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SHORT COMMUNICATION

Acoustic crypsis in southern right whale mother–calf pairs: infrequent, low-output calls to avoid predation?

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ABSTRACT

Southern right whales (*Eubalaena australis*) invest substantial amounts of energy in their calves, while facing the risk of having them predated upon by eavesdropping killer whales (*Orcinus orca*). We tested the hypothesis that southern right whale mother–calf pairs employ acoustic crypsis to reduce acoustic detectability by such predators. Specifically, we deployed multi-sensor DTAGs on nine lactating whales for a total of 62.9 h in a Western Australian breeding ground, and used a SoundTrap to estimate the concomitant acoustic background noise. Vocalisations were recorded at low rates of <10 calls h^{-1} (1 call per dive) and at low received levels between 123±8 and 134±10 dB re. 1 µPa RMS depending on call type. We conclude that such acoustic crypsis in southern right whales and other baleen whales decreases the risk of alerting potential predators and hence jeopardizing a substantial energetic investment by the mother.

INTRODUCTION

Many baleen whale species are capital breeders that undertake long-distance annual migrations between high-latitude feeding grounds in summer and low-latitude breeding grounds in winter (Lockyer, 2007). For the slowly reproducing baleen whales, producing and nursing a calf is a large energetic investment (Christiansen et al., 2018) that may be compromised by predation from eavesdropping killer whales (*Orcinus orca*) (Pitman et al., 2015). The underlying reasons for the long-range migrations to coastal low-latitude breeding grounds by pregnant baleen whales have been proposed to include (i) reduced heat loss of calves in the warmer waters on the breeding grounds (Clapham, 2001, but see Corkeron and Connor, 1999), (ii) skin regeneration (Durban and Pitman, 2012) and (iii) a lower predation risk on newborn calves (Corkeron and Connor, 1999), involving the use of shallow-water coastal areas as a refuge from potential predators (Ford and Reeves, 2008).

Many migrating baleen whales exhibit behaviours, such as seeking shallow water in the presence of killer whales, that could have evolved as a response to predation on newborn calves and the risk of losing a substantial energetic investment (Ford and Reeves,

2008; Reeves et al., 2006). Migrating mother–calf pairs of grey whales (*Eschrictus robustus*), right whales (*Eubalaena* spp.) and humpback whales (*Megaptera novaeangliae*) move close to shore in shallow waters while on their breeding grounds, compared with conspecific adults unaccompanied by a calf (Whitehead and Moore, 1982; Payne, 1986; Swartz, 1986; Pack et al., 2017). Specifically, on their breeding grounds, southern right whale (*Eubalaena australis*) mother–calf pairs primarily reside in very shallow water of 5–10 m depth close to shore, in close proximity to or in the surf zone (Payne, 1986). However, little is known about potential advantages and risks of bringing newly born calves within metres of the breaking waves in a low-visibility (<20 m), acoustically noisy environment such as South Australian breeding habitats, with the risk of stranding (Australian Government Species Profile and Threats Database; Groom and Coughran, 2012).

On the breeding ground, the contact between baleen whale mother and calf is critical to ensure calf protection, access to milk and maternal care, all of which increase the chances of calf survival and augmented maternal fitness. The use of acoustic communication between mother and calf in a low-visibility habitat may therefore be crucial for maintaining contact and facilitate reunion in the case of separation (King et al., 2016; Videsen et al., 2017). However, the use of acoustic signals has the risk of revealing the location of the vulnerable calf to possible predators such as killer whales or sharks (Durban and Pitman, 2012; Pirzl and Burnell, 2005; Pitman et al., 2015). Recently, it has been shown that humpback whale mother–calf pairs employ cryptic behaviours on the breeding grounds to decrease a potential risk of predation and minimize the risk of losing the considerable energetic investment by their mother (Videsen et al., 2017).

In this study, we address the acoustic behaviour of southern right whale mother–calf pairs by quantifying call parameters on a breeding ground in Western Australia, as well as the behavioural context of the acoustic signals. Specifically, we hypothesised that acoustic signals of mother–calf pairs are frequent (i.e. >1 call per dive) but produced at low amplitudes, to facilitate contact in low-visibility habitats while decreasing the risk of alerting eavesdropping killer whales. Finally, we investigated the potential for acoustic masking in or close to the surf zone, which may benefit mother–calf pairs by leading to a high level of acoustic crypsis from predators.

MATERIALS AND METHODS

Data collection

Research was approved by Aarhus University, Denmark (IACUC) and carried out under research permits from the Western Australian Department of Parks and Wildlife (#SF010712 and #08-000694-2) and a Murdoch University animal ethics permit (#R2820/16). Data were collected in Flinders Bay, south-west Western Australia (34° 20′S, 115°15′E) in July–August 2016 and August 2017. This region is a re-emerging breeding ground for the Australian southern right

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whale [*Eubalaena australis* (Desmoulins 1822)] population (Australian Government Conservation Management Plan 2011–2021), where mother–calf pairs generally aggregate <1 km offshore in shallow water (<10 m) close to or in the surf zone. Mother–calf pairs were approached with a 5.5 m aluminium-hulled boat for deployment of DTAG3 (Johnson and Tyack, 2003) using the methods described in Videsen et al. (2017). The tagging approach was initiated when mother–calf pairs were observed to be logging or travelling slowly. Prior to starting our tagging approach, we observed the behaviour of the mother–calf pair for 1 h, maintaining a distance of >200 m. When tagging, the mother–calf pair were approached parallel from behind at slow speeds (<2 knots) with the boat in forward idle. The reaction to tagging was mild for all mothers and calves. The typical reaction to tagging was a slow dive, with the calf moving into a back-riding position, while the pair moved slowly away from the tagging boat. After a short period of time (about 15 min) during which the whales were diving slowly, the mother–calf pair resumed their original behaviour. During the field season of 2017, both mothers and calves were approached for tagging; however, for tagged calves [Table S1; age 0–3 months (Christiansen et al., 2018)], the duration of a deployment lasted only 5–42 min, as tags quickly detached because of frequent body contact between mothers and calves, typically initiated by the calves (Nielsen et al., 2019). Accordingly, no data from the tagged calves were used for further analyses. For the lactating females, one tag stayed on until pre-programmed release (20 h), while the rest detached prematurely, likely due to close body contact between the mother and calf. This was verified by a large peak in both minimum specific acceleration (MSA) and sound level at the time when the tag detached, which indicated direct physical contact with the tag. The DTAG3 used in this study sampled pressure, 3-axis magnetometers and accelerometer (dynamic range of ±2 g) data at a predetermined sampling rate of 200 Hz, and 16-bit resolution. Sound was recorded by two hydrophones in the tag at a sampling rate of 120 kHz, 16-bit and a flat (±2 dB) frequency response between 0.04 and 45 kHz, and a clip level of 172 dB re. 1 µPa.

Data analyses

Dives were determined based on the pressure measurements of the tag (62.9 h from nine whales), and a depth threshold of 1.5 m was set to distinguish dives from occasional short duration submergence due to swell movements. During dives, MSA was estimated from the acceleration by taking the norm in three axes and subtracting the strength of the gravitational field of the earth (i.e. $9.81\ \mathrm{m\ s^{-2}}$) (see Simon et al., 2012). The orientation of the tag was converted to the orientation of the whale throughout deployments (Johnson and Tyack, 2003). Minimum specific acceleration was used as a proxy for activity of the tagged animal. For each dive the median normalised MSA (nMSA) was calculated by dividing the median MSA of each dive with the median MSA for all dives with the same tag placement, to account for acceleration differences arising from differences in tag placement between tagged animals. Shifts in tag placement during a deployment were determined based on the 3-axis accelerometer data.

Whale sound analyses

Sound recordings were examined in 15 s sequences both acoustically and visually in a spectrogram display (Hamming window, N for FFT: 4096–8192, 90% overlap). Start time and duration of recorded sounds were marked and identified. Sounds were detected as either harmonic or non-harmonic vocalisations in line with established definitions (Dombroski et al., 2016; Webster

et al., 2016), where harmonic cues had either an up- or down-sweep in frequency compared with non-harmonic sounds (Fig. 2). Additionally, rubbing sounds were identified as high-amplitude, broadband sounds that occurred concomitantly with large peaks in the jerk (differential to the acceleration) (Videsen et al., 2017), which suggests that rubbing sounds are an indication of physical contact between mother and calf. Only sounds recorded during dives, constituting ∼30% of the durations of recordings, were included in this study, because of the high probability of missing sounds when the whale was at the surface. Call rates were calculated based on all calls regardless of signal-to-noise ratios (SNRs) and were accordingly expressed as calls per unit time underwater or as calls per dive.

Sound cues with SNRs >10 dB were retained for further analyses. The SNRs of sound cues were calculated as the difference between root-mean-square (RMS) ambient noise level and the RMS sound level in a window covering the entire duration of calls on a dB scale. For each call, the RMS ambient noise level was estimated from the ambient noise prior to each call. This was done from the 50th percentile RMS from 20 successive 100 ms sequences starting 100 ms before each vocalisation. Prior to the RMS calculations, the recordings were corrected for the 400 Hz single-pole high-pass filter in the DTAGs, using a script from the DTAG MATLAB toolbox that corrects for the impulse response of this filter. Both call types and ambient noise were low-pass filtered at 3 kHz with a 4th order Butterworth bandpass filter prior to the RMS calculations. Before estimating RMS bandwidth ($\mathrm{RMS_{BW}}$) and centroid frequency (CF) a rectangular Tukey window with a taper length defined as samples 10 ms before and after the signal divided by the length of the signal was applied to the sound signal. $\mathrm{RMS_{BW}}$ and CF were calculated using the established definitions (Au, 1993; Madsen and Wahlberg, 2007). Due to the close proximity of mother–calf pairs (<15 m) it was not possible to determine if calls were produced by the mother or the calf and calls were therefore treated as the acoustic output of the group. Other whales in the vicinity may also have been recorded on the tag during the deployments. However, the number of conspecifics in Flinders Bay during the time of data collection was low. Specifically, seven mother–calf pairs and one single adult whale were observed in the Bay in 2016 and four mother–calf pairs and three single adults were observed in 2017. Only three mother–calf pairs and two single adults were re-sighted across the field season, indicating that the whales had either left the bay after first observation or moved further East in the bay. The distance between individual whales observed in the bay on the same day was generally more than 1–2 km. Vocalisations from non-focal southern right whales at a distance of 1.5 km from the tag would lead to received levels on the tag of between ∼74–99 rms re. 1 µPa m, using source levels (SLs) of 137 and 162 dB rms re. 1 µPa m (Parks and Tyack, 2005). As these numbers are much lower than the recorded noise levels, non-focal calls produced at these ranges and SLs would not have been included in the analyses as we used an SNR of 10 dB. This would therefore make it unlikely that non-focal calls have been included in the analyses. Further, focal follows were conducted from the boat at distances >200 m with the engine switched off for a duration of about 2 h following tagging, while the behaviour of the focal mother–calf pair was recorded visually.

To test the hypothesis that vocalisations are used to keep contact during active dives (Videsen et al., 2017), we examined the presence of acoustic cues and rubbing sounds against the nMSA of all dives (N=598), in separate models. This was done using a binomial (logit link function) generalised linear mixed model (GLMM; lme4 package in R software v3.4.3) with the presence of acoustic signals

(calls or rubbing sounds) during dives modelled as a binomial response variable and nMSA and duration of dives as fixed effects. To account for individual variation in the date, ID was included as a random effect in the model. The final 15 h of animal 'ea230a' was left out of acoustic analyses due to a discrepancy in the accelerometer data occurring 6 h into the deployment, which led to an increasing mismatch between the acoustic and accelerometer data. This was verified by matching acoustic recordings with the sensor data for each surfacing.

Ambient noise analyses

A SoundTrap (Ocean Instruments, Auckland, New Zealand) was deployed for 24 h to estimate the ambient noise in the environment in relatively calm weather (34°18′56″S, 115°15′07″E). The SoundTrap was deployed with weights and buoys at 4 m depth in an area with a water depth of 8 m and recorded continuously at a sampling rate of 288 kHz, rendering a flat (±2 dB) frequency response between 20 Hz and 100 kHz. The masking of vocalisations from the ambient noise was estimated using the 24 h SoundTrap recording by calculating the mean RMS noise level over the 250 Hz octave level band covering the peak frequencies of the calls recorded.

RESULTS AND DISCUSSION

A total of nine lactating southern right whales were tagged in Flinders Bay, Australia, on 25 July–6 August 2016 and 17–23 August 2017. A total of 62.9 h of data were recorded with whales wearing the tags for a mean (±s.d.) duration of 7±5.2 h (Table S1). The mother–calf pairs were generally found in close proximity to the coast (<1 km) at depths of 5–10 m. Out of the 62.9 h of on-animal recordings, the tags were out of the water for ~30% of the time, when the whales were at the surface, during which acoustic

signals could not be reliably identified. For a total of 793 dives the median dive duration was 2.3 min [interquartile range (IQR): 1–5 min; Table S1] and the mean (±s.d.) maximum depth of dives was 4.3±2.4 m (Table S1; Fig. 1). Similarly to the suckling dives reported for humpback whales by Videsen et al. (2017), the general dive pattern of resting southern right whale mothers was slow, shallow dives (<5 m) of ~5 min duration, followed by extended periods of remaining stationary at the surface (i.e. logging behaviour). Conversely, active dive behaviour included deeper dives (5–10 m) and short surfacing times (Fig. 1).

Vocal behaviour and masking noise

A total of 189 harmonic and 379 non-harmonic sounds (Fig. 2A,B) were classified and used to calculate call rate. 155 of 204 (~75%) harmonic and 242 out of 391 (~60%) non-harmonic sounds had SNRs>10 dB and were kept for acoustic analyses. The average call rate of both non-harmonic and harmonic calls was 6±7 calls h^{-1} (Table S2). Given an overall call rate of 0.75 calls per dive, it is likely that southern right whale mother–calf pairs employ a similar strategy to that observed in humpback whale mother–calf pairs, where contact is primarily visual and tactile, rather than acoustic, in contexts associated with energy transfer, i.e. suckling (Thomas and Taber, 1984; Videsen et al., 2017). Furthermore, the probability that a call was recorded during a dive was significantly affected by the nMSA (GLMM, d.f.=1, χ^2=5.05, P=0.02) and duration (GLMM, d.f.=1, χ^2=4.72, P=0.03) of the dive, with calls being more likely to occur during longer dives with higher nMSA (Fig. 3A,B). Thus, similar to what was found by Videsen et al. (2017) for humpback whales, acoustic signals of southern right whale mother–calf pairs in this study are more likely to be recorded during dives with a higher activity level which are unlikely to be associated with nursing. Instead, nursing dives in southern right whales are likely to
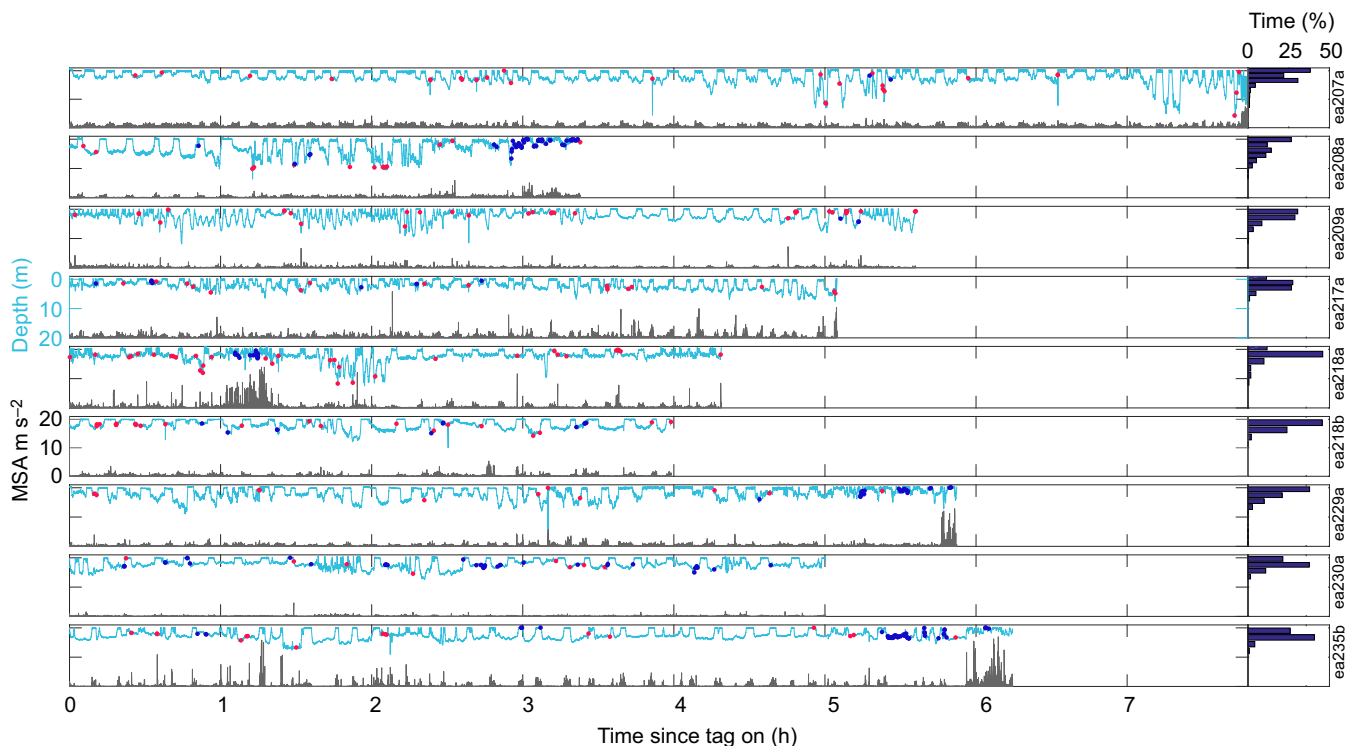

Fig. 1. Dive behaviour of lactating southern right whales. Depth profiles (left) and the corresponding histogram of dive depth distribution (right) for lactating southern right whales (n=9). Depth profiles (blue lines) include minimum specific acceleration (MSA, grey lines) and the recorded acoustic signals (harmonic and non-harmonic, dark blue points) and rubbing sounds (red points).
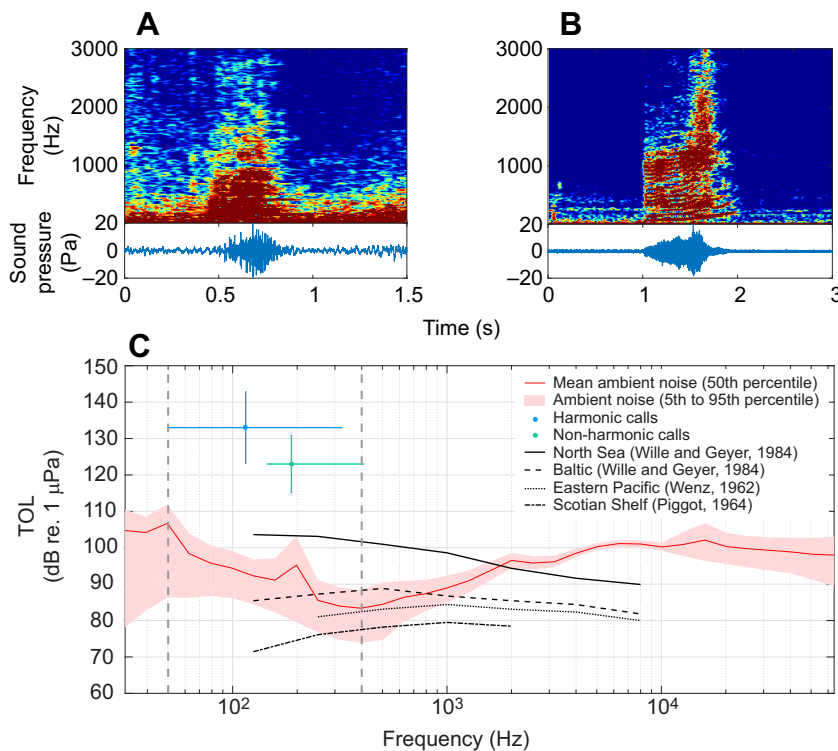
Fig. 2. Spectrograms of harmonic and non-harmonic sounds and ambient noise levels on the breeding ground. Spectrograms (Hamming window, nfft: 4096, 90% overlap) of a (A) non-harmonic sound and a (B) harmonic sound, with the waveform of each sound shown below. (C) Ambient noise level (dB re. 1 μPa) as a function of third octave level (TOL) frequency bands with mean and 5th and 95th percentiles. Black lines represent recordings from coastal habitats (adapted from Madsen et al., 2006): North Sea (Wille and Geyer, 1984; 28 m depth), Baltic (Wille and Geyer, 1984; 28 m depth), Eastern Pacific (Wenz, 1962; 45 m depth), Scotian Shelf (Piggott, 1964; 36 m depth). Vertical grey dashed lines indicate the recorded frequency bandwidth. The range of the received level and RMS bandwidth of both harmonic and non-harmonic calls are indicated in blue and green, respectively.

be related to low activity levels of the mother, where she will remain stationary, often submerged, while the calf dives down beneath her to suckle (Smultea et al., 2017; Thomas and Taber, 1984; Zoidis and Lomac-Macnair, 2017). This indicates that acoustic signals are cohesion calls for maintaining contact when moving. Furthermore, the infrequent acoustic signals of southern right whale mother–calf pairs in this study is in accordance with these mother–calf pairs remaining in close proximity (<15 m), which is likely to be within visible range, of each other for most of the time (>90%) whilst on their breeding grounds (Nielsen et al., 2019).

Interestingly, the probability of recording a rubbing sound was not affected by the nMSA (GLMM, d.f.=1, χ^2=1.30, P=0.25; Fig. 3C). However, the duration of dives (GLMM, d.f.=1, χ^2=29.15, P<0.001; Fig. 3D) affected the probability of rubbing being recorded, with rubbing being more likely to occur during longer dives (Fig. 3D). This indicates that rubbing occurs during both active and resting dives, and that physical contact may have an important function of maintaining contact between the mother and her calf to compensate for the low calling rates.

Non-harmonic sounds had an overall mean (±s.d.) received level of 123±8 dB re. 1 μPa RMS, while harmonic sounds had an overall mean received level of 133±10 dB re. 1 μPa RMS. Also, sounds recorded during focal follows had a received level of 124.3±5.5 and 120.8±3.8 dB re. 1 μPa RMS, while sounds recorded after focal follows had ended had a received level of 122.9±8.4 and 134.1± 9.9 dB re. 1 μPa RMS, for non-harmonic and harmonic sounds, respectively. The substantial difference in received levels of harmonic sounds may indicate that non-focal animals were recorded on the tag. It also suggests that the harmonic calls in particular are weaker than the reported overall mean (120 compared with 133 dB re. 1 μPa). However, only six harmonic sounds were recorded during the periods of focal follow, compared with 160 sounds recorded after. The average CF and RMS$_{BW}$ (median and

inter-quartile range, IQR) for non-harmonic sounds were 188 (IQR: 137–320) Hz and 249 (IQR: 144–411) Hz, respectively, while for harmonic sounds they were 115 (IQR: 96–216) Hz and 109 (IQR: 50–326) Hz, respectively (Table S2; Fig. 2). Given the distance of more than 1 km between individuals in the study area, it is unlikely that the recorded received levels arose from other individuals than the tagged mother–calf pairs. Variability in the recorded amplitudes may stem from variations in call outputs, mother–calf spacing and from physical effects of recording in the near field and shadowing effects of the body of either the tagged female or her calf. It is accordingly not possible to calculate source levels. However, if assuming that these low frequency calls indeed are produced by the mother–calf pair that are within a distance of 15 m of each other >90% of the time (Nielsen et al., 2019), it is possible to evaluate the magnitude of the resulting active space if the ambient noise that will mask such communication is known.

The ambient noise level was estimated in calm seas to be 103± 11 dB re. 1 μPa RMS in the frequency band overlapping the frequency band of mother–calf calls (Fig. 2C). At such ambient noise levels, the differences between the ambient noise levels and the recorded southern right whale call amplitudes were on average 30 and 20 dB, for harmonic and non-harmonic calls, respectively. Assuming SLs are around 150 dB re. 1 μPa (Parks and Tyack, 2005) call signals would be below the ambient noise level (SNR<0) at distances below 200 m at the ambient noise levels reported here. This supports our prediction that the acoustic environment in and close to the surf zone increases the acoustic crypsis of mother–calf pairs.

While such low output calling comes at the risk of increasing mother–calf separation, it greatly reduces the risk of detection by eavesdropping killer whales. Although the risk of killer whale predation on baleen whales and the ecological role of such prey remain controversial (e.g. Williams et al., 2004; Mehta et al., 2007; Pitman et al., 2015), even a minor risk of predation and loss of large
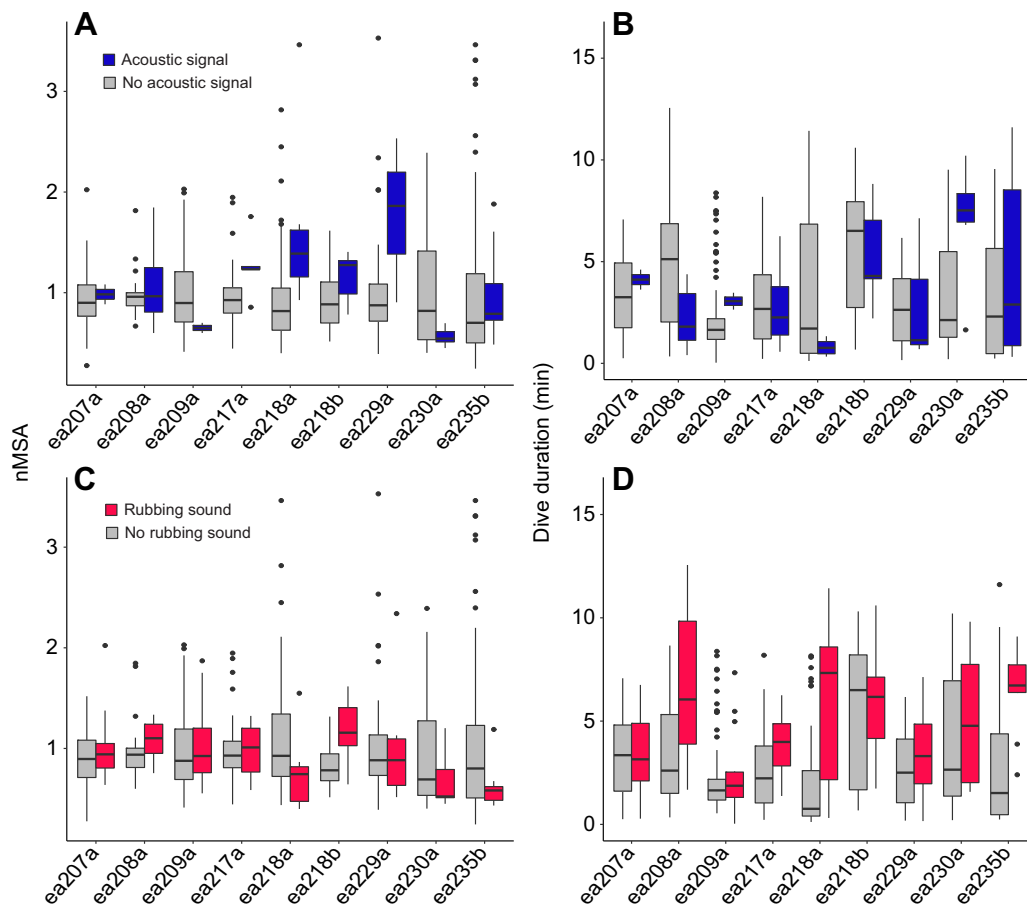
Fig. 3. Box plots of normalised specific acceleration (nMSA) and dive durations. (A) nMSA (GLMM, d.f.=1, χ^2=5.05, P=0.02) and (B) dive durations (GLMM, d.f.=1, χ^2=4.72, P=0.03) for dives where acoustic signals were recorded (blue, n=103) and dives where no acoustic signals were recorded (grey, n=496) for each deployment. (C) nMSA (GLMM, d.f.=1, χ^2=1.30, P=0.25) and (D) dive durations (GLMM, d.f.=1, χ^2=29.15, P<0.001) for dives where rubbing sounds were recorded (red, n=127) and dives where no rubbing sounds were recorded (grey, n=471). Black dots represent outliers.

energetic investments have the potential of affecting the behaviour of a slowly reproducing species such as the southern right whale (Corkeron and Connor, 1999; Ford and Reeves, 2008). The low received levels reported here are similar to received levels of tag recordings of humpback whale mother–calf communication (Videsen et al., 2017), indicating that several species of baleen whales communicate to mediate behavioural transitions and maintain contact with their offspring but do so at low output levels to reduce the potential risk of alerting eavesdropping predators or male conspecifics that may compromise calf fitness (Corkeron and Connor, 1999; Ford and Reeves, 2008; but see Fournet et al., 2018). A similar cryptic acoustic behaviour has been observed in species across the animal kingdom, including moths (Nakano et al., 2009), birds (Dabelsteen et al., 1998) and ungulates (Padilla de la Torre and Mcelligott, 2017), where low-amplitude signals are used to balance important interactions, such as courtship, group cohesion or nursing, against the risk of being detected by eavesdroppers.

The elevated ambient noise levels reported here for a calm 24 h period (Fig. 2C) originate from mother–calf pairs primarily occupying areas in close proximity to the shoreline in or right behind the surf zone, where they face an apparent risk of separation or stranding (Australian Government, Department of the Environment and Energy, 2016). Here, we show that the noise in the surf zone and the low output levels of infrequent calls offers

southern right whale mother–calf pairs a much smaller risk of acoustically mediated interception by killer whales compared with quieter habitats. We therefore speculate that the risks related to the apparently rough nursing environment is offset by the anti-predatory advantages highlighted here in concert with the added benefits of defending a calf from attack in shallow water (Ford and Reeves, 2008; Swartz, 1986).

In summary, acoustic signals recorded between southern right whale mothers and calves were infrequent and more likely to occur during active dives, indicating that these signals are used as cohesion calls that function to maintain contact when the whales are moving or become separated, rather than a signal that initiates suckling. Furthermore, the acoustic signals were recorded at low amplitudes in a habitat with elevated ambient noise levels due to breaking waves, which, in combination, lead to a small active space. As such, the ambient noise of the coastal shallow-water habitat in combination with low call amplitudes intensifies the challenge for mother–calf pairs of maintaining cohesion and reuniting after separation by use of acoustic signals, perhaps explaining why they consistently maintain close contact within approximately a body length of the mother. However, importantly, low-amplitude calling also reduces the risk of alerting eavesdropping killer whales of the location of the newborn calf, suggesting that this acoustic crypsis may have evolved as an antipredator strategy.

Supplementary information
Supplementary information available online at
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