, calls were louder and had a lower peak frequency, indicating mechanisms for coping with varying conditions. However, the vulnerability of pilot whales to anthropogenic noise is still of concern as the ability to cope with increasing background noise may be limited. Our study shows that combining propagation modelling and actual tag recordings provides new insights into the communicative potential for social calls in orientation and reunion with group members for deep-diving pilot whales.

INTRODUCTION

Communication among members of social groups is an essential element of their social behaviour, allowing them to share information, find mates, defend territories, recognise offspring, and many other life functions (Kondo and Watanabe, 2009; Ladich and Winkler, 2017; Snijders and Naguib, 2017). Group living can provide safety from predators (Lehtonen and Jaatinen, 2016), enhance foraging efficiency (e.g. local enhancement, group-hunting: Thiebault et al. 2014; Herbert-Read et al. 2016) and create opportunities for reproduction (e.g. aggregating and lekking, social breeding: Ryder et al. 2009). However, group-living requires a way of communicating that allows associated animals to maintain or re-establish contact, particularly for wide-ranging animals. A powerful sensory modality to keep track of group members is the hearing of each other's sounds, especially if distances between individuals become greater or visibility is limited (Kondo and Watanabe, 2009).

Odontocetes, or toothed whales, are sound-oriented animals that typically live for long periods in the same social groups. Group-stability ranges from short-term, fission-fusion societies in some species to long-term, stable matrilineal groups in others (Connor et al., 1998; Hartman et al., 2008; Ottensmeyer and Whitehead, 2003; Whitehead et al., 1991). As light attenuates rapidly in water, odontocetes predominantly use sound for orientation, foraging, and social communication. Odontocetes use social calls for a wide variety of functions, including recognition and relocation of close associates (Cantor et al., 2015; Deecke et al., 2010). Bottlenose dolphins (*Tursiops truncatus*), for example, use individual-specific vocalisations to identify and relocate specific group members (Janik and Slater, 1998).

Interestingly, some deep-diving odontocete species that live in the most stable groups, such as sperm whales and pilot whales (*Globicephala spp.*) do not seem to coordinate hunting effort but typically catch prey individually at depth (Whitehead et al. 1998; Ottensmeyer and Whitehead 2003; Watwood et al. 2006; Visser et al. 2014; but see Aoki et al. 2013 for an exception). Foraging sperm whales, for example, form rank formations, potentially to avoid targeting the same prey (Whitehead, 1989). Foraging at depth can therefore lead to spatial separation between group members, which must be relocated when individuals return to the sea surface. Acoustic relocation may be possible through acoustic tracking of echolocation cues from group members and/or directed acoustic signalling through social calls (Parks et al., 2014). Long-finned pilot whales produce more social calls during foraging bouts, when individuals are dispersed, than during non-foraging periods when individuals are several body lengths apart (Visser et al., 2017). However, it is still unknown if their social calls during foraging have the capacity to effectively transmit information between deep-diving and shallow-diving or surfacing group members, or which call features facilitate communication over larger distances.

Besides distance, call detectability can be influenced by the ambient noise level at the receiver and by call characteristics (Brumm and Slabbekoorn, 2005; Wiley, 2013). Both natural and anthropogenic sources can increase the ambient noise level, leading to a reduction in the range of call detectability (David, 2006; Janik, 2000; Jensen et al., 2009). Call characteristics that may enhance detection include long duration, high call amplitude, a signal bandwidth that does not overlap with ambient noise, a caller orientation directed to the receiver and low peak frequency (Brumm and Slabbekoorn, 2005). These can be tuned by the producer and thereby adapted to situations with poor conditions for call detection. For example, in response to anthropogenic sound, killer whales produced longer calls than in low ambient noise conditions, potentially facilitating detection (Foote et al., 2004).

Propagation of marine mammal calls has mostly been studied in horizontal contexts, because species living in shallow waters are more easily studied and are likely to be limited by horizontal rather than vertical propagation distance (David, 2006; Janik, 2000; Miller, 2006). However, propagation between horizontally and vertically dispersed animals is not easy to compare. Call propagation in horizontal contexts can be heavily influenced by the sound speed profile and boundary effects from the water surface and the bottom in shallow waters, which creates multiple acoustic pathways (Marsh and Schulkin, 1962). These boundary effects are less complex for propagation between vertically dispersed animals, because of the steep angles at which the sound travels through the water column and interacts with the surface boundary. At (near) vertical angles, the sound undergoes little refraction or reflection when it crosses thermoclines, thus keeping only one acoustic pathway (Ainslie, 2010). Furthermore, if the horizontal distance between caller and receiver is within 1-3 times the water depth, the direct pathway of the sound will be dominant, because of the smallest relative distance compared to other pathways.

Call propagation can be determined empirically, by measuring a call at the producer and at the receiver (Piza and Sandoval, 2016), or theoretically, by calculating transmission loss of the call (Jensen et al., 2012; Mercado III and Frazer, 1999; Miller, 2006). Up till now, studies on marine mammal call propagation relied on theoretical modelling, because of the difficulties involved in measuring calls at both the producer and receiver at larger spatial scales on free-ranging whales in the marine environment. Here, we overcome this limitation by applying suction-cup attached sensors, which record sound, movement and depth, on multiple individuals in one group. (Palmer et al., 2017; Pasquaretta et al., 2015; Snijders et al., 2017).

We examined relocation of close associates through acoustic communication and reception of social calls in a deep-diving odontocete: the long-finned pilot whale (*Globicephala melas*, Traill 1809). Using a combined theoretical and empirical approach, we tested 1) whether pilot whales have the theoretical potential to communicate when vertically dispersed, 2) whether calls produced by or close to a tagged whale were detectable in recordings of tags attached to a potential receiver and 3) how call detectability was influenced by call characteristics and the acoustic environment at the receiving whale. We hypothesize that pilot whales have evolved social calls with transmission properties adapted for acoustic communication over spatial scales that allow for communication and reunion with dispersed group members during and following foraging dives. Environmental noise could hamper this potentially critical relocation process, but its effect might also be mitigated to some extent by potential signal adjustments of the sound producing animals.

MATERIALS AND METHODS

Theoretical call propagation and detection

To explore the theoretical detection range of deep diving pilot whale social calls, we adopted a propagation model in RStudio (version 3.5.2) to simulate propagation between vertically dispersed animals in deep waters, based on the assumption of spherical spreading (Urick, 1983):

$$RL = SL - 20 \log_{10}(R/1m) \text{ dB} - \alpha R \quad (1)$$

Here, RL = received level (dB re 1 μPa), SL = source level (dB re 1 $\mu\text{Pa}\cdot\text{m}$), R = distance between producer and receiver (m) and α = frequency-specific attenuation (Ainslie and McColm, 1998) (dB/m). Boundary effects such as Lloyd's mirror effect were ignored, because we focused on transmission between vertically dispersed animals, in which surface reflections will be very limited. In our specific dataset, the measured sound speed at 50 m water depth and 200 m water depth showed little variation (1472 and 1487 m/s at 50 and 200 m, respectively, (Miller et al., 2011)). This meant that the angle at which boundary effects could occur was ~ 5 degrees from the horizontal, indicating a negligible effect of refraction on the sound propagation. Furthermore, reflected waves of different frequencies will have alternating interference patterns, leading to an overall neutral effect on signal strength of a broadband signal (Jensen et al., 2011). Pilot whale social calls are typically composed of frequency modulated tonal calls with harmonics, also termed whistles (Visser et al., 2017). Individuals therefore can potentially perceive calls through multiple frequency channels spread over a wide bandwidth (3-9 kHz as found by Rendell et al. 1999).

Whether an animal detects a call depends on whether the received level is above the hearing threshold, the signal-to-noise ratio in the presence of a masking sound, and the orientation of the animal relative to the masker (Erbe et al., 2016). Detection of tonal signals is not yet possible when signal and noise at the same frequency are equal in sound level. Detection of tonal sounds only occurs when there is a slightly higher level of the signal compared to the noise (Moore, 2013). This minimal signal-to-noise ratio at which an animal can detect a sound, the critical ratio (CR; Fletcher 1940; Erbe et al. 2016) is frequency dependent. It is defined as the minimal level difference in sound pressure (SPL) of the signal and the level of the power spectral density of the root-mean-square sound pressure (PSD) of the masking noise that is required for hearing. Therefore, the modelled detection per frequency was based on received level, critical ratio and ambient noise level.

As critical ratios for long-finned pilot whales have not been measured, the model was based on average critical ratios from other delphinids, at 18, 23 and 28 dB re 1 Hz for 1, 5 and 20 kHz signals respectively (Erbe et al., 2016). Ambient noise levels were taken from the acoustic recordings of the suction-cup attached archival tags (DTAG-2, SOUNDTAG lab, University of St Andrews, United Kingdom), used on the tagged pilot whales for the empirical data collection. The PSD of ambient noise was measured within one-third octave frequency bands (10-base, also referred to as *decidecade*). The average PSD was computed by dividing the one-third octave band SPL by the frequency bandwidth in Hz over which they were measured, corrected for flow noise by taking the level of correlated noise as the ambient noise level (von Benda-Beckmann et al. 2016). After comparison of the mean and median of the PSD measurements, we took median and 25 and 75 percentiles to describe the general variation in the noise levels, because the median was least sensitive for outliers in the data. At 20 kHz, ambient noise levels could not be reliably measured due to high levels of system noise in the deployed tags. Instead, a typical ambient noise level at 20 kHz for sea state 2 (highest sea state in which data were collected) was used (Wenz, 1962).

Calls were considered to be detectable by the pilot whales when the received level (RL) within a frequency band exceeded the level of ambient noise mean spectral density plus the critical ratio. When the masking sound source is at a different direction than the calling animal, spatial masking release can reduce the degree of masking (e.g. Erbe et al. 2016). Since the focus of this study was on relatively low frequency calls with limited masking release (Au and Moore, 1984; Brumm and Slabbekoorn, 2005), we did not control for masking release, which provided a conservative measure of the detectability of the calls.

Long-finned pilot whales produce social calls with varying peak frequencies (frequency with highest SPL; Taruski 1979; Visser et al. 2017). The main range of peak frequencies was determined from an empirical dataset. The minimum (1 kHz), maximum (20 kHz) and mean peak frequency (5 kHz) were used to model call detectability. The used source levels were based on levels found for short-finned pilot whales, 145-160 dB re 1 $\mu\text{Pa}\cdot\text{m}$ (Turl and Fish, 1976), which are in the range of reported source levels for other odontocetes (Janik, 2000; Miller, 2006). The source levels were verified by calculating source levels from a subset of calls collected from one of the tag pairs, for which absolute distance between the tag pair could be calculated. The 1/3-octave band SPL at the peak frequency was back-propagated from the receiver, assuming spherical spreading and accounting for frequency-dependent absorption (likely to have a small effect at these distances). Mean (s.d.) source levels found were 146.5 (9.5) dB re 1 $\mu\text{Pa}^2\text{m}^2$, which fell within the range of earlier reported source levels (Fig. 1).

Empirical call propagation and detection

Ethical statement

All research activities were carried out under permits issued by the Norwegian Animal Research Authority (permit no. S2011/38782), in compliance with ethical and local use of animals in experimentation. The research protocol was approved by the University of St Andrews Animal Welfare and Ethics Committee and Woods Hole Oceanographic Institution's Animal Care and Use Committee.

Data collection

Pilot whale social call and dive data were collected using DTAGs in 2009-2010, off Lofoten, Norway, as part of a larger project to study the effects of naval sonar on cetaceans (3S project) (Miller et al., 2012). All data used in this study were recorded during baseline pre-exposure periods. Tagged whale pairs were always two individuals from the same group (Visser et al., 2014). Dive depth was sampled every second. Acoustic recording sampling frequency was 192 kHz, except for tag 138a (96 kHz), with 16-bit resolution and sensitivity of -189 ± 3 dB (mean \pm s.d.) (Johnson and Tyack, 2003). The acoustic tags were calibrated in an anechoic tank prior to the experiments (Wensveen, 2016).

Call selection

Calls were selected using a step-wise procedure. First, acoustic recordings were analysed by two independent observers who visually marked high amplitude calls from the recordings (amplitude colouration close to the maximum of the fixed colour scale and higher on the scale than most other sounds). All recordings were analysed with identical spectrogram settings: colour scale limits = $-90 - 0$ dB; FFT block size = 512; Hamming window; overlap = 256; display length = 15 s. High amplitude calls were considered to be calls produced by the tagged whale or an individual in its close vicinity (Alves et al., 2014).

Second, a subset was created with calls with a signal-to-noise ratio (SNR) of ≥ 10 dB at the producer to minimize measurement errors due to the ambient noise (following Jensen et al. 2011). The SNR level was calculated as call-SPL minus total ambient noise-SPL (uncorrected for flow noise, since all noise could influence the acoustic measurements) at the one-third octave band

around the peak frequency of the call. To determine the peak frequency of the call, the PSD was measured for one-third octave frequency bands. Peak frequencies were identified in the spectrogram as the frequencies with maximum amplitude in the PSD of the pulse using the entire pulse duration as integration time. The peak third octave was also used to measure the PSD in 200 ms of ambient noise within 4 s before or after a call (the ambient noise section). The period of 200 ms concurs with the typical aural integration time of marine mammals (Erbe et al., 2016; Kastelein et al., 2010).

Call detection

Acoustic recordings of paired tags were time-synchronised, initially by using the internal clock of each tag. Second, we corrected for clock-drift by averaging travel times of clicks produced on tag A and received on tag B, and for near simultaneously produced clicks on tag B and received on tag A (DTAG toolbox, Johnson 2005). Clock-drift was then determined as the time-difference from the mean travel time. Clicks produced by the tagged whale were determined from the angle of arrival of the click on the tag, calculated from the difference in time of arrival between the two tag hydrophones. Since one of the tag-pairs with dual-hydrophone tags did not have simultaneous clicking, the precise clock-drift could only be determined for one out of three tag pairs (clock drift for tag-pair 137: 0.268-0.280 s). For the other tag pairs, time-synchronisation was less accurate, but still accurate enough (error in order of milliseconds) to link produced and received calls.

Detectability of the selected calls of one tag on the other tag was scored visually per call (Fig. 2). A call was considered detected if the call contour could be reliably identified on the spectrogram of the receiving tag. Harmonics did not have to be visible for reliable identification, but often were. Calls that were produced while the receiver whale was surfacing were excluded, because of the high level of flow noise and surface splashes that typically coincide with the surfacing event. Detectability was scored as 1 (detectable) or 0 (undetectable). As calls were often produced in distinct sequences, the position of the produced call relative to other calls was used to check whether no detectable call was missed in the analysis.

Noise filtering

Ambient noise sections and calls were filtered to exclude echolocation clicks using a custom-built script (Supplements; Miller et al. 2012). This procedure was undertaken post analysis of call detection, so that the acoustic background when detecting calls would be similar to the acoustic

background experienced by the whales. A click was detected when the rise between two subsequent root-mean-square levels (of a centred moving average with a window length of 2 and 10 ms, respectively) in the >30 kHz frequency range was ≥ 3 dB. Start and end of a click was found using a third RMS level, with a window length of 6 ms. Each detected click was then replaced with zeroes in the pressure wave form.

We explored the ambient noise in the 0-7 kHz frequency range for every section to investigate whether ambient noise recordings were dominated by flow noise (*sensu* von Benda-Beckmann et al. 2016). Flow noise can be measured by differentiating the noise that is similar between the two hydrophones of the tag (correlated noise) and noise that is not (uncorrelated noise). Only correlated noise is likely to be part of the ambient noise that surrounds the tagged animal, while uncorrelated noise is created by flow noise. Calls at the producer tag for which correlated noise was <6 dB greater than uncorrelated (flow) noise were considered to be influenced too much by flow noise and were removed from the dataset.

Call characteristics

For each selected call, we recorded production time, peak frequency, PSD at peak frequency, duration (all on producer tag), call arrival time at recorder tag and PSD of total ambient noise at producer and at receiver tag. Call duration was then taken as the 90% energy contour of the call, using a 1-50 kHz band-pass 4-pole Butterworth filter. For detected calls, ambient noise level at the receiver was measured within 4 s surrounding the received calls. For undetected calls, ambient noise level at the receiver was measured at the time the call would have been received. For detected calls, we calculated the signal excess above the ambient noise as:

$$SE = RL - DT \quad (2)$$

With

$$DT = NL - 10 \log_{10}(\text{bandwidth}) \text{ dB} + CR \quad (3)$$

Where SE = signal excess (dB), RL = received SPL of the call at peak frequency (dB re 1 μ Pa), DT = detection threshold (dB re 1 μ Pa), NL = total ambient noise level at receiver at call peak frequency (dB re 1 μ Pa), bandwidth = bandwidth of third octave level around peak frequency (Hz) and CR = critical ratio for peak frequency (dB re 1 Hz), taken from the average critical ratio found for odontocetes (Erbe et al., 2016).

Vertical distance

Vertical distance between the producer and receiver at the time of calling was determined by calculating the difference in depth between the two tagged animals at time of call production. To investigate whether vertical distance could serve as a proxy for absolute distance between two calling individuals, absolute distance was assessed for a subset of the calls. Distances were calculated from the travel time of detected calls (time the call travelled from the producer to the recorder tag). Because the time-synchronisation had to be very precise for this method, only calls from sections in which both individuals vocalised could be included in our analysis. Consequently, absolute distance measurements were only possible for one of the three tag pairs, due to the lack of a second hydrophone or not enough simultaneous calling or clicking for the other two pairs. Absolute distance measures for calls were verified by calculating absolute distance from temporally close clicks, which have a clear onset time and are therefore less prone to measurement error. All acoustic analyses were performed in Matlab R2017a (the Math Works Inc., USA) using the DTAG toolbox (Johnson 2005).

Statistics

The effect of call characteristics at the producer on call detectability at the receiver was modelled using a generalised linear model (GLM) with a binomial distribution. The full model included 1) call duration, 2) peak frequency, 3) ambient noise level at the receiver, 4) call PSD at peak frequency at the producer and 5) tag pair as explanatory variables, as well as all possible two-way interaction terms. It did not include distance, as analysis of vertical vs. absolute distance showed that these two were not correlated and absolute distance could only be measured for the periods when calls were produced and detected on both tags. The difference between absolute and vertical distance, where it could be assessed, ranged from 16 to 418 m (N = 33).

The relation between all three call characteristics that could be influenced by the producer (duration, peak frequency, call PSD at peak frequency) and two environmental variables (total ambient noise level at the producer and producer depth) was modelled using three separate linear models with each of the call characteristics as the response variable and the other call and environmental variables as explanatory variables, including all two-way interactions between the two explanatory call characteristics and depth. Peak frequency and depth were log-transformed to maintain the assumption of normality and modelled using a Gaussian distribution. Call duration

was modelled using a Gamma distribution. There was one outlier for peak frequency, which was excluded from the model.

Model selection was performed using dredging, based on lowest Akaike Information Criterion corrected for small sample sizes (AICc). All models that had AICcs within 2.0 points of the model with the lowest AICc were ranked based on lowest degrees of freedom (df). For all these models, R^2 values were calculated using the package *piecewiseSEM* (Lefcheck et al., 2018). The best model was the one with the lowest df. All statistics were performed in Rstudio 3.3.2. (R Core Team 2015).

RESULTS

Theoretical call propagation and detection

Our model revealed that the detection range for call components with a peak frequency at 1 kHz should be 230-1279 m. Higher frequency call components at 5 and 20 kHz would be detectable at minimally 1786 and 1414 m, respectively, with maximum ranges reaching beyond the modelled 2000 m. The maximum separation distance we could assess empirically (433 m) fell within these modelled ranges. Examination of click-based absolute distance measures that were close in time to calls showed an overestimation of 41-54 m for the call-based distance measures, caused by a larger measurement error in the call arrival-time. The empirically assessed maximum separation distance therefore became ~385 m.

The counterintuitive increase in detection range at higher frequencies was due to the markedly decreased ambient noise levels at 5 and 20 kHz compared to 1 kHz. Tones at 1 and 5 kHz showed no significant difference in propagation distance due to limited attenuation (α) at low frequencies (Fig. 3). Comparison of modelled ambient noise levels against the pilot whale audiogram indicated that all ambient noise levels were above unmasked hearing thresholds, hence detection was ambient noise limited. Ambient 1/3-octave band PSD levels at the receiver tag decreased with increasing frequency from 68-80 to 45-57 dB re 1 $\mu\text{Pa}^2/\text{Hz}$ (25-75% quantiles) at 1 and 5 kHz, respectively, and were estimated by a Wenz-curve noise level at 50 dB re 1 $\mu\text{Pa}^2/\text{Hz}$ at 20 kHz. Average ambient noise levels for 1 and 5 kHz (78 and 56 dB re 1 $\mu\text{Pa}^2/\text{Hz}$) were similar to reported ambient noise levels for sea state conditions at the time of measurement (sea state = 1-2 Beaufort; Wenz 1962). Since the critical ratios that were used increased with frequency, the net result was a similar average detection threshold for 5 and 20 kHz, and a much higher detection threshold for 1 kHz.

Empirical evidence for social call detectability

We analysed social call detection probability in three pairs of tagged pilot whales. Recording duration ranged from 17-170 minutes, with a mean (s.d.) of 53 (27) calls per tag (Table 1). Individuals dove to a maximum depth of 401 m. The maximum depth difference between the tag pairs was 400 m (mean-s.d. depth difference = 43-97 m, N = 315). Absolute distance for the subset of calls where it could be estimated, ranged from 60-385 m (mean-s.d. = 276-89 m N = 33). This was within the threshold detection range as predicted by the propagation model (1786 m), indicating that the tagged pairs remained within detection distance for at least part of the separation period. On average, 65% of calls produced by a tagged individual were detectable on the tag of the receiver (90% observer agreement). Calls that were detected on the receiver tag had a mean signal excess (*eq. (2)*) of 31 dB (range: 8-65 dB; Fig. S1). Detected calls had a lower peak frequency than undetected call (median 5 vs. 6 kHz) and were recorded at lower levels of ambient noise across the frequency range (Fig. 4)

Variation in call characteristics with context

Call detectability in the empirical dataset was influenced by peak frequency, duration, call PSD level at the producer and ambient noise PSD level at the receiver ($R^2 = 0.48$, $df = 13$; Table S1). Detected calls were significantly longer than undetected calls (estimate = -1.24; $p < 0.005$; Table 2) and had a slightly lower peak frequency ($p < 0.005$, estimate = 0.000108). Detected calls of pair 158 were also produced at higher call PSD level than undetected calls ($p < 0.05$; Fig. 5A-C). Furthermore, for detected calls, ambient noise PSD levels at the receiver side were significantly lower than for undetected calls, with a larger difference for pairs 138 and 158 than for pair 137 (Table 2; Fig. 5D).

Independent of detectability, call characteristics at the producer showed a number of interesting correlations, often dependent on environmental conditions. The best models of the call characteristics showed several correlations: longer calls were louder and the relationship between call duration and call PSD changed with call peak frequency (interaction $p < 0.05$; Fig. 6A, Table S1). Call characteristics were also influenced by depth of the producer: calls at depth were shorter and louder, especially higher frequency calls (Fig. 6B & C). Calls produced in higher ambient noise conditions were also louder and lower in peak frequency (Fig. 6D).

DISCUSSION

Our results demonstrate that social, deep-diving toothed whales can use social calls for acoustic relocation of close associates. Model propagation results showed that pilot whale social calls have the potential to be used for communication or as an acoustic beacon between vertically dispersed group members over 230-1786 m. Empirical data from three pairs of synchronously tagged animals confirmed our modelling results. 50% of produced calls were detected on receiver tags up to at least 385 m. Call characteristics influenced their propagation capacity. Modelled calls with a peak frequency of 1 kHz could be detected over shorter ranges than their counterparts at higher frequencies (5 or 20 kHz). This was caused by higher ambient noise levels at 1 kHz than at higher frequencies (propagation model results). Detected calls were also longer, had a higher power spectral density (PSD) level at the producer and were received in environments with lower ambient noise levels (empirical data). Plasticity of call production was indicated from differences in call characteristics under varying levels of ambient noise. In a noisier environment, calls were slightly louder and had a slightly lower peak frequency.

Acoustic potential for group relocation

The predicted large detection range for calls of 5-20 kHz (1414-1786 m) suggests that dispersed long-finned pilot whales maintain the potential to communicate during periods of vertical separation. These distances are at or exceeding pilot whale maximum dive depths recorded across populations (~600 m Baird et al. 2002; Sivle et al. 2012; Aoki et al. 2013; Visser et al. 2014; Aoki et al. 2017; Isojunno et al. 2017; Visser et al. 2017). Although the propagation model did not account for complexity in the transmission loss pattern when whales would also be horizontally dispersed, at short horizontal compared to vertical ranges these patterns are likely of minor influence to the overall propagation distance (Ainslie, 2010). Group members calling at the surface may serve as an acoustic beacon for listening group members that have been foraging at depth and aim to return to the group, similar to male frogs searching for chorusing conspecifics they can join (Bee, 2007). These results complement previous findings, reporting context-dependent occurrence of calls in long-finned pilot whales with peaks in production of social calls at the start and end of foraging bouts of individuals (Visser et al., 2017). Thus, social calls were produced at or close to the surface while other group members might still have been foraging or returning to the surface. Empirical evidence for the communicative role of these calls, however, remains difficult, as it would require proof of

vocally mediated shifts in upward swimming directions or turning angles in response to the location of a known producer.

As the detection of calls in this study was determined by human observers, we cannot exclude the possibility that pilot whales may have detected fewer or more calls than were detected by the observers. Since we excluded low-amplitude calls, the number of detected calls in this study is a conservative estimate. However, it is highly likely that all “detected” calls were also detected by the receiving whale. The maximum distance found for the subset of detected calls fell within the range predicted by the theoretical propagation model. Estimated call source levels from a subset of calls from one tag pair were consistent with the assumed range of source levels based on source levels reported in the literature. Furthermore, detected calls had a received level that was considerably higher than the detection threshold (mean signal excess: 30 dB; based on measured ambient noise levels and known critical ratios). Other mechanisms, such as comodulation masking release and directional masking release, might also contribute to higher rates of detected calls (Branstetter et al., 2008; Erbe et al., 2016). Nevertheless, it remains unknown at what signal excess level and with how much spectral information call detection translates to actual information transfer.

Even though it may appear obvious that social calls, often referred to as contact calls, serve in keeping contact with group members and relocating the group when separated (Ford, 1989), actual proof is not abundant in any taxon and distinct call categories are far from clear (e.g. birds: Hamilton 1962; Marler 2004). However, several studies on terrestrial mammals reported the production of separation calls (Alberghina et al., 2013; Mumm et al., 2014). In a field study on chacma baboons (*Papio cynocephalus ursinus*) for example, so-called contact barks in adult females were induced by separation from the group at large or when separated from dependent infants (Rendall et al., 2000). A rare actual test of phonotactic potential of such calls in free-ranging capybaras (*Hydrochoerus hydrochaeris*) showed that playback of conspecific click calls interrupted the capybaras’ behaviour and made them approach (Nogueira et al. (2012).

Odontocetes may be vocally active for other reasons than keeping the group together (Taruski, 1979; Weilgart and Whitehead, 1990; Zwamborn and Whitehead, 2016) and do not need to have the intention to allow homing by sound for foraging group members. However, the temporal patterns of vocal activity are so that group cohesion can be mediated by phonotactic behaviour (Jensen et al., 2011; Marrero Pérez et al., 2017; Visser et al., 2017). Being more silent when in larger, more tightly spaced groups, and more vocal during foraging bouts when group members are repeatedly leaving and returning for deep foraging bouts also seems to be quite widespread

among whales and dolphins (Tyack, 2000; Visser et al., 2014) and supports the hypothesis that acoustic communication is used to maintain contact between group members.

How call characteristics influence detection

Our finding that several call features such as duration, amplitude and frequency at the producer correlated with the detection probability at the receiver is in line with our knowledge about the effect of propagation and ambient noise on evolutionary shaping of acoustic signals (Brumm and Slabbekoorn, 2005; Endler, 1992; Ryan and Brenowitz, 1985). As expected, longer and louder calls were better detectable. The empirical data further showed a statistically significant difference in peak frequency between detected and undetected calls, but this difference was so small that it was likely not biologically relevant. It could be because system noise in the higher frequencies limited our ability to detect high frequency calls. Propagation model results showed that calls of 1 kHz would actually be less detectable than higher frequency calls, due to high ambient noise levels at that frequency. These modelled detection thresholds suggested that calls of 5 and 20 kHz would be equally well detectable, with a possible increase in detection at 20 kHz when the increased hearing directionality with increasing frequencies is taken into account.

Interestingly, the pilot whale calls measured had substantial energy at frequencies below 5 kHz, which would be suboptimal for the range of call detection. However, the high ambient noise level at 1 kHz that caused the shorter detection range is likely due to increased anthropogenic activity, an evolutionary recent phenomenon. At low ambient noise levels, calls of 1 kHz would likely have a larger detection range than calls at higher frequencies, due to a smaller loss from frequency-specific attenuation. There could also be trade-offs between optimal call features for propagation and constraints on production or limitations by depth. Indeed, we found that calls at depth were shorter, similar to results found for short-finned pilot whales (Jensen et al., 2011), but also louder, especially the high-frequency calls (Fig. 6). An alternative route, diminishing these potential trade-offs, is the evolution of more extreme call features or higher auditory sensitivity. Sperm whales, for example, are highly social deep divers, foraging at depths up to 1800 m. Their echolocation clicks are the most intense animal-borne signals known to date (Møhl et al., 2002).

Rising levels of ambient noise

The potential importance of hearing calls from group members and the fine-tuning to the acoustic environment may make deep-diving odontocetes vulnerable to current changes in the oceans. Ambient noise levels have increased due to a wide variety of human activities, including container shipping, seismic exploration, pile driving and deep-sea mining (Frisk, 2012; Hildebrand, 2009; McDonald et al., 2006), though the trends in ambient noise may be site-specific (Miksis-Olds and Nichols, 2016). Although masking issues can be relieved through differences in location between the anthropogenic source and the caller (directional masking release), or through the fluctuating amplitude in the ambient noise levels (co-modulation masking release) (Branstetter et al., 2008; Brumm and Slabbekoorn, 2005; Moore, 2013), it is important to investigate what the implications will be when group members do get separated by increasing ambient noise levels.

Pilot whale social calls that were produced during higher levels of ambient noise in the current study had a higher PSD level and a lower peak frequency than calls produced during quieter periods (Fig. 6D). This indicates a level of plasticity that can be employed in natural ambient noise level fluctuations, e.g. through increased sea state, and could to some degree also be successful in response to a rise in anthropogenic ambient noise levels (c.f. Foote et al. 2004; Miller 2006; Parks et al. 2011). However, a proper cost-benefit analysis is required to explore whether the extent and volitional control of such plasticity is sufficient to prevent negative consequences to the individual or population (Holt et al., 2015; Southall et al., 2007).

Conclusion

We have shown that deep-water foraging pilot whales have the capacity to communicate with their group members at the surface, using frequency-modulated tonal calls. This potential was found both through propagation modelling and empirical data of produced and received calls on simultaneously tagged group members. The variation in social call characteristics such as PSD level and duration influence the communication range, representing call-type plasticity which might be utilized to overcome masking in situations of increased ambient noise levels. However, as call structure also changes with depth, there might be physical restrictions to this variability. It is therefore of great importance to investigate whether anthropogenic activity at

sea will lead to impaired communication between vertically dispersed group members of this highly social species.

ACKNOWLEDGMENTS

The authors are grateful for the effort put in by all members of the 3S-cruise in 2009 and 2010 for collecting the data. Paul Wensveen kindly made his script for click extraction available to us. Michael Ainslie, Ozkan Sertlek, Mark Prior, Mark Johnson, Coen Elemans and Philip Bijl aided with the acoustic analyses and with constructing several versions of the propagation model.

COMPETING INTERESTS

The authors declare to have no competing interests.

FUNDING

Data collection for this project was funded by Office of Naval Research awards [N00014-08-1-0984, N00014-10-1-0355, N00014-15-1-2341], the Dutch Royal Navy, and the Norwegian Navy (FFD).

REFERENCES

- Ainslie, M. A.** (2010). *Principles of Sonar Performance Modelling*.
- Ainslie, M. A. and McColm, J. G.** (1998). A simplified formula for viscous and chemical absorption in sea water. *J. Acoust. Soc. Am.* **103**, 1671–1672.
- Alberghina, D., Caudullo, E., Bandi, N. and Panzera, M.** (2013). A comparative analysis of the acoustic structure of separation calls of Mongolian wild horses (*Equus ferus przewalskii*) and domestic horses (*Equus caballus*). *J. Vet. Behav. Clin. Appl. Res.* **9**, 254–257.
- Alves, A. C., Antunes, R. N., Bird, A., Tyack, P. L., Miller, P. J. O., Lam, F.-P. A. and Kvadsheim, P. H.** (2014). Vocal matching of naval sonar signals by long-finned pilot whales (*Globicephala melas*). *Mar. Mammal Sci.* **30**, 1248–1257.
- Aoki, K., Sakai, M., Miller, P. J. O., Visser, F. and Sato, K.** (2013). Body contact and synchronous diving in long-finned pilot whales. *Behav Process.* **99**, 12–20.
- Aoki, K., Sato, K., Isojunno, S., Narazaki, T. and Miller, P. J. O.** (2017). High diving metabolic rate indicated by high-speed transit to depth in negatively buoyant long-finned pilot whales. *J Exp Biol* **220**, 3802–3811.
- Au, W. W. L. and Moore, P. W. B.** (1984). Receiving beam patterns and directivity indices of the Atlanti bottlenose dolphin *Tursiops truncatus*. *J. Acoust. Soc. Am.* **75**, 255–262.
- Baird, R. W., Borsani, J. F., Hanson, M. B. and Tyack, P. L.** (2002). Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. *Mar. Ecol. Prog. Ser.* **237**, 301–305.
- Bee, M. A.** (2007). Selective phonotaxis by male wood frogs (*Rana sylvatica*) to the sound of a chorus. *Behav. Ecol. Sociobiol.* **61**, 955–966.
- Branstetter, B. K., Finneran, J. J., Green, L. S., Robinson, E. E., Tormey, M. N. and Dear, R. L.** (2008). Comodulation masking release in the bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **123**, 2985–2985.
- Brumm, H. and Slabbekoorn, H.** (2005). Acoustic Communication in Noise. *Adv. Study Behav.* **35**, 151–209.

- Cantor, M., Shoemaker, L. G., Cabral, R. B., Flores, C. O., Varga, M. and Whitehead, H.** (2015). Multilevel animal societies can emerge from cultural transmission. *Nat. Commun.* **6**,.
- Connor, R. C., Mann, J., Tyack, P. L. and Whitehead, H.** (1998). Social evolution in toothed whales. *Trends Ecol Evol* **13**, 228–231.
- David, J. A.** (2006). Likely sensitivity of bottlenose dolphins to pile-driving noise. *Water Environ. J.* **20**, 48–54.
- Deecke, V. B., Barrett-Lennard, L. G., Spong, P. and Ford, J. K. B.** (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*). *Naturwissenschaften* **97**, 513–518.
- Endler, J. A.** (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125–S153.
- Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K. and Dooling, R.** (2016). Communication masking in marine mammals: A review and research strategy. *Mar. Pollut. Bull.* **103**, 15–38.
- Fletcher, H.** (1940). Auditory Patterns. *Rev. Mod. Phys.* **12**, 47–66.
- Foote, A. D., Osborne, R. W. and Hoelzel, A. R.** (2004). Whale-call response to masking boat noise. *Nature* **428**, 910.
- Ford, J. K. B.** (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Can. J. Zool.* **67**, 727–745.
- Frisk, G. V.** (2012). Noiseconomics: The relationship between ambient noise levels in the sea and global economic trends. *Sci. Rep.* **2**, 2–5.
- Hamilton, W. J.** (1962). Evidence concerning the Function of Nocturnal Call Notes of Migratory Birds. *Condor* **64**, 390–401.
- Hartman, K. L., Visser, F. and Hendriks, A. J. E.** (2008). Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: a stratified community based on highly associated social units. *Can. J. Zool.* **86**, 294–306.
- Herbert-Read, J. E., Romanczuk, P., Krause, S., Strömbom, D., Couillaud, P., Domenici, P., Kurvers, R. H. J. M., Marras, S., Steffensen, J. F., Wilson, A. D. M., et al.** (2016).

Proto-Cooperation: Group hunting sailfish improve hunting success by alternating attacks on grouping prey. *Proc. R. Soc. B Biol. Sci.* **283**,

Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Mar. Ecol. Prog. Ser.* **395**, 5–20.

Holt, M. M., Noren, D. P., Dunkin, R. C. and Williams, T. M. (2015). Vocal performance affects metabolic rate in dolphins: implications for animals communicating in noisy environments. *J. Exp. Biol.* **218**, 1647–1654.

Isojunno, S., Sadykova, D., DeRuiter, S. L., Curé, C., Visser, F., Thomas, L., Miller, P. J. O. and Harris, C. M. (2017). Individual, ecological, and anthropogenic influences on activity budgets of long-finned pilot whales. *Ecosphere* **8**,

Janik, V. M. (2000). Source levels and the active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. *J Comp Physiol A* **186**, 673–680.

Janik, V. M. and Slater, P. J. B. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim. Behav.* **56**, 829–838.

Jensen, F. H., Bejder, L., Wahlberg, M., Aguilar de Soto, N., Johnson, M. P. and Madsen, P. T. (2009). Vessel noise effects on delphinid communication. *Mar. Ecol. Prog. Ser.* **395**, 161–175.

Jensen, F. H., Marrero Pérez, J., Johnson, M. P., Aguilar de Soto, N. and Madsen, P. T. (2011). Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. *Proc Biol Sci* **278**, 3017–3025.

Jensen, F. H., Beedholm, K., Wahlberg, M., Bejder, L. and Madsen, P. T. (2012). Estimated communication range and energetic cost of bottlenose dolphin whistles in a tropical habitat. *J Acoust Soc Am* **131**, 582–592.

Johnson, M. P. and Tyack, P. L. (2003). A Digital Acoustic Recording Tag for Measuring the Response of Wild Marine Mammals to Sound. *IEEE J. Ocean. Eng.* **28**, 3–12.

Kastelein, R. A., Hoek, L., de Jong, C. A. F. and Wensveen, P. J. (2010). The effect of signal duration on the underwater detection thresholds of a harbor porpoise (*Phocoena phocoena*) for single frequency-modulated tonal signals between 0.25 and 160 kHz. *J. Acoust. Soc. Am.* **128**, 3211–3222.

- Kondo, N. and Watanabe, S.** (2009). Contact calls: Information and social function. *Jpn. Psychol. Res.* **51**, 197–208.
- Ladich, F. and Winkler, H.** (2017). Acoustic communication in terrestrial and aquatic vertebrates. *J Exp Biol* **220**, 2306–2317.
- Lehtonen, J. and Jaatinen, K.** (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behav. Ecol. Sociobiol.* **70**, 449–458.
- Marler, P.** (2004). Bird calls: a cornucopia for communication. In *Nature's music, the science of birdsong* (ed. Marler, P.) and Slabbekoorn, H.), pp. 132–177. London: Elsevier Academic Press.
- Marrero Pérez, J., Jensen, F. H., Rojano-Doñate, L. and Aguilar de Soto, N.** (2017). Different modes of acoustic communication in deep-diving short-finned pilot whales (*Globicephala macrorhynchus*). *Mar. Mammal Sci.* **33**, 59–79.
- Marsh, H. W. and Schulkin, M.** (1962). Shallow-water transmission. *J Acoust Soc Am* **34**, 863–864.
- McDonald, M. A., Hildebrand, J. A. and Wiggins, S. M.** (2006). Increases in deep ocean ambient noise in the Northeast Pacific west of San Nicolas Island, California. *J. Acoust. Soc. Am.* **120**, 711–718.
- Mercado III, E. and Frazer, L. N.** (1999). Environmental constraints on sound transmission by humpback whales. *J. Acoust. Soc. Am.* **106**, 3004–3016.
- Miksis-Olds, J. L. and Nichols, S. M.** (2016). Is low frequency ocean sound increasing globally? *J. Acoust. Soc. Am.* **139**, 501–511.
- Miller, P. J. O.** (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **192**, 449–459.
- Miller, P. J. O., Antunes, R. N., Alves, A. C., Wensveen, P. J., Kvadsheim, P. H., Kleivane, L., Nordlund, N., Lam, F.-P. A., van IJsselmuide, S., Visser, F., et al.** (2011). *The 3S experiments: studying the behavioural effects of naval sonar on killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and long-finned pilot whales (*Globicephala melas*) in Norwegian waters*. St Andrews, UK: Scottish Oceans Institute.

- Miller, P. J. O., Kvadsheim, P. H., Lam, F.-P. A., Wensveen, P. J., Antunes, R. N., Alves, A. C., Visser, F., Kleivane, L., Tyack, P. L. and Sivle, L. D.** (2012). The Severity of behavioral changes observed during experimental exposures of killer (*Orcinus orca*), long-finned Pilot (*Globicephala melas*), and sperm (*Physeter macrocephalus*) whales to naval sonar. *Aquat. Mamm.* **38**, 362–401.
- Møhl, B., Wahlberg, M., Madsen, P. T., Miller, L. A. and Surlykke, A.** (2002). Sperm whale clicks: Directionality and source level revisited. *J. Acoust. Soc. Am.* **107**, 638–648.
- Moore, B. C. J.** (2013). *An Introduction to the Psychology of Hearing*. Sixth. Leiden, the Netherlands: Brill.
- Mumm, C. A. S., Urrutia, M. C. and Knörnschild, M.** (2014). Vocal individuality in cohesion calls of giant otters, *pteronura brasiliensis*. *Anim. Behav.* **88**, 243–252.
- Nogueira, S. S. C., Pedroza, J. P., Nogueira-Filho, S. L. G. and Tokumar, R. S.** (2012). The Function of Click Call Emission in Capybaras (*Hydrochoerus hydrochaeris*). *Ethology* **118**, 1001–1009.
- Ottensmeyer, C. A. and Whitehead, H.** (2003). Behavioural evidence for social units in long-finned pilot whales. *Can. J. Zool.* **81**, 1327–1338.
- Palmer, C., Baird, R. W., Webster, D. L., Edwards, A. C., Patterson, R., Withers, A., Withers, E., Groom, R. and Woinarski, J. C. Z.** (2017). A preliminary study of the movement patterns of false killer whales (*Pseudorca crassidens*) in coastal and pelagic waters of the Northern Territory, Australia. *Mar. Freshw. Res.* **68**, 1726–1733.
- Parks, S. E., Johnson, M. P., Nowacek, D. and Tyack, P. L.** (2011). Individual right whales call louder in increased environmental noise. *Biol Lett* **7**, 33–35.
- Parks, S. E., Cusano, D. A., Stimpert, A. K., Weinrich, M. T., Friedlaender, A. S. and Wiley, D. N.** (2014). Evidence for acoustic communication among bottom foraging humpback whales. *Sci. Rep.* **4**.
- Pasquaretta, C., Busia, L., Ferrari, C., Bogliani, G., Reale, D. and Von Hardenberg, A.** (2015). Helpers influence on territory use and maintenance in Alpine marmot groups. *Behaviour* **152**, 1391–1412.
- Piza, P. and Sandoval, L.** (2016). The differences in transmission properties of two bird calls show relation to their specific functions. *J. Acoust. Soc. Am.* **140**, 4271–4275.

- Rendall, D., Cheney, D. L. and Seyfarth, R. M.** (2000). Proximate factors mediating “contact” calls in adult female baboons (*Papio cynocephalus ursinus*) and their infants. *J. Comp. Psychol.* **114**, 36–46.
- Rendell, L. E., Matthews, J. N., Gill, A., Gordon, J. C. D. and Macdonald, D. W.** (1999). Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. *J Zool L.* **249**, 403–410.
- Ryan, M. J. and Brenowitz, E. A.** (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* **126**, 87–100.
- Ryder, T. B., Parker, P. G., Blake, J. G. and Loiselle, B. A.** (2009). It takes two to tango: Reproductive skew and social correlates of male mating success in a lek-breeding bird. *Proc. R. Soc. B Biol. Sci.* **276**, 2377–2384.
- Sivle, L. D., Kvadsheim, P. H., Fahlman, A., Lam, F.-P. A., Tyack, P. L. and Miller, P. J. O.** (2012). Changes in dive behavior during naval sonar exposure in killer whales, long-finned pilot whales, and sperm whales. *Front Physiol* **3**, 400.
- Snijders, L. and Naguib, M.** (2017). Communication in Animal Social Networks, pp. 297–359.
- Snijders, L., van Oers, K. and Naguib, M.** (2017). Sex-specific responses to territorial intrusions in a communication network: Evidence from radio-tagged great tits. *Ecol. Evol.* **7**, 918–927.
- Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Jr., C. R. G., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., et al.** (2007). Aquatic Mammals- Marine Mammal Noise Exposure Criteria: Initial Scientific Recommendations. *Aquat. Mamm.* **33**, 411–521.
- Taruski, A. G.** (1979). The whistle repertoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment. In *Behavior of marine mammals, vol 3* (ed. Winn, H. E.) and Olla, B. L.), pp. 345–368. New York.
- Thiebault, A., Mullers, R. H. E., Pistorius, P. A. and Tremblay, Y.** (2014). Local enhancement in a seabird: Reaction distances and foraging consequence of predator aggregations. *Behav. Ecol.* **25**, 1302–1310.
- Turl, C. W. and Fish, J. F.** (1976). *Acoustic source levels of four species of small whales*. San Diego.

- Tyack, P. L.** (2000). Functional aspects of cetacean communication. In *Cetacean Societies. Field Studies of Dolphins and Whales* (ed. Mann, J.), Connor, R. C.), Tyack, P. L.), and Whitehead, H.), pp. 270–307. Chicago and London: The University of Chicago Press.
- Urick, R. J.** (1983). *Principles of underwater sound (third edition)*. (ed. Davis, J.) Los Altos Hills, USA: Peninsula Publishing.
- Visser, F., Antunes, R. N., Oudejans, M. G., Miller, P. J. O., Lam, F.-P. A., Kvadsheim, P. H., Huisman, J., Tyack, P. L., Mackenzie, M. L. and Aoki, K.** (2014). The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). *Behaviour* **151**, 1453–1477.
- Visser, F., Kok, A. C. M., Oudejans, M. G., Scott-Hayward, L. A. S., DeRuiter, S. L., Alves, A. C., Antunes, R. N., Isojunno, S., Pierce, G. J., Slabbekoorn, H., et al.** (2017). Vocal foragers and silent crowds: context-dependent vocal variation in Northeast Atlantic long-finned pilot whales. *Behav Ecol Sociobiol* **71**, 170.
- von Benda-Beckmann, A. M., Wensveen, P. J., Samarra, F. I., Beerens, S. P. and Miller, P. J. O.** (2016). Separating underwater ambient noise from flow noise recorded on stereo acoustic tags attached to marine mammals. *J Exp Biol* **219**, 2774.
- Watwood, S. L., Miller, P. J. O., Johnson, M. P., Madsen, P. T. and Tyack, P. L.** (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J Anim Ecol* **75**, 814–825.
- Weilgart, L. S. and Whitehead, H.** (1990). Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behav. Ecol. Sociobiol.* **26**, 399–402.
- Wensveen, P. J.** (2016). Detecting , Assessing , and Mitigating the Effects of Naval Sonar on Cetaceans.
- Wenz, G. M.** (1962). Acoustic ambient noise in the ocean: spectra and sources. *J. Acoust. Soc. Am.* **34**, 1936–1956.
- Whitehead, H.** (1989). Formations of foraging sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Can. J. Zool.* **67**, 2131–2139.
- Whitehead, H., Waters, S. and Lyrholm, T.** (1991). Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behav. Ecol.*

Sociobiol. **29**, 385–389.

Whitehead, H., Dillon, M., Dufault, S., Weilgart, L. S. and Wright, A. J. (1998). Non-geographically based population structure of South Pacific sperm whales: dialects, fluke markings and genetics. *J. Anim. Ecol.* **67**, 253–262.

Wiley, R. H. (2013). A receiver–signaler equilibrium in the evolution of communication in noise. *Behaviour* **150**, 1–37.

Zwamborn, E. M. J. and Whitehead, H. (2016). Repeated call sequences and behavioural context in long-finned pilot whales off Cape Breton, Nova Scotia, Canada. *Bioacoustics* **26**, 1–15.

Figures

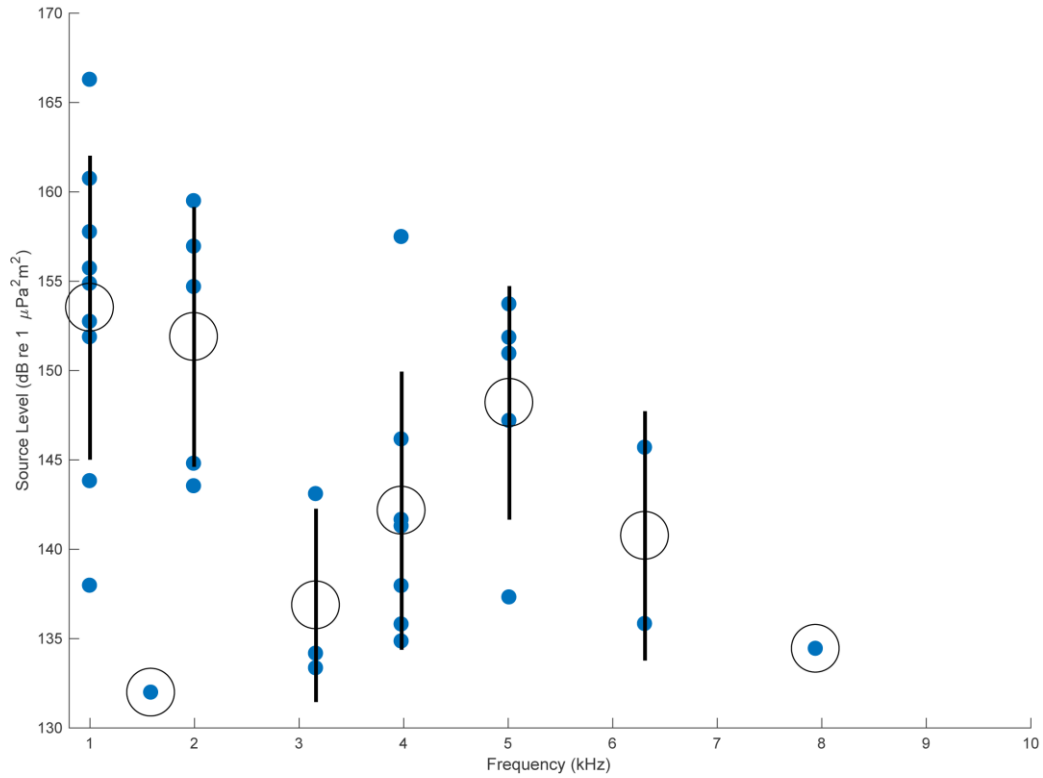


Figure 1: Back-propagated source levels calculated from 1/3 octave peak frequency bands (N = 33). Blue dots represent individual calls, open circles are means per frequency band and vertical lines represent standard deviation.

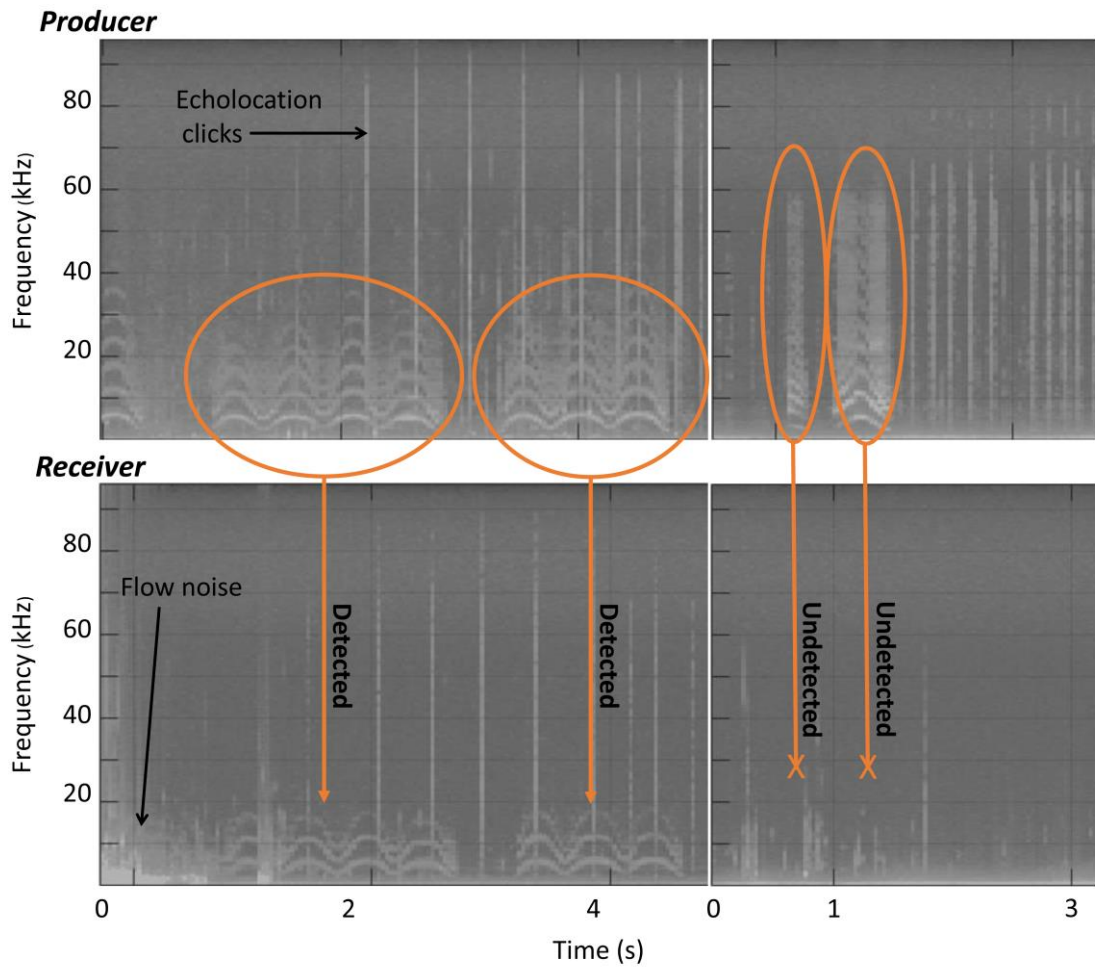


Figure 2. Time-synchronised spectrograms of recordings on producer and receiver tags showing examples of detected (left) and undetected (right) calls. Note that the detected calls are longer than the undetected calls, which makes the noise at the start of the recording less influential for detection.

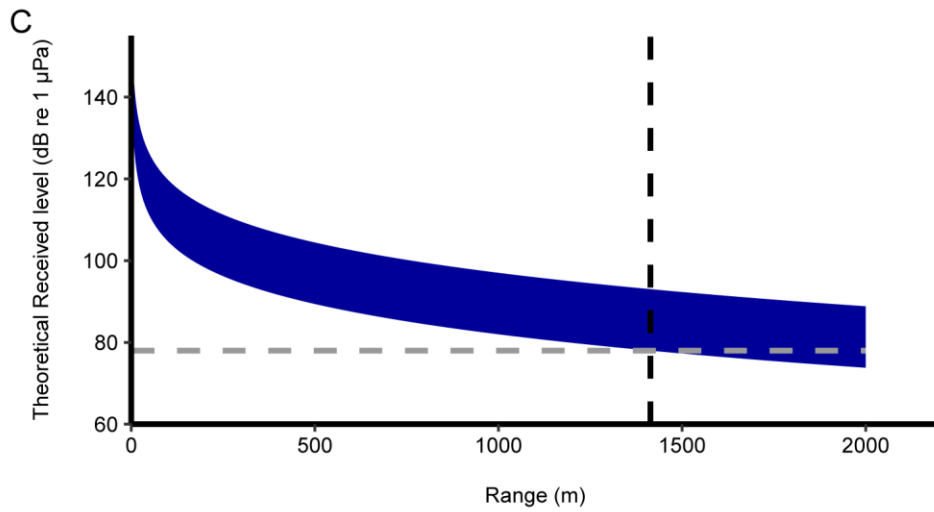
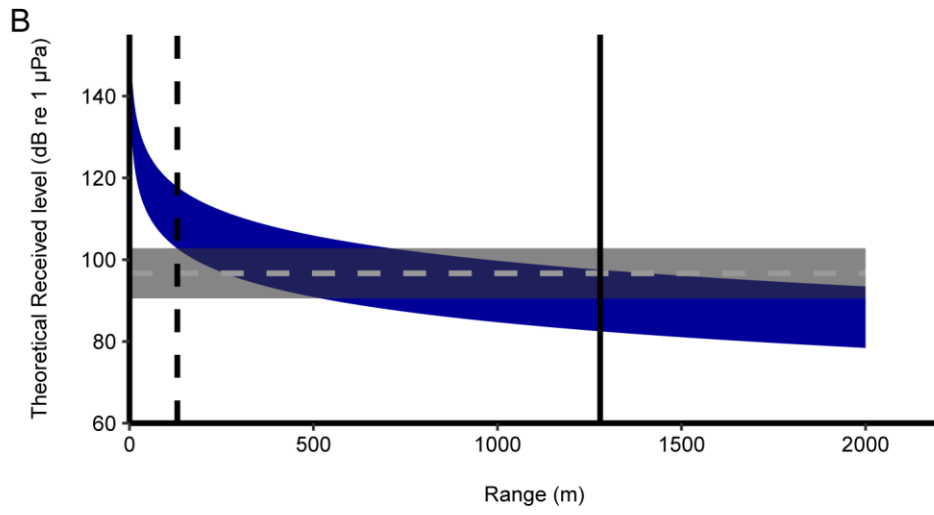
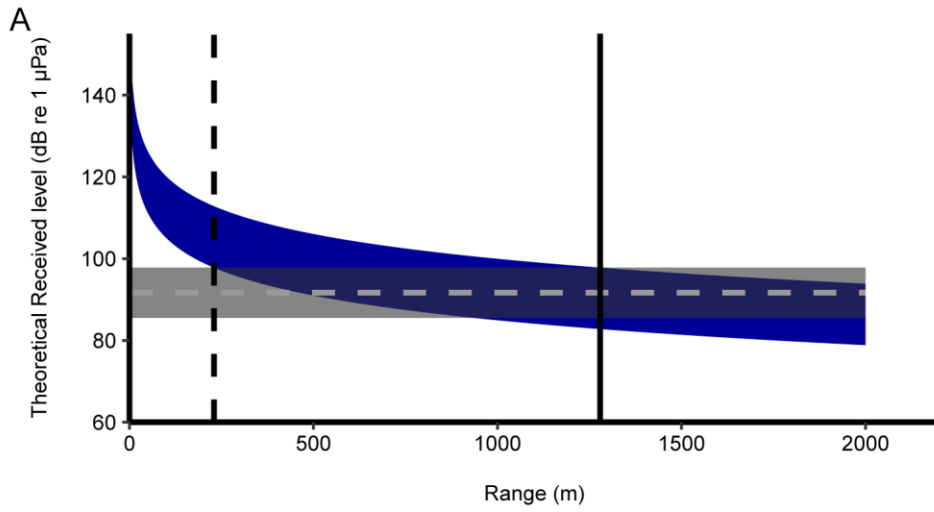


Figure 3. Sound propagation modelling for a pure tone (dark blue) of A) 1 kHz, B) 5 kHz, and C) 20 kHz with source level = 145-160 dB over a range of 2000 m. Median with 25 and 75 percentile detection thresholds (grey shaded area) and Wenz ambient noise level (grey dashed line) influenced signal detection at frequency-specific distances. Signals with a low source level dropped below the maximum detection threshold at some point for all frequencies (black dashed vertical lines). For 1 kHz signals, also signals with a high source level dropped below the detection threshold at 501 m (solid black line).

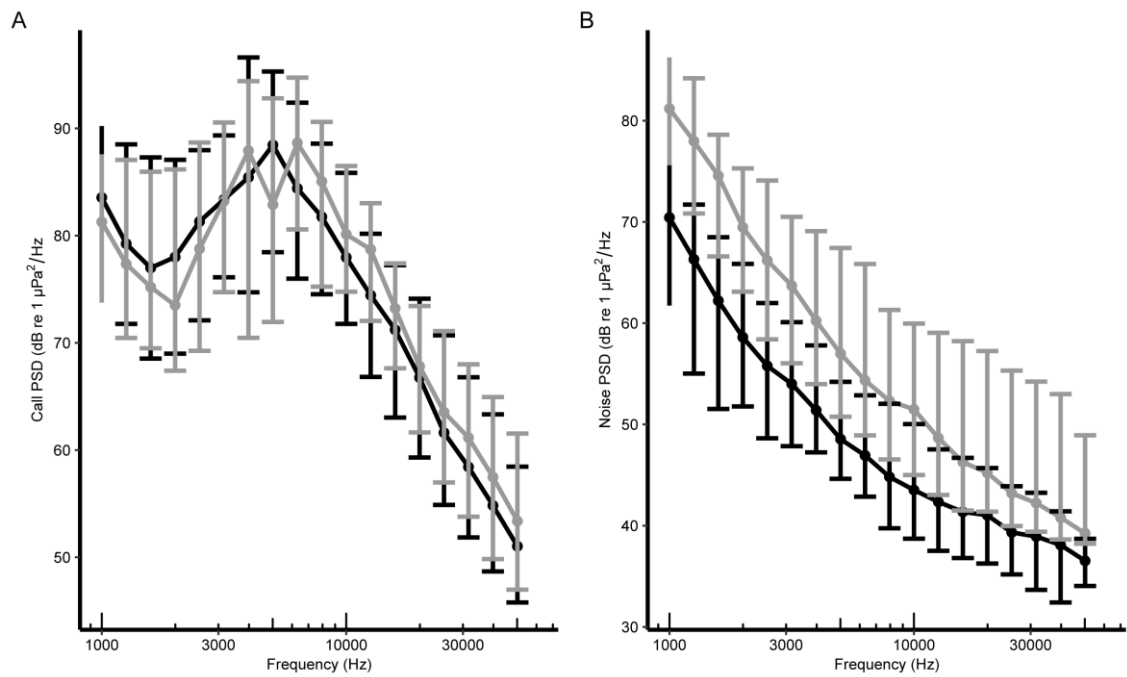


Figure 4: Average social call and ambient noise power spectral density of root-mean-square sound pressure (PSD) level for social calls and ambient noise, comparing conditions for detected (black, N = 183) and undetected (grey, N = 121) calls. Measures represent third octave band levels from 1-50 kHz of A) median call level at the producer and B) median ambient noise level at the receiver (corrected for flow noise). Error bars represent 25 and 75 percentiles.

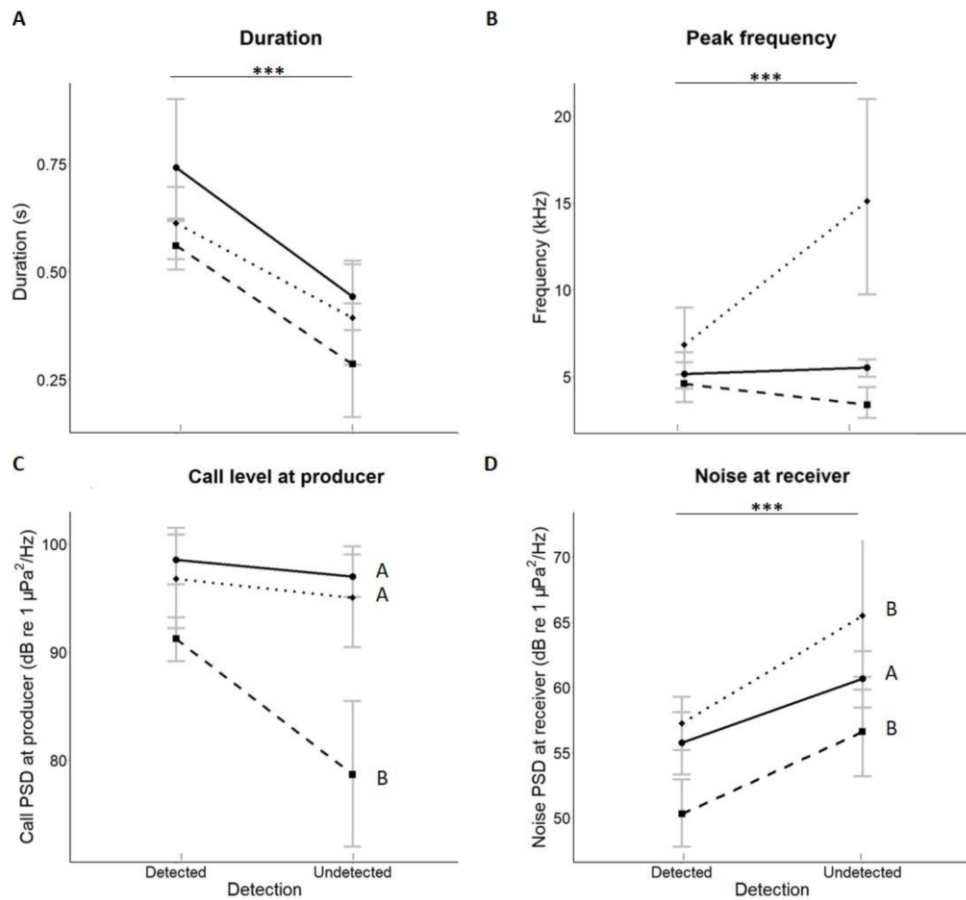


Figure 5: Call and environmental characteristics influencing social call detection. Detected and undetected calls were compared for A) call duration, B) call peak frequency, C) producer call power spectral density (PSD) at peak frequency, and D) ambient noise PSD at call peak frequency, at receiver. Comparisons are shown separately for each tagged pair (pair gm137: filled circle and solid line, Detected N = 72, Undetected N = 94; pair gm138: filled square and interrupted line, Detected N = 41, Undetected N = 22; pair gm158 = filled diamond and dotted line, Detected N = 75, Undetected N = 11). Error bars show bootstrapped 95% c.i. * indicates significance at $* < 0.05$, $** < 0.01$ and $*** < 0.0001$, letters indicate pairs that showed equal trends.

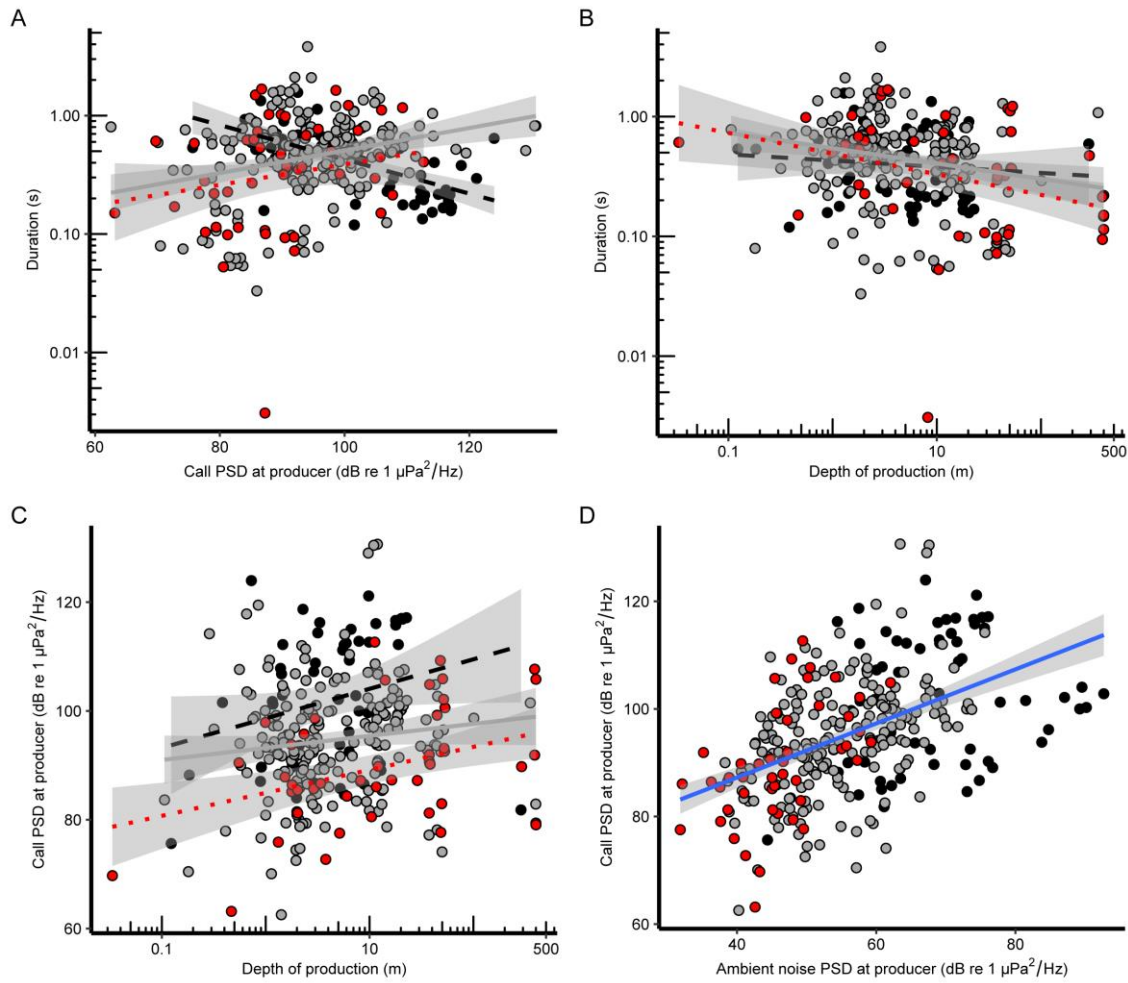


Figure 6. Call characteristics at the producer in relation to environmental features as a function of call peak frequency. The call peak frequency influenced the relation between A) producer call Power Spectral Density (PSD) at peak frequency and call duration, B) depth of call production and call duration, C) depth of production and call PSD and D) PSD of the ambient noise at the producer, at peak frequency and call PSD. Call peak frequency was divided into three subgroups for visualisation purposes: <2.5 kHz (black dots, black interrupted line, N = 61), 2.5-7.5 kHz (grey dots, grey solid line, N = 196), and >7.5 kHz (red dots, red dotted line, N = 58). Shaded areas represent 95% c.i. Note that depth of production and duration are presented on a \log_{10} scale.

TABLES

Table 1: Summary of tagged pair datasets.

Tag ID	Record duration analysed (s)¹	No. Produced calls	No. Detected calls	Max dive depth in used data(m)	Deployment
137a	10223	70	25	288	17-5-'09 14:52
137c	10223	96	47	293	17-5-'09 15:52
138a	1482	46	29	401	18-5-'09 12:17
138b	1482	17	12	120	18-5-'09 13:19
158c	1301	45	41	18	07-06-'10 17:52
158d	1301	41	34	17	07-06-'10 17:55

¹Record duration analysed was determined as a subset from temporal overlap between tagged-pair records.

Table 2: GLM results testing how call detectability was affected by call and environmental characteristics.

Coefficients	Estimate	SE	Z	P
Intercept	0.15	2.00		
<i>Pair</i>				
138	-6.00	3.45	-1.74	0.08
158	8.26	5.15	1.61	0.11
Peak frequency	0.000108	0.0000371	2.99	<0.005
Noise at receiver	0.0554	0.0187	2.96	<0.005
Call at producer	-0.0303	0.0196	-1.55	0.12
Duration	-1.24	0.415	-2.99	<0.005
Duration:138	-2.59	1.57	-1.65	0.10
Duration:158	-4.61	2.09	-2.20	<0.05
Noise at receiver:138	0.0962	0.0485	1.99	<0.05
Noise at receiver:158	0.0995	0.0493	2.02	<0.05
Call at producer:138	-0.00269	0.0371	-0.072	0.94
Call at producer:158	-0.171	0.0719	-2.38	<0.05

SUPPLEMENTS

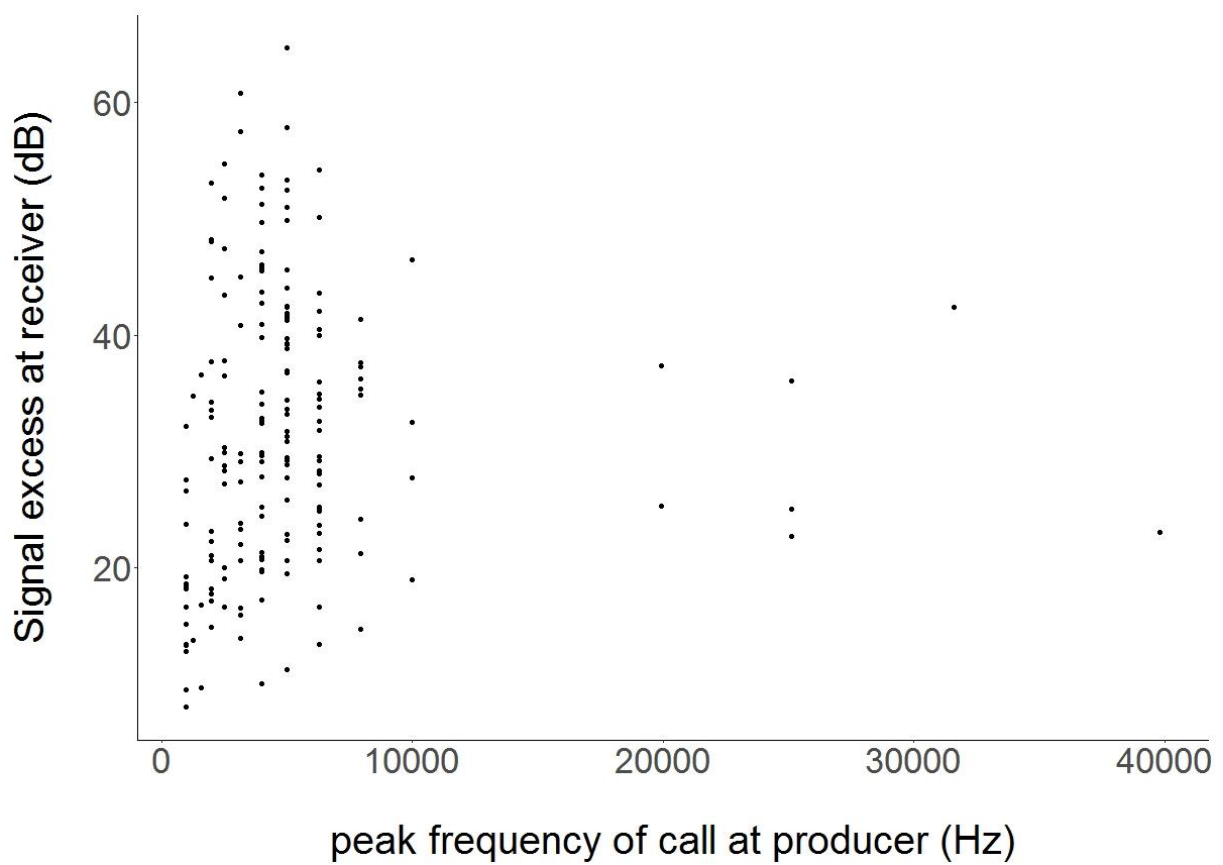


Figure S1: Signal excess (the level of the signal above the detection threshold) of calls that were detected on the tag of the receiving whale. These values give an indication of the audibility of the calls for the receiving whale.

Table S1: GLM model selection. Best model selection was based on lowest Akaike Information Criterion corrected for small sample size (AICc), after which the final model was selected from all models with a non-significant difference from the lowest AICc ($\Delta AICc < 2$). The final model (bold) was then selected to be the model with the lowest degrees of freedom (df). Interaction terms are indicated with “:” between variables. All variables were measured on the tag of the producer, except ambient noise levels (Noise Receiver).

Pair	Duration	Peak frequency	Noise Receiver	Call producer	Pair:Duration	Pair:Frequency	Pair:Noise Receiver	Pair:Call producer	Duration:Frequency	Duration:Noise Receiver	Duration:Call Producer	Noise Receiver:Call Producer	df	R ²	AICc	$\Delta AICc$
x	x	x	x	x	x		x	x	x				14		311.1	0
x	x	x	x	x	x		x	x					13	0.48	312.3	1.20
x	x	x	x	x	x		x	x	x	x			15		312.9	1.82
x	x	x	x	x	x		x	x	x		x		15		313.0	1.94

Table S2: LM results investigating how duration, call PSD at the producer, and peak frequency were correlated with several call variables and depth. Duration, peak frequency and depth were log transformed to maintain normality assumption. Interaction terms are indicated with “:” between variables. Only the variables retained in the final models are included.

Model	Coefficients	Estimate	SE	T	P	R ²	AICc
Duration	Intercept	19.59	4.11			0.21	150.4
	log(Depth)	1.15	0.27	4.25	<0.0001		
	Call SPSD at prod	-0.24	0.045	-5.32	<0.0001		
	log(Frequency)	-2.48	0.49	-5.02	<0.0001		
	Call:log(freq)	0.030	0.0055	5.45	<0.0001		
	log(Depth):log(Freq)	-0.15	0.031	-4.85	<0.0001		
Call PSD at prod	Intercept	62.40	13.74			0.43	2297.8
	log(Depth)	-9.99	3.58	-2.79	<0.01		
	log(Duration)	-38.49	9.21	-4.18	<0.0001		
	log(Frequency)	1.31	1.35	0.98	0.33		
	Noise at prod	0.38	0.069	5.57	<0.0001		
	<i>Tag</i>						
	137c	1.70	1.53	1.11	0.27		
	138a	-0.88	1.79	-0.49	0.62		
	138b	11.33	2.59	4.37	<0.0001		
	158c	-2.77	1.83	-1.51	0.13		
	158d	-8.09	1.89	-4.29	<0.0001		
	log(Depth):log(Freq)	1.32	0.41	3.21	<0.005		
	log(Dur):log(Freq)	4.73	1.09	4.34	<0.0001		
Frequency	Intercept	10.82	0.49			0.57	466.3
	log(Depth)	-0.55	0.15	-3.73	<0.0005		
	Call SPSD at prod	-0.00011	0.0052	-0.021	0.98		
	log(Duration)	-0.70	0.34	-2.07	<0.05		
	Noise at prod	-0.042	0.0032	-12.99	<0.0001		
	<i>Tag</i>						
	137c	-0.063	0.087	-0.73	0.47		
	138a	-0.11	0.10	-1.09	0.28		
	138b	0.21	0.15	1.42	0.16		
	158c	-0.35	0.10	-3.57	<0.0005		

158d	-0.54	0.10	-5.20	<0.0001
log(Depth):log(Dur)	-0.072	0.024	-2.93	<0.005
Call at prod:log(Dur)	0.0097	0.0038	2.56	<0.05
log(Depth):Call at prod	0.0063	0.0015	4.27	<0.0001
