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RESEARCH ARTICLE

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

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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 385 m (empirical) and 1800 m (theoretical). These distances match or exceed 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.

KEY WORDS: Active space, Communication, Contact call, Noise, Odontocete, *Globicephala melas*

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 locate 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, adopt 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 whether 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

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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 with 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 and Frazer, 1999; Miller, 2006). Until now, studies on marine mammal call propagation have 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 overcame 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 hypothesise 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 (Urlick, 1983):

$$RL = SL - 20 \log_{10}(R/R_0) \text{dB} - \alpha R. \quad (1)$$

Here, RL is the received level (dB re. 1 μPa), SL is the source level (dB re. 1 μPa m), R is the distance between producer and receiver (m), R_0 is the distance at which SL is measured (1 m) and α is frequency-specific attenuation (Ainslie and McColm, 1998) (dB m^{-1}). 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^{-1} at 50 and 200 m, respectively; Miller et al., 2011). This meant that the angle at which boundary effects could occur was ~ 5 deg from the horizontal, indicating a negligible effect of refraction on 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 RL is above the hearing threshold, the signal-to-noise ratio (SNR) 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 with noise (Moore, 2013). This minimal SNR 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 difference in sound pressure level (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 RL, CR and ambient noise level.

As CRs for long-finned pilot whales have not been measured, the model was based on average CRs 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, SOUND TAG lab, University of St Andrews, UK), 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 decade). 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 noise level, because the median was least sensitive for outliers in the data. At 20 kHz, ambient noise levels could not be reliably measured because of high levels of system noise in the deployed tags. Instead, a typical ambient noise level at 20 kHz for sea state 2 (the highest sea state in which data were collected) was used (Wenz, 1962).

Calls were considered to be detectable by the pilot whales when the RL within a frequency band exceeded the level of ambient noise mean spectral density plus the CR. When the masking sound source is from a different direction to the calling animal, spatial masking release can reduce the degree of masking (e.g. Erbe et al., 2016). As the focus of this study was on relatively low frequency calls with limited masking release (Au and Moore, 1984; Brumm and Slabbekoom, 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 μPa 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 one-third 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 (\pm s.d.) source levels found were 146.5 \pm 9.5 dB re. 1 μPa^2 m², 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 the coast of Lofoten, Norway, as part of a larger

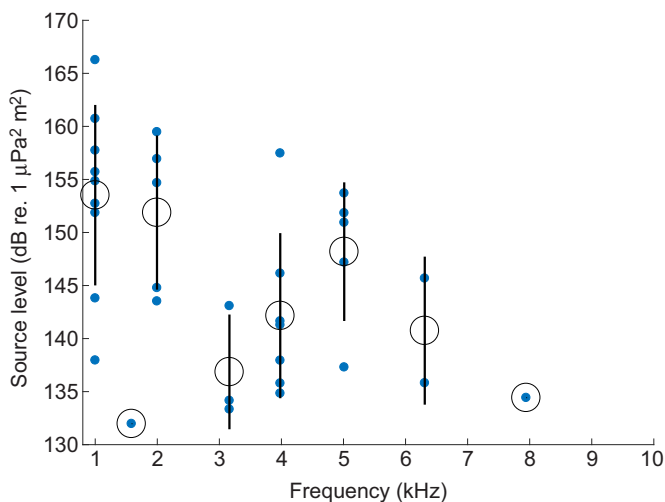


Fig. 1. Back-propagated source levels calculated from one-third octave peak frequency bands. $N=33$. Blue dots represent individual calls, open circles are means per frequency band and vertical lines represent standard deviation.

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 gm138a (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 SNR of ≥ 10 dB at the producer to minimise measurement errors due to ambient noise (following Jensen et al., 2011). The SNR level was calculated as call SPL minus total ambient noise SPL (uncorrected for flow noise, as 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 one-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. Additionally, 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 clicks on tag A (DTAG toolbox; <http://animaltags.org/doku.php>). 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. As 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 gm137: 0.268–0.280 s). For the other tag pairs, time synchronisation was less accurate, but still accurate enough (error of the 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,

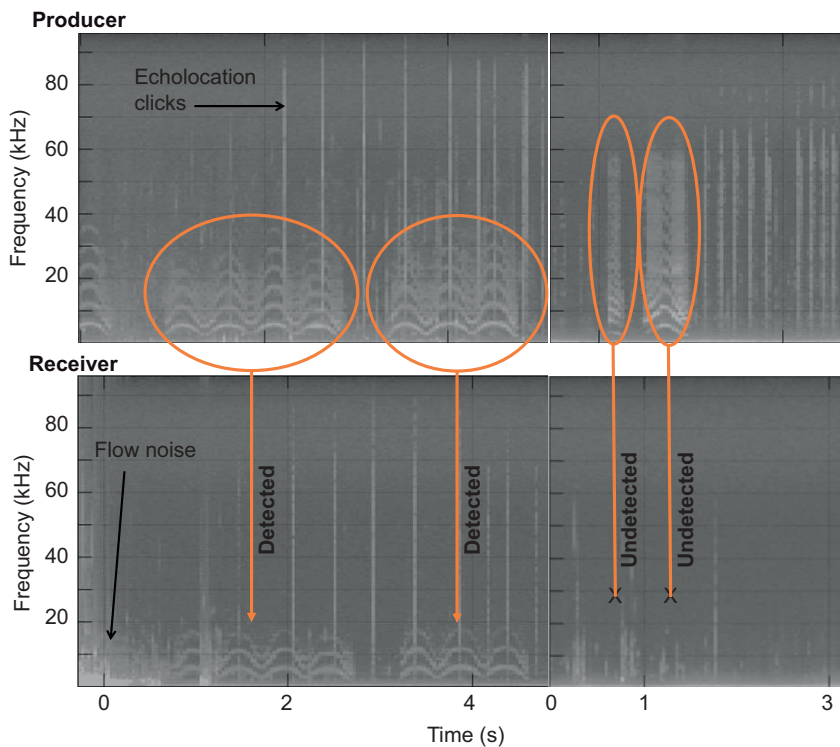


Fig. 2. Time-synchronised spectrograms of recordings on producer and receiver tags showing examples of detected (left) and undetected (right) calls. Note that the detected calls are longer than the undetected calls, which makes the noise at the start of the recording less influential for detection.

the position of the produced call relative to other calls was used to check that no detectable call was missed in the analysis.

Noise filtering

Ambient noise sections and calls were filtered to exclude echolocation clicks using a custom-written script (Scripts 1, 2) (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. The start and end of a click were 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 the producer tag), call arrival time at the recorder tag and PSD of total ambient noise at the producer and 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 is signal excess (dB), RL is received SPL of the call at peak frequency (dB re. 1 μPa), DT is the detection threshold (dB re. 1 μPa), NL is the total ambient noise level at the receiver at call peak frequency (dB re. 1 μPa), bandwidth is that of the one-third octave level around peak frequency (Hz) and CR is the critical ratio for peak frequency (dB re. 1 Hz), taken from the average CR 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 the 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 took to travel 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, because of 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., Natick, MA, USA) using the DTAG toolbox (<http://animaltags.org/doku.php>).

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 versus 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 relationship between all three call characteristics that could be influenced by the producer (duration, peak frequency and 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 the lowest Akaike information criterion corrected for small sample sizes (AICc). All models that had AICc within 2.0 points of the model with the lowest AICc were ranked based on lowest degrees of freedom (d.f.). For all these models, R^2 values were calculated using the package `piecewiseSEM` (<https://CRAN.R-project.org/package=piecewiseSEM>). The best model was the one with the lowest d.f. All statistics were performed in Rstudio 3.3.2. (<http://www.R-project.org/>).

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 a minimum of 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 with those at 1 kHz. Tones at 1 and 5 kHz showed no significant difference in propagation distance because of 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 one-third octave band PSD levels at the receiver tag decreased with increasing frequency from 68–80 to 45–57 dB

re. $1 \mu\text{Pa}^2 \text{Hz}^{-1}$ (25–75 percentiles) at 1 and 5 kHz, respectively, and were estimated by a Wenz curve noise level at 50 dB re. $1 \mu\text{Pa}^2 \text{Hz}^{-1}$ at 20 kHz. Average ambient noise levels for 1 and 5 kHz (78 and 56 dB re. $1 \mu\text{Pa}^2 \text{Hz}^{-1}$) were similar to reported ambient noise levels for sea state=1–2 Beaufort; Wenz, 1962). Because the CRs 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 to 170 min, with a mean (\pm s.d.) of 53 ± 27 calls per tag (Table 1). Individuals dived to a maximum depth of 401 m. The maximum depth difference between the tag pairs was 400 m (mean \pm s.d. depth difference of 43 ± 97 m, $N=315$). Absolute distance for the subset of calls, where it could be estimated, ranged from 60 to 385 m (mean \pm s.d. of 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 the 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 (Eqn 2) of 31 dB (range: 8–65 dB; Fig. S1). Detected calls had a lower peak frequency than undetected calls (median 5 versus 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 ($R^2=0.48$, d.f.=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 gm158 were also produced at a 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 gm138 and gm158 than for pair gm137 (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 S2). 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

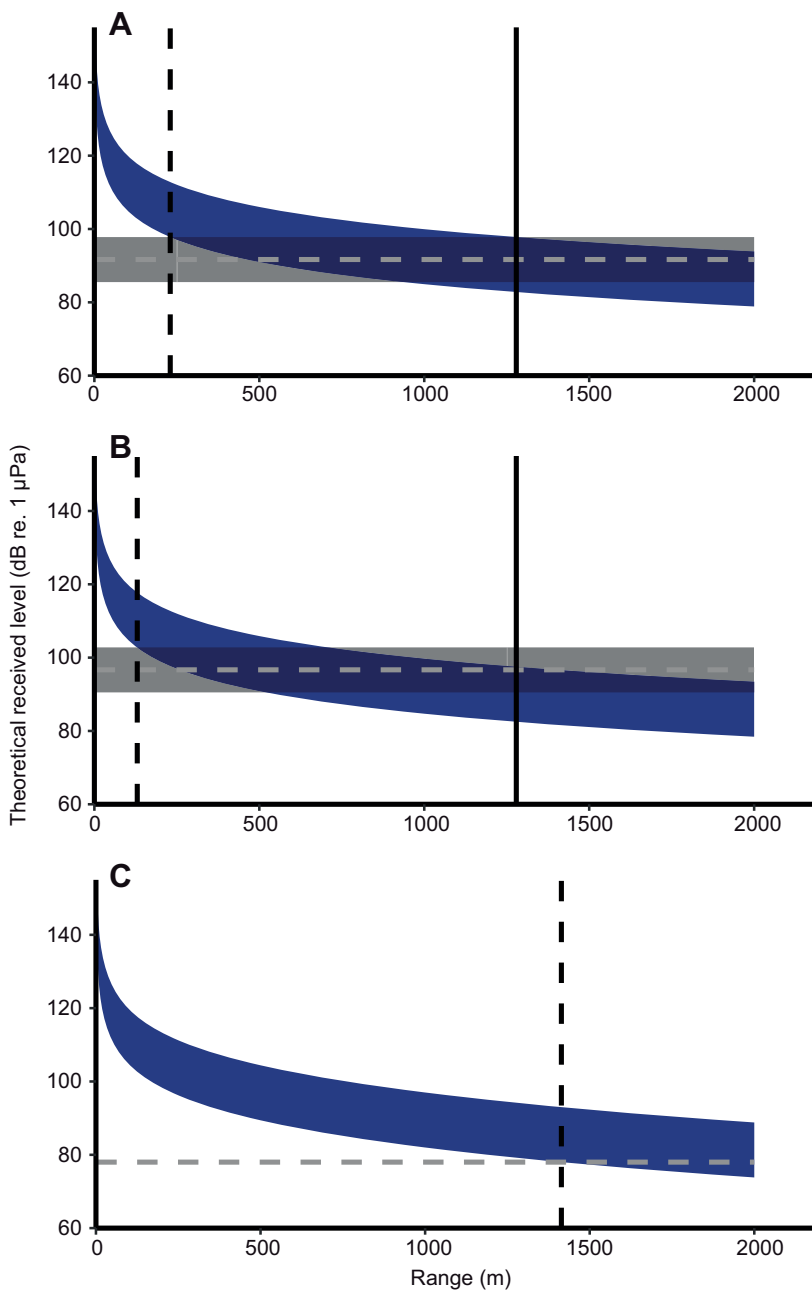


Fig. 3. Sound propagation modelling for a pure tone (dark blue) over a range of 2000 m. (A) 1 kHz, (B) 5 kHz and (C) 20 kHz pure tone with source level of 145–160 dB. Medians with 25 and 75 percentile detection thresholds (A and B, grey dashed line and grey shaded area, respectively) and Wenz ambient noise level (C, 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 (vertical dashed black lines). For 1 kHz signals, signals with a high source level also dropped below the detection threshold at 1279 m (vertical solid black line).

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 because of higher ambient noise levels at 1 kHz than at higher frequencies (propagation model results). Detected calls were also

longer, had a higher 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.

Table 1. Summary of tagged pair datasets

Tag ID	Record duration analysed (s)	No. produced calls	No. detected calls	Max. dive depth in used data (m)	Deployment
gm137a	10,223	70	25	288	17 May 2009 14:52 h
gm137c	10,223	96	47	293	17 May 2009 15:52 h
gm138a	1482	46	29	401	18 May 2009 12:17 h
gm138b	1482	17	12	120	18 May 2009 13:19 h
gm158c	1301	45	41	18	7 June 2010 17:52 h
gm158d	1301	41	34	17	7 June 2010 17:55 h

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

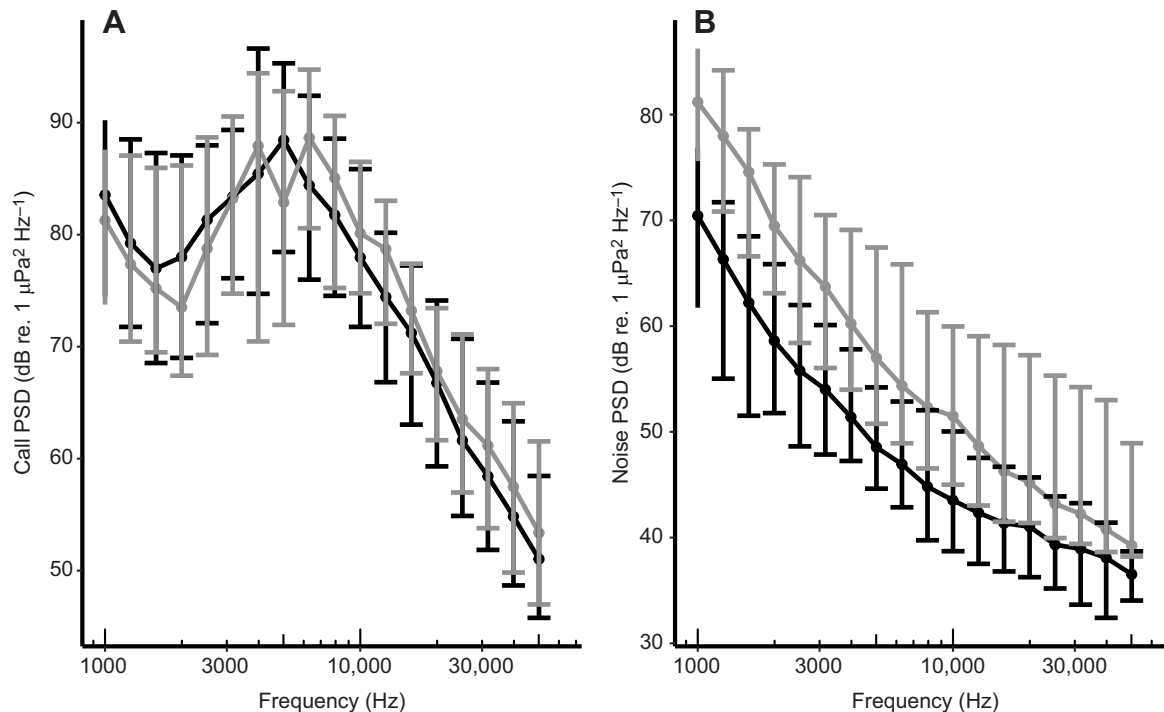


Fig. 4. Average social call and ambient noise power spectral density of root-mean-square sound pressure (PSD) level for social calls and ambient noise. Comparison of conditions for detected (black, $N=183$) and undetected (grey, $N=121$) calls. Measures represent one-third octave band levels from 1 to 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.

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 exceed pilot whale maximum dive depths recorded across populations (~600 m; Baird et al., 2002; Sivle et al., 2012; Aoki et al., 2013, 2017; Visser et al., 2014, 2017; Isojunno 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 with vertical ranges, these patterns are likely to be 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

chourusing 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. Because 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 of 30 dB, based on measured ambient noise levels and known CRs). Other mechanisms, such as co-modulation 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 maintaining contact with group members

Table 2. Effect of call and environmental characteristics on call detectability (GLM results)

Coefficients	Estimate	s.e.	Z	P
Intercept	0.15	2.00		
Pair				
gm138	-6.00	3.45	-1.74	0.08
gm158	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: gm138	-2.59	1.57	-1.65	0.10
Duration: gm158	-4.61	2.09	-2.20	<0.05
Noise at receiver: gm138	0.0962	0.0485	1.99	<0.05
Noise at receiver: gm158	0.0995	0.0493	2.02	<0.05
Call at producer: gm138	-0.00269	0.0371	-0.072	0.94
Call at producer: gm158	-0.171	0.0719	-2.38	<0.05

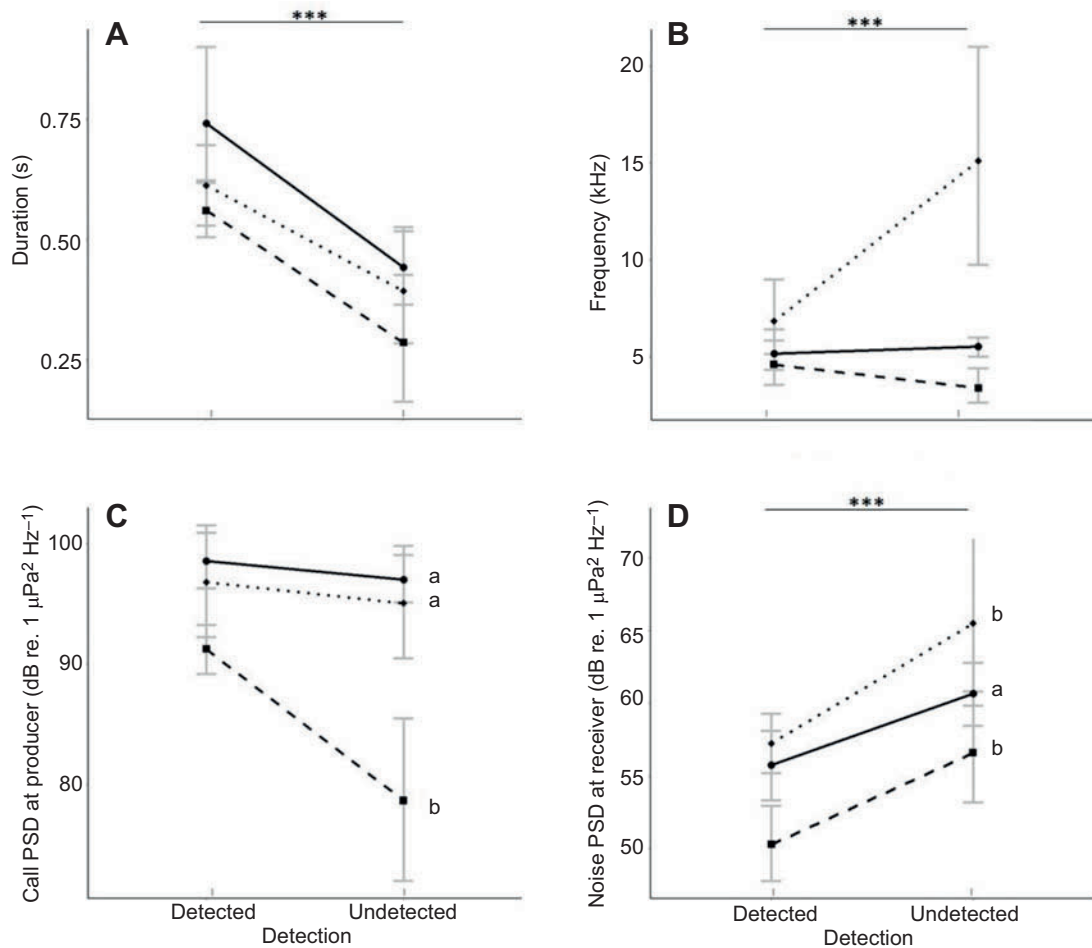


Fig. 5. Call and environmental characteristics influencing social call detection. Detected and undetected calls were compared for (A) call duration, (B) call peak frequency, (C) producer call PSD at peak frequency and (D) ambient noise PSD at call peak frequency at the receiver. Comparisons are shown separately for each tagged pair (pair gm137: filled circles and solid line, detected $N=72$, undetected $N=94$; pair gm138: filled squares and dashed line, detected $N=41$, undetected $N=22$; pair gm158: filled diamonds and dotted line, detected $N=75$, undetected $N=11$). Error bars show bootstrapped 95% confidence interval (CI). Asterisks indicate a significant difference ($***P<0.0001$); letters indicate pairs that showed equal trends.

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., 2014; 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 from dependent infants (Rendall et al., 2000). A rare actual test of the 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 reasons other than keeping the group together (Taruski, 1979; Weilgart and Whitehead, 1990; Zwamborn and Whitehead, 2016) and not necessarily for the purpose of homing by sound for foraging group members. However, the temporal patterns of vocal activity are such 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 for and returning

from 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 correlate with the detection probability at the receiver is in line with our knowledge about the effect of propagation and ambient noise on the evolutionary shaping of acoustic signals (Brumm and Slabbekoorn, 2005; Endler, 1992; Ryan and Brenowitz, 1985). As expected, longer and louder calls were more easily 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 probably not biologically relevant. It could be because system noise at 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, as a result of high ambient noise levels at that frequency. These modelled detection thresholds suggested that calls of 5 and 20 kHz would be equally well detected, with a possible increase in detection

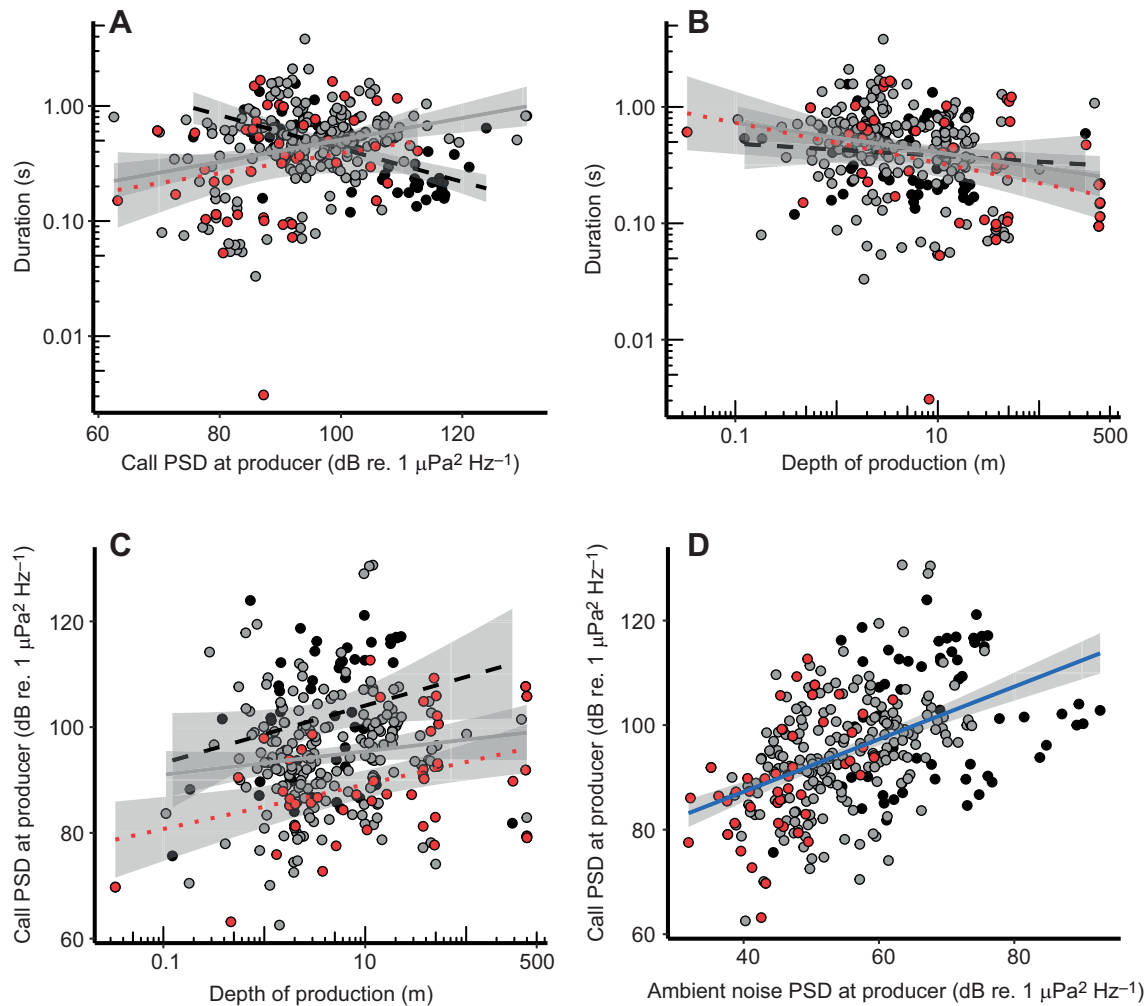


Fig. 6. Call characteristics at the producer in relation to environmental features as a function of call peak frequency. The call peak frequency influenced the relationship between (A) producer call PSD at peak frequency and call duration, (B) depth of call production and call duration, (C) depth of 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 circles and dashed line, $N=61$), 2.5–7.5 kHz (grey circles and solid line, $N=196$) and >7.5 kHz (red circles and dotted line, $N=58$). Shaded areas represent 95% CI. Note that depth of production and duration are presented on a log₁₀ scale.

at 20 kHz when the increased directionality of hearing with increasing frequency 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 probably due to increased anthropogenic activity, an evolutionarily recent phenomenon. At low ambient noise levels, calls of 1 kHz would probably have a larger detection range than calls at higher frequencies, as a result of 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 as a consequence of 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 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 (cf. 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 through both 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 influences 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.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.C.M.K., A.M.v.B.-B., P.J.O.M., H.S., F.V.; Methodology: A.C.M.K., J.A.C., A.M.v.B.-B., P.J.O.M., F.V.; Formal analysis: A.C.M.K., L.v.K.; Investigation: P.J.O.M., F.V.; Data curation: P.J.O.M., F.V.; Writing - original draft: A.C.M.K.; Writing - review & editing: L.v.K., J.A.C., A.M.v.B.-B., P.J.O.M., H.S., F.V.; Visualization: A.C.M.K.; Supervision: H.S., F.V.; Funding acquisition: P.J.O.M., F.V.

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Supplementary information

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