# Short moan call reveals seasonal occurrence and diel-calling pattern of crabeater seals in the Weddell Sea, Antarctica

Fannie W. Shabangu[a,b*] and Russell A. Charif[c]

[a]*Fisheries Management, Department of Environment, Forestry and Fisheries, Foreshore, Cape Town, South Africa*

[b]*Mammal Research Institute Whale Unit, University of Pretoria, Private Bag X20, Hatfield, Pretoria 0028, South Africa*

[c]*Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, NY, 14850, USA*

*E-mail: fannie.shabangu@yahoo.com

Notes on contributors

FWS participated in the design of the study and drafted the manuscript; FWS collected field data; FWS and RAC performed the acoustic data analyses; FWS carried out the statistical analyses; FWS and RAC wrote the manuscript. Authors gave final approval for publication.

## Abstract

Crabeater seals (*Lobodon carcinophaga*) are an important component of the Southern Ocean as they are the most abundant pinniped species in this krill-based ecosystem; however, their acoustic repertoire and ecology remains to be fully described. Seasonal occurrence and diel-calling pattern of crabeater seal off the Maud Rise, eastern Weddell Sea, are described using passive acoustic monitoring data collected over eight months (mid-January to mid-September) in 2014. We describe a new call type of crabeater seals, the short moan call (mean 90% duration: 2.2 ± 0.3 (SD) s, peak frequency: 596.5 ± 109.4 Hz, and frequency range: 122–1024 Hz), which was the only detected call type and 1871 calls were enumerated. Those crabeater seal calls were detected from April until mid-September (with peak in calling around September), which coincided with the appearance of sea ice. Short moan call rates were highest at night in August (i.e., 6.4 calls per minute) and September, and showed no diel variations for April through July. Distance to the sea ice edge and month of the year were the most important predictors of call occurrence and call rates of crabeater seals. This study highlights the Maud Rise as a useful habitat for this species.

Keywords: Crabeater seals; seasonal occurrence; diel behaviour; short moan call, acoustic repertoire

## Introduction

As the most abundant and widespread ice-inhabiting pinniped in the Southern Ocean and worldwide (Bengtson 2009; Bengtson et al. 2011; Hückstädt 2015), crabeater seals are one of the key species of the Southern Ocean krill-based food web (Southwell et al. 2008; Brault et al. 2019). Satellite linked dive recorders and compound-specific isotopes indicate that the distribution and foraging behaviour of crabeater seals corresponds well with the life history of their prey, Antarctic krill (*Euphausia superba*) (Nachtsheim et al. 2017; Brault et al. 2019). Unfortunately, most of the available information about crabeater seals is from ship-based visual observations using transect methods that provide limited information on their distribution, habitat use and responses to climate change (e.g., Southwell et al. 2008; Botta et al. 2018). Furthermore, Hückstädt (2015) states that additional research is needed on the population size, distribution, threats and population trends of crabeater seals. However, due to its widespread occurrence and very large population size, the International Union for the Conservation of Nature Red List of Threatened Species classifies crabeater seals as Least Concern (Hückstädt 2015).

Habitats of crabeater seals are difficult to survey during certain times of the year, as they are inaccessible due to heavy pack ice, remoteness of those areas and the requirement for the use of expensive icebreaker ships and/or helicopters (Stirling and Kooyman 1971; Stirling and Siniff 1979; Thomas and DeMaster 1982; Southwell et al. 2003; Bengtson et al. 2011). Passive acoustic monitoring serves in this regard as a reliable and cost effective method to study the year round ecology of these marine mammals (e.g., Klinck et al. 2010; van Opzeeland et al. 2010). Crabeater seals produce two kinds of calls during the breeding season (late September through late December (Laws et al. 2003; Southwell et al. 2003)): the low (mean duration: 2.5 s, frequency range: 126–4269 Hz) and high (mean duration: 2.6 s, frequency range: 835–6671 Hz) moan calls (Stirling and Siniff 1979; Rogers 2003; McCreery and Thomas 2009; Klinck et al. 2010; van Opzeeland et al. 2010). The low moan call (Klinck et al. 2010) corresponds to the long groan call described by McCreery and Thomas (2009). Grunts, whistles, screeches and short groans are produced during the non-breeding season, and the function of these sounds remain unclear but some are likely associated with foraging (McCreery and Thomas 2009).

Up to now, there were five publicly available acoustic studies of crabeater seals (Stirling and Siniff 1979; Thomas and DeMaster 1982; McCreery and Thomas 2009; Klinck et al. 2010; van Opzeeland et al. 2010). Three of the five publications were based on short-term recordings (Stirling and Siniff 1979; Thomas and DeMaster 1982; McCreery and Thomas 2009) whereas the other two studies were based on long-term recordings off the Eckström Iceshelf, eastern Weddell Sea (Klinck et al. 2010; van Opzeeland et al. 2010). Erbe et al. (2017) reported crabeater seal low moan call as an “underwater burst-pulse sound” recorded in Antarctica without giving any acoustic characteristics of the call. Many aspects of the acoustic ecology of this species remain to be investigated, including the completeness of the known call type repertoire, variations of call rates in relation to changing environmental conditions and acoustic functions of each crabeater seal sound.

Here we describe a new type of crabeater seal call, the short moan call, and use it to describe the seasonal occurrence and diel-calling pattern of this species in association with sea ice off the Maud Rise, Antarctica. Information on seasonal occurrence and behaviour produced through this study will support future conservation and management efforts of this seal species in the Southern Ocean as a long term acoustic presence is established in the Maud Rise.

## Materials and Methods

### *Acoustic recordings*

Passive acoustic monitoring data were collected off the Maud Rise, eastern Weddell Sea (Figure 1) as part of the South African Blue Whale Project (SABWP; Shabangu et al. 2019). The Maud Rise is a seamount centred at 65°S, 2.5°E in the eastern Weddell Sea of the Southern Ocean, and the Autonomous Underwater Recorder for Acoustic Listening (hereafter called recorder) Model 2 version 04.1.3 (AURAL; Multi-Electronique Inc., Canada) rated to 300 m depth was deployed to record acoustic data on the centre of the seamount (Figure 1). The recorder was positioned at 250 m below the sea surface, which corresponds to the sound fixing and ranging (SOFAR) channel at 65°S (Garner 1967), and secured on a dedicated mooring fixed at a water depth of 1267 m. The mooring of the recorder was located ~667 km from the nearest landmark on the Antarctic continent (Figure 1). The recorder was deployed from 12 January 2014 to 17 January 2015 but it stopped recording on 17 September 2014 due to battery depletion and only eight months of acoustic data were recorded. A sampling rate of 2048 Hz was used for a single block of 25 minutes per hour (i.e. sampling scheme) throughout the day for the whole deployment period to preserve the battery life.

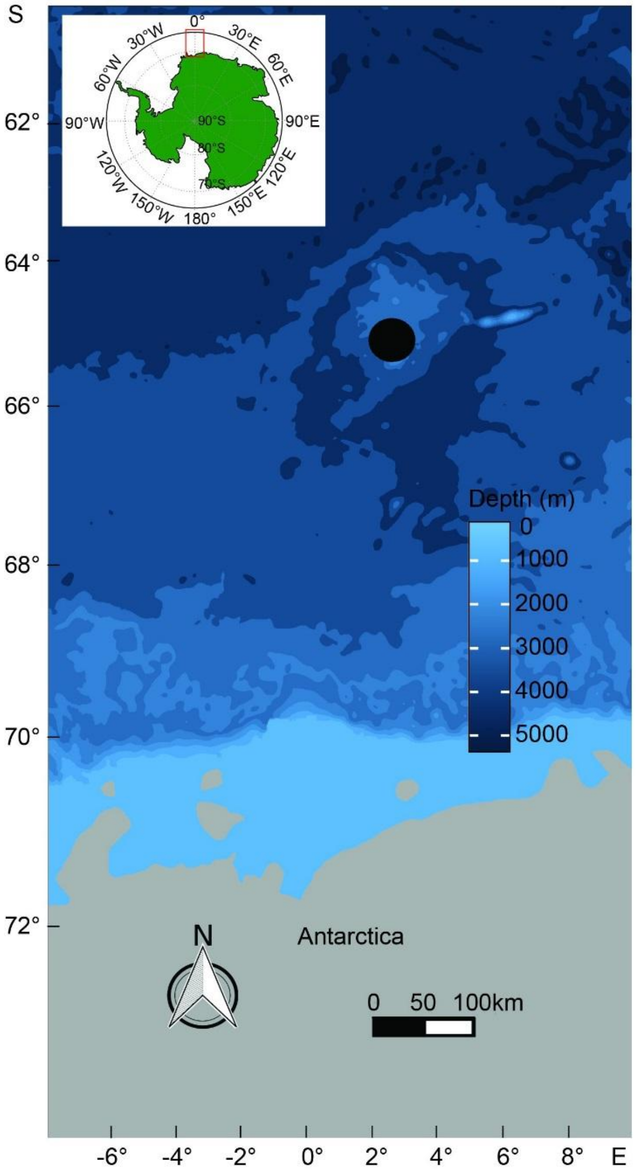

**Figure 1.** Position of the recorder mooring (●) off the Maud Rise, eastern Weddell Sea.

### *Detection of calls*

Following the evaluation of acoustic characteristics of calls relative to previously published descriptions (Stirling and Siniff 1979; McCreery and Thomas 2009; Klinck et al. 2010) and confirmation from a colleague (2019 email conversation from H Klinck to FWS; unreferenced); we consider calls detected here to be produced by crabeater seals. Calls of crabeater seals (Figure 2(a–d)) were visually detected (using spectrograms) and reviewed aurally (when calls were visually identified) from the whole dataset in Raven

Pro (Bioacoustics Research Program 2017). Previously described types of crabeater seal calls are characterized by a rapidly pulsed structure that results in sidebands when calls are viewed spectrographically (Klinck et al. 2010). Sounds that spectrally resembled crabeater seal calls but had harmonics instead of sidebands and were longer in duration than normal crabeater seal calls (McCreery and Thomas 2009; Klinck et al. 2010) were not considered as crabeater seal sounds due to the uncertainty with respect to their source. Call rates were calculated for each sampling interval by counting the number of calls in each sampling interval and then dividing by 25, to give calls per minute. A sampling interval was defined as the time between which data was recorded, which was 25 minutes. Acoustic presence or absence was scored for each sampling interval. Acoustic presence refers to instances when one or more calls were detected within a sampling interval, whereas acoustic absence refers to the lack of calls in a sampling interval. Monthly proportion of species occurrence was calculated as the number of sampling intervals with presence of calls divided by the total number of sampling intervals per month. Austral seasons of the year are used to define our data: summer (December to February), autumn (March to May), winter (June to August), and spring (September to November). Since time of day is a circular variable, diel mean values of call rates per season were smoothed through penalized cyclic cubic regression splines (Wood 2017) in generalized additive models (GAMs; Guisan et al. 2002).

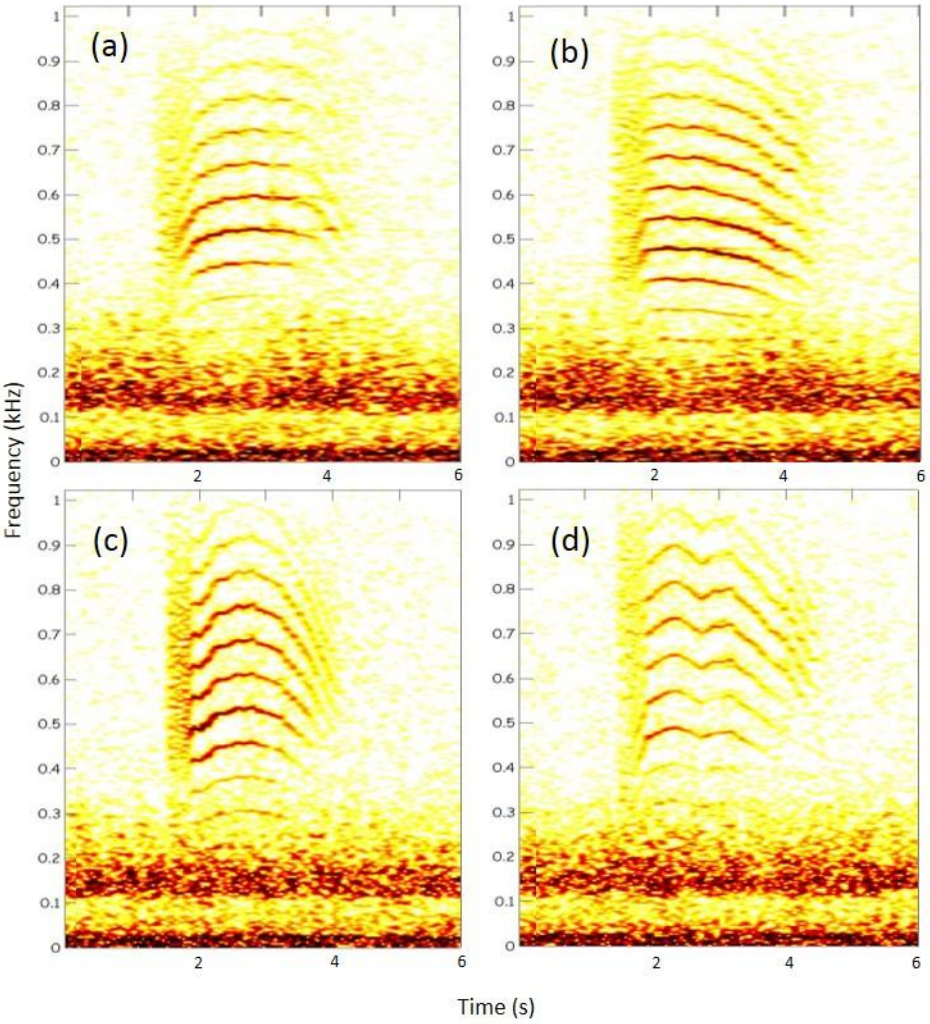

**Figure 2.** Four examples of short moan calls (a–d) recorded in September off the Maud Rise, Antarctica. Spectrograms were generated in XBAT (Figueroa 2006), using parameters: (a) – (c) frame size 0.4 s, 25% overlap, FFT size 630 points, Hann window; (d) frame size 0.2 s, 25% overlap, FFT size 530 points, Hann window.

### *Characterisation of calls*

The minimum, peak and maximum frequencies (Hz), duration (seconds) and pulse repetition rate (PRR) of calls of crabeater seals (Figure 3) were measured from 275 calls with high signal-to-noise ratio (>10 dB) in Raven Pro. Peak frequency was defined as the frequency of the spectrogram cell with the highest power density in the selection. The 90% duration and 90% bandwidth of the call were measured by manually drawing a box around the call, then using the 5% and 95% measurements for time and frequency to determine the bounds of the box that encompasses 90% of the energy in the call (Figure 3(a)). This approach of using 90% of the energy distribution in frequency and time to measure features less sensitive to background noise is the same as that used by Klinck et al. (2010) in a previous description of crabeater seal calls. Mellinger and Bradbury (2007) explain the rationale and background for this approach. We also included in our measurements the 0% minimum frequency, 100% maximum frequency and 100% duration of the call (Figure 3(a)) for easier comparison with results of a previous study of McCreery and Thomas (2009). To measure the PRR, we used the frequency spacing between sidebands in the spectrogram (Figure 3(b)). When a tonal carrier signal is rapidly pulsed or amplitude-modulated, sidebands (spectral peaks) appear in the spectrogram below and above the carrier whenever the spectral analysis window is long enough to encompass several or many pulses. The frequency interval between adjacent sidebands is equal to the rate of amplitude modulation or pulse repetition (Gerhardt 1998).

Since the PRR changes over the course of the call, we made the PRR measurements at the centre time of the call (i.e. the median time of total energy distribution for the call, with 50% of the energy in the selection before this time, 50% after) as there were fully formed and well-spaced spectral peaks (Figure 3). PRR measurements at the centre time of the call served as an objective method of determining PRR. Spectrogram slice view in Raven Pro was used to measure the difference, in Hz, between the sidebands adjacent to the peak frequency (Figure 3(b)). Because there was a lot of low-frequency background noise, the acoustic data were high-pass filtered at 200 Hz to enable clear evaluation of the structure of the pulse in the waveform.

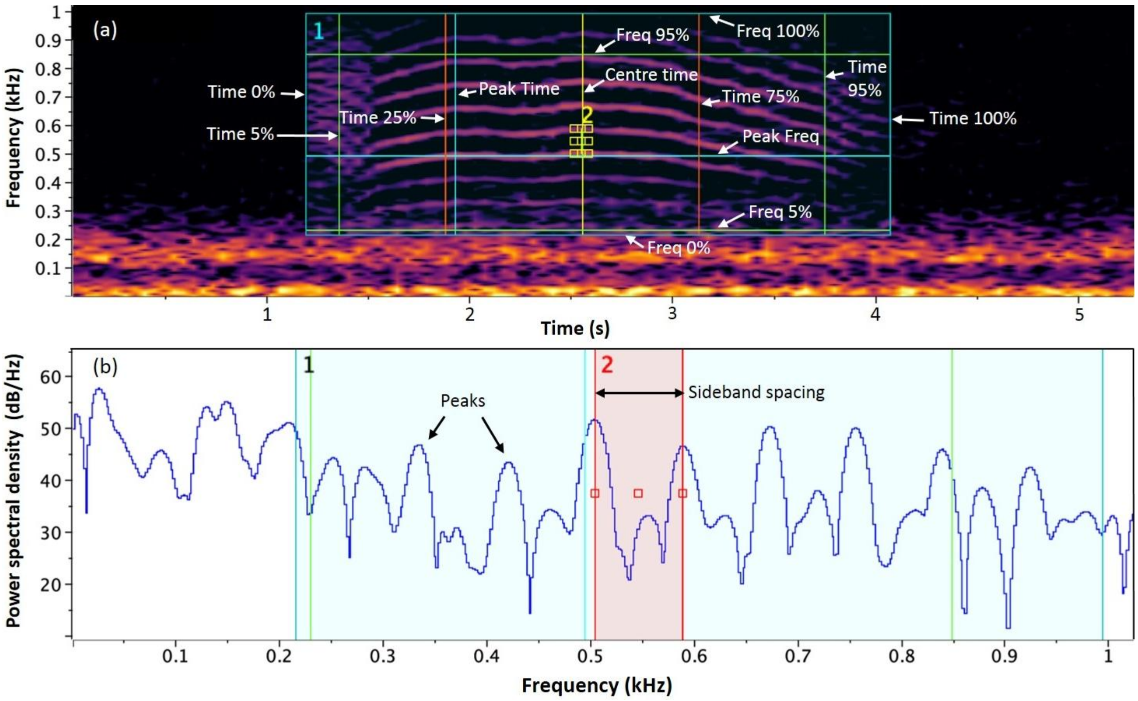

**Figure 3.** (a) Spectrogram of crabeater seal short moan call illustrating all the call measurements conducted in this study, and (b) spectrogram slice from the centre time used to measure the sideband spacing from one spectral peak to the next. Numbers 1 and 2 in (a) and (b) represent the call frequency bandwidth and pulse repetition rate (PRR) measurement position respectively. Small yellow squares in (a) at the centre time delimit the frequency span of selection box 2, used for measuring the PRR in (b). Freq is for frequency, and dB is decibels relative to an arbitrary reference. The PRR at the centre time of the call, given by the sideband spacing in (b), is 84 Hz. Spectrogram parameters: frame size 0.07 s, 50% overlap, DFT size 256 samples, Hann window.

Summary statistics of the call acoustic repertoire were computed using the ‘pastces’ package (Grosjean and Ibanez 2018) in R (version 4.0.1; R Core Team 2020). Welch two sample t-tests were performed to compare the 5% minimum frequency, peak frequency, 90% duration, and PRR between Klinck et al. (2010) measurements and this study using the mean, standard deviation (SD) values and sample sizes provided in each study. Similarly, Welch two sample t-tests were performed between the 0% minimum frequency and 100% duration of McCreery and Thomas (2009) measurements and this study using the mean, SD values and sample sizes provided in each study. Welch two-sample t-tests were used as they do not assume that the variance is the same between the two groups, and were performed using the ‘DescTools’ package (Signorell et al. 2020) in R. GAMs were fitted to evaluate if there was significant interaction between call characteristics (0% minimum frequency, 5% minimum frequency, 95% maximum frequency, peak frequency, 90% duration, 100% duration, and PRR) and months (April through mid-September). GAMs were fitted with Gaussian distributions using the ‘mgcv’ package (Wood, 2001) in R.

### *Sea ice extent*

Monthly sea ice extents were downloaded from the G02135 dataset (Fetterer et al. 2016) at the National Snow and Ice Data Centre data pool server: ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/south/monthly/shapefiles/shp_extent/. From the monthly sea ice extents, the distance of the nearest sea ice edge to the recorder mooring position was measured to determine the effects of sea ice on the acoustic occurrence and behaviour of crabeater seals off the Maud Rise. Daily sea ice concentrations (%) were obtained from the satellite sea ice concentration product of the Advanced Microwave Scanning Radiometer-2 with a 3.1 km grid resolution (Spreen et al. 2008; Beitsch et al. 2014).

### *Modelling predictors of call occurrence and call rates*

Random forest (RF) modelling (Ho 1995; Breiman 2001) was used to investigate the influences of predictor variables (i.e., distance to the sea ice edge (km), time of day (hours) and month of the year) on the seasonal acoustic occurrence and call rates of crabeater seals. Based on generalized variance inflation factors (GVIFs; Fox and Monette 1992), no multi-collinearity was found between predictor variables (month of the year, time of day and distance to the sea ice edge) prior to fitting the RF model as GVIF values were around one. The RF model was chosen for use in this study as it is an ensemble modelling approach that is used in a wide range of problems but mostly classification, regression, time series and survival data with non-parametric inferential properties (Breiman 2001; Hastie et al. 2009; Kane et al. 2014). Furthermore, the RF model has been found to have higher predictive capabilities for modelling the occurrence and behaviour of other marine mammals (Shabangu et al. 2017, 2019, 2020a).

The relative importance of each of the variables in the RF model was determined by measuring the total decrease in node impurities from splitting on the variable, averaged over all trees (Liaw and Wiener 2002). The node impurity was measured by the Gini index, measuring homogeneity from zero (homogeneous) to one (heterogeneous) (Hastie et al. 2009). The changes in Gini coefficients were summed for each variable, and normalized at the end of the calculation. Variables that resulted in nodes with higher purity had a higher decrease in Gini coefficient. In order to expand RF model output interpretability, we computed p-values for the feature importance metric via permutation, whereby variables were permuted and changes in feature importance after permuting was used to measure significance. Significance (p-value) of feature importance values were computed through the method of Altmann et al. (2010).

To perform the RF modelling in R, the ‘randomForest’ package (Liaw and Wiener 2002) was used. The ‘ranger’ package was used as a computational-time-saving method for implementing RF models (Wright and Ziegler 2017) to determine the values of optimal parameter configuration for RF models. The predictive accuracy of each model with different parameter configurations was measured using the area under the receiver operating characteristic curve (AUC). RF models with optimal parameter configurations had the highest AUC values. Optimal parameter configurations for each RF model used to investigate the effect and importance of predictors on crabeater seal occurrence and call rates were: 500 growing trees, default number of variables randomly selected at each tree node were used, and the splitting minimum size of terminal nodes of trees of one were applied.

## Results

### *Call detection output*

A total of 5950 25-minute sampling periods were recorded and examined, which produced a total of 53 hours with short moan calls from the 2479 hours of recorded audio (Table 1). Only 39 days of the 249 sampled days contained short moan calls, and 1871 short moan calls were counted from those days in April through mid-September (Table 1). September had the highest number of days (14) with short moan calls, followed by August with nine days and April had the lowest number of days (one) with short moan calls (Table 1). Short moan calls were the only crabeater seal sounds detected in this acoustic dataset. Short moan calls did not tend to cluster but occurred serially within a sampling interval.

**Table 1**. Summary of the recorded number of days, recorded hours and number of short moan calls per month.

| Month of the year | Number of days recorded | Number of days with short moan calls | Total sampling intervals recorded (hours) | Total sampling intervals with calls (hours) | Total number of calls per month |
|---|---|---|---|---|---|
| January | 20 | 0 | 196.7 | 0 | 0 |
| February | 28 | 0 | 282 | 0 | 0 |
| March | 31 | 0 | 310 | 0 | 0 |
| April | 30 | 1 | 300 | 0.4 | 16 |
| May | 31 | 5 | 310 | 3.4 | 31 |
| June | 30 | 4 | 300 | 3.8 | 66 |
| July | 31 | 6 | 310 | 2.9 | 46 |
| August | 31 | 9 | 310 | 14.3 | 478 |
| September | 17 | 14 | 162.5 | 28.6 | 1234 |
| **Total** | **249** | **39** | **2479** | **53.4** | **1871** |

### *Characteristics of the short moan calls*

Short moan calls have a rapidly pulsed or amplitude-modulated structure (Figure 4). In spectrograms, the rapid pulse rate gives rise to sidebands symmetrically placed below and above a carrier frequency (Figures 3 and 5; Gerhardt 1998). The carrier frequency and associated sidebands of short moan calls initially sweep up in frequency and then down to the end of the call. The inflection point from upsweep to downsweep varies from approximately one quarter to halfway through the call. The rate of the upsweeping and downsweeping varied from call to call (e.g., Figure 2(a–d)). Divergent sidebands were clearly visible at the start of most calls, indicating accelerating pulse rates (Figure 5).

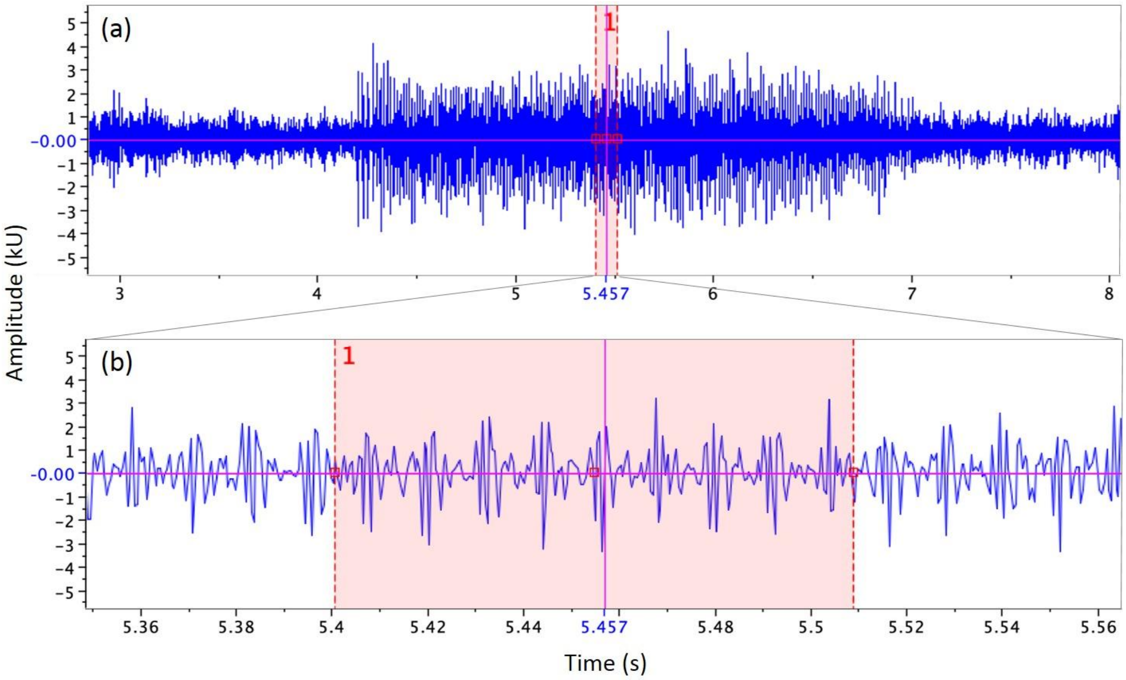

**Figure 4.** Waveforms of acoustic data high-pass filtered at 200 Hz (a) and a zoomed in section of the waveforms (b) of a short moan call, showing pulsed structure.

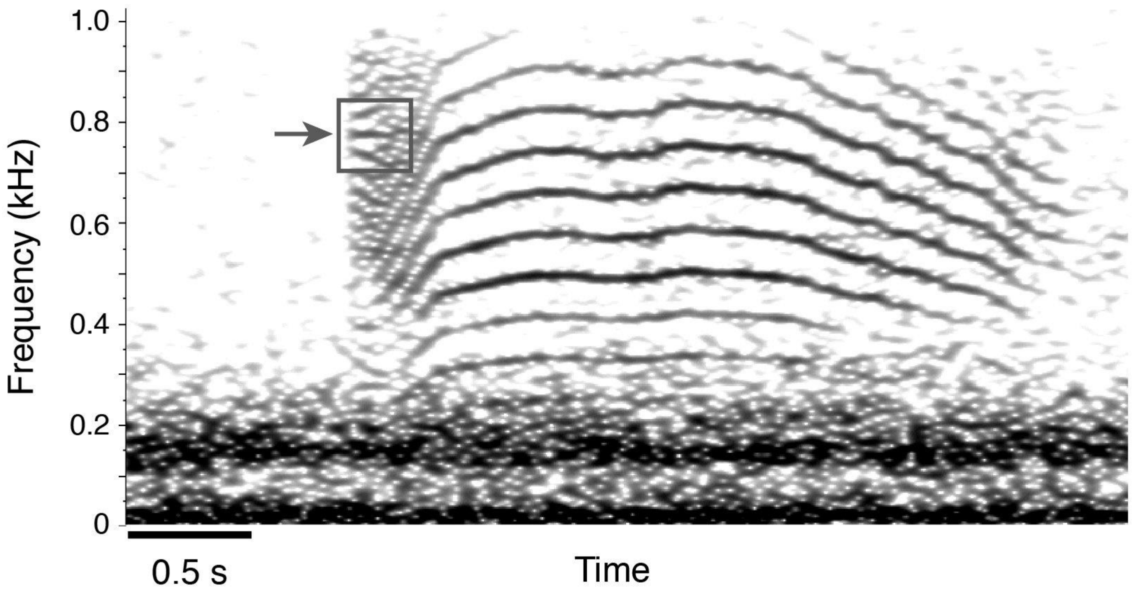

**Figure 5.** A short moan call illustrating the divergent sidebands at the start of the call. The arrow indicates the carrier frequency, and the box encloses the first sidebands below and above the carrier, which diverge in frequency as the pulse rate of the signal increases. Spectrogram parameters: 0.134 s, 92.7% overlap, DFT size 512 samples, Hann window.

Sidebands of the call had a mean 5% minimum frequency of 409.3 ± 83.9 Hz and a mean 95% maximum frequency of 886 ± 66.5 Hz, the 0% minimum frequency and 100% maximum frequency are also provided in Table 2. Since the 95 and 100% maximum frequencies were so close to the recording Nyquist frequency of our recordings (1024 Hz), it is possible that the exact actual maximum frequency of the call was not measured. The mean peak frequency of this call was 596.5 ± 109.4 Hz, and the minimum and maximum peak frequencies were 264 and 880 Hz respectively (Table 2). The short moan calls were 2.2 ± 0.3 s in duration for the 90% duration but 2.7 ± 0.4 s for the 100% duration measurement (Table 2). The mean PRR at the centre time of call was 76.7 ± 6.3 Hz, minimum PRR was 58.2 Hz and the maximum PRR was 109.58 Hz (Table 2). Minimum (0 and 5%) and peak frequencies were significantly different between all months (Table 2). GAMs indicated significant difference for 95%

maximum frequency in May, June, and September; 100% maximum frequency were significantly different in May and August (Table 2). The 90 and 100% call durations were consistent from April through August but were significantly high in September, and the PRR was significantly different in May and June (Table 2).

Welch two-samples t-tests comparing the averages of 5% minimum frequency (264 ± 89 Hz), 95% maximum frequency (2520 ± 735 Hz), 90% duration (2.5 ± 0.3 s), and PRR (75 ± 8 Hz) between low moan call measurements of Klinck et al. (2010) and the short moan calls measured in this study (Table 2) yielded significant difference (p-values of 0.05 or less) but no significant difference was found between peak frequencies (p-value>0.05). The 100% duration (2.887 ± 3.148 s) of the McCreery and Thomas (2009) long groan call and the short moan call measured in this study were not significantly different (p-value >0.05). The 0% minimum frequency (315.3 ± 308.9 Hz) and 100% duration (1.034 ± 0.6 s) of the short groan call (McCreery and Thomas 2009) were significantly different to those of the short moan call (p<0.05). Given the above statistical results, the general structure and rough frequency range of our call suggests that this may be a different moan call type. Since the durations of the calls reported here are significantly shorter than the low moan call described by Klinck et al. (2010), we here term the call type described herein as *short moan call*.

**Table 2.** Monthly statistics [mean ± SD (range)] of the acoustic characteristics of short moan calls. April was the GAM reference level for month. Significant ($p$-value<0.05) results are bold-faced, and n is the sample size. Overall statistics present the total of n (population size) and the mean ± SD (range) call characteristics for all months, and these overall statistics were used for Welch's t-tests.

| Month | n | 0% Min frequency (Hz) | 5% Min frequency (Hz) | Peak frequency (Hz) | *95% Max frequency (Hz) | *100% Max frequency (Hz) | 90% duration (s) | 100% duration (s) | PRR (Hz) |
|---|---|---|---|---|---|---|---|---|---|
| April | 13 | 484.8 ± 37.8 | 511.4 ± 35.1 | 670.2 ± 77.9 | 932.3 ± 12.1 | 1000.1 ± 18.1 | 2.1 ± 0.2 | 2.4 ± 0.2 | 75 ± 2.6 |
| | | (407.5–524.5) | (440–544) | (528–768) | (912–952) | (957.8–1024) | (1.8–2.3) | (2.2–2.7) | (70.3–79) |
| May | 5 | **323.3 ± 134.7** | **350.4 ± 149.3** | **478.4 ± 208.5** | **748.8 ± 185.4** | **890.9 ± 149.6** | 2.2 ± 0.3 | 2.6 ± 0.3 | **64.4 ± 3.8** |
| | | (121.9–477.2) | (128–512) | (264–752) | (544–936) | (654.8–1020.5) | (1.9–2.6) | (2.3–3.1) | (58.2–67.4) |
| June | 5 | **321.2 ± 95.3** | **347.2 ± 95.9** | **403.2 ± 182.9** | **849.6 ± 149.6** | 926.6 ± 149.1 | 2.1 ± 0.3 | 2.4 ± 0.4 | **88.7 ± 14.3** |
| | | (268.2–491.1) | (288–512) | (304–728) | (600–960) | (670.7–1024) | (1.7–2.4) | (1.9–2.8) | (74.7–103.8) |
| July | 3 | **320.1 ± 61.2** | **357.3 ± 78.9** | **536 ± 52.5** | 936 ± 21.2 | 1017.2 ± 6.2 | 1.9 ± 1 | 2.4 ± 1.2 | 77.4 ± 27.9 |
| | | (276.3–390.1) | (304–448) | (480–584) | (912–952) | (1011.8–1024) | (0.8–2.5) | (1.1–3.2) | (59.6–109.6) |
| August | 50 | **413.9 ± 47.6** | **450.9 ± 49.8** | **592.9 ± 91** | 896.9 ± 52.4 | **955.5 ± 67.4** | 2.2 ± 0.4 | 2.5 ± 0.4 | 76.1 ± 6.4 |
| | | (264.1–503.9) | (280–544) | (432–856) | (744–960) | (776.1–1024) | (1.3–3) | (1.5–3.6) | (62.6–93.6) |
| September | 199 | **339. 4 ± 79.5** | **396.1 ± 82.7** | **601.4 ± 104** | **884.5 ± 59.7** | 981.1 ± 69.9 | **2.3 ± 0.2** | **2.8 ± 0.4** | 77 ± 5 |
| | | (179.1–539.7) | (184–568) | (448–880) | (688–976) | (728.3–1024) | (1.3–2.8) | (1.6–3.6) | (64–87.3) |
| Overall statistics | 275 | 359 ± 84.3 | 409.3 ± 83.9 | 596.5 ± 109.4 | 886 ± 66.5 | 975.1 ± 73 | 2.2 ± 0.3 | 2.7 ± 0.4 | 76.7 ± 6.3 |
| | | (121.9–539.7) | (128–568) | (264–880) | (544–976) | (654.8–1024) | (0.8–3) | (1.1–3.6) | (58.2–109.58) |

*Maximum frequencies are likely limited by the Nyquist frequency of the recorder.

### *Seasonal occurrence and diel call rates*

Short moan calls of crabeater seals were first detected towards the end of April until mid-September when the recorder stopped working, and the highest proportion of call occurrence (17%) was in September (Figure 6). The recorder mooring location was submerged under sea ice from the beginning of May through mid-September (Figure 6). From January 12th to April 20th, the sea ice concentration within the 3.1 km block from the recorder mooring location was 0% but increased to 50% by the end of April. Sea ice concentration further increased to ~80% at beginning of May, and then increased to 100% by mid-May through mid-September. Short moan calls started to occur when the sea ice edge was closer to the recorder mooring location and increased as the recorder mooring location was fully submerged under the sea ice (Figure 6). The highest call rates were recorded towards the end of August and beginning of September, and the highest call rate was 6.4 calls per minute recorded in August (Figure 7). Since the mean call rates per day for each day was around zero, the highest call rates for each day are presented in Figure 7. There were big breaks in periods of calling between days from April (calls detected in one day) through mid-August, and small breaks were seen between days from the end of August through mid-September (Figure 7). A few low double trills (Stirling and Siniff 1979) of the leopard seal (*Hydrurga leptonyx*) were the only sounds of another seal species that were detected from this acoustic dataset on few occasions in January, April and September.

Figure 8 shows mean diel call rates for August and September. Mean call rates did not vary between different times of the day for April through July, and are not included in Figure 8. August was marked with low mean call rates between 09:00 and 14:00 (i.e. daytime hours), whereas September had low call rates between 07:00 and

18:00 (Figure 8). The highest mean call rates were observed from 21:00 to 03:00 (i.e. nighttime to early morning) for August and September (Figure 8).

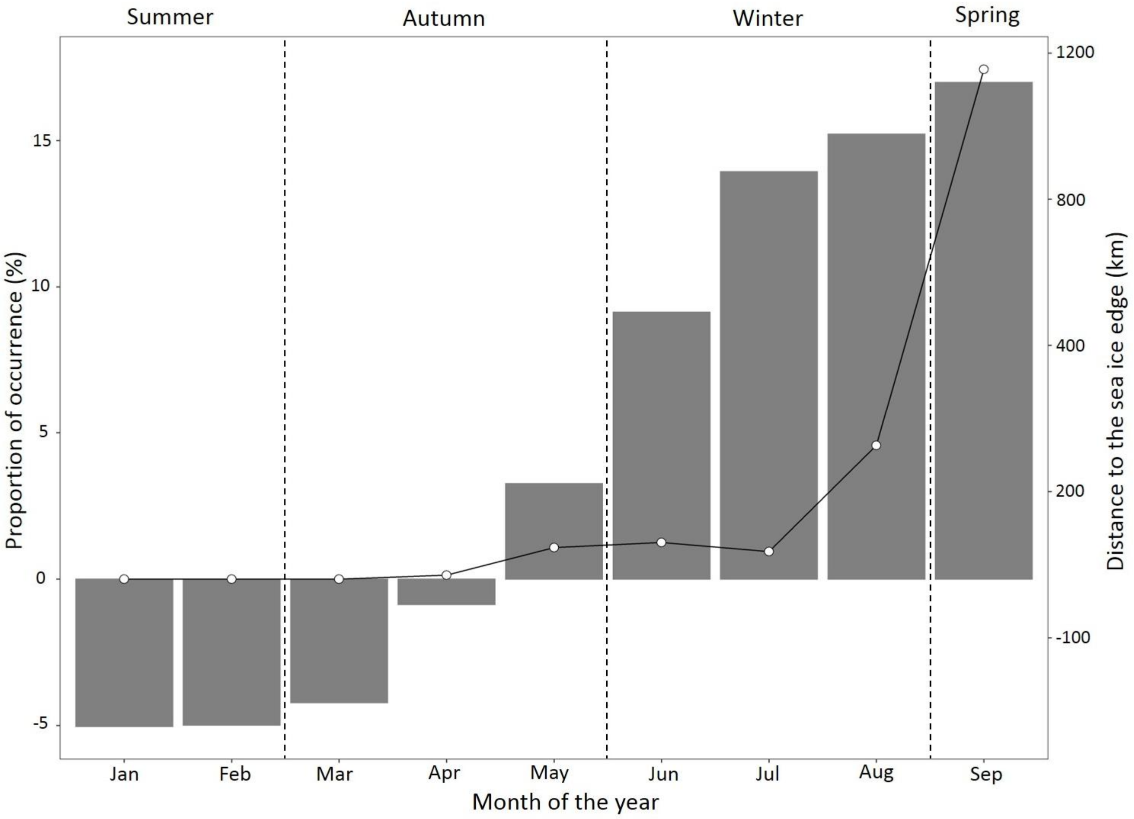

**Figure 6.** Monthly proportion of sampling intervals in which short moan calls occurred (line plot) in relation to the distance to the sea ice edge (bar plot). Negative values of distance to the sea ice edge represent instances when the recorder deployment position was not submerged under sea ice, and positive values of distance to the sea ice edge represent instances when the recorder deployment position was submerged under sea ice. Austral seasons are shown on the top axis and outlined by dashed lines.

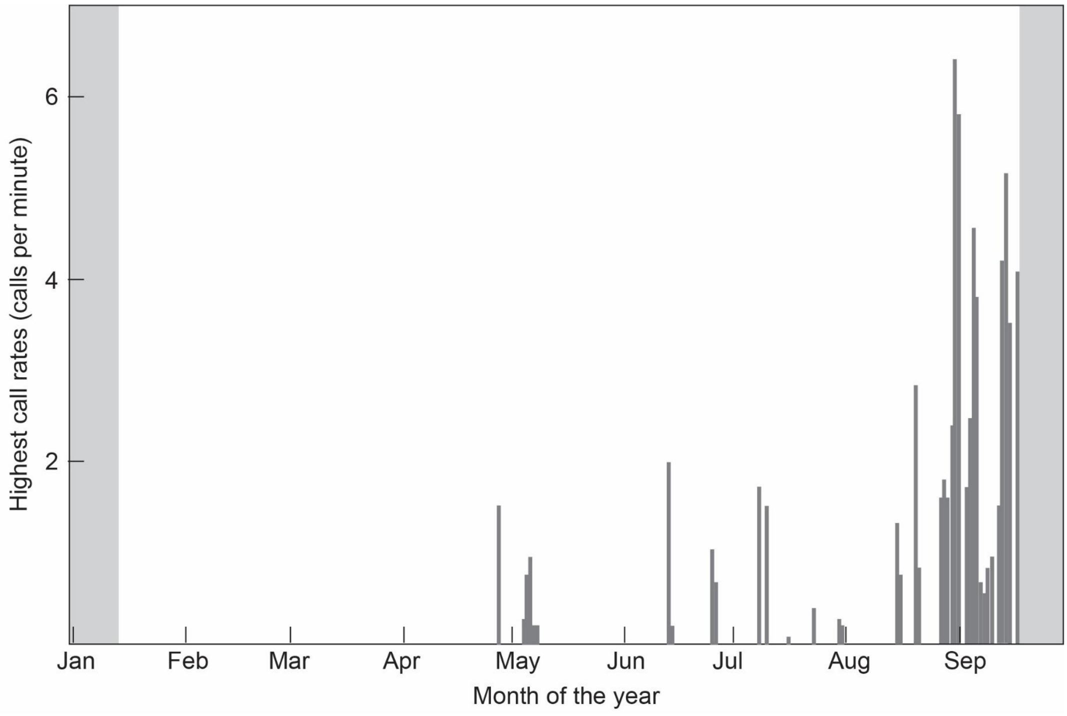

**Figure 7.** Highest call rates of short moan call for each day of the month. The highest call rates represent the maximum of the 24 samples for each day. Labels on the time axis indicate the start of each month, and grey shadings indicate times before and after the recording period.

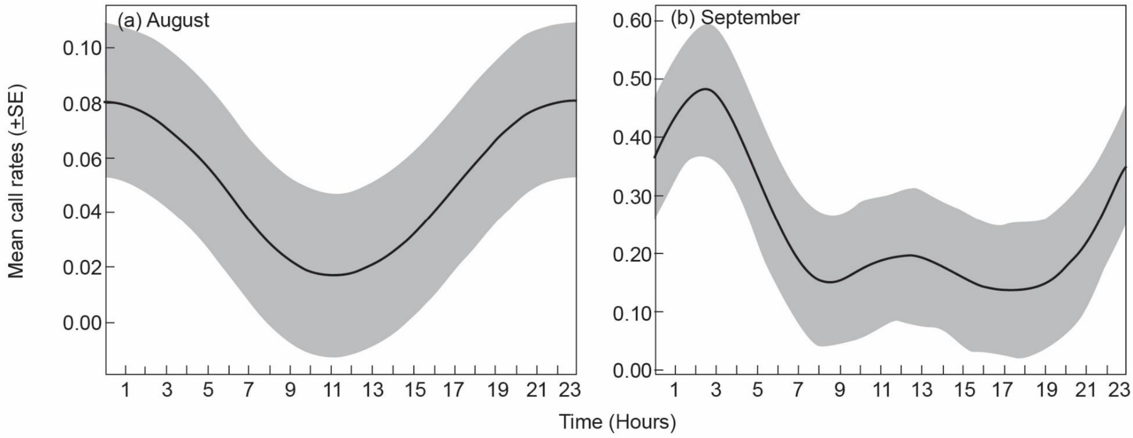

**Figure 8.** Circular smoothed mean diel call rates (calls per minute) of short moan calls for August (a) and September (b) off the Maud Rise, Antarctica. Grey shaded region represents the standard error (SE) of the mean. Coordinated Universal Time is used.

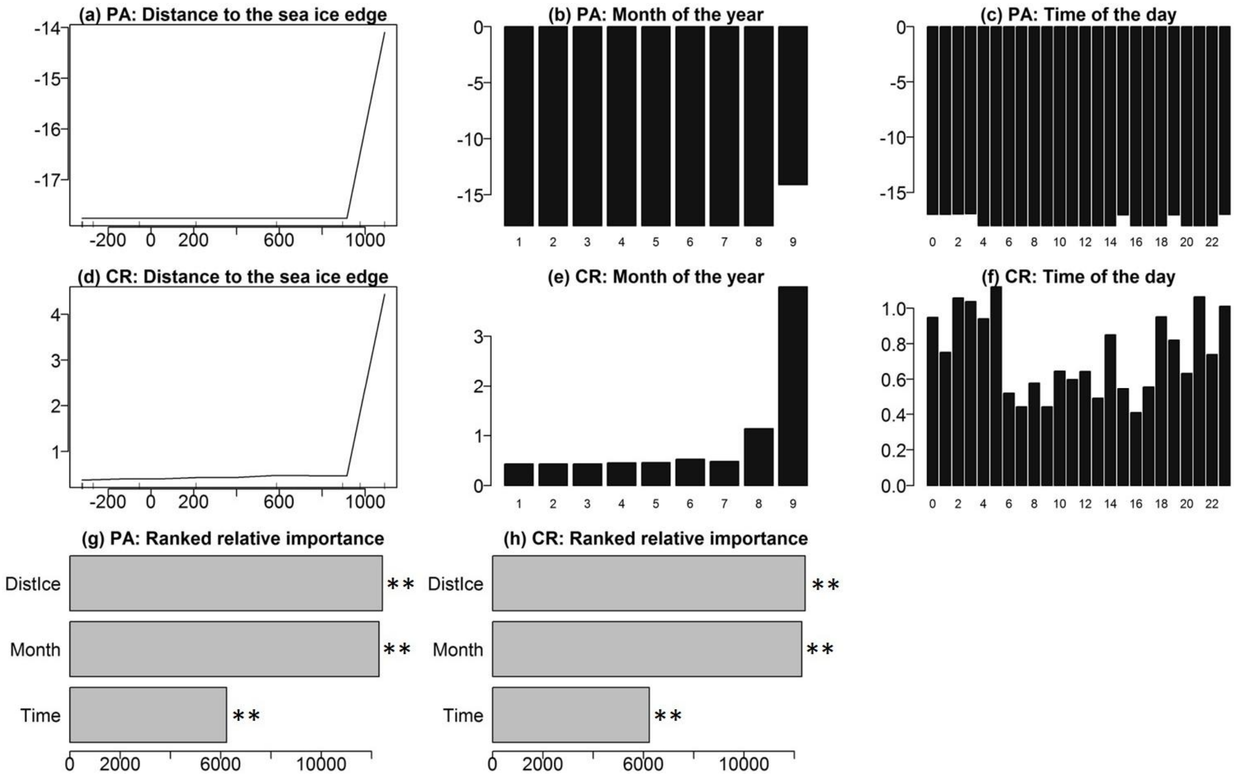

**Figure 9**. Relative effects and importance of predictor variables on the call occurrence (a–c, g) and call rates (d–f, h) of short moan calls. Vertical axes of (a) – (f) are relative effects of predictor variables on call occurrence and call rate (Note the difference in scales.). Horizontal axes of (g) and (h) are relative importance of predictor variables on call occurrence and call rates. PA is presence/absence to indicate acoustic occurrence, CR is for call rates and DistIce is distance to the sea ice edge. Negative values of distance to the sea ice edge represent instances when the recorder deployment position was not submerged under sea ice, and positive values of distance to the sea ice edge represent instances when the recorder deployment position was submerged under sea ice. ** indicates significant ($p<0.05$) of variable importance.

### *Predictors of short moan call occurrence and call rates*

Distances to the sea ice edge from -323 to 977 km and months of the year from January through August had the highest effect on the acoustic occurrence of short moan calls (Figure 9(a,b)). No clear pattern of which hour of the day had the highest effect on short moan call occurrence (Figure 9(c)). Distance to the sea ice edge (with a breaking point at 1091 km), September, and nighttime to early morning hours had the highest effects on the call rates of short moan calls given the high call rates during those levels (Figure

9(d,e,f)). RF models ranked distance to the sea ice edge and month of the year as equally the most important predictors of short moan call occurrence and call rates (Figure 9(g,h)). The RF model ranked time of day as the least important predictor of short moan call rates (Figure 9(g.h)). Distance to the sea ice edge, month of the year and time of day were all significant predictors of call occurrence and call rates (Figure 9(g,h)), indicating that these are informative predictors of the crabeater seal behaviour and ecology.

## Discussion

### *Acoustic structure of the short moan call*

The divergent sidebands at the very start of the short moan call indicate that the pulse rate or amplitude modulation frequency is increasing since the pulse rate determines the spacing between the sidebands (Gerhardt 1998; Frommolt 1999). For a short interval at the start of most short moan calls, the carrier frequency was close to a constant frequency, and the sidebands diverged with the higher sideband having an upward slope, and the lower sideband having a downward slope (Gerhardt 1998; Elemans et al. 2008). We consider sidebands observed here to be produced by sound generating organs of seals and not originating from the electronics of the recording device since the intervals (i.e. PRR) from the peak frequency are greater than 50 Hz (Table 2; Frommolt 1999). Sidebands diminished symmetrically in amplitude above and below the carrier frequency when the spectral peak of the carrier frequency was highest, which is typical of sidebands (Elemans et al. 2008).

The mean 95 and 100% maximum frequencies were significantly high or low for two to three months out of the six months with calls, indicating some stability in the acoustic characteristics of this call type over time. The mean 90 and 100% durations were not significantly different from April to August but a significantly longer duration was found only in September (although still shorter than the low moan of Klinck et al. (2010)), indicating that the call duration changed slightly before the start of the breeding season likely due to change in reproductive status of seals. PRRs were less varied between months as per GAM results, reflecting that this acoustic characteristic of the species did not change over time but changed their call rates over months. Call rates for other Antarctic ice-inhabiting phocid seals such as Ross (*Ommatophoca rossii*) and leopard seals also changed over months (van Opzeeland et al. 2010).

Short moan calls described here have on average, higher 5% minimum frequencies, shorter 90% duration, and higher PRR compared to the low moan call of Klinck et al. (2010). Peak frequency of low moan calls described by Klinck et al. (2010) is comparable to that of the short moan call given their non-significance test result, suggesting that the energy of these calls is concentrated in similar frequency bands and that these calls are produced by the same species (e.g., Mizuguchi et al. 2016). Furthermore, these comparable call peak frequencies could indicate that seals of similar body size produced the calls detected from our study area and that of Klinck et al. (2010) since peak frequencies of most terrestrial mammals such as bats, elephants, humans and dogs have been found to decrease with increasing body size (Fletcher 2004; Thiagavel et al. 2017).

The significantly lower mean 0% minimum frequency of short moan calls in this study compared to the 0% minimum frequency (962.2 ± 349.6 Hz) of long groan call described by McCreery and Thomas (2009), suggests that these are different call types. The 100% duration of the short moan call (2.7 ± 0.4 s) did not differ significantly from that of the McCreery and Thomas (2009) long groans, which were highly variable in duration (2.9 ± 3.2 s). Given the short recording length (15.1 minutes) and big standard deviations (± 3.2 s) of the mean 100% duration of the long groan call described by McCreery and Thomas (2009), these recordings might represent calls from just one or a few individuals. Duration of short moan calls did not significantly change between months except in September although the peak frequency significantly changed between months, showing that call duration did not change with peak frequency. The mean 0 and 5% minimum frequencies of short moan calls were significantly different between months, although May, June, July and September had comparable minimum frequencies. Such comparable frequency changes in four out of six months could indicate that crabeater seals did not change their vocalization frequencies in response to changing seasonal noise levels as found for other seal species (Tripovich et al. 2012; Zhao et al. 2018).

Because the mean 95 and 100% maximum frequencies that Klinck et al. (2010) and McCreery and Thomas (2009) reported were well above the Nyquist frequency of our recorder, we cannot compare these measurements, as our sampling rate was too low to reliably capture the upper frequency limit of these calls. It is possible that the loss of energy at the high end might also influence the minimum frequency, but if the full frequency range was captured, the only possible effect this would have had on the minimum frequency would have been to shift it up slightly. Given that the 5% minimum frequency measurements observed are higher than those of Klinck et al. (2010) low moan call but significantly lower than the 0% minimum frequency of long groan call of McCreery and Thomas (2009), it is safe to say that the t-test is conservative in finding a significant difference. For example, the minimum (0 and 5%) frequencies and duration are different from those of low and high moan calls (Klinck et al. 2010); grunts, whistles, screeches and short groans (McCreery and Thomas 2009)- we suggest that this is a new moan call type that was previously undescribed since most of the measured parameters are different from previous crabeater seal studies. Description of this call type create useful information that contributes towards the understanding of the acoustic repertoire and acoustic ecology of crabeater seals.

It is possible that there could be continuous geographic variation in the crabeater seal calls that was not documented previously. For example, Mizuguchi et al. (2016) found differences in the acoustic characteristics of ribbon seals (*Histriophoca fasciata*) underwater vocalizations from three geographically discrete populations. Nevertheless, the distance between our study area (Maud Rise) and Ekström Ice Shelf (Klinck et al. 2010) is 758 km, and 2914 km between Ezcurra Inlet (McCreery and Thomas 2009) and this study’s location, which is shorter than the maximum tracked distance of 4554 km travelled by a crabeater seal over six months (Nachtsheim et al. 2017). The above distances between different studies, likely made it possible for seals to overlap in the distribution between the three locations. Given the spacing between Ekström Ice Shelf, Ezcurra Inlet and Maud Rise, we eliminate the hypothesis that geographic isolation could have led to different acoustic characteristics of crabeater seal calls. Since there is a big temporal gap between our study and previous studies (McCreery and Thomas 2009; Klinck et al. 2010), it is unlikely that there could have been temporal shift in the frequency of crabeater seal calls as long groan calls recorded in 1978 (McCreery and Thomas 2009) have similar spectral characteristics to the low moan recorded in 2007 (Klinck et al. 2010).

### ***Seasonal and diel occurrence of short moan calls***

Short moan calls started to occur towards the end of April and continued to persist until mid-September, indicating that seals arrived in the Maud Rise area with the extension of the sea ice edge as this is a pack-ice seal species (e.g., Southwell et al. 2003, 2008;

Bengtson 2009; Bengtson et al. 2011; Nachtsheim et al. 2017). Thus, RF models ranked distance to the sea ice edge and month of the year as the most important predictors of crabeater seal acoustic occurrence and call rates, which support in-part findings of previous studies that sea ice concentration is one of the important variables for predicting the distribution of crabeater seals (e.g., Joiris 1991; Bester et al. 2002; Nachtsheim et al. 2017). Detection of crabeater seal calls when the recorder was fully submerged under sea ice and the distance to the sea ice edge was great (May through mid-September), indicates that seals were in the close vicinity of the recorder mooring location as Klinck et al. (2010) estimated that the calls of crabeater seals can travel a maximum detectable range of 15 km. These seals could have maintained their presence in areas that were fully ice covered by using breathing holes (Stirling and Kooyman 1971; Stirling and Siniff 1979). In addition to breathing holes, they could have used polynyas to maintain their distribution in this region as similarly observed for Antarctic minke whales (Schevill and Watkins 1972; Ribic et al. 1991; Plötz et al. 1991; Scheidat et al. 2011; Shabangu et al. 2020a); blue and fin whales (Shabangu et al. 2020b).

Although the function of short moan calls is currently unknown, they could be used for territorial defence, foraging and other social contact including mating as found with other calls of crabeater seals (Thomas and DeMaster 1982; Rogers 2003; McCreery and Thomas 2009; Klinck et al. 2010, van Opzeeland et al. 2010). Previous long-term acoustic studies detected crabeater seal sounds (i.e., low and high moan calls) in August (very few calls), October (peak calling period) and December off the Ekström Iceshelf, eastern Weddell Sea (Klinck et al. 2010; van Opzeeland et al. 2010). The short moan call provides more information about the seasonal presence and acoustic ecology of seals in an Antarctic area that could not have been derived using other call types of the species (e.g., Klinck et al. 2010; van Opzeeland et al. 2010). A previous acoustic study (van Opzeeland et al. 2010) carried out during the same seasons detected sounds of other seal species (such as Ross seal and Weddell seals (*Leptonychotes weddellii*)) that are not detected in this study, possibly indicating that the Maud Rise is not a preferred habitat for those species. We detected leopard seal calls on few occasions; even though the low sampling rate used in this study was intended for the study of baleen whale low-frequency sounds (Shabangu et al. 2020b). Nevertheless, this low sampling rate was sufficient for detecting Ross seals, as the lower components of the calls of this species have been detected below 500 Hz (Shabangu and Rogers, unpublished data).

The total of 1871 short moan calls detected in this study is comparable to 2126 crabeater seal calls counted by van Opzeeland et al. (2010) but drastically lower than the 16370 (i.e., 96% of 17052 total) low moan calls enumerated by Klinck et al. (2010). The highest call rate of 6 calls per minute observed in this study is higher than 1 call per minute for short groan call (McCreery and Thomas 2009) but lower than the highest call rates from other previous crabeater seal acoustic studies: 7 calls per minute (Thomas and DeMaster 1982), 10 calls per minute (van Opzeeland et al. 2010), 11 calls per minute (Klinck et al. 2010) and 21 calls per minute for low groan call (McCreery and Thomas 2009). The observed low call rate of this study could be from isolated seals (e.g., Stirling and Kooyman 1971) that inhabit this region from mid-autumn through early spring since these recordings were conducted outside the breeding season of crabeater seals. Short groan call of McCreery and Thomas (2009) also had a low call rate since it was recorded during the non-breeding season of these seals. Additionally, the difference in call rates between studies could be due to different duty cycles applied to each study (e.g., Thomisch et al. 2015) and depth of the recorder in the water column relative to the SOFAR channel (e.g., Lurton 2002). The big calling breaks between days from mid-April through mid-August, likely indicate that there were few seals around the Maud Rise whereas small vocalizing breaks between days from the end of August through early September probably reflect an increase in the number of seals. Crabeater seals are known to aggregate in high numbers before their migration or foraging (Bengtson 2009), and during their breeding season (Southwell et al. 2003).

Low call rates observed during daytime in August and September could be because most of the seals were hauled out on ice floes or pack ice during the day to rest or avoid predators (Thomas and DeMaster 1982; Bengtson 2002; Southwell et al. 2008). The RF model also showed that nighttime to early morning had the highest effect on call rates of crabeater seal, which supports the nocturnal vocal activity of this species. Van Opzeeland et al. (2010) also observed low call rates of crabeater seal calls during the day in October and December but more calls at night, suggesting that this seal species is more vocally active at nighttime regardless of the call type (e.g., Thomas and DeMaster 1982). Alternatively, seals could just have been silent underwater during the day as an anti-predator strategy (e.g., Thomas et al. 1987). High call rates of the short moan call type at night could also imply that animals could have produced this call type when foraging (McCreery and Thomas 2009) on big swarms of Antarctic krill that migrate to shallow depths at night (Demer and Hewitt 1995; Gaten et al. 2008; Nachtsheim et al. 2017). Seals could have as well used sound to maintain contact with conspecific at night. The lack of diel-calling pattern for April through July could be due to low call numbers during those months. The RF model ranked time of day as the least important predictor of both call occurrence and call rates, indicating that month of the year and distance to the sea ice edge are the most reliable predictors of call occurrence and call rates although all variables are informative for explaining the response variables.

## *Conclusions*

Using the crabeater seal short moan call, this study provides novel information about the occurrence, acoustic ecology and vocal behaviour of this species that were previously undescribed using other call types. The duration, minimum frequency, and PRR of the short moan call are different from other previously published call types of crabeater seals, suggesting that this is a new call type for crabeater seals. A quantitative description of the short moan call is provided here for the first time, making this call type easily identifiable to future studies. The Maud Rise is likely a useful habitat of crabeater seals since they were within its vicinity for extended periods, depending on sea ice conditions and month of the year. Passive acoustic monitoring has here provided essential knowledge that is important for understanding the species ecology to improve the conservation and management efforts of this species in the Southern Ocean.

## Acknowledgements

Special thanks to the National Research Foundation and South African National Antarctic Programme for funding the SABWP (Grant No. SNA 2011112500003). We are sincerely grateful to numerous colleagues, collaborators, Captains and crew of the RV *SA Agulhas II* for their assistance with the deployment and recovery of the acoustic instrument used in this study.

## References

Altmann A, Tolos L, Sander O, Lengauer T. 2010. Permutation importance: a corrected feature importance measure. Bioinformatics 26 (10):1340–1347.

Beitsch A, Kaleschke L, Kern S. 2014. Investigating high resolution AMSR2 sea ice concentrations during the February 2013 fracture event in the Beaufort Sea. Remote Sens. 6:3841–3856.

Bengtson JL. 2002. Crabeater seal *Lobodon carcinophagus*. In: Perrin WF, Würsig B, Thewissen JGM, editor. Encyclopedia of marine mammals. San Diego: Academic Press, p. 302–304.

Bengtson JL. 2009. Crabeater seal *Lobodon carcinophagus*. In: Perrin WF, Würsig B, Thewissen JGM, editors. Encyclopedia of marine mammals. 2nd ed. San Diego: Academic Press, p. 290–292.

Bengtson JL, Laake JL, Boveng PL, Cameron MF, Hanson MB, Stewart BS. 2011. Distribution, density, and abundance of pack-ice seals in the Amundsen and Ross Seas, Antarctica. Deep-Sea Res Pt II 58:1261–1276.

Bester MN, Ferguson JWH, Jonker FC. 2002. Population densities of pack ice seals in the Lazarev Sea, Antarctica. Antarct. Sci. 14:123–127.

Bioacoustics Research Program 2017. Raven Pro: Interactive sound analysis software (Version 1.5) [Computer Software]. Ithaca, NY: The Cornell Lab of Ornithology. Available from http://www.birds.cornell.edu/raven.

Botta S, Secchi ER, Rogers TL, Prado JH, de Lima RC, Carlini P, Negrete J. 2018. Isotopic niche overlap and partition among three Antarctic seals from the western Antarctic Peninsula. Deep-Sea Res. II 149:240–249.

Brault EK, Koch PL, Costa DP, McCarthy MD, Hückstädt LA, Goetz KT, McMahon KW, Goebel ME, Karlsson O, Teilmann J, Harkonen T, Harding KC. 2019. Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. Mar Ecol Prog Ser. 611:1–18.

Breiman L. 2001. Random forests. Mach Learn. 45:5−32.

Demer DA, Hewitt RP. 1995. Bias in acoustic biomass estimates of *Euphausia superba* due to diel vertical migration. Deep-Sea Res. I 42(4):455–475.

Elemans CPH, Heeck K, Muller M. 2008. Spectrogram analysis of mechanical events in sound production of animals. J Bioacoustics 18:183–212.

Erbe C, Dunlop R, Jenner KCS, Jenner MNM, McCauley RD, Parnum I, Parsons M, Rogers TL, Salgado-Kent C. 2017. Review of underwater and in-air sounds emitted by Australian and Antarctic marine mammals. Acoust Aust. 45:179–241.

Fetterer F, Knowles K, Meier W, Savoie M. 2016. Sea Ice Index, Version 2. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center. [accessed 2016 Aug 28]. http://dx.doi.org/10.7265/N5736NV7.

Figueroa HK. 2006. XBAT: Extensible BioAcoustic Tool. [accessed 2015 June 22]. http://xbat.org.

Fletcher NA. 2004. A simple frequency-scaling rule for animal communication. J Acoust Soc Am. 115:2334–2338.

Fox J, Monette G. 1992. Generalized collinearity diagnostics. J Am Stat Assoc. 87:178–183.

Frommolt K-H. 1999. Sidebands – facts and artefacts. Bioacoustics 10:219–224.

Garner DM. 1967. Oceanic sound channels around New Zealand. New Zeal J Mar Fresh. 1:3–15.

Gaten E, Tarling G, Dowse H, Kyriacou C, Rosato E. 2008. Is vertical migration in Antarctic krill (*Euphausia superba*) influenced by an underlying circadian rhythm? J Genet. 87:473–483.

Gerhardt HC. 1998. Acoustic signals of animals: recording, field measurements, analysis and description. In: Hopp SL, Owren ML, Evans CS, editors. Animal Acoustic Communication: Sound Analysis and Research Methods. Berlin: Springer-Verlag, p. 1–25.

Grosjean P, Ibanez F. 2018. pastecs: Package for analysis of space-time ecological series. R package version 1.3.21. https://CRAN.R-project.org/package=pastecs.

Guisan A, Edwards TC, Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol Model. 157:89−100.

Hastie TJ, Tibshirani R, Friedman J. 2009. The elements of statistical learning. New York: Springer.

Ho TK. 1995. Random decision forests. Proceedings of the 3rd International Conference on Document Analysis and Recognition, 14–16 August 1995, Montreal, QC. p. 278–282.

Hückstädt L. 2015. *Lobodon carcinophaga*. The IUCN Red List of Threatened Species 2015: e.T12246A45226918. https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T12246A45226918.en. Downloaded on 15 January 2020.

Joiris CR. 1991. Spring distribution and ecological role of seabirds and marine mammals in the Weddell Sea, Antarctica. Polar Biol. 11:415–424.

Kane MJ, Price N, Scotch M, Rabinowitz P. 2014. Comparison of ARIMA and Random Forest time series models for prediction of avian influenza H5N1 outbreaks. BMC Bioinformatics 15:276.

Klinck H, Mellinger DK, Klinck K, Hager J, Kindermann L, Boebel O. 2010. Underwater calls of the crabeater seal (*Lobodon carcinophaga*). J Acoustic Soc Am. 128:474–479.

Laws RM, Baird A, Bryden MM. 2003. Breeding season and embryonic diapause in crabeater seals (*Lobodon carcinophagus*). Reproduction 126:365–370.

Liaw A, Wiener M. 2002. Classification and Regression by randomForest. R News 2(3):18–22.

Lurton X. 2002. An introduction to underwater acoustics: principles and applications. London: Springer. 347 pp.

McCreery L, Thomas JA. 2009. Acoustic analysis of underwater vocalizations from crabeater seals (*Lobodon carcinophagus*): Not so monotonous. Aquatic Mammals 35(4):490–501.

Mellinger DK, Bradbury JW. 2007. Acoustic measurements of marine mammal sounds in noisy environments. In: Proceedings of the Second International Conference on Underwater Acoustic Measurements: Technologies and Results, June 25–29, Heraklion, Greece. p. 273–280.

Mizuguchi D, Mitani Y, Kohshima S. (2016). Geographically specific underwater vocalizations of ribbon seals (*Histriophoca fasciata*) in the Okhotsk Sea suggest a discrete population. Mar Mam Sci. 32(3):1138–1151.

Nachtsheim DA, Jerosch K, Hagen W, Plötz J, Bornemann H. 2017. Habitat modelling of crabeater seals (*Lobodon carcinophaga*) in the Weddell Sea using the multivariate approach Maxent. Polar Biol. 40:961–976.

Plötz J, Weidel H, Bersch M. 1991. Winter aggregations of marine mammals and birds in the north-eastern Weddell Sea pack ice. Polar Biol. 11:305–309.

R Core Team. 2020. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Ribic CA, Ainley DG, Fraser WR. 1991. Habitat selection by marine mammals in the marginal ice zone. Antarctic Science 3:181–186.

Rogers TL. 2003. Factors influencing the acoustic behaviour of male phocid seals. Aquatic Mammals 29(2):247–260.

Scheidat M, Friedlaender A, Kock KH, Lehnert L, Boebel O, Roberts J, Williams R. 2011. Cetacean surveys in the Southern Ocean using icebreaker supported helicopters. Polar Biol. 34:1513–1522.

Schevill WE, Watkins WA. 1972. Intense low-frequency sounds from an Antarctic minke whale, *Balaenoptera acutorostrata*. Breviora 388:1–8.

Shabangu FW, Yemane D, Stafford KM, Ensor P, Findlay KP. 2017. Modelling the effects of environmental conditions on the acoustic occurrence and behavior of Antarctic blue whales. PLoS ONE 12(2):e0172705.

Shabangu FW, Findlay KP, Yemane D, Stafford KM, van den Berg M, Blows B, Andrew RK. 2019. Seasonal occurrence and diel calling behavior of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa. J Marine Syst. 190:25–39.

Shabangu FW, Findlay K, Stafford KM. 2020a. Seasonal acoustic occurrence, diel-vocalizing patterns and bioduck call-type composition of Antarctic minke whales off the west coast of South Africa and the Maud Rise, Antarctica. Mar Mam Sci. 36:658–675.

Shabangu FW, Andrew RK, Yemane D, Findlay KP. 2020b. Acoustic seasonality, behaviour and detection ranges of Antarctic blue and fin whales under different sea ice conditions off Antarctica. Endanger Species Res. DOI: https://doi.org/10.3354/esr01050.

Signorell A, Aho K, Alfons A, Anderegg N, Aragon T, Arppe A, Baddeley A, Barton K, Bolker B, Borchers HW, Caeiro F, Champely S, Chessel D, Chhay L, Cummins C, Dewey M, Doran HC, Dray S, Dupont C, Eddelbuettel D, Enos J, Ekstrom C, Elff M, Erguler K, Farebrother RW, Fox J, Francois R, Friendly M, Galili T, Gamer M, Gastwirth JL, Gel YR, Gross J, Grothendieck G, Harrell Jr FE, Heiberger R, Hoehle M, Hoffmann CW, Hojsgaard S, Hothorn T, Huerzeler M, Hui WW, Hurd P, Hyndman RJ, Villacorta Iglesias PJ, Jackson C, Kohl M, Korpela M, Kuhn M, Labes D, Temple Lang D, Leisch F, Lemon J, Li D, Maechler M, Magnusson A, Malter D, Marsaglia G, Marsaglia J, Matei A, Meyer D, Miao W, Millo G, Min Y, Mitchell D, Mueller F, Naepflin M, Navarro D, Nilsson H, Nordhausen K, Ogle D, Ooi H, Parsons N, Pavoine S, Plate T, Rapold R, Revelle W, Rinker T, Ripley BD, Rodriguez C, Russell N, Sabbe N, Seshan VE, Snow G, Smithson M, Soetaert K, Stahel WA, Stephenson A, Stevenson M, Templ M, Therneau T, Tille Y, Trapletti A, Ulrich J, Ushey K, Van Der Wal J, Venables B, Verzani J, Warnes GR, Wellek S, Wickham H, Wilcox RR, Wolf P, Wollschlaeger D, Yee T, Zeileis A. 2020. DescTools: Tools for descriptive statistics. R package version 0.99.36. https://cran.r-project.org/package=DescTools.

Southwell CJ, Kerry KR, Ensor PH, Woehler EJ, Rogers TL. 2003. The timing of pupping by pack-ice seals in East Antarctica. Polar Biol. 26:648–652.

Southwell CJ, Paxton CGM, Borchers D, Boveng P, de la Mare W. 2008. Taking account of dependent species in management of the Southern krill fishery: Estimating crabeater seal abundance off East Antarctica. J Appl Ecol. 45:622–631.

Spreen G, Kaleschke L, Heygster G. 2008. Sea ice remote sensing using AMSR-E 89-GHz channels. J Geophys Res Oceans 113:C2S03, doi:10.1029/2005JC003384.

Stirling I, Kooyman GL. 1971. The crabeater seal (*Lobodon carcinophagus*) in McMurdo Sound, Antarctica and the origin of mummified seals. J Mammal. 52:175–180.

Stirling I, Siniff DB. 1979. Underwater vocalizations of leopard seals (*Hydrurga leptonyx*) and crabeater seals (*Lobodon carcinophagus*) near the South Shetland Islands, Antarctica. Can J Zool. 57:1244–1248.

Thiagave J, Santana SE, Ratcliffe JM. 2017. Body size predicts echolocation call peak frequency better than gape height in vespertilionid bats. Sci Rep. 7: 828.

Thomas JA, DeMaster DP. 1982. An acoustic technique for determining diurnal activities in leopard (*Hydrurga leptonyx*) and crabeater (*Lobodon carcinophagus*) seal. Can J Zool. 60:2028–2031.

Thomas JA, Ferm LM, Kuechle VB. 1987. Silence as an anti predation strategy by Weddell seals. Antarct J. 22:232–234.

Thomisch K, Boebel O, Zitterbart DP, Samaran F, Van Parijs S, and Van Opzeeland I. 2015. Effects of subsampling of passive acoustic recordings on acoustic metrics. J Acoust Soc Am. 138(1):267–278.

Tripovich JS, Hall-Aspland S, Charrier I, Arnould JPY. 2012. The behavioural response of Australian fur seals to motor boat noise. PLoS ONE 7(5):e37228.

van Opzeeland I, van Parijs S, Bornemann H, Frickenhaus S, Kindermann L, Klinck H, Plötz J, Boebel O. 2010. Acoustic ecology of Antarctic pinnipeds. Mar Ecol Prog Ser. 414:267–291.

Wood SN. 2001. mgcv: GAMs and generalized ridge regression for R. R News 1(2):20–25.

Wood SN. 2017. P-splines with derivative based penalties and tensor product smoothing of unevenly distributed data. Stat Comput. 27(4):985–989.

Wright MN, Ziegler A. 2017. ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. J Stat Softw. 77(1):1–17.

Zhao L, Sun X, Chen Q, Yang Y, Wang J, Ran J, Brauth SE, Tang Y, Cui J. 2018. Males increase call frequency, not intensity, in response to noise, revealing no Lombard effect in the little torrent frog. Ecol Evol. 8:11733–11741.