



Acoustic seasonality, behaviour and detection ranges of Antarctic blue and fin whales under different sea ice conditions off Antarctica

Fannie W. Shabangu^{1,2,*}, Rex K. Andrew³, Dawit Yemane¹, Ken P. Findlay^{2,4}

¹Fisheries Management Branch, Department of Environment, Forestry and Fisheries, Foreshore, Cape Town 8001, South Africa

²Mammal Research Institute Whale Unit, University of Pretoria, Private Bag X20, Hatfield, Pretoria 0028, South Africa

³Applied Physics Laboratory, University of Washington, Seattle, WA 98105, USA

⁴Cape Peninsula University of Technology, PO Box 652, Cape Town 8000, South Africa

ABSTRACT: Descriptions of seasonal occurrence and behaviour of Antarctic blue and fin whales in the Southern Ocean are of pivotal importance for the effective conservation and management of these endangered species. We used an autonomous acoustic recorder to collect bioacoustic data from January through September 2014 to describe the seasonal occurrence, behaviour and detection ranges of Antarctic blue and fin whale calls off the Maud Rise, Antarctica. From 2479 h of recordings, we detected D- and Z-calls plus the 27 Hz chorus of blue whales, the 20 and 99 Hz pulses of fin whales and the 18–28 Hz chorus of blue and fin whales. Blue whale calls were detected throughout the hydrophone deployment period with a peak occurrence in February, indicating continuous presence of whales in a broad Southern Ocean area (given the modelled detection ranges). Fin whale calls were detected from January through July when sea ice was present on the latter dates. No temporal segregation in peaks of diel calling rates of blue and fin whales was observed in autumn, but a clear temporal segregation was apparent in summer. Acoustic propagation models suggest that blue and fin whale calls can be heard as far as 1700 km from the hydrophone position in spring. Random forest models ranked month of the year as the most important predictor of call occurrence and call rates (i.e. behaviour) for these whales. Our work highlights areas around the Maud Rise as important habitats for blue and fin whales in the Southern Ocean.

KEY WORDS: Blue whales · Fin whales · Seasonality · Behaviour · Detection ranges · Antarctica · Sea ice

1. INTRODUCTION

The Southern Ocean ecosystem is an important habitat for large baleen whales, including Antarctic blue whales *Balaenoptera musculus intermedia* and fin whales *B. physalus*, as productivity in this region supports high biomass of the whales' prey, Antarctic krill *Euphausia superba* (Everson 2000, Knox 2006). Modern whaling in the Southern Ocean was responsible for the loss of numerous baleen whales (around

360 000 blue whales and 725 000 fin whales) during the austral summer between 1904 and the early 1970s (IWC 1995, Clapham & Baker 2002), which reduced most large baleen whale populations to very low numbers (e.g. Branch et al. 2007). After feeding throughout the austral summer in the Southern Ocean (e.g. Mackintosh 1942, Branch et al. 2007), most animals migrate to the low latitudes in winter where they are assumed to mate and calve (Best 1998). While some animals overwinter in the South-

*Corresponding author: fannie.shabangu@yahoo.com

ern Ocean, others overwinter at low latitudes (Širović et al. 2004, Best 2007, Thomisch et al. 2016, 2019, Buchan et al. 2018, Samaran et al. 2019, Shabangu et al. 2019). The International Union for the Conservation of Nature Red List of Threatened Species classifies Antarctic blue whales as Critically Endangered (Cooke 2018) and fin whales as Endangered (Reilly et al. 2013). Low abundances of these species after the extensive whaling pressure means that visual surveys are generally not cost-effective for monitoring population distributions or seasonal abundances, and automated acoustic methodologies are being increasingly used (e.g. Branch et al. 2007, Thomas & Marques 2012, Miller et al. 2015, Balcazar et al. 2017, Shabangu et al. 2019). Effects of environmental conditions on the seasonal call occurrence and call rates of Antarctic blue and fin whales in the Southern and Atlantic Oceans have recently been documented (Shabangu et al. 2017, 2019).

Antarctic blue whales produce D- and Z-calls (Ljungblad et al. 1998, Rankin et al. 2005, Oleson et al. 2007a). D-calls are slightly higher in frequency than Z-calls, are frequency modulated (FM) and down-sweep from 106–22 Hz (e.g. Rankin et al. 2005, Saddler et al. 2017). D-calls are believed to be used for short-range communication, last about 2–6 s and might be produced by males and females during feeding (Oleson et al. 2007a, Saddler et al. 2017). A recent study has shown that blue whale males also produce D-calls at high call rates (60–200 calls h⁻¹) as an agonistic mating display during reproductive competition; females produce this call type as a receipt of the males' acoustic displays and might also be involved in the agonistic display (Schall et al. 2020). Z-calls are low frequency tonal sounds consisting of stereotyped 3-unit sequences; the duration of a complete Z-call can range from 18–26 s (Ljungblad et al. 1998, Rankin et al. 2005). The first unit (Unit A) of the Z-call is 8–12 s long (Rankin et al. 2005, Miller et al. 2015) and is constant in frequency at ~27 Hz (McDonald et al. 2009, Gavrilov et al. 2012, Leroy et al. 2016, Ward et al. 2017). The second unit (Unit B) is short (2 s) and downsweeps from ~27–20 Hz, and the third unit (Unit C) is 8–12 s in length with a slight modulation from 20 to ~18 Hz (Rankin et al. 2005). Z-calls can be detected in any of the following combinations: (1) all 3 unit calls, (2) 2 unit calls consisting of Units A and B or (3) just as 1 unit calls consisting only of Unit A.

Only male Antarctic blue whales are presumed to produce Z-calls, likely as a long-distance contact call for sexual advertisement or other social interactions, similar to the function of other blue whale calls (McDonald et al. 2001, Oleson et al. 2007a). These

calls are sometimes produced in repeated, stereotyped sequences at regular intervals, termed songs (Payne & McVay 1971, McDonald et al. 2001, 2006, Oleson et al. 2007b, Leroy et al. 2016, Thomisch et al. 2016). Songs are call phrases uttered in a recognizable and repeated sequence and used chiefly for attracting mates (Janik 2009). They can last from minutes to days or weeks with slight pauses as the animals surface to breathe (Cummings & Thompson 1971, Payne & McVay 1971, McDonald et al. 2001, 2006).

Fin whale calls consist of short FM downsweeps from ~28–15 Hz (hereafter called 20 Hz pulse) that last for less than 1 s, which are sometimes accompanied by a concurrent higher frequency pulse (Širović et al. 2004, 2009). Two regional differences in the fin whale higher frequency pulses have been described: pulses from the Eastern Antarctica Peninsula had a secondary frequency peak in the pressure spectrum at 99 Hz, whereas pulses from the Western Antarctic Peninsula had a frequency peak at 89 Hz (Širović et al. 2009). Only male fin whales are believed to produce the 20 Hz pulses, which can be uttered as either a unit or song (Croll et al. 2002). Fin whales also produce another short (usually under 1 s) pulse that downsweeps from 70–40 Hz (Širović et al. 2013); hereafter termed the 40 Hz pulse. The 40 Hz pulses are irregularly produced, like blue whale D-calls (Rankin et al. 2005, Širović et al. 2013), thus they can sometimes be mistaken for D-calls because they both extend over parallel frequency bands. The distinguishing feature between the 2 call types is the call duration; D-calls have extended durations compared to the 40 Hz pulses (Rankin et al. 2005, Širović et al. 2013). The 20 Hz pulse is used for social contacts (McDonald et al. 1995, Edds-Walton 1997), while the 40 Hz pulse might be used for foraging purposes (Širović et al. 2013).

The Maud Rise is a seamount or plateau centred at 65°S, 2.5°E in the Weddell Sea of the Southern Ocean (see Fig. 1). Its peak rises almost 3000 m from the seafloor and its summit is positioned just less than 1000 m beneath the sea surface (Brandt et al. 2011). The flow of deep circumpolar waters is disturbed by the rise, which causes relatively warm (>1°C), nutrient-rich deep waters to rise up (upwell) to the sea surface resulting in significant phytoplankton growth (Comiso & Gordon 1987, Gordon & Huber 1995, Hellmer 2007). The newly upwelled warm waters fragment the sea ice cover in winter, resulting in the formation of polynyas (areas of open water surrounded by sea ice) and initiates the spring melt of sea ice to benefit the biological ecosystem of the area (Comiso & Gordon 1987, Hellmer 2007, Gordon 2009,

Martin 2009). The presence of large swarms of Antarctic krill around the Maud Rise has been associated with the upwelling-driven phytoplankton blooms as well as the presence of sea ice algae for krill to feed off (Everson 2000, Hellmer 2007). This, consequently, also drives the seasonal occurrence of marine top predators in the area such as whales, seabirds, seals and fish (e.g. Everson 2000, Širović et al. 2004, Knox 2006).

To date, only short-term acoustic research on Antarctic blue and fin whales has been conducted, during the Southern Ocean Whale and Ecosystem Research programme of the International Whaling Commission (IWC SOWER) between 1996 and 2009 in the vicinity of the Maud Rise (Shabangu et al. 2017, in press). A study on Antarctic minke whales is the single long-term acoustic study that has been conducted off the Maud Rise (Shabangu et al. 2020). Findlay et al. (2014) conducted a 10 d blue whale sighting survey around the Maud Rise and sighted 24 Antarctic blue whales and 33 fin whales. Here, we present the first study of seasonal detection ranges, call occurrence, call rates and diel calling patterns of Antarctic blue and fin whales off the Maud Rise, eastern Weddell Sea, recorded through passive acoustic monitoring. Such information is pivotal for improving our understanding and knowledge of the acoustic behaviour and ecology of recovering Antarctic blue and fin whale populations in the Southern Ocean.

2. MATERIALS AND METHODS

2.1. Acoustic data collection

Passive acoustic recordings of Antarctic blue and fin whale calls were collected at 65° S, 2.5° E on the Maud Rise in the eastern Weddell Sea region of the Southern Ocean (Fig. 1). An autonomous underwater recorder for acoustic listening (AURAL model 2, v.04.1.3, Multi-Electronique; hereafter termed recorder), rated to 300 m depth, was used to passively record acoustic data. The recorder was equipped with a HTI-96-MIN (High Technology) hydrophone with a factory-calibrated sensitivity of -164.10 dBV μPa^{-1} . The recorder was positioned 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 approximately 1260 m. The recorder was deployed from 12 January 2014 to 17 January 2015 but stopped recording on 17 September 2014 due to battery depletion, so that only 8 mo of acoustic data

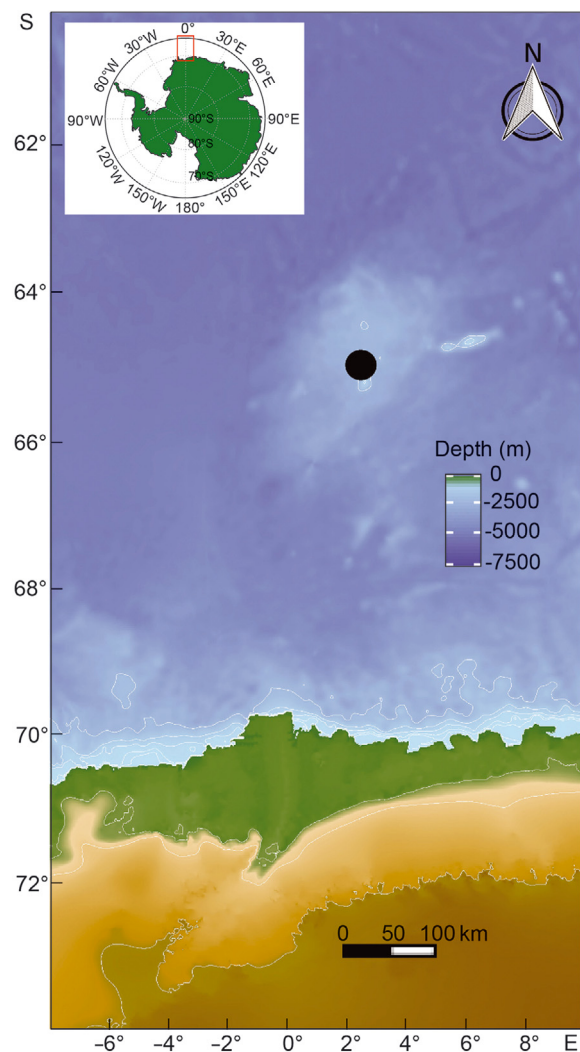


Fig. 1. Position of the recorder mooring (●) off the Maud Rise, eastern Weddell Sea

were recorded. During this time, the recorder sampled the acoustic environment at a rate of 2048 Hz and recording 1 block of 25 min h^{-1} throughout the day to preserve the battery life.

2.2. Autonomous call detections

The whole acoustic data set was reviewed visually through spectrograms, and aurally when Antarctic blue and fin whale calls were visually identified using Raven Pro (Bioacoustics Research Program 2017). The autonomous detection of fin whale 20 Hz pulses and Z- and D-calls of blue whales was performed using a detection template method developed and implemented in eXtensible Bio-Acoustic Tool (XBAT) software (Figueroa 2006) as a MATLAB

routine (MathWorks 2014). No detector was implemented for fin whale 40 Hz pulses since this call type was not detected during the visual review of the acoustic data. Whale calls were recognized autonomously from spectrograms by cross-correlating with the detection template kernel (Mellinger & Clark 2000) based on a similarity level above the set threshold (the lowest detectable similarity percentage between a template and call within the metric produced for each detection by the detection algorithm). Unit A of the Z-call (Fig. 2a) was used as a detection template since our data did not contain any complete 3-unit or 2-unit Z-calls. A single template of D-calls (Fig. 2c) downsweeping from 75–40 Hz was used as a detection template, since similar calls were present in our similar data set—hence there was no need for multiple detectors to accommodate the high variability of this FM call type. A fin whale 20 Hz pulse (Fig. 2b) was used as a template for detecting other similar calls in our acoustic data set. Some individual Unit A Z-calls were not discernible in bands of continuous calling (chorusing) when the call rate of the species was very high (Fig. 2b,c); thus, such calling periods were poorly quantified in this analysis due to the difficulty in delineating calls. Z-call chorus (hereafter called the 27 Hz chorus) is produced by distant

Antarctic blue whales (Thomisch et al. 2016), and its detection range is currently unknown. The presence of the continuous calling band of the Antarctic blue whale and fin whale chorus between 18 and 28 Hz (the 18–28 Hz chorus) was noted, as it could have possibly masked some of the fin whale 20 Hz pulses and blue whale Z-calls. The presence of a chorus around 99 Hz (Fig. 2c) was noted as it possibly represented 99 Hz pulses from distant fin whales.

Seven different thresholds from 15–75% in increments of 10% were tested to determine optimal thresholds for the detection of blue and fin whale calls (Fig. 3). From preliminary testing on 5% of the acoustic data, the 15% detection threshold was best suited for detections of the fin whale 20 Hz pulses, D- and Z-calls as it produced the fewest missed calls compared to other thresholds. We visually assessed the whole acoustic data set in XBAT to estimate the number of false positive (detections that were not real blue or fin whale calls) and false negative (missed blue and fin whale calls) calls. The true positive rate (also called sensitivity or recall) was used to measure the percentage of blue and fin whale calls that were automatically detected, and was calculated as the number of true positives divided by the total number of calls detected (number of true positives plus num-

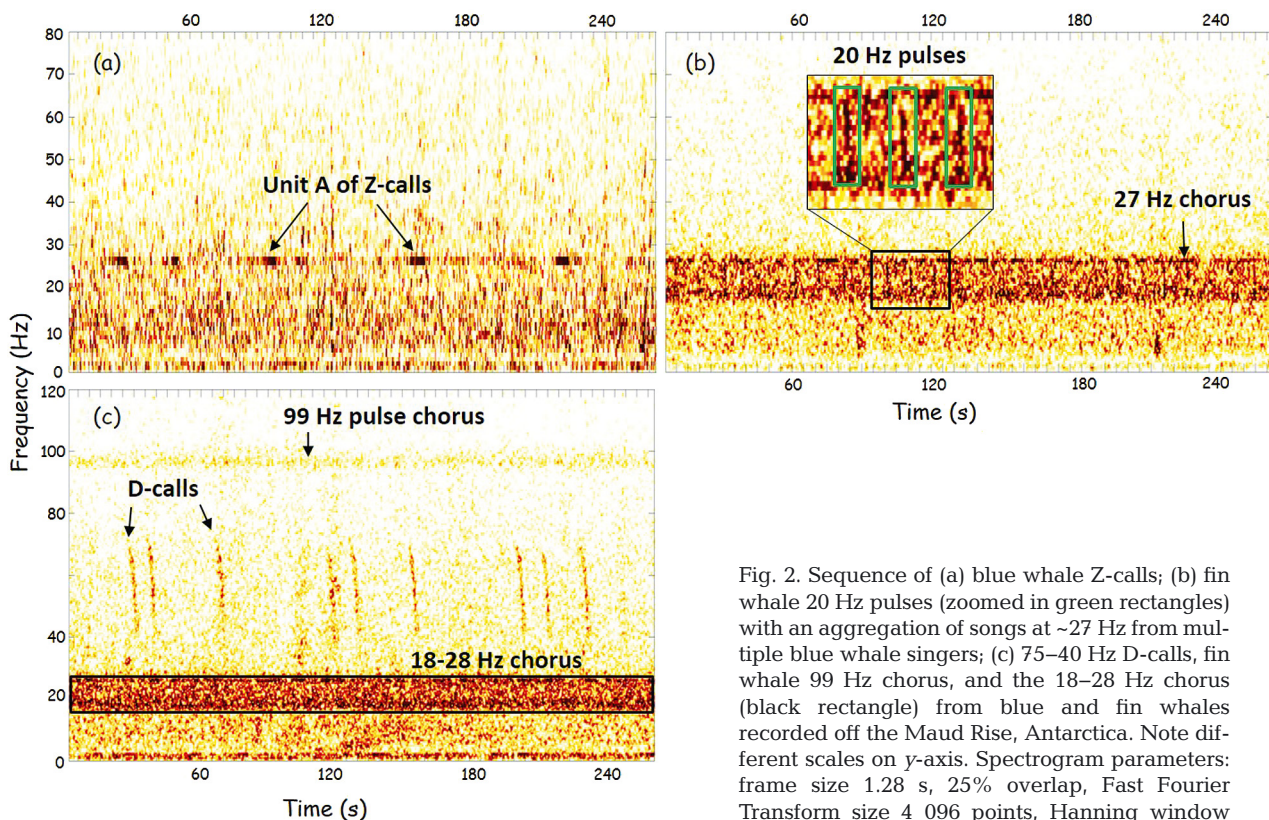


Fig. 2. Sequence of (a) blue whale Z-calls; (b) fin whale 20 Hz pulses (zoomed in green rectangles) with an aggregation of songs at ~27 Hz from multiple blue whale singers; (c) 75–40 Hz D-calls, fin whale 99 Hz chorus, and the 18–28 Hz chorus (black rectangle) from blue and fin whales recorded off the Maud Rise, Antarctica. Note different scales on y-axis. Spectrogram parameters: frame size 1.28 s, 25% overlap, Fast Fourier Transform size 4 096 points, Hanning window

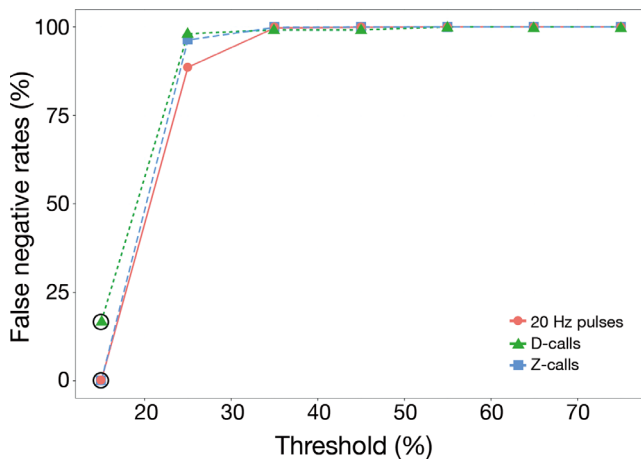


Fig. 3. False negative rates at different thresholds for the fin whale 20 Hz pulses and blue whale D- and Z-calls recorded off the Maud Rise, Antarctica. Used thresholds are circled

ber of missed detections). Visually identified false positive detections (<2% of the detected calls) were manually excluded from further acoustic analyses, while visually identified false negatives were manually incorporated into the total call number counts. Detection templates produced false negative rates of 17 and 0% for D- and Z-calls respectively, and true positive rates of 83 and 100% for D- and Z-calls respectively. The fin whale detection template produced 0% false negative and 100% true positive rates (Fig. 3).

2.3. Determination of call occurrence and rates

Acoustic presence refers to instances when a whale call type was detected in a sampling interval, whereas acoustic absence refers to the lack of any call detection within a sampling interval. A sampling interval was defined as the time between which data was recorded, which was 25 min. Proportion of species occurrence was calculated as the number of sampling intervals with presence of Z-calls for blue whales, and 20 and 99 Hz pulses for fin whales, divided by the total number of sampling intervals per month. We did not use the presence of the 18–28 Hz chorus to establish occurrence of either species since the chorus consists of calls from both species and it is currently impossible to separate the source of the calls. Call rates were determined as the number of calls in a sampling interval divided by the duration of the sampling interval (0.42 h), which described how often animals were calling. We used austral seasons of the year to define our data: summer (December–

February), autumn (March–May), winter (June–August) and spring (September–November). Different light regimes for plots were defined over different seasons according to the altitude of the sun (nautical twilight [dawn and dusk], daytime and nighttime) based on averages of hourly sun altitudes over austral seasons. Sun altitudes were obtained from the United States Naval Observatory Astronomical Applications Department (<http://aa.usno.navy.mil>). We defined the nautical dawn hours as periods when the centre of the sun was geometrically between 0 and 12° below the horizon before sunrise. Daytime hours were between sunrise and sunset and nautical dusk hours were between sunset and the evening (defined as when the sun was <12° below the horizon). Night-time hours were when the geometric centre of the sun was >12° below the horizon between dusk and dawn. Given that 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).

2.4. Sea ice extent

Monthly sea ice extensions were downloaded from the G02135 data set (Fetterer et al. 2016) at the National Snow and Ice Data Centre data pool server: (ftp://sidacs.colorado.edu/DATASETS/NOAA/G02135/south/monthly/shapefiles/shp_extent/). From the monthly sea ice extensions, we measured the distance of the nearest sea ice edge to the recorder mooring position. Processed daily sea ice concentrations (%) were obtained from the satellite sea ice concentration product of the Advanced Microwave Scanning Radiometer-2 (AMSR-2) with a 3.125 km grid resolution (Sprenn et al. 2008, Beitsch et al. 2014).

2.5. Detection range estimation

The communication space is the region around a cetacean throughout which the detectability of calls from distant conspecifics is generally good. A detection range can roughly quantify the size of this space. Detectability (D) itself is a geographically specific function that depends on complex acoustical propagation. D will be defined as a binary metric, with value unity if the signal-to-noise ratio (SNR) is above a detection threshold (DT) value, zero otherwise:

$$D = 0 \text{ for } \text{SNR} \leq \text{DT} \text{ or } D = 1 \text{ for } \text{SNR} > \text{DT} \quad (1)$$

Using the passive sonar equation (where all quantities are in decibels), the SNR for a listener (recorder) at location Y and for a call from location X is:

$$\text{SNR}_{X,Y} = \text{SL} - \text{TL}_{X,Y} - \text{NL}_Y \quad (2)$$

where SL is the source level, TL is the transmission loss and NL is the noise level. Eqs. (1) & (2) were used to define the detection range of low frequency (18–28 Hz) Antarctic blue and fin whale vocalizations near the Maud Rise off Antarctica for 4 time periods: January, April, July and September.

The average SL was assumed to be 189 dB re 1 μPa @ 1 m for both blue and fin whales (Širović et al. 2007). TL was computed using the BELLHOP beam tracing model (Porter 2011) at 20 Hz. The BELLHOP model requires several environmental parameters to estimate TL. The bathymetry in the region was extracted from the Smith-Sandwell database (Smith & Sandwell 1997). Sound speed profiles for the region were built by extracting monthly averaged temperature and salinity profiles (for the appropriate months) from the World Ocean Atlas 2013 (Locarnini et al. 2013, Zweng et al. 2013), then converting temperature and salinity to sound speed using routines from the Thermodynamic Equation of Seawater-2010 (<http://www.teos-10.org>). Sound-speed attenuation was obtained from the Thorp model (Thorp 1967). The sound-speed profile at the Maud Rise only extends to 2400 m; profiles for the surrounding deeper regions were made by linearly extrapolating the values at 2300 and 2400 m. The vocalizing whale was assumed to be at a depth of 30 m (Oleson et al. 2007b); the receiver was at 250 m (to coincide with the actual deployment depth of the hydrophone). TL curves were computed every 18 km along 16 radials starting at the receiver location and spaced every 22.5° in azimuth. Reciprocity was used to assume that the loss from the receiver to the whale (the direction the BELLHOP model used) was equivalent to the loss from a distant vocalizing whale to the receiver.

'Background' ambient NLs were taken from four 25 min recordings captured in January, April, July and September. NL had the most significant effect on detection range in this analysis. In general, the noise, especially at these low frequencies, is considerably quieter when the sea surface is covered by pack ice in austral winter and spring. During these times (particularly for the July and September scenarios), the 'background' level at the hydrophone in the blue and fin whale vocalization frequency band is dominated by conspecific chatter (the 18–28 Hz chorus), which can be as much as 10 dB over levels that would exist in the absence of all marine mammal vocalizations. NLs rise across the band for the January (sea ice

break-up) and April (open ocean) scenarios, as the ocean surface becomes more active. There is no noticeable chatter dominance in the January record, but it is strong in the April record, even though levels across adjacent bands are also higher (Fig. 4).

Since there is no definitive understanding of detection threshold for these species, we assumed that the conspecific chatter acts like noise for the single point-to-point communication effort of a distant whale to this receiver. Accordingly, the operational NL was chosen as roughly the average level near the peak of the band as follows: 92 dB for January; 99 dB for April; 95 dB for July; 87 dB for September (Fig. 4). DT was assumed to be 0 dB (Miller et al. 1951); this threshold is consistent with Širović et al. (2007). An alternative definition might define the 'background' noise as the value interpolated between the NLs lacking dominant biophony at the nearest lower and higher frequencies, in which case a positive DT would be chosen. For example, Stafford et al. (2007) chose a threshold of 8 dB. For the April, July and September scenarios, these 2 definitions are similar. Complicated BELLHOP TL curves yield complex detectability throughout the region. There is rarely an abrupt change in detectability at a range that would define a unique detection range. Detection range, therefore, is at best a qualitative metric, and may depend on azimuth.

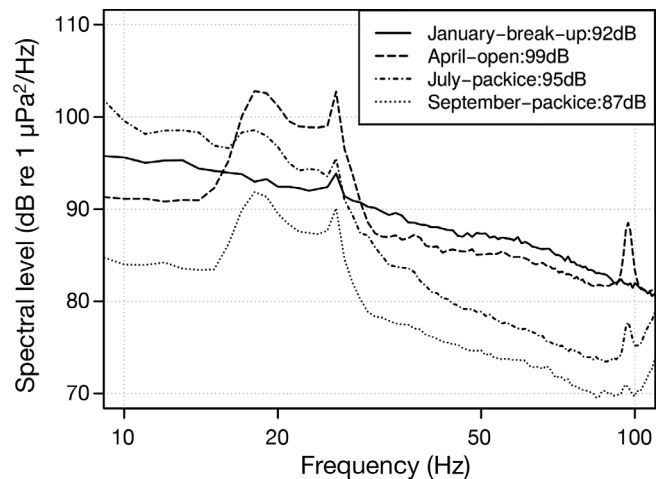


Fig. 4. Observed ocean sound spectra for the 4 scenarios. Vocalizing energy is dominant for April, July and September between 18 and 28 Hz chorus frequency band. The legend provides the 'background' level chosen for modelling with the associated data month and nominal sea surface conditions, where January-break-up:92dB is 92 dB for January when ice breaks up; April-open:99dB is 99 dB for April during open ocean; July-packice:95dB is 95 dB for July during pack ice conditions; September-packice:87dB is 87 dB for September during pack ice conditions

2.6. Modelling occurrence and behaviour

We used random forest (RF) models (Ho 1995, Breiman 2001) to investigate the influence of different predictor variables (time of day [h], distance to the sea ice extent [km] and month of the year) on the acoustic occurrence and call rates of Antarctic blue and fin whales. RF models are an ensemble modelling approach for classification (for factor variables such as call occurrence), regression (for continuous variables such as call rates) and other functions with non-parametric inferential properties (Breiman 2001, Hastie et al. 2009). As a machine learning method, RF models provide higher performances and have considerable benefits over standard regression methods such as GAMs (Elith et al. 2008, James et al. 2013). RF models have also been found to perform better in terms of prediction accuracies than GAM and generalised boosted regression models (Friedman et al. 2000) for modelling blue and fin whale occurrence and call rates in the Southern and Atlantic Oceans (Shabangu et al. 2017, 2019). The advantages and rationale of using RF models for this kind of data are provided in Shabangu et al. (2017, 2019). The relative importance of each of the variables in the model was determined by measuring the Gini index (used as goodness-of-fit for the RF model), which measures homogeneity from 0 (homogeneous) to 1 (heterogeneous) from the total decrease in node impurities (Hastie et al. 2009). Gini coefficients decrease drastically across every tree of the forest for variables that produce nodes with higher purity, then are summed for each variable and divided by the number of trees in the forest to provide an average importance.

Before fitting the RF models, we investigated multicollinearity between different predictor variables (time of day, distance to the sea ice extent and month of the year) using generalised variance inflation factors (GVIFs; Fox & Monette 1992) implemented through the 'car' package (Fox and Weisberg 2011) in R v.3.6.0 (R Core Team 2019). Our GVIF values indicated no collinearities, as they were around one (Fox & Monette 1992, O'Brien 2007, Hair et al. 2009), and no variable was excluded due to multicollinearity. RF models were fitted using the optimal configuration values (best settings): tree node of one for all models, splitting minimum size of terminal nodes of trees of one, and 500 growing trees for all models except for the D-call's RF model, which was 2000. The 'randomForest' package (Liaw & Wiener 2002) was used to perform RF modelling in R, whereas the 'ranger' package was used to determine the RF

model optimal parameter settings as a computational-time-saving method (Wright & Ziegler 2017) to implement the RF models. To improve interpretability of RF model output, we calculated p-values for the feature importance metric via permutation, whereby features/variables were permuted, and changes in feature importance after permuting were used to measure significance. Altmann et al.'s (2010) method was used to compute the significance (p-value) of the feature importance value.

3. RESULTS

3.1. Whale acoustic occurrence

A total of 2479 h of audio files were recorded within the 8 mo of the recorder deployment. Blue whale Z-calls were present in 94% of the recorded time (2330 h of audio files), and fin whale 20 Hz pulses were present in 0.7% of the recorded time (17 h of audio files). We detected a total number of 50407 blue whale Z-calls, 475 blue whale D-calls and 5381 fin whale 20 Hz pulses. Fin whale 40 Hz pulses were not detected in our data set. Z-calls were present throughout the entire period of the recorder deployment (January–September); the monthly proportion was above 81% for each month, with the highest proportion (100%) in February (Fig. 5). The blue whale 27 Hz chorus was present throughout the recorder deployment, and the 18–28 Hz chorus was present from February through September (Fig. 5). D-calls were detected in small proportions during February (5.1%), March (4%) and April (0.6%) (Fig. 5). Monthly proportions of the fin whale 20 Hz pulse occurrence were 2 and 4% for January and March respectively, and the 99 Hz chorus was present from March until July (Fig. 5).

3.2. Seasonal diel calling rates

During winter, Z-call rates increased from immediately after sunset to early morning and then sharply decreased from dawn to dusk (Fig. 6a). In spring, Z-call rates increased from dawn until 09:00 h but slightly decreased from 10:00–12:00 h before stabilising and then increased again from 17:00 h until midnight (Fig. 6b). Z-call rates increased from 13:00–18:00 h in summer (Fig. 6c) and from dawn to 16:00 h in autumn (Fig. 6d). D-call rates increased from 08:00–10:00 h and sharply decreased until 12:00 h in summer (Fig. 6e). In autumn, D-call rates increased

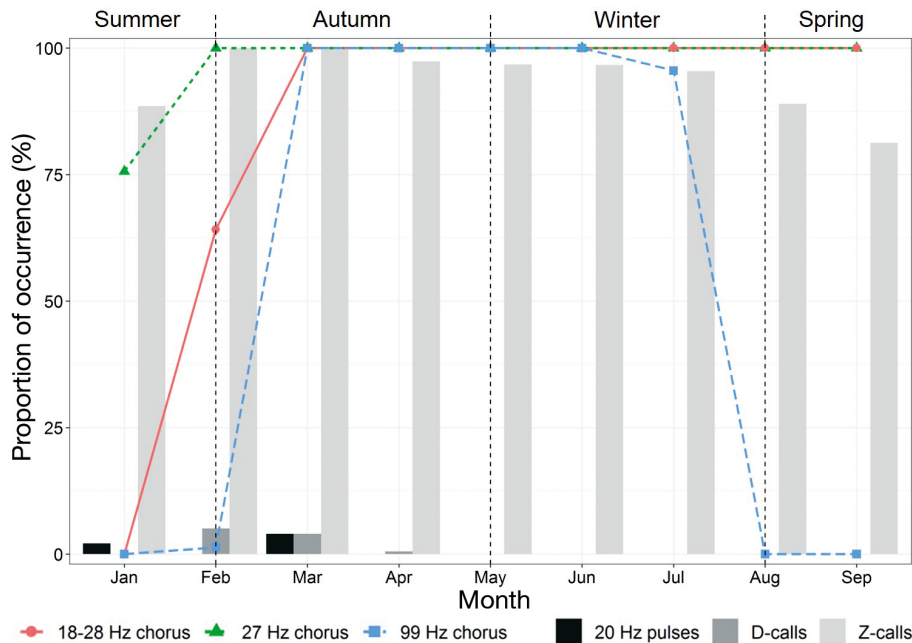


Fig. 5. Monthly proportion of Antarctic blue and fin whale call occurrence off the Maud Rise from January–September 2014

dramatically between 12:00 and 16:00 h and dropped towards midnight (Fig. 6f); there were no calls recorded in winter and spring. Fin whale 20 Hz pulse rates increased from 04:00–10:00 h in summer and decreased sharply thereafter (Fig. 6g). In autumn, the fin whale 20 Hz pulses increased from 05:00–08:00 h and stabilised until 14:00 h, when there was a slight drop until 17:00 h, and then sharply increased from 18:00–22:00 h (Fig. 6h). There was no temporal segregation in the peaks of diel calling rates of blue whale Z-calls and fin whale 20 Hz pulses in autumn but clear temporal segregation in peaks of diel calling rates during summer (Fig. 6). D-call rates had a similar diel pattern to the 20 Hz pulses but the opposite pattern of Z-calls in summer (Fig. 6c,e,g).

3.3. Detection range output

In general, a high-latitude sound-speed profile channels sound away from the bottom, providing enhanced propagation ranges (Fig. 7). The combination of ducted propagation and lower noise can dictate potential detection ranges in excess of 1000 km (Fig. 7) in the sea-ice covered months of spring but were significantly lower at 250–500 km for other times of the year. In the late austral summer a near-surface duct can form, again providing enhanced ducting, and hence, propagation range, as seen for mid-autumn in the April simulation (Fig. 7a). Additionally, this is particularly evident for the September scenario, for propagation under full pack ice condi-

tions where background levels aside from biophony were very quiet (Fig. 7d). In both these simulations, the major range restriction is the bathymetry to the south (123.75–213.75°), where the seafloor slopes up to the Antarctic continent. In the other 2 scenarios, the maximum range is <500 km, with evidence of convergence zone influence in all directions but no bathymetric restrictions (Fig. 7).

3.4. Predictors of whale occurrence and behaviour

From 12 January–20 April, the sea ice concentration was 0% before increasing to 50% by the end of April. The recorder mooring was submerged under sea ice from the beginning of May through mid-September; sea ice concentrations were around 80% at the start of May but increased to 100% from mid-May through mid-September. We observed a negative Pearson correlation between distance to the sea ice edge and acoustic occurrence of blue ($r = -0.58$) and fin ($r = -0.55$) whales. Negative distances to the sea ice edge were when the recorder deployment position was not immersed under sea ice, and positive distances to the sea ice edge were when the recorder deployment position was immersed under sea ice (Figs. 8 & 9). The following factors had the largest effects on Antarctic blue whale Z-call occurrence: the months of February and March (Fig. 8a); distances before and after (between –200 and 800 km) the recorder position was fully submerged under sea ice (Fig. 8b); and nighttime and daytime

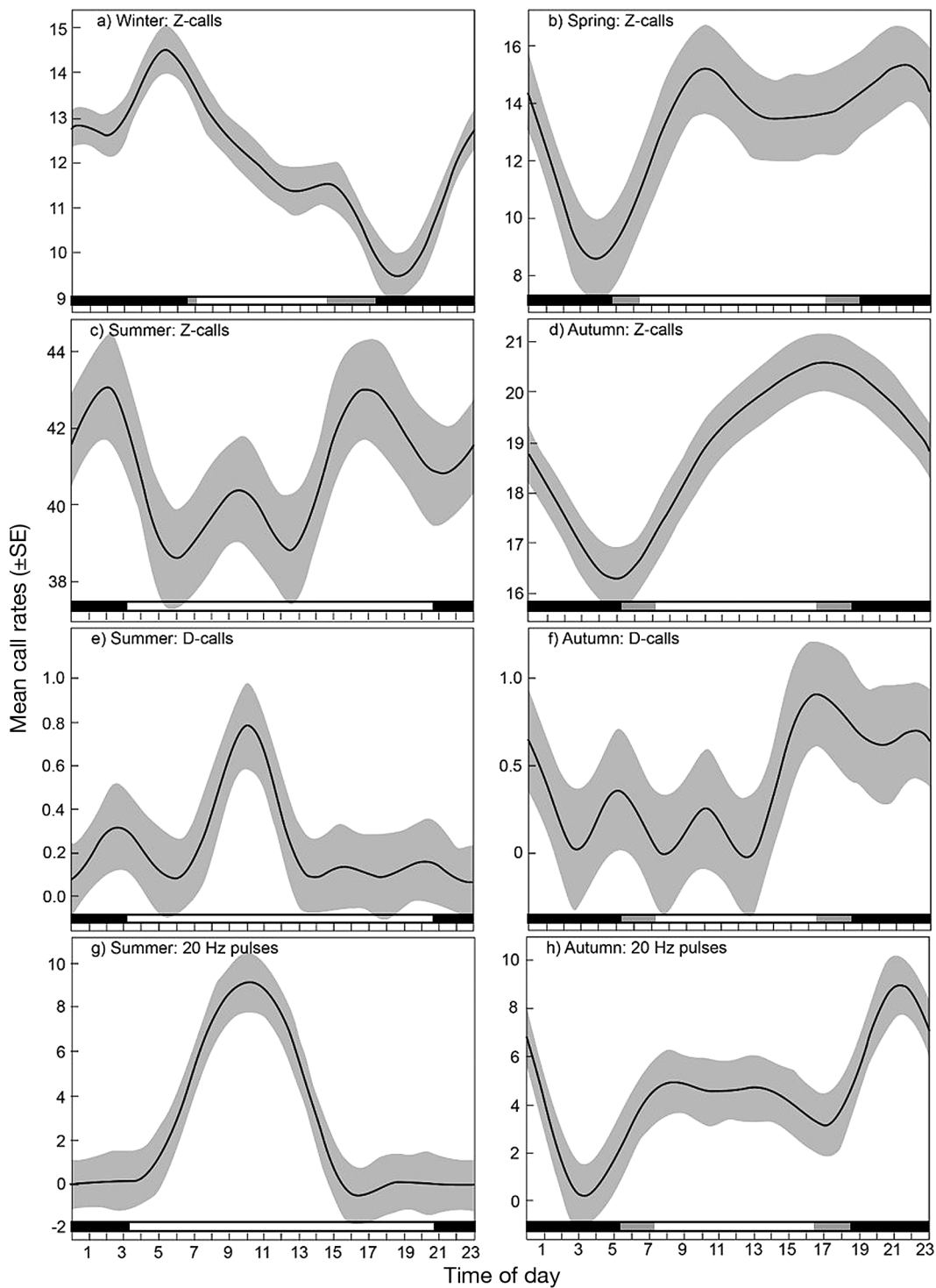


Fig. 6. Seasonal circular smoothed mean \pm SE (black lines with grey shading) diel call rates for (a–d) Z-calls, (e,f) D-calls, (g,h) fin whale 20 Hz pulses. No D-calls or 20 Hz pulses were detected in winter and spring. Note different scales on y-axis. Horizontal diel bar shading: black: average nighttime hours; grey: average twilight hours; white: average daytime hours; no dawn and dusk for summer. Universal Coordinated Time is used

hours (Fig. 8c). For fin whales, the months of January and March had the highest effect on the 20 Hz pulse occurrence (Fig. 8d); negative distances to the sea ice

edge (Fig. 8e); and nighttime and daytime hours (Fig. 8f). Month of the year was the most important predictor of Antarctic blue and fin whale occurrence

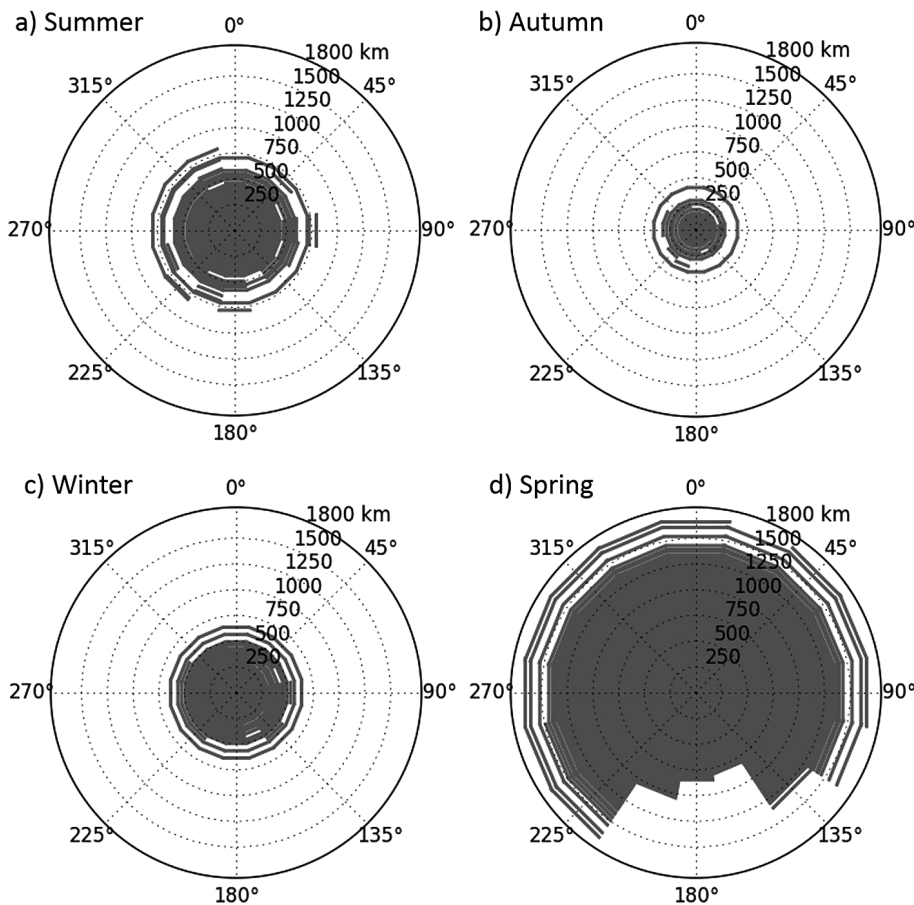


Fig. 7. Polar plots of BELLHOP model estimates for seasonal detection ranges of Antarctic blue and fin whale calls at different bearings in (a) summer, (b) autumn, (c) winter and (d) spring. Grey patches: regions from which calls would be detectable at the hydrophone location (centre of plot)

(Fig. 8g,h). Distance to the sea ice edge was a moderately important predictor, while time of the day was the least of important predictor of both Antarctic blue and fin whale call occurrence (Fig. 8g,h). All variables were significant predictors for blue whale occurrence, whereas month of the year and distance to sea ice edge were significant predictors of fin whale occurrence and time of day was an insignificant predictor (Fig. 8g,h).

February and March, daytime (early and late morning) and nighttime hours (midday to midnight) and distance to the sea ice edge <200 km had the highest effect on D-call rates (Fig. 9a–c). February and negative distance to the sea ice edge had the highest effect on Z-call rates (Fig. 9d,e); no visible effect of a particular hour was observed on Z-call rates (Fig. 9f). January and March, daytime and nighttime hours and distance to the sea ice edge <250 km had the highest effect on the fin whale 20 Hz pulse rates (Fig. 9g–i). Month of the year was the most important predictor, time of day was a moderate predictor and distance to the sea ice edge was the least important of D-call and fin whale 20 Hz pulse rates (Fig. 9j,l). Month of the year was the most

important predictor of Z-call rates, followed by distance to the sea ice edge as a moderate predictor and time of day as the least important predictor (Fig. 9k). Month of the year, distance to the sea ice edge and time of day were significant predictors of Z- and D-call rates (Fig. 9j,k). Month of the year and distance to the sea ice edge were significant predictors of fin whale 20 Hz pulse rates, whereas time of day was an insignificant predictor of this call type (Fig. 9l).

4. DISCUSSION

The reduced detection of calls by our automated call detection method, due to the difficulty of delineating individual Z-calls from the 27 Hz chorus during periods with intense calling, potentially induced a negative bias in the total number of detected blue whale calls in our data during those periods. Thomisch et al. (2016) used the blue whale index (BWI) to quantify the proportion of time when the chorus had higher energy levels than ambient noise, and Leroy et al. (2016) used a similar technique but termed it the 'chorus to noise-without-chorus ratio' (CNR). The

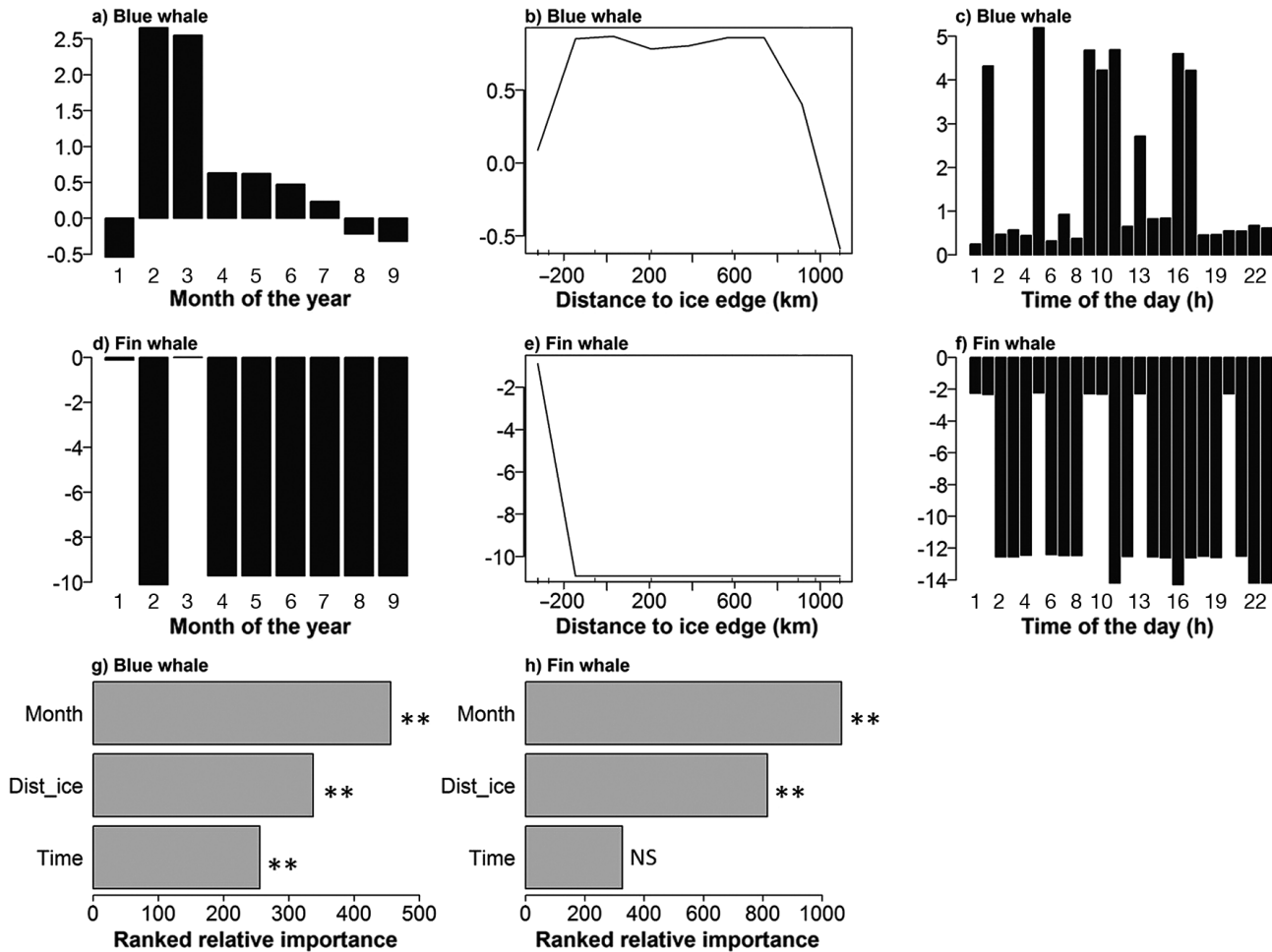


Fig. 8. (a–f) Relative effects and (g,h) relative importance of predictor variables for the occurrence of Antarctic blue whale Z-call and fin whale 20 Hz calls as determined by random forest models. Dist_ice: distance to the sea ice extent; ** indicates significance ($p < 0.05$); NS: not significant ($p > 0.05$). The y-axes of (a–f) and x-axes of (g,h) are in arbitrary units and have different scales

BWI and CNR time series generally followed the same trend as the seasonal variations of call numbers (Leroy et al. 2016, Thomisch et al. 2016); we found the same trend with the 27 Hz chorus but less so with the 18–28 Hz chorus. Consequently, the automated template detector method routinely underestimated Z-call numbers during chorus presence (as noted by Thomisch et al. 2016) but was effective in assessing and providing an indication of whale call occurrence and acoustic behaviour (Shabangu et al. 2017, 2019). The sole detection of Unit A of Z-calls suggests that vocalizing whales were distant from the recorder. The recent increase in the number of researchers recording the 27 Hz chorus of Antarctic blue whales might indicate an increase in the Antarctic blue whale population since the chorus is assumed to comprise songs from multiple distant whales. For example, there were no 27 Hz choruses recorded

during circumpolar cruises conducted by the IWC SOWER programme (Shabangu et al. 2017), but this 27 Hz chorus is now commonly recorded in low latitude areas such as Namibia (Thomisch et al. 2019) and around the Equator in the Atlantic Ocean (Samaran et al. 2019).

February and March had the highest proportion of blue whale call occurrence and rates, suggesting that most animals were more vocally active during those months or that most migratory whales had arrived in the eastern Antarctic waters from their overwintering grounds after most of the sea ice extent had retracted, as determined from acoustic research (Širović et al. 2004) and seasonal catch data (Mackintosh & Wheeler 1929). February and March is also the period when the sea ice edge was farthest from our recorder location and krill biomass was high at the end of summer (Hewitt et al. 2004). Furthermore, such detection dif-

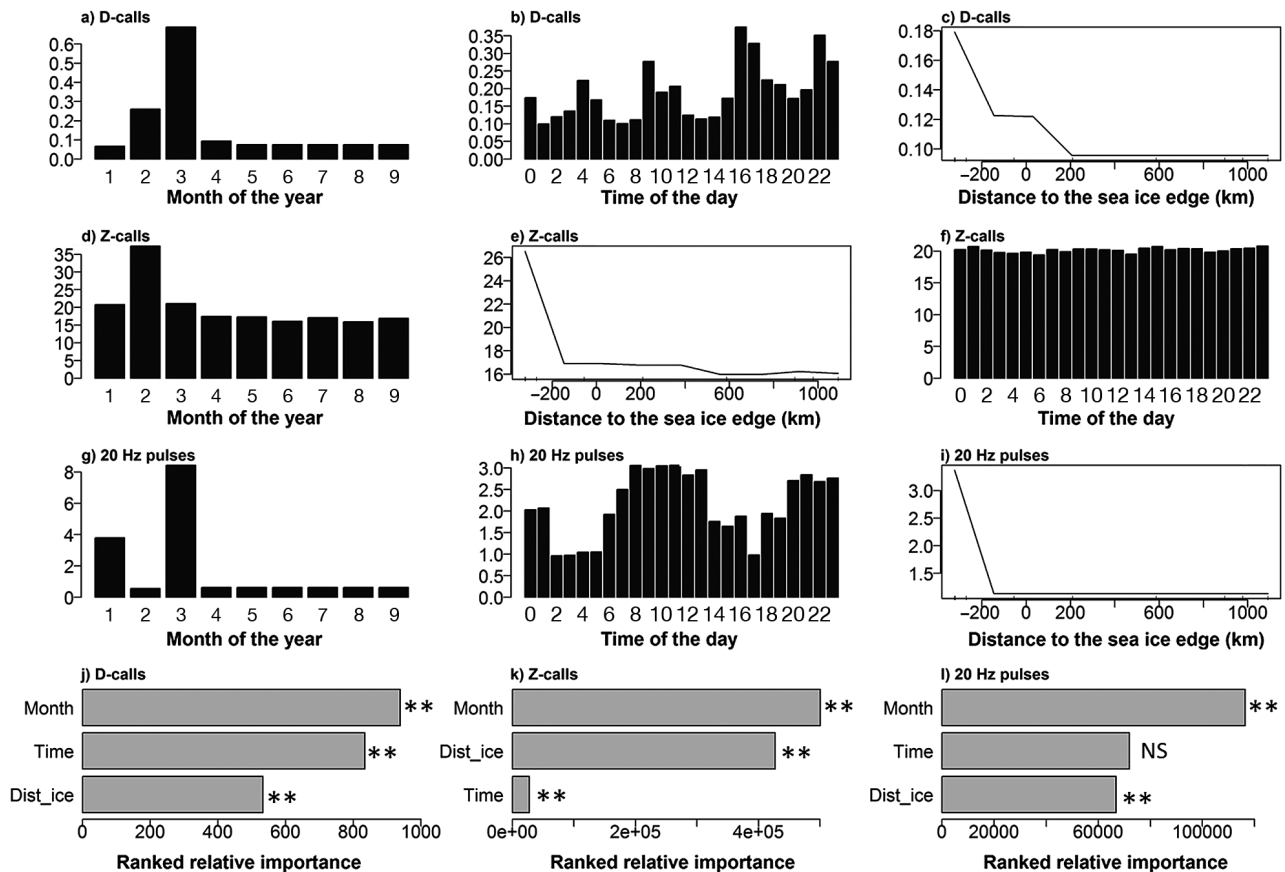


Fig. 9. (a–i) Effects and (j–l) relative importance of predictor variables for the call rates of Antarctic blue (D- and Z-calls) and fin (20 Hz pulses) whales according to random forest models. The y-axes of (a–i) and x-axes of (j–l) are in arbitrary units and have different scales. See Fig. 8 for further details on significance levels

ferences could have been caused by changes in detection ranges in relation to changing NLs and sound propagation over seasons as indicated by our BELL-HOP model results. The fin whale 20 Hz pulse was only recorded in January and March, a phenomenon that was unexpected as fin whales usually occur simultaneously and to some extent sympatrically with blue whales (Širović et al. 2004, 2009, Shabangu et al. 2019). The only calls of the fin whale occurring in eastern Antarctica were detected off the Maud Rise, suggesting longitudinal isolation between fin whales occurring in the eastern and western Antarctic (Širović et al. 2009).

The highest fin whale call rates in March could be from departing whales socializing as they move out of the Maud Rise region. Širović et al. (2004, 2009) also observed peaks in calling around that time of the year from circumpolar locations. Since the 99 Hz chorus of fin whales was present in periods when the 20 Hz pulses were not detected, it is likely that the 18–28 Hz chorus overshadowed the 20 Hz pulse, suggesting that fin whales could have been present from

January through September. Furthermore, the presence of the fin whale 99 Hz chorus from March through July suggests that a portion of the fin whale population might be in Antarctica during periods of high sea ice concentrations. The absence of the 40 Hz pulses of fin whales in our acoustic data set suggest that fin whales around the Maud Rise might not have produced the call when feeding, since this call type is associated with a foraging function (e.g. Širović et al. 2013). Aulich et al. (2019) also detected no 40 Hz pulses in Australian waters, but did not provide a reason for the lack of this fin whale call type in that area.

D-calls were only detected from February through April, which is towards the end of summer through mid-autumn, but not throughout the summer season as expected for Antarctic blue whale feeding distributions (Mackintosh 1942, Branch et al. 2007). D-call occurrence (lowest sample size of the 3 call types described here) was rather low with an average of 0.2 calls h^{-1} (range: 0–119 calls h^{-1}). It should be noted that this was based on a data set in which 98.5% of all data were characterised by zero D-calls. The average

D-call rates from this study are drastically lower than the average of 16 calls h^{-1} (range: 0–451, with 77.2% of all data characterised by zero D-calls) estimated in summer during the IWC SOWER cruises (Shabangu et al. 2017). The above difference in D-call rates could be because blue whales rarely produce this call type at this latitude; they could have been feeding further south of the Maud Rise at the sea ice edge, as detected during the circumpolar IWC SOWER cruises (Shabangu et al. 2017). Oleson et al. (2007a) also reported low call rates (4 ± 3.7 D-calls h^{-1}) during feeding activities off the California coast. Call rates in the present study are very low compared to Shabangu et al. (2017) and Schall et al. (2020), which could indicate that whales were not mating in this region. Additionally, low D-call detections might be due to propagation effects; this call type could be travelling shorter distances than Z-calls since they have been observed to function for short-range communication (Oleson et al. 2007b) and likely have lower SLs than Z-calls given their slightly high frequency.

The negative correlation that we observed between distance to the sea ice edge and blue and fin whale occurrence agrees with a negative correlation observed by Širović et al. (2004) between sea ice concentration and the acoustic presence of blue and fin whales in the Southern Ocean. Our RF model results suggest that month of the year and distance to the sea ice edge are important predictors of call occurrence and call rates of blue and fin whales in the Southern Ocean. The continuous presence of Antarctic blue and fin whales observed here could indicate that areas around the Maud Rise have year-round favourable environmental conditions and prey availability for these whales (Širović et al. 2004, 2009, Thomisch et al. 2016). Areas around the Maud Rise are known to have recurring large polynyas (generally referred to as the Weddell Polynyas) over the deep ocean during the winter (Comiso & Gordon 1987, Hellmer 2007), which might provide suitable habitats for blue and fin whales during winter. Shorter distance of the sea ice edge to the recorder mooring position was a moderately important predictor of Z-call occurrence and rates, probably reflecting that blue whales were calling closer to the sea ice extent where sea conditions are calm (Shabangu et al. 2017) and krill is abundant (Everson 2000). Although we estimated 100% sea ice concentrations around the mooring location during late autumn through spring, it is likely that polynyas were present around Maud Rise. Alternatively, the detections of blue whale Z-calls and fin whale 99 Hz chorus in months when the recorder was fully submerged under sea ice reflect

that these low frequency sounds could have been produced by whales in open waters at the sea ice edge; these sounds can travel long distances—over 1000 km as depicted by our BELLHOP model results at this time of the year.

Detection roses of the BELLHOP model showed a loss of detection range in the southern direction, which could be due to interruption by the Antarctic continent. Širović et al. (2007) estimated a maximum detection range of 1300 km for blue and fin whales in the Southern Ocean, whereas Thomisch et al. (2016) estimated a maximum detection range of 700 km for blue whales in the Southern Ocean. Samaran et al. (2010) estimated a maximum detection range of 200 km for Antarctic blue whales in the Indian Ocean. Our estimated maximum detection range of 1700 km for both blue and fin whales in spring is comparable to Širović et al.'s (2007) range of 1300 km. Detection ranges >1000 km support the theory of Payne & Webb (1971) that the low frequency sounds produced by baleen whales can travel such long ranges. The detection ranges of Thomisch et al. (2016) and Samaran et al. (2010) are considerably lower than the 1700 km detection range estimate in spring but comparable to the 250–500 km estimates in summer, autumn and winter. Differences in the estimates of whale call detection ranges between our study and previous studies could be due to different TL in the ocean, sea state conditions, NLs, SLs used, recorder types, recorder depths, sound propagation models used, SNR thresholds and bathymetric properties of different regions (e.g. Lurton 2002, Širović et al. 2007, Samaran et al. 2010, Thomisch et al. 2016). For example, the recorder of Širović et al. (2007) was deployed on the seafloor (3000 m water depth), whereas our recorder was positioned closer on the SOFAR channel. Propagation down to the deep receiver (Širović et al. 2007) would be less than that to the shallow receiver (present study), particularly at longer range. Remarkably, using a 0 dB SNR threshold (as in the present study) and BELLHOP to model TL (as in the present study), Širović et al. (2007) found a maximum range that is very consistent with, but slightly less than ours, which would follow for a deeper receiver experiencing greater TL. In general, there is no consistency in the computation of maximum detection range in the above studies. A useful exercise would be to try to compare these approaches, but that is beyond the scope of this paper.

Blue whale Z-call rates peaked between 05:00 and 17:00 h, suggesting that most blue whales are vocally active during the day (Shabangu & Findlay 2014, Leroy et al. 2016, Shabangu et al. 2017, 2019).

Early (~04:00 h) and late morning (09:00–11:00 h) and midday to nighttime (15:00–23:00 h) were important for the D-call rates, suggesting that blue whales could have been foraging on deep krill swarms during the day and more on ascending krill at night (Piakowski 1985, Gaten et al. 2008, Shabangu et al. 2019). According to our RF model results, time of day was the least important predictor of blue whale Z-calls but a moderately important predictor of D-calls and fin whale 20 Hz pulses, reflecting that call occurrence and rates vary over different times of the day depending on the call type. However, significance tests indicated that time of day was a non-informative predictor of fin whale occurrence and call rates, and cannot be reliably used to predict those responses.

Seasonal variations in diel Z-call rates could be due to changes in sound propagation properties or NLs around the recorder location. Additionally, these animals could have adjusted their behaviour in response to the different light regimes and environmental conditions of the Antarctic. Z-call rates in summer and autumn trended similarly since those seasons are closer to each other, whereas winter call rates were the opposite of summer and autumn. Spring (only the first 2 wk of spring were sampled) Z-call rates showed some similarity to summer and autumn call rates as these seasons might have similar environmental conditions. There was a clear difference in fin whale 20 Hz pulse diel calling rates between autumn and summer; this is possibly because the sample size of fin whale calls from our study was too low to reliably and accurately depict diel calling behaviour. Absence of temporal segregation between the peaks of diel calling rates of Z-calls and 20 Hz pulses in autumn shows that blue and fin whales might not vocally compete but vocalise at similar times during certain seasons of the year, as found in the Benguela ecosystem (Shabangu et al. 2019). Interestingly, there was a strong temporal segregation between Z-calls and 20 Hz pulse rates in summer—possibly reflecting that these whales avoided vocal competition during that season when whales are present in high numbers. Furthermore, D-calls had a similar diel pattern to 20 Hz pulses in summer but had an opposite diel pattern than Z-calls, likely reflecting a slight frequency shift by blue whales to avoid conflict with fin whales and that blue whales do not simultaneously produce these call types. Tripovich et al. (2015) found Antarctic blue whales off Australia to be more vocally active during nighttime, possibly to avoid vocal competition with pygmy blue whales during daytime.

Our current efforts to describe the diel calling behaviour, detection ranges and seasonal call occurrence of Antarctic blue and fin whales in the Southern Ocean provide useful information to better understand the occurrence and behavioural ecology of these endangered whale species. Based on detection ranges estimated by our BELLHOP model, Antarctic blue and fin whale calls could be used for longer range communication than previously documented if environmental conditions (such as temperature, NLs, wind speed, etc.) permit. Deployment of recorders on oceanographic moorings (Shabangu et al. 2019) could be a cost-effective way to collect future passive acoustic data in the Southern Ocean.

Acknowledgements. We are grateful to the National Research Foundation and the South African National Antarctic Programme (Grant No. SNA 2011112500003) for financially supporting the South African Blue Whale Project. We thank Meredith Thornton, Kirsty Venter, Ian Thompson, and Ove Fabriciussen for their kind assistance with the deployment of the recorder. We give special thanks to Sinekhaya Bilana, Jarred Voorneveld and Jethan d’Hotman for their outstanding and expert technical assistance with the acoustic transponder releases of the recorder mooring during recovery. Many heartfelt thanks to captains and crew of the RV ‘SA Agulhas II’ for their great assistance with recorder deployment and recovery. Marcel van den Berg is thanked for his invaluable advice and guidance with the procedure for recorder mooring deployment and recovery. MetOcean Services are thanked for the loan of a satellite transponder, while Mr. Bruce Spolander of MetOcean Services is thanked for providing satellite positions of the recorder during the recovery at late hours of the day.

LITERATURE CITED

- ✦ Altmann A, Tolos L, Sander O, Lengauer T (2010) Permutation importance: a corrected feature importance measure. *Bioinformatics* 26:1340–1347
- ✦ Aulich MG, McCauley RD, Saunders BJ, Parsons MJG (2019) Fin whale (*Balaenoptera physalus*) migration in Australian waters using passive acoustic monitoring. *Sci Rep* 9:8840
- ✦ Balcazar NE, Klinck H, Nieuwkerk SL, Mellinger DK, Klinck K, Dziak RP, Rogers TL (2017) Using calls as an indicator for Antarctic blue whale occurrence and distribution across the southwest Pacific and southeast Indian Oceans. *Mar Mamm Sci* 33:172–186
- ✦ 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
- Best PB (1998) Blue whales off Namibia—a possible wintering ground for the Antarctic population. Paper SC/50/CAWS14 presented to the IWC Scientific Committee, April 1998, Muscat
- Best PB (2007) Whales and dolphins of the Southern African subregion. Cambridge University Press, Cape Town

- Bioacoustics Research Program (2017) Raven Pro: interactive sound analysis software version 1.5. www.birds.cornell.edu/raven
- Branch TA, Stafford KM, Palacios DM, Allison C and others (2007) Past and present distribution, densities and movements of blue whales (*Balaenoptera musculus*) in the southern hemisphere and northern Indian Ocean. *Mammal Rev* 37:116–175
- Brandt A, Bathmann U, Brix S, Cisewski B and others (2011) Maud Rise—a snapshot through the water column. *Deep Sea Res II* 58:1962–1982
- Breiman L (2001) Random forests. *Mach Learn* 45:5–32
- Buchan SJ, Hucke-Gaete R, Stafford KM, Clark CW (2018) Occasional acoustic presence of Antarctic blue whales on a feeding ground in southern Chile. *Mar Mamm Sci* 34:220–228
- Clapham PJ, Baker CS (2002) Modern whaling. In: Perrin WF, Würsig B, Thewissen JGM (eds) *Encyclopedia of marine mammals*. Academic Press, New York, NY, p 1328–1332
- Comiso JC, Gordon AL (1987) Recurring polynyas over the Cosmonaut Sea and the Maud Rise. *J Geophys Res* 92: 2819–2833
- Cooke JG (2018) *Balaenoptera musculus* ssp. *intermedia*. The IUCN Red List of Threatened Species 2018:e.T41713 A50226962. doi:10.2305/IUCN.UK.2018-2.RLTS.T41713 A50226962.en
- Croll DA, Clark CW, Acevedo A, Tershy B, Flores S, Gedamke J, Urban J (2002) Only male fin whales sing loud songs. *Nature* 417:809–811
- Cummings WC, Thompson PO (1971) Underwater sounds from the blue whale, *Balaenoptera musculus*. *J Acoust Soc Am* 50:1193–1198
- Edds-Walton PL (1997) Acoustic communication signals of mysticete whales. *Bioacoustics* 8:47–60
- Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *J Anim Ecol* 77:802–813
- Everson I (2000) *Krill: biology, ecology and fisheries*. Blackwell Sciences, Malden, MA
- Fetterer F, Knowles K, Meier W, Savoie M (2016) Sea ice index, version 2. National Snow and Ice Data Center, Boulder, CO (accessed 28 August 2016)
- Figueroa HK (2006) XBAT: extensible bioacoustic tool. <http://xbat.org> (accessed 22 June 2015)
- Findlay K, Thornton M, Shabangu F, Venter K, Thompson I, Fabriciussen O (2014) Report of the 2013/14 South African Antarctic blue whale survey, 000–020° E. Paper SC/65b/SH01 presented to the IWC Scientific Committee, May 2014, Bled
- Fox J, Monette G (1992) Generalized collinearity diagnostics. *J Am Stat Assoc* 87:178–183
- Fox J, Weisberg S (2011) *An R companion to applied regression*, 2nd edn. SAGE Publications, Thousand Oaks, CA
- Friedman JH, Hastie T, Tibshirani R (2000) Additive logistic regression: a statistical view of boosting. *Ann Stat* 28: 337–407
- Garner DM (1967) Oceanic sound channels around New Zealand. *N Z J Mar Freshw Res* 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
- Gavrilov AN, McCauley R, Gedamke J (2012) Steady inter and intra-annual decrease in the vocalization frequency of Antarctic blue whales. *J Acoust Soc Am* 131:4476–4480
- Gordon AL (2009) Bottom water formation. In: Steele JH, Thorpe SA, Turekian KK (eds) *Encyclopedia of ocean sciences*, 2nd edn, Vol 1. Academic Press, London, p 415–421
- Gordon AL, Huber BA (1995) Warm Weddell Deep Water west of Maud Rise. *J Geophys Res Oceans* 100: 13747–13753
- Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol Modell* 157:89–100
- Hair JF, Black WC, Babin BJ, Anderson RE (2009) *Multivariate data analysis*, 7th edn. Pearson Education, Upper Saddle River, NJ
- Hastie TJ, Tibshirani R, Friedman J (2009) *The elements of statistical learning*. Springer, New York, NY
- Hellmer H (2007) Oceanography of Weddell Sea. In: Riffenburgh B (ed) *Encyclopedia of the Antarctic*. Routledge, New York, NY, p 1053–1056
- Hewitt RP, Kim S, Naganobu M, Gutierrez M and others (2004) Variation in the biomass density and demography of Antarctic krill in the vicinity of the South Shetland Islands during the 1999/2000 austral summer. *Deep Sea Res II* 51:1411–1419
- Ho TK (1995) Random decision forests. In: Kavavaugh M, Storms P (eds) *Proc 3rd Int Conf Document Analysis and Recognition*, Montreal, 14–16 August 1995. IEEE Computer Society Press, Los Alamitos, CA, p 278–282
- IWC (1995) Report of the scientific committee. *Rep Int Whaling Comm* 45:53–221
- James G, Witten D, Hastie T (2013) *An introduction to statistical learning: with applications in R*. Taylor & Francis, New York, NY
- Janik VM (2009) Whale song. *Curr Biol* 19:R109–R111
- Knox GA (2006) *Biology of the Southern Ocean*, 2nd edn. Taylor & Francis, New York, NY
- Leroy EC, Samaran F, Bonnel J, Royer JY (2016) Seasonal and diel vocalization patterns of Antarctic blue whale (*Balaenoptera musculus intermedia*) in the Southern Indian Ocean: a multi-year and multi-site study. *PLOS ONE* 11:e0163587
- Liaw A, Wiener M (2002) Classification and regression by RandomForest. *R News* 2:18–22
- Ljungblad DK, Clark CW, Shimada H (1998) A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the Madagascar Plateau and those attributed to 'true' blue whales (*Balaenoptera musculus*) recorded of Antarctica. *Rep Int Whaling Comm* 48:439–442
- Locarnini RA, Mishonov AV, Antonov JI, Boyer TP and others (2013) *World Ocean Atlas 2013*, Vol 1: temperature. NOAA Atlas NESDIS 73, National Oceanographic Data Center, Silver Spring, MD
- Lurton X (2002) *An introduction to underwater acoustics: principles and applications*. Springer, London
- Mackintosh NA (1942) The southern stocks of whalebone whales. *Discov Rep* 22:197–300
- Mackintosh NA, Wheeler JFG (1929) Southern blue and fin whales. *Discov Rep* 1:259–540
- Martin WR (2009) Polynyas. In: Steele JH, Thorpe SA, Turekian KK (eds) *Encyclopedia of ocean sciences*, 2nd edn, Vol 4. Academic Press, London, p 540–545
- MathWorks (2014) *MATLAB R2014a version 8.3.0.532*. The MathWorks, Natick, MA
- McDonald MA, Hildebrand JA, Webb SC (1995) Blue and fin whales observed on a seafloor array in the Northeast Pacific. *J Acoust Soc Am* 98:712–721

- McDonald MA, Calambokidis J, Teranishi AM, Hildebrand JA (2001) The acoustic calls of blue whales off California with gender data. *J Acoust Soc Am* 109:1728–1735
- McDonald MA, Hildebrand JA, Mesnick SL (2006) Biogeographic characterization of blue whale song worldwide: using song to identify populations. *J Cetacean Res Manag* 8:55–65
- McDonald MA, Hildebrand JA, Mesnick SL (2009) Worldwide decline in tonal frequencies of blue whale songs. *Endang Species Res* 9:13–21
- Mellinger DK, Clark CW (2000) Recognizing transient low-frequency whale sounds by spectrogram correlation. *J Acoust Soc Am* 107:3518–3529
- Miller GA, Heise GA, Lichten W (1951) The intelligibility of speech as a function of the context of the test materials. *J Exp Psychol* 41:329–335
- Miller BS, Barlow J, Calderan S, Collins K and others (2015) Validating the reliability of passive acoustic localisation: a novel method for encountering rare and remote Antarctic blue whales. *Endang Species Res* 26:257–269
- O'Brien RM (2007) A caution regarding rules of thumb for variance inflation factors. *Qual Quant* 41:673–690
- Oleson EM, Calambokidis J, Barlow J, Hildebrand JA (2007a) Blue whales visual and acoustic encounter rates in the Southern California Bight. *Mar Mamm Sci* 23: 574–597
- Oleson EM, Calambokidis J, Burgess WC, McDonald MA, LeDuc CA, Hildebrand JA (2007b) Behavioral context of call production by eastern North Pacific blue whales. *Mar Ecol Prog Ser* 330:269–284
- Payne RS, McVay S (1971) Songs of humpback whales. *Science* 173:585–597
- Payne R, Webb D (1971) Orientation by means of long range acoustic signaling in baleen whales. *Ann N Y Acad Sci* 188:110–141
- Piakowski U (1985) Distribution, abundance and diurnal migration of macrozooplankton in Antarctic surface waters. *Meeresforschung* 20:264–279
- Porter MB (2011) The BELLHOP manual and user's guide. Technical Report, Heat, Light and Sound Research, La Jolla, CA
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rankin S, Ljungblad D, Clark C, Kato H (2005) Vocalisations of Antarctic blue whales, *Balaenoptera musculus intermedia*, recorded during the 2001/2002 and 2002/2003 IWC/SOWER circumpolar cruises, Area V, Antarctica. *J Cetacean Res Manag* 7:13–20
- Reilly SB, Bannister JL, Best PB, Brown M and others (2013) *Balaenoptera physalus*. The IUCN Red List of Threatened Species 2013:e.T2478A44210520. doi:10.2305/IUCN.UK.2013-1.RLTS.T2478A44210520.en (accessed 28 December 2019)
- Saddler MR, Bocconcelli A, Hickmott LS, Chiang G and others (2017) Characterizing Chilean blue whale vocalizations with DTAGs: a test of using tag accelerometers for caller identification. *J Exp Biol* 220:4119–4129
- Samaran F, Adam O, Guinet C (2010) Detection range modeling of blue whale calls in Southwestern Indian Ocean. *Appl Acoust* 71:1099–1106
- Samaran F, Berne A, Leroy EC, Moreira S, Stafford KM, Maia M, Royer JY (2019) Antarctic blue whales (*Balaenoptera musculus intermedia*) recorded at the Equator in the Atlantic Ocean. *Mar Mamm Sci* 35:641–648
- Schall E, Di Iorio L, Berchok C, Filún D and others (2020) Visual and passive acoustic observations of blue whale trios from two distinct populations. *Mar Mamm Sci* 36: 365–374
- Shabangu FW, Findlay K (2014) Passive acoustic monitoring of marine mammals in South Africa, with special reference to Antarctic blue whales. In: Funke N, Claassen M, Meissner R, Nortje K (eds) Reflections on the state of research and development in the marine and maritime sectors in South Africa. Council for Scientific and Industrial Research, Pretoria, p 153–173
- Shabangu FW, Yemane D, Stafford KM, Ensor P, Findlay KP (2017) Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales. *PLOS ONE* 12:e0172705
- Shabangu FW, Findlay KP, Yemane D, Stafford KM, van den Berg M, Blows B, Andrew RK (2019) Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa. *J Mar Syst* 190:25–39
- Shabangu FW, Findlay K, Stafford KM (2020) Seasonal acoustic occurrence, diel-vocalizing patterns and bio-duck call-type composition of Antarctic minke whales off the west coast of South Africa and the Maud Rise, Antarctica. *Mar Mamm Sci* 36:658–675
- Shabangu FW, Stafford KM, Findlay KP, Rankin S and others (in press) Overview of the IWC SOWER cruise circumpolar acoustic survey data and analyses of Antarctic blue whale calls within the dataset. *J Cetacean Res Manag* (Spec Issue)
- Širović A, Hildebrand JA, Wiggins SM, McDonald MA, Moore SE, Thiele D (2004) Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep Sea Res II* 51:2327–2344
- Širović A, Hildebrand JA, Wiggins SM (2007) Blue and fin whale call source levels and propagation range in the Southern Ocean. *J Acoust Soc Am* 122:1208–1215
- Širović A, Hildebrand JA, Wiggins SM, Thiele D (2009) Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. *Mar Mamm Sci* 25:125–136
- Širović A, Williams LN, Kerosky SM, Wiggins SM, Hildebrand JA (2013) Temporal separation of two fin whale call types across the eastern North Pacific. *Mar Biol* 160:47–57
- Smith WHF, Sandwell D (1997) Global seafloor topography from satellite altimetry and ship depth soundings. *Science* 277:1956–1962
- Spreen G, Kaleschke L, Heygster G (2008) Sea ice remote sensing using AMSR-E 89-GHz channels. *J Geophys Res Oceans* 113:C2S03
- Stafford KM, Mellinger DK, Moore SE, Fox CG (2007) Seasonal variability and detection range modeling of baleen whale calls in the Gulf of Alaska, 1999–2002. *J Acoust Soc Am* 122:3378–3390
- Thomas L, Marques TA (2012) Passive acoustic monitoring for estimating animal density. *Acoust Today* 8:35–44
- Thomisch K, Boebel O, Clark CW, Hagen W, Spiesecke S, Zitterbart DP, Van Opzeeland I (2016) Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea. *Endang Species Res* 30:239–253
- Thomisch K, Boebel O, Bachmann J, Filun D, Neumann S, Spiesecke S, Van Opzeeland I (2019) Temporal patterns in the acoustic presence of baleen whale species in a presumed breeding area off Namibia. *Mar Ecol Prog Ser* 620:201–214

-
- ✦ Thorp WH (1967) Analytic description of the low-frequency attenuation coefficient. *J Acoust Soc Am* 42:270
 - ✦ Tripovich JS, Klinck H, Nieukirk SL, Adams T and others (2015) Temporal segregation of the Australian and Antarctic blue whale call types (*Balaenoptera musculus* spp.). *J Mammal* 96:603–610
 - ✦ Ward R, Gavrilov AN, McCauley RD (2017) 'Spot' call: a common sound from an unidentified great whale in Australian temperate waters. *J Acoust Soc Am* 142: EL231–EL236
 - ✦ Wood SN (2017) P-splines with derivative based penalties and tensor product smoothing of unevenly distributed data. *Stat Comput* 27:985–989
 - ✦ Wright MN, Ziegler A (2017) ranger: a fast implementation of random forests for high dimensional data in C++ and R. *J Stat Softw* 77:1–17
 - Zweng MM, Reagan JR, Antonov JI, Locarnini RA and others (2013) World ocean atlas 2013, Vol 2: salinity. NOAA Atlas NESDIS 74, National Oceanographic Data Center, Silver Spring, MD

*Editorial responsibility: Mike Noad,
Gatton, Queensland, Australia*

*Submitted: March 16, 2020; Accepted: June 23, 2020
Proofs received from author(s): August 25, 2020*