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ORIGINAL PAPER

Year-round acoustic monitoring of Antarctic blue and fin whales in relation to environmental conditions off the west coast of South Africa

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Abstract

Antarctic blue and fin whales were once abundant in the southeastern Atlantic Ocean, yet their occurrence and ecology in this region is still poorly understood. Seasonal acoustic occurrence and behaviour of Antarctic blue and fin whales off the South African west coast were determined using bio-acoustic data collected through two autonomous acoustic recorders between December 2015 and January 2017. Blue whale Z-calls were detected year-round with a peak in July, while fin whale 20 Hz pulses were detected seasonally with a peak in June by a recorder deployed at 1118 m water depth. Blue and fin whale calls were detected seasonally with a similar peak in May by a recorder deployed at 4481 m water depth. The blue whale 27 Hz chorus, and blue and fin whale 18–28 Hz chorus followed a similar trend as the seasonal acoustic occurrence of individual Z-calls and 20 Hz pulses. A maximum detection range of 800 km estimated by acoustic propagation modelling suggests that detected calls originate from whales within the South African west coast waters. Random forest models classified month of the year, wind speed, log-transformed chlorophyll-a, and sea surface temperature anomaly as the most important predictors of blue and fin whale acoustic occurrence and behaviour. Our study highlights the South African west coast as an important year-round habitat and seasonal breeding or overwintering habitat of these whales. Additionally, the year-round acoustic occurrence in this region supports the notion that blue whale migration patterns are more dynamic than previously perceived.

Keywords Antarctic blue whales · Fin whale calls · Diel calling behaviour · Seasonal occurrence · Southeast Atlantic Ocean · Passive acoustic monitoring

Introduction

Sightings of Antarctic blue (*Balaenoptera musculus intermedia*) and fin (*B. physalus*) whales remain rare off the west coast of South Africa, some four decades after the termination of modern whaling (carried out between 1909 and the mid-1960s) (Branch et al. 2007; Figueiredo and Weir 2014). Such paucity of sightings given their low population numbers and wide distribution (Baker and Clapham 2002; Branch et al. 2007), means it is not feasible to assess the seasonal presence and distribution of these whales in this region using visual surveys. However, passive acoustic monitoring has been shown to be a cost effective and reliable method of monitoring these whales (e.g. Shabangu et al. 2019; Thomisch et al. 2019). The most recent (1996) population assessment estimated that approximately 1–3% of the Antarctic blue whale population remains, with an annual increasing rate of about 7% per year (Branch et al.

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2004). Current population levels and recovery rate of fin whales in the Southern Hemisphere are not well understood because surveys have typically not covered the area where they are primarily distributed during the summer. However, this population is suspected to be increasing (Branch and Butterworth 2001). Like most baleen whales, blue and fin whales are traditionally thought to migrate seasonally between summer high-latitude feeding grounds and winter breeding grounds in low-latitude warmer waters where they mate and calve, though the precise locations of breeding grounds remain unknown (Mackintosh 1966; Branch et al. 2004, 2007; Best 2007; Samaran et al. 2013). However, recent evidence shows that the migratory behaviour of these species is more dynamic than initially thought, as these species have been reported to acoustically occur year-round in both high (e.g. Širović et al. 2004; Shabangu et al. 2020a) and low latitudes (e.g. Samaran et al. 2013, 2018; Thomisch et al. 2016, 2019).

The Benguela ecosystem is a low-latitude region in the southeast Atlantic Ocean that extends from the south coast of South Africa to the southern boundary of Angola (Shannon et al. 1985; Shannon and Nelson 1996), and Antarctic blue whales were previously observed to overwinter and breed in this region (e.g. Olsen 1914; Best 1998). This ecosystem is characterised by the Benguela Current (Fig. 1) that is mainly driven by prevailing south-easterly trade winds that produce nutrient-rich coastal upwelling that results in high primary productive areas (Shannon et al. 1985; Hutchings et al. 2009). This primary productivity supports high densities of zooplankton which subsequently contributes to the presence of top marine predators, such as blue and fin whales (e.g. Shabangu et al. 2019). Little is known of the migration dynamics of these particular species in the Benguela ecosystem (Best 1998; Thomisch et al. 2019). Continuous population monitoring of these threatened species is therefore crucial for increasing our knowledge of the importance of these species in the Benguela ecosystem, particularly since blue and fin whales face threats from anthropogenic activities and may undergo climate-induced range shifts (Record et al. 2019).

Blue and fin whales produce low-frequency and high intensity calls that may be detectable up to distances of 200–1700 km (Clark et al. 1995; Širović et al. 2007; Samaran et al. 2010; Thomisch et al. 2019; Shabangu et al. 2020a). Antarctic blue whales produce two different call types, namely a stereotyped Z-call (Rankin et al. 2005) and a D-call (Oleson et al. 2007a). Z-calls have three components that are frequency modulated and range from 18 to 26 s in duration (Rankin et al. 2005). The first component occurs at frequency ~ 27 Hz and is 8–12 s long, the second component's frequency downsweeps from ~ 27 Hz to 20 Hz and is 2 s in duration, and the third component is somewhat frequency modulated from 20 Hz to ~ 18 Hz and is 8–12 s in duration (Rankin et al. 2005). These Z-calls can occur

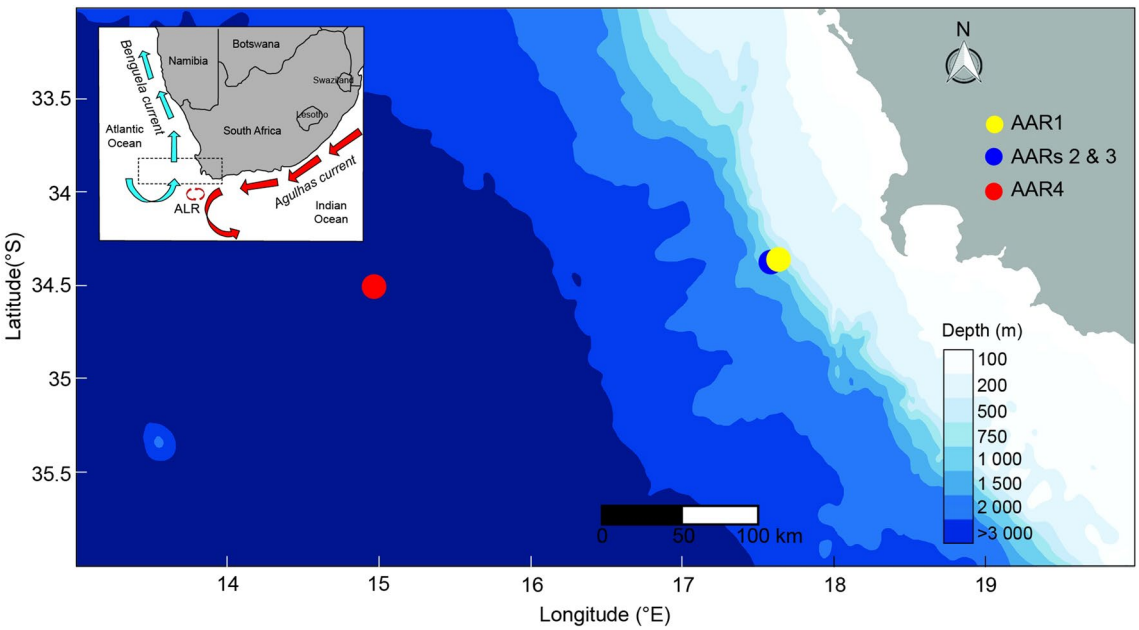

Fig. 1 Location of autonomous acoustic recorders (AARs) off the west coast of South Africa. Flow direction of the cold Benguela Current (blue arrows) on the west coast, Atlantic Ocean, and the warm Agulhas Current (red arrows) together with its Agulhas Leakage Rings (ALR) on the east coast of South Africa, Indian Ocean, are shown in the inset map. The dotted box in the inset map highlights the study area (AARs; coloured circles). Results of acoustic occurrence and behaviour from AARs 1 and 2 are detailed in Shabangu et al. (2019), and this study focusses on data from AARs 3 and 4. Please note that colour on the map shows bathymetry

with either all three components, only the first and second component, or just the first component. The frequency of the Z-call declined from 28 to 26 Hz over the last few decades. Although the reason for this decline is unclear, hypotheses include anthropogenic noise and climate change (McDonald et al. 2009; Ward et al. 2017; Leroy et al. 2018). Z-calls are repeatedly produced in long bouts (as songs) that form a recognisable pattern in time and are believed to be a male reproductive display (McDonald et al. 2001; Janik 2009; Thomisch et al. 2016). On the other hand, D-calls exhibit a frequency downsweep from 106 to 22 Hz, a duration of 0.7–7.5 s, and are produced by both males and females during feeding and mating (Rankin et al. 2005; Oleson et al. 2007a, 2007b; Schall et al. 2020).

Fin whales produce short (~ 1 s) repetitive pulses (hereafter referred to as 20 Hz pulses) that are from 15 to 28 Hz, and are at times accompanied by simultaneous higher frequency components (Širović et al. 2004, 2007). Higher frequency components with a frequency peak around 89 Hz have been attributed to the Western Antarctic Peninsula acoustic population and those with a frequency peak around 99 Hz attributed to the Eastern Antarctic Peninsula acoustic population (Gedamke 2009; Širović et al. 2009). The 20 Hz pulses are the most commonly reported calls, and are primarily produced by males for reproductive advertisement as either a unit or song (Croll et al. 2002). Fin whales also produce a less common short duration pulse (under 1 s) that downsweeps from 70 to 40 Hz (Širović et al. 2013), termed the 40 Hz pulse, and is used as a foraging call (Romagosa et al. 2021).

Leroy et al. (2017) recently described two calls from an unknown source that could possibly be produced by baleen whales. The first call, termed P-call, can be confused with the first component of the blue whale Z-call, as it is centered around 27 Hz with a duration of 10 s and is also declining in frequency (Leroy et al. 2017). The second call, termed the M-call, has a single component which occurs at ~ 22 Hz with a duration of 10 s (Leroy et al. 2017). These calls were recently detected with both blue and fin whale calls (Leroy et al. 2017; Thomisch et al. 2019).

Given that the spatio-temporal distribution patterns of Antarctic blue and fin whales are still poorly understood in the southern African region, the primary aim of this study was to investigate the seasonal acoustic occurrence and acoustic behaviour of Antarctic blue and fin whale calls in relation to environmental conditions in the southeast Atlantic Ocean, off the South African west coast. Recorders were deployed at stations with different depths and physical environments, and detection range modelling and environmental data analysis were conducted to identify predictors for seasonal acoustic occurrence and behaviour of these species. This study improves our understanding of the seasonal acoustic occurrence and behaviour of these species, and subsequently informs conservation efforts in this region and globally.

Methods

Collection of acoustic data

Acoustic data were collected between December 2015 and January 2017 off the west coast of South Africa in the southeast Atlantic Ocean (Fig. 1) using four autonomous acoustic recorders (AARs) of type Autonomous Underwater Recorder for Acoustic Listening (AURAL) Model 2 version 04.1.3 manufactured by Multi-Électronique Inc., Canada. These AARs were deployed on oceanographic moorings of the South Atlantic Meridional Overturning Circulation Basin-wide Array (SAMBA) project (Ansorge et al. 2014). This data collection was conducted as part of the South African Blue Whale Project (SABWP) to study the acoustic occurrence and behaviour of Antarctic blue whales in South African (Shabangu et al. 2019) and Antarctic (Shabangu et al. 2020a) waters. Results of acoustic occurrence and behaviour from AARs 1 and 2 are detailed in Shabangu et al. (2019), and this study focusses on data from AARs 3 and 4 (Fig. 1). Both AARs were deployed on 04 December 2015 and retrieved on 04 April 2017; however, due to battery depletion AAR3 stopped recording on 01 January 2017 and AAR4 stopped recording on 13 January 2013. AARs were deployed at different depths in the water columns (Table 1). AAR3 was deployed approximately 74 km from the coast at a water depth of 1118 m, and AAR4 was approximately 240 km east of AAR3 at a water depth of 4481 m (Fig. 1). Both AARs were set up to record for 25 min of every hour of the day as a sampling protocol over the duration of the deployment to maximise battery lifespan.

Table 1 Location and configurations of each hydrophone (AAR)

AAR ID	Hydrophone depth (m)	Water depth (m)	Hydrophone sensitivity (dB V/μPa)	Gain (dB)	Sample rate (samples/s)	A/D conversion (dB)
AAR3	300	1118	− 164.1	22	8192	84.3
AAR4	200	4481	− 164.2	22	8192	84.3

ID is identification. The analog-to-digital (A/D) conversion is 16 bits into ± 2 V, which corresponds to 84.3 dB counts/V

Whale call detection

Initial analyses comprised of a manual review of the whole acoustic dataset for blue and fin whale calls using spectrograms in Raven Pro (Bioacoustics Research Program 2015). This manual review method entailed visually and aurally identifying signals based on their species-specific/characteristic call as seen in previous literature (e.g. Sirovic et al. 2004; Thomisch et al. 2019). Spectrogram parameters, as indicated in Fig. 2, were used for identification of all whale call types. Acoustic presence of these whales was noted if at least one call attributed to these species was detected within a recording session. For recording sessions with confirmed acoustic presence, the automatic detection of Z-calls and 20 Hz pulses was conducted through spectrogram correlation (Mellinger and Clark 2000; Mellinger 2001), using a MATLAB (MathWorks 2014) driven eXtensible Bio-Acoustic Tool (XBAT; Figueroa 2006) which uses automatic detection templates. The automated template detection method uses cross-correlation with a detection image kernel (pixel-by-pixel) to detect calls (Mellinger and Clark 2000) based on a similarity level above a set threshold (i.e. the lowest detectable similarity percentage between a template and call within the metric produced for each detection by the detection algorithm) within the spectrogram. Blue and fin whale calls with high signal-to-noise-ratio (SNR) were chosen manually from the acoustic data and used as templates for the automatic detection of calls. One complete Z-call with all three-units (Fig. 2a) was used as the blue whale primary detection template since it comprised all units of the call. Nonetheless, three detectors with three combinations of Z-call units as recommended by Shabangu et al. (2017) were implemented by Miller et al. (2021) after data analyses of this study were completed. One 20 Hz pulse (Fig. 2b) was used as a primary detection template of fin whales since it was the most frequent and reliably detected sound of this species. The fin whale higher frequency 99 Hz pulses were considerably few, and hence were not included in the analysis since the 20 Hz pulses are a reliable proxy of fin whale presence and behaviour. There was no template developed for M-calls (Fig. 2c) since they were recorded infrequently and hence were manually noted (at least one M-call detected within a recording session). Similarly, there were no templates developed for D-calls, P-calls and 40 Hz pulses as these were not detected during the manual review of the acoustic data.

A Z-call chorus (hereafter referred to as 27 Hz chorus) occurs around 27 Hz and is typically produced by distant Antarctic blue whales in bands when continuously calling, often associated with a high call rate (Thomisch et al. 2016, 2019). The presence of these choruses in spectrograms essentially makes it difficult to detect the first component of Z-calls, and call rates might be underestimated due to the difficulty in separating individual calls. When fin whales

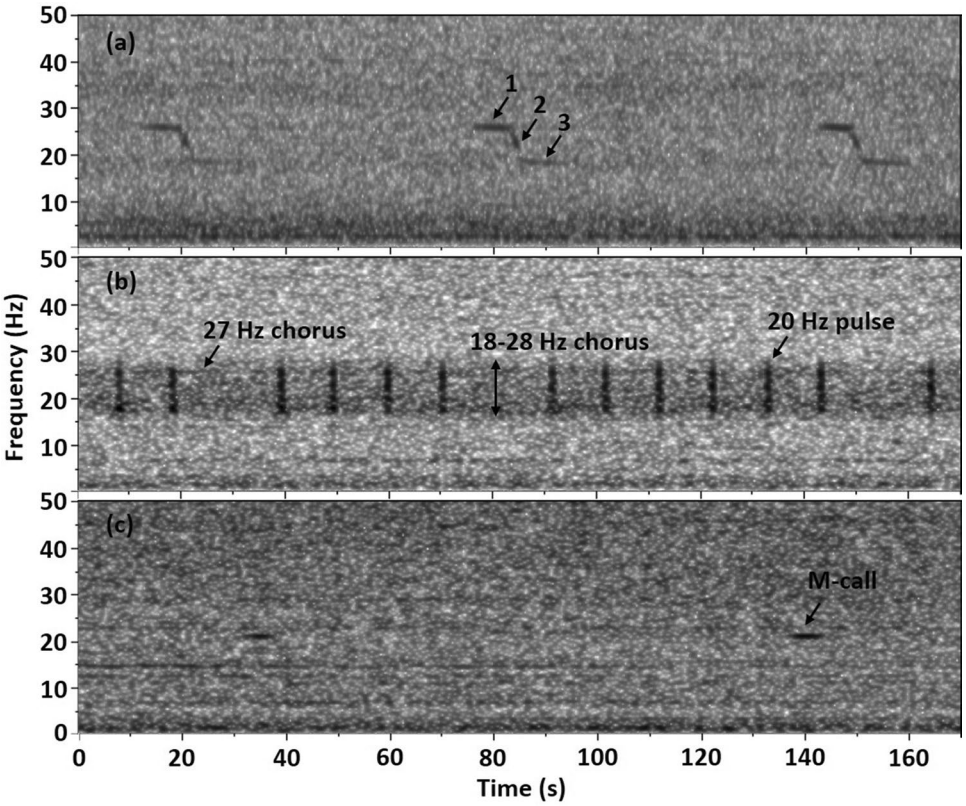

Fig. 2 Spectrogram showing (**a**) three components (1, 2 and 3) of Antarctic blue whale Z-calls, (**b**) blue whale 27 Hz chorus, blue and fin whale 18–28 Hz chorus and fin whale 20 Hz pulse, and (**c**) M-call. Spectrogram parameters: (**a**) 6803 hop size, 50% overlap, DFT size 16,384 samples, Hann window (**b**) 6357 hop size, 50% overlap, DFT size 16,384 samples, Hann window, (**c**) 9742 hop size, 50% overlap, DFT size 32,768 samples, Hann window

are also calling, a combined Antarctic blue and fin whale chorus occurs between 18 and 28 Hz (hereafter referred to as 18–28 Hz chorus), and similarly makes it difficult to detect individual Z-calls and fin whale 20 Hz pulses. The presence of both the 18–28 Hz and 27 Hz (Fig. 2b) choruses were manually noted (at least one chorus detected within a recording session) to account for call rate underestimation by possible masking of some of the Z-calls and 20 Hz pulses.

Call detector precision

To assess the efficacy of the above spectrogram cross correlation of automated detectors at correctly identifying whale calls (i.e. precision), each of the automated detectors was tested using variable detection thresholds. A subsample of the data representing 20% of the entire dataset that contained each of the target whale calls was randomly chosen from each station. Three thresholds (10%, 15% and 20%) were used on the representative subsample from both AARs, and data were manually reviewed for the estimation of the number of false positives (automated detections that were neither blue nor fin whale calls) and false negatives (blue and fin whale calls that were missed by the automated detector). The above thresholds were based on results of Shabangu et al. (2019) who tested a range of thresholds from 10 to 70% by increments of 10% on randomly selected 5% of the acoustic data, and found that the 10–20% thresholds had less false positives and negatives compared to the higher thresholds. Similarly, Mellinger and Clark (2000) also recommend using low thresholds on large datasets for obtaining fewer false positives.

Overall, the 10% and 15% detection thresholds were found to be best suited for detection of Z-calls and 20 Hz pulses respectively from both AARs as they produced the fewest missed (false negatives) calls compared to other thresholds, and these threshold settings were subsequently used for the entire acoustic dataset analysis. The 20% detection threshold was not used for blue and fin whales in both stations as it yielded higher false positives and negatives. After implementing the above thresholds, false positive calls were manually identified and excluded from further data analyses. Manually identified false negative detections were incorporated into the calculations of the final total call numbers and call rates.

Acoustic occurrence and behaviour

Acoustic presence of blue and fin whale calls represents instances when one or more calls of either whale species were detected within a 25 min recording session. Acoustic absence represents the lack of blue or fin whale calls within such a recording session. As the most abundant call types, Z-calls and 20 Hz pulses were used to determine the acoustic presence of blue and fin whales, respectively. To investigate seasonal acoustic occurrence, the data were parsed into the Southern Hemisphere (austral) seasons of the year by month: autumn (March–May), winter (June–August), spring (September–November) and summer (December–February). The percentage of each species acoustic occurrence was calculated as the number of recording sessions containing calls divided by the total number of recording sessions per month. Similarly, the seasonal acoustic occurrence of 18–28 Hz chorus, 27 Hz chorus and M-calls were calculated using the method described above.

Call rates (described as calls per hour) of both species were calculated as the total number of calls recorded within a recording session divided by the duration of a recording session (i.e. 0.416 h) for both stations. Call rates generally describe the acoustic behaviour of whales around our study area by showing the number of calls produced by all animals that were within the recorder detection range at a given time. Whale behaviour is consequently described by call rates, although it is acknowledged that the recording of such rates is underpinned by occurrence. Since time of day is a circular variable, smoothed means of the Diel call rate patterns per season were calculated using penalized cyclic cubic regression splines (Wood 2017) using the 'mgcv' package (Wood 2001) in R (version 4.0.5; R Core Team 2021).

To investigate Diel calling patterns, different light regimes (dawn (nautical twilight), daytime, dusk (nautical twilight) and night time) were classified over different seasons according to the altitude of the sun by averaging hourly sun altitudes over the austral seasons. Sun altitudes were retrieved from the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil). Time of twilight between nautical twilight start and sunrise was defined as dawn, the time of twilight between sunset and nautical twilight end was defined as dusk. The time between nautical twilight and sunrise was defined as night, and the time between sunrise and sunset was defined as day.

Sound propagation modelling

The objective of this analysis was to characterize the changes in detection range for seasonal effects at the AARs 3 and 4 mooring locations off the west coast of South Africa, with a focus on the 20 Hz frequency band to provide information on detection area for all target species. Both receivers captured low-frequency sound at a sample rate of 8192 samples/s (Table 1). The parameters for these two receivers are documented in Table 1. The hydrophone sensitivity of − 149 dB re 1 V/µPa quoted in Shabangu et al. (2019) was incorrect; the true value is − 58.7 dB count/µPa or written out more explicitly as − 165 dB re 1 V/µPa, 22 dB, and 84.3 dB re 1 count/V, and the latter was used consistently throughout this analysis. Transmission loss was computed using

BELLHOP beam tracing model (Porter 2011) operating on an annual average sound speed derived from World Ocean Atlas 2013 (Boyer et al. 2013) and Thermodynamic Equation of Seawater-2010 (www.teos-10.org), bathymetry from the Smith-Sandwell database (Smith and Sandwell 1997), and Thorp attenuation (Thorp 1967; Focke et al. 1982). Ray trace models such as the BELLHOP beam tracing model are justified when the water column is approximately 10 wavelengths deep or deeper. For a frequency of 20 Hz, this holds for both AAR3 and AAR4 at their deployment locations. Transects away from the receivers have adequate depth (by this measure) to the west and south; to the east the bottom shoals up, and at some point, the ray model loses validity in this direction. But away from the coastline, the ray model should be adequate. Similarly, Thomisch et al. (2019) used the BELLHOP model for water depths exceeding 700 m, for a location off the Namibian coast. The detection ranges and their associated errors were computed as described in Shabangu and Andrew (2020) and Shabangu et al. (2019, 2021). Detection ranges were estimated using a source level of 189 dB re 1 μPa @1 m (Širović et al. 2007) and an animal vocalizing depth of 30 m (Oleson et al. 2007b).

Acoustic files from both AARs without any blue or fin whale calls were selected to provide crude estimates of the seasonal ambient noise level at 20 Hz to determine SNR for each mooring. Data captures were analysed for each season for both AARs. Each file contained three 25 min data segments. One power spectral density (PSD) estimate was generated for each sub-segment. The PSDs were computed in units of dB re 1 μPa^2/Hz using the manufacturer's hydrophone calibration, a gain of 22 dB and an A/D conversion of 84.3 dB (see Table 1). PSD estimation used Octave pwelch command, with a unity-weighted taper and a block-size equal to the sample rate. This conveniently produces spectral density on a 1 Hz grid. One PSD value was extracted from each PSD to represent the noise level at 20 Hz. The effective ambient noise level was the average of the sub-segment levels. The standard error of the sub-segment levels was computed to provide a crude measure of uncertainty. The effective ambient noise levels are shown in Table 2. The files were carefully selected for stability at 20 Hz, and this is reflected in the short error bars for all seasons and AARs. The detection threshold was assumed to be 0 dB (Miller et al. 1951), since the detection threshold for blue and fin whales is currently unknown as also used by Širović et al. (2007). Using the above parameters, BELLHOP model was used to produce detection coverage maps for 32 bearings around each AAR location for all seasons.

Table 2 Measured ambient noise levels for both autonomous acoustic recorders (AARs) for all seasons

AAR ID	Season	Ambient noise level ± standard error (dB re 1 μPa^2/Hz)
AAR3	Summer	96 ± 0.39
	Autumn	98.6 ± 0.88
	Winter	96.5 ± 0.13
	Spring	89.1 ± 1.15
AAR4	Summer	108.0 ± 0.55
	Autumn	105.6 ± 0.76
	Winter	101.9 ± 0.50
	Spring	86.2 ± 0.42

Environmental condition data

To get a proxy of the sea state condition, daily global wind speed (m s^{-1}) data were sourced from https://www.ncei.noaa.gov/data/blended-global-sea-surface-wind-products/access/winds/daily/. As a proxy of ocean circulation, daily global sea surface height anomaly (SSHA; m) was sourced from ftp://my.cmems-du.eu/Core/SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047/dataset-duacs-rep-global-merged-allsat-phy-l4. Daily global chlorophyll-a (mg m^{-3}; chl-a) were downloaded from ftp://ftp.hermes.acri.fr/GLOB/merged/day/, and used as a proxy of phytoplankton pigment concentration. Sea surface temperature anomaly (SSTA, °C) data were sourced from ftp://nrt.cmems-du.eu/Core/SST_GLO_SST_L4_NRT_OBSERVATIONS_010_001/METOFFICE-GLO-SST-L4-NRT-OBS-ANOM-V2 as an indication of the upper ocean thermal conditions.

Given the seasonal differences in modelled detection ranges of blue and fin whale calls between AARs, each AAR position was treated as an independent sampling point. We averaged environmental variables within the average seasonal detection ranges for each AAR to describe the variation in each environmental variable to which whales were likely exposed. The seasonal radius of the average detection range around each AAR adjacent to the latitudinal and longitudinal grids of each AAR mooring position gave the spatial scale domain of environmental variable integration per season. For example, we averaged by 70.8 km grid for AAR3 mooring in summer where the value of four 70.8 km blocks adjacent to that location were averaged to get comparable daily environmental conditions within the AAR average detection range (Shabangu et al. 2019; Shabangu and Andrew 2020).

Less than 30% of daily chl-a data were missing due to satellite data limitation, and were interpolated using available data from the day before or after the date with the missing environmental data as there is a strong temporal and spatial autocorrelation in chl-a (e.g. Shabangu et al. 2019; Shabangu and Andrew 2020). Chl-a was log-transformed because of data skewness before any statistical analyses, and will henceforth be abbreviated as lchl-a. Given that these AARs sampled year-round, mean monthly values of

environmental variables for plots were circular smoothed through penalized cyclic cubic regression splines in Generalized Additive Models (GAMs).

Statistical data analyses

We investigated the relative influence and importance of six predictor variables (time of day, month of the year, lchl-a, SSHA, SSTA and wind speed) on the acoustic occurrence and behaviour of blue and fin whales from the two AARs using four random forest (RF) models (Ho 1995; Breiman 2001) for each AAR. As a machine learning and ensemble modelling approach with non-parametric inferential properties, the RF model provides higher statistical performance (i.e. high prediction accuracy) than commonly used regression methods, such as the generalized boosted regression trees model (Friedman et al. 2000; Shabangu et al. 2017) and GAM (Elith et al. 2008; James et al. 2013; Shabangu et al. 2019). The RF modelling approach is principally useful and preferred for our kind of data and specific analysis given its observed higher predictive capabilities for modelling acoustic occurrence and behaviour of other marine mammals (Shabangu et al. 2017, 2019, 2020a, b; Shabangu and Charif 2021; Shabangu and Rogers 2021). The relative importance of each variable in the RF models was calculated by permuting the out-of-the bag data where the prediction error is recorded for each tree as described in Shabangu et al. (2017, 2019). Preceding fitting of RF models, the effects of multi-collinearity between predictor variables (time of day, month of the year, lchl-a, SSHA, SSTA and wind speed) were determined using generalized variance inflation factors (GVIFs; Fox and Monette 1992) implemented through the 'car' package (Fox and Weisberg 2019). High multicollinearities were found between SSHA and other predictor variables for AAR3 (highest GVIF was 24.45) and AAR4 (highest GVIF was 9.01); however, the highest GVIF values decreased to 3.42 and 3.10 for AARs 3 and 4, respectively, when excluding SSHA as a predictor variable. Thus, SSHA was eliminated as a predictor variable.

The area under the receiver operating characteristic curve (AUC) and root mean square prediction error (RMSE) were used to estimate optimal parameter configurations for each RF model corresponding to each AAR to investigate the influence and importance of predictors on blue and fin whale acoustic occurrence and behaviour, respectively. AUC and RMSE measured the predictive accuracy of a range of RF models with different combinations of the number of growing trees (ntrees; range: 500–3000 by increment of 500), the splitting minimum size of terminal nodes of trees (nodesize; range: 1–5), and the number of acoustic occurrence randomly selected at the tree node (mtry; range: 1–5). Values for optimal parameter configuration of RF models were determined using the 'ranger' package (Wright and Ziegler 2017) to save computational-time for implementing RF models. Estimated optimal parameter configurations for each RF model corresponding to each AAR are given in Table 3. The above derived optimal parameter configurations were used to perform RF modelling in R using the 'randomForest' package (Liaw and Wiener 2002). The significance of each predictor variable was measured by computing *p* values for feature importance metric through permutation using a technique of Altmann et al. (2010); this metric makes the interpretation of RF model easier as significant variables are highlighted. Time of day was eliminated for blue whale occurrence from AAR3 and for fin whale occurrence from AARs 3 and 4 due to negative relative importance that indicated that this variable was not important at all and did not have a role in the prediction as done in Shabangu et al. (2019).

Results

A total of 3982 h of acoustic data from 25 min recording sessions were recorded by AAR3, where 1353 h contained Z-calls and 202 h contained 20 Hz pulses. A total of 4098 h of acoustic data from 25 min recording sessions were recorded by AAR4; only 377 h contained Z-calls and 139 h contained fin whale 20 Hz pulses. Overall, 88,859 Z-calls and 28,697 20 Hz pulses were detected from AAR3. A sum of 23,190 Z-calls and 23,403 fin whale 20 Hz pulses were detected from AAR4. No D-calls and 40 Hz pulses were detected from either AAR. The blue whale 27 Hz chorus was detected in 124 h and Antarctic blue and fin whale 18–28 Hz chorus was detected in 773 h from AAR3. The blue whale 27 Hz chorus was detected in 11 h whereas the Antarctic blue and fin whale 18–28 Hz chorus was detected in 74 h

Table 3 Optimal settings of random forest model parameters estimated for acoustic behaviour and occurrence of blue and fin whales for each autonomous acoustic recorder (AAR)

AAR ID	Species	Category	Model parameters		
			mtry	nodesize	ntree
AAR3	Blue whales	Behaviour	4	1	1000
		Occurrence	3	1	500
	Fin whales	Behaviour	1	1	500
		Occurrence	1	1	2500
AAR4	Blue whales	Behaviour	2	1	500
		Occurrence	4	1	1500
	Fin whales	Behaviour	2	1	3000
		Occurrence	1	1	500

Number of growing trees (ntree; range: 500–3000 by increment of 500), the splitting minimum size of terminal nodes of trees (nodesize; range: 1–5), and the number of acoustic occurrence randomly selected at the tree node (mtry; range: 1–5)

from AAR4. M-calls were detected in 12 and 40 h from AARs 3 and 4 respectively.

Detection ranges

There was evidence of anthropogenic noise and biological noise in some files. The noise levels are lowest in spring for both moorings. With the exception of spring, the noise levels at mooring AAR4 are higher than at mooring AAR3 (Table 2). Spring produced the farthest average detection ranges for both AARs, and winter produced the second farthest average detection range for both AARs (Tables 4). On the other hand, autumn produced the shortest average detection ranges for both AARs (Table 4). The large detection ranges for spring are a result of the low ambient noise levels for this season (Table 2). The observed detection range solution and its sensitivity are generally strongly driven by the ambient noise terms (Table 2).

Table 4 Average ± standard error detection ranges for both moorings for all seasons

Mooring	Season	Average detection range ± standard error (km)
AAR3	Autumn	70.8 ± 34.5
	Winter	98.2 ± 55.9
	Spring	448.3 ± 356.0
	Summer	111.2 ± 62.4
AAR4	Autumn	16.8 ± 8.1
	Winter	27.8 ± 18.1
	Spring	372.9 ± 99.7
	Summer	19.6 ± 6.5

Environmental conditions

A higher overall lchl-a concentration was found within AAR3 detection ranges than within AAR4 detection ranges (Fig. 3a, e). Higher SSHA were observed in February within AAR3 detection ranges (Fig. 3b), and in May and October within AAR4 detection ranges (Fig. 3f). SST anomalies were positive (warmer) for most months within AAR3 detection ranges but dropped to zero °C from March through May and between October and November (Fig. 3c). Negative SST anomalies were observed in May and between October and November within AAR4 detection ranges (Fig. 3g). Monthly mean wind speeds were comparable for both AARs, and ranged similarly between corresponding months (Fig. 3d, h).

Monthly acoustic occurrence

Within AAR3 recordings, Z-calls were detected each month from December 2015 through December 2016 (Fig. 4a). The blue whale 27 Hz chorus was recorded only in March and

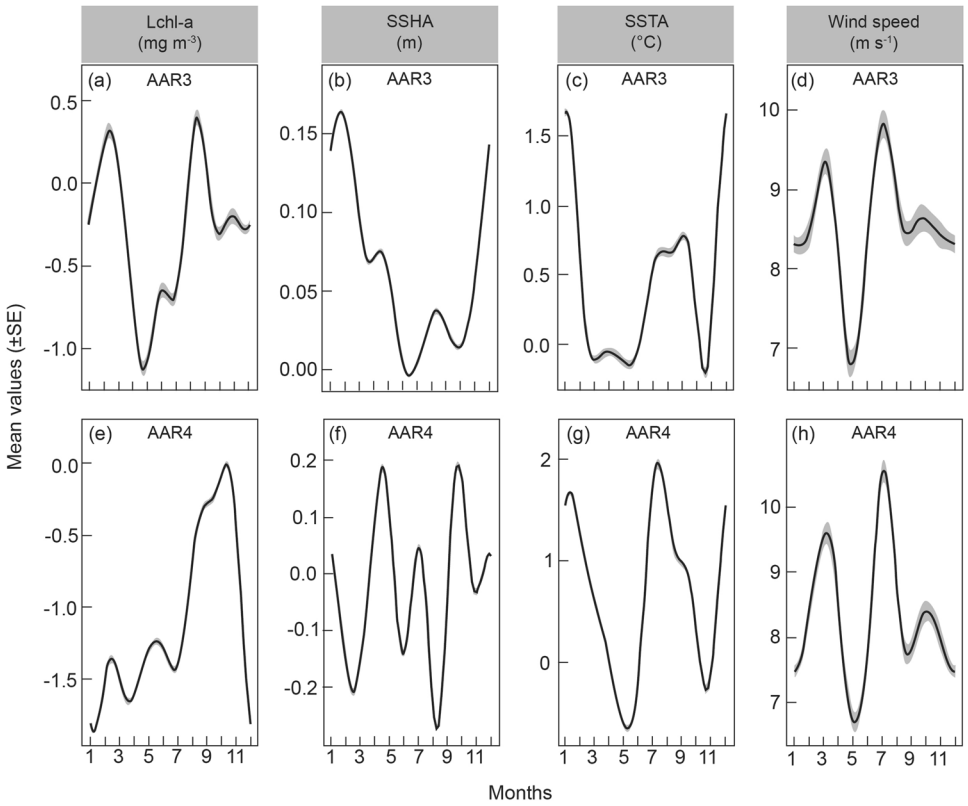

Fig. 3 Circular smoothed monthly mean values (line plot) of log-transformed chlorophyll-a (lchl-a), sea surface height anomaly (SSHA), sea surface temperature anomaly (SSTA) and wind speed around (**a**–**d**) AAR3 and (**e**–**h**) AAR4. SE is standard error shaded in grey around the mean. Note the different scales for y-axes

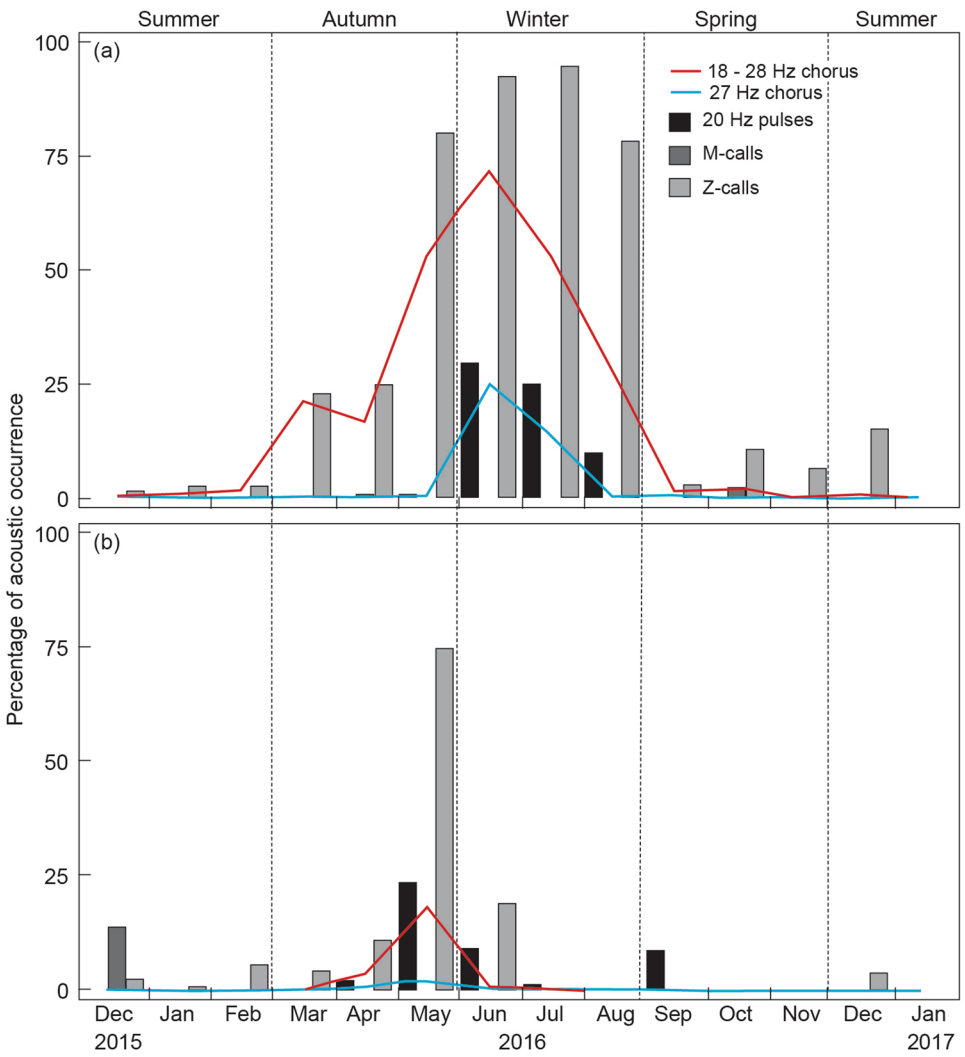

Fig. 4 Monthly percentages of acoustic occurrence of Antarctic blue and fin whale calls and M-calls off the west coast of South Africa from December 2015 to January 2017 for (**a**) AAR3 and (**b**) AAR4. It should be noted that only a single day was sampled in January 2017 around AAR3, and 13 days were sampled in January 2017 around AAR4

from May to September 2016; no chorus was detected in November (Fig. 4a). The blue and fin whale 18–28 Hz chorus was detected each month from December 2015 through October 2016, and again in December 2016. Fin whale 20 Hz pulses were recorded seasonally from May through August 2016 (Fig. 4a). M-calls were detected in April 2016, June 2016 and October to November of 2016 (Fig. 4a). The peak monthly occurrence for Z-calls (95%) was recorded in late winter, i.e. July 2016, while peaks for both 27 Hz (25%) and 18–28 Hz (72%) choruses were detected in June 2016, i.e. mid-winter (Fig. 4a). The peak monthly acoustic occurrence for fin whales (30%) was recorded in June 2016 i.e. mid-winter (Fig. 4a). The peak monthly acoustic occurrence for M-calls (0.02%) was recorded in October 2016 i.e. mid-spring.

Within AAR4 recordings, Z-calls were detected seasonally between December 2015 and July 2016, and again in December 2016 (Fig. 4b). The 27 Hz chorus was recorded between April and June 2016, while the 18–28 Hz chorus was recorded between January and July 2016 (Fig. 4b). Fin whale 20 Hz pulses were recorded seasonally between April and July 2016, and again in September 2016 (Fig. 4b). M-calls were detected in December 2015 and May 2016 (Fig. 4b). The peak in monthly acoustic occurrence of Z-calls (75%), 27 Hz chorus (3%), 18–28 Hz chorus (18%) and 20 Hz pulses (24%) occurred in May 2016 from AAR4 recordings (Fig. 4b), a month earlier than the June peak reported for AAR3 (Fig. 4b). The peak monthly acoustic occurrence for M-calls (14%) was recorded in December 2015, i.e. early summer.

Observed Diel calling patterns

Within AAR3 recordings, Z-call rates decreased from 02:00 to 14:00, and increased thereafter in summer (Fig. 5a). In autumn, Z-call rates increased from 07:00 to 15:00, and decreased thereafter (Fig. 5b). In winter, Z-call rates showed more of a crepuscular pattern with increases from 01:00

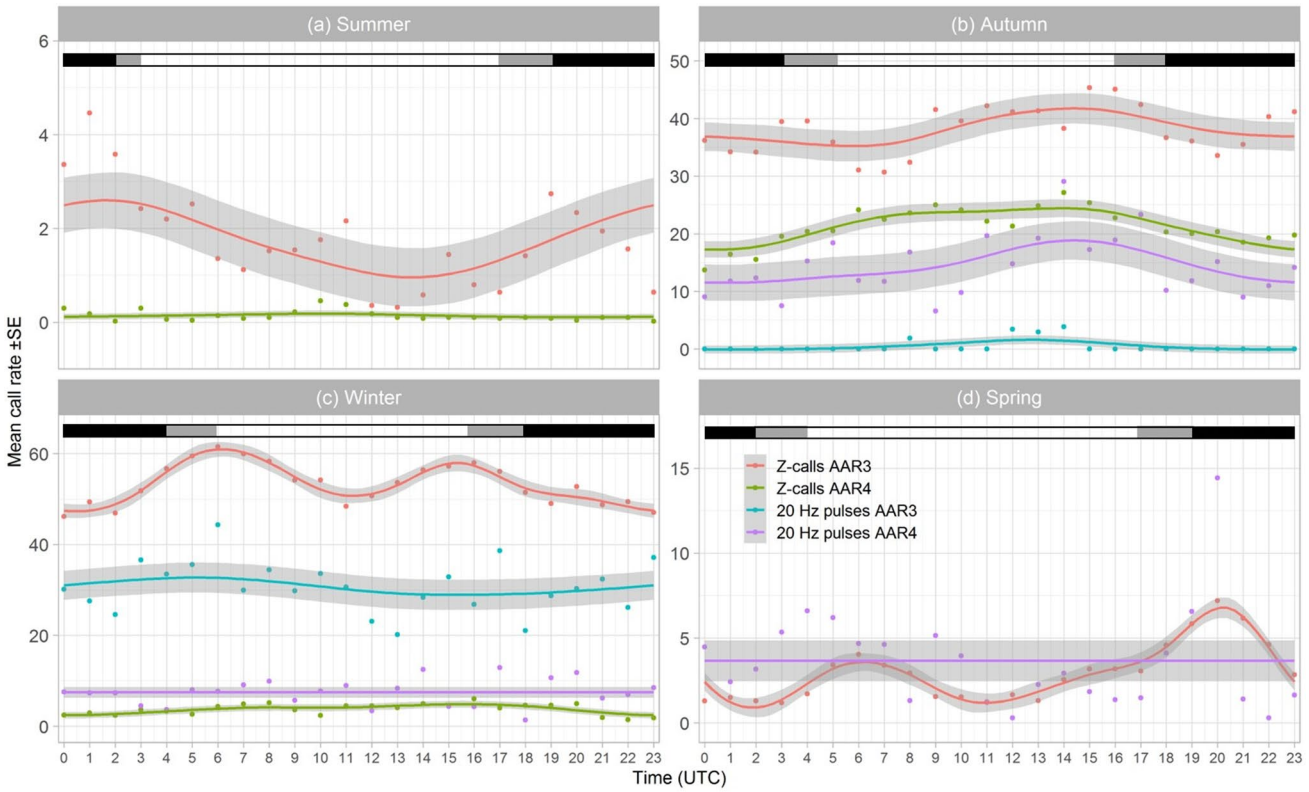

Fig. 5 Seasonal circular smoothed mean ± standard error (SE) Diel call rates (calls per hour) of blue and fin whales represented by lines with different shading colours from AAR3 and AAR4. UTC is Coordinated Universal Time. Horizontal Diel bar shading: black represents average night-time hours; grey represents twilight hours; white represents average daytime hours. Closed circles represent unsmoothed data points

through 06:00, and another increase from 12:00 through 15:00 (Fig. 5c). Similarly in spring, Z-calls showed more of a crepuscular pattern with increases from 02:00 to 06:00, and another increase from 12:00 till 20:00 (Fig. 5d). Within AAR4 recordings, no Diel Z-call rate pattern was observed for summer (Fig. 5a). Z-calls rates increased slightly from 01:00 through 15:00, and decreased thereafter in autumn (Fig. 5b). Z-call rates showed small increases between 03:00 and 20:00 in winter, and no calls were detected in spring (Fig. 5c, d). Call rates of 20 Hz pulses from AAR3 showed slight increase between 09:00 and 17:00 in autumn, slight decrease from 00:00 through 12:00 in winter, and no calls were detected in summer and spring (Fig. 5). Within the AAR4 recordings, call rates of the 20 Hz pulses increased from 06:00 to 15:00 and decreased thereafter in autumn; call rates were constant during different times of day in winter and spring; no calls were detected in summer (Fig. 5).

Occurrence and behaviour predictors

May through August, wind speeds between 7 and 8 m s^{-1}, cool SSTA below 1.5 °C, and lchl-a around − 0.5 and 1.5 mg m^{-3} had the highest influence on blue whale acoustic occurrence within AAR3 detection ranges (Fig. 6a–d). May, wind speed around 16 m s^{-1}, low lchl-a below − 1.3 mg m^{-3}, colder SSTA below 0 °C, and varying times of day had the highest influence on blue whale acoustic occurrence around AAR4 (Fig. 6e–i). June through August, low (< 5 m s^{-1}) and high (> 15 m s^{-1}) wind speeds, colder SSTA below 0 °C, and low lchl-a below 0 mg m^{-3} highly influenced fin whale acoustic occurrence around AAR3 (Fig. 6j–m). Low (~ 2 m s^{-1}) and high (~ 17 m s^{-1}) wind speeds, May, June and September, cool SSTA below 1.5 °C, and lchl-a around 0.8 mg m^{-3} had the highest influence on fin whale acoustic occurrence around AAR4 (Fig. 6n–q). Month of the year was the most important predictor of blue whale acoustic occurrence around both AARs and of fin whale acoustic occurrence around AAR3 (Fig. 6r–t), whereas wind speed and month of the year were the most important predictors of fin whale acoustic occurrence around AAR4 (Fig. 6u). Wind speed was the moderate important predictor of blue whale acoustic occurrence recorded by both AARs (Fig. 6r, s); wind speed and SSTA were moderate predictors of fin whale acoustic occurrence around AAR3 (Fig. 6t); SSTA was a moderate predictor of fin whale acoustic occurrence around AAR4 (Fig. 6u). SSTA and lchl-a were the least important

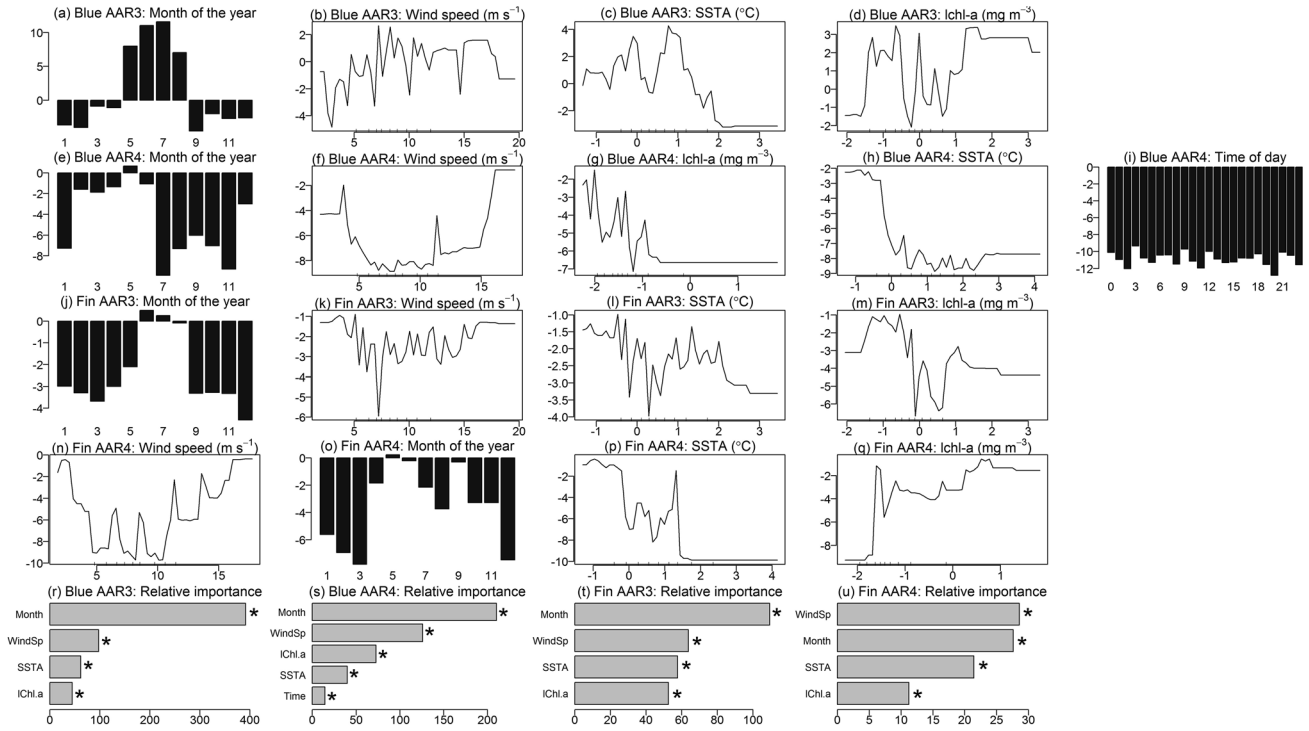

Fig. 6 (**a**-**q**) Relative influence and (**r**–**u**) ranked relative importance of predictor variables on acoustic occurrence of blue and fin whales estimated by random forest models. Blue and fin in main title of figures respresent blue and fin whale acoustic occurrence. WindSp: wind speed; lChl.a: logtransformed chl-a. The x- and y-axes are in arbitrary units and have different scales. * indicates predictor variables with significant ($p < 0.05$) importance

predictors of blue whale acoustic occurrence around AAR3 (Fig. 6r); lchl-a, SSTA and time of day were the least important predictors of blue whale acoustic occurrence around AAR4 (Fig. 6s); lchl-a was the least important predictor of fin whale acoustic occurrence around both AARs 3 and 4 (Fig. 6t, u). All variables were significant predictors of acoustic occurrence (Fig. 6r–u).

March through August, SSTA between 0.5 and 0.9 °C, wind speeds above 5 m s^{-1}, and lchl-a around − 0.8 mg m^{-3} had the highest influence on Z-call rates from AAR3 (Fig. 7a–d). April through June, low wind speed around 2 m s^{-1}, cooler SSTA below 0 °C, and lchl-a above − 1 mg m^{-3} had the highest influence on Z-call rates from AAR4 (Fig. 7e–h). June through August, lchl-a below − 0.4 mg m^{-3}, cool SSTA around − 0.4 °C, and wind speeds below 5 m s^{-1} had the highest influence on 20 Hz pulses from AAR3 (Fig. 7i–l). Lchl-a around − 1.7 mg m^{-3}, SSTA around − 1 °C, wind speed around 2 m s^{-1}, and May through July and September had the highest influence on 20 Hz pulse call rates from AAR4 (Fig. 7m–p). Month of the year was an important predictor of Z-call rates from both AARs and of 20 Hz pulse call rates from AAR3 (Fig. 7q–s), whereas lchl-a and SSTA were the most important predictors of 20 Hz pulse call rates from AAR4 (Fig. 7t). SSTA and wind speed for Z-call rates from AAR3, wind speed for Z-call rates and 20 Hz pulse call rates from AAR4, and lchl-a and SSTA for 20 Hz pulse rates from AAR3 were moderate predictors (Fig. 7q–t). Lchl-a for Z-call rates from AAR3, SSTA and lchl-a for Z-call rates from AAR4, wind speed for 20 Hz pulse call rates form AAR3, and months of the year from AAR4 were the least important predictors (Fig. 7q–t). All variables were significant for call rates of Z-calls and 20 Hz pulses from both AARs, except for month of the year that was not significant for 20 Hz pulses from AAR4 (Fig. 7q–t).

Discussion

Passive acoustic monitoring enabled the investigation of seasonal acoustic occurrence and behaviour of Antarctic blue and fin whales in a low-latitude region, expanding our knowledge of these species. Our results indicate that blue whale Z-calls were present year-round around AAR3, and only seasonally around AAR4. Shabangu et al. (2019) detected Z-calls only seasonally in water depths of 850 m (AAR1) and 1100 m (AAR2; deployed at the same location as AAR3) off the west coast of South Africa. This inter-annual variability in acoustic occurrence between this study and Shabangu et al. (2019) suggests that individuals in a population may alter migration patterns between years

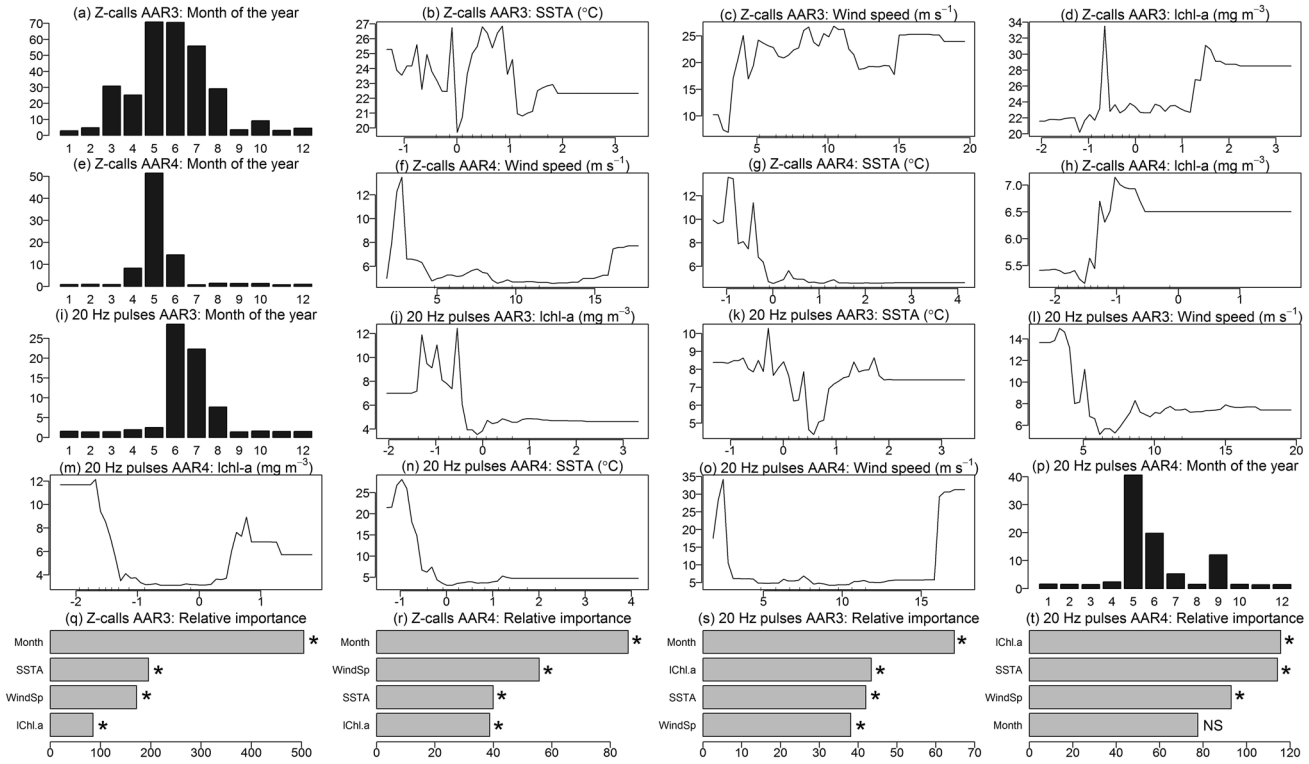

Fig. 7 (**a**–**p**) Relative influence and (**q**–**t**) ranked relative importance of predictor variables on call rates of blue and fin whales estimated by random forest models. WindSp: wind speed; lChl.a: logtransformed chl-a. The x- and y-axes are in arbitrary units and have different scales. * indicates predictor variable with significant ($p < 0.05$) importance, and NS represent nonsignificant importance ($p > 0.05$)

or seasons, likely in response to changing environmental conditions. For instance, AAR3 had higher lchl-a and wind speed than what was found by Shabangu et al. (2019) around AAR2. This suggests that environmental conditions around AAR3 may have been suitable for blue whales during this period hence the year-round presence.

Shabangu et al. (2019) detected blue whale feeding associated D-calls which suggests that some blue whales may feed when in the Benguela ecosystem. Best (1967) observed stomachs of blue whales whaled off the west coast of South Africa to contain crab larvae (megalopa), indicating that these whales were feeding in South African waters. However, it is intriguing that the D-calls were not detected from our data with a year-round acoustic occurrence. The absence of D-calls during this year-round blue whale presence could indicate that blue whales were not feeding in the region, or were doing so out of range of our instruments, as D-calls would have a shorter detection range given their higher frequency (Oleson et al. 2007a). It is possible that D-calls detected by Shabangu et al. (2019) may have been an anomaly, which essentially suggests changes in the distribution and/or behaviour of these whales. Alternatively, those D-calls detected by Shabangu et al. (2019) could have been mating related as Schall et al. (2020) recently observed blue whales to use this call type for antagonistic display during mating since this region is considered a possible breeding ground (Olsen 1914; Best 2007).

The year-round acoustic occurrence of blue whales off the west coast of South Africa contrasts the traditional migration theory that all blue whales are distributed at higher latitudes during the austral summer (Brown 1954; Best 1998, 2007), suggesting that their migration behaviour is more complex and not obligate (Thomisch et al. 2016). Similar year-round acoustic occurrence of blue whales has also been reported in the Equatorial Atlantic (Haver et al. 2017; Samaran et al. 2018), Indian Ocean (Samaran et al. 2010, 2013; Leroy et al. 2016) and more recently off Namibia (Thomisch et al. 2019). Equally, Thomisch et al. (2019) suggested this year-round presence to be heavily influenced by availability of prey in high-productive waters of the Benguela region and the associated high-turbulence eddy regime. Eddy regimes are important as they serve as retention zones and resultantly affect the distribution of nutrients (Hutchings et al. 1995). The continued high productivity of the Benguela ecosystem upwelling regime reflected through indicators, such as lchl-a, SSTA, SSHA and wind speed, supports the notion that these animals may sustain themselves year-round through possible opportunistic feeding on available prey.

Low lchl-a, SSTA and wind speed had the highest influence of both blue and fin whale acoustic occurrence and

behaviour from both AARs, according to the RF models, suggesting their importance on driving other ecological processes (coastal upwelling) that are important to these animals. Shabangu et al. (2019) reported that peak blue and fin whale acoustic occurrence and behaviour in winter coincided with a seasonal decrease in biological productivity (characterized by environmental predictors, such as low lchl-a, SSHA, SSTA and wind speed) off the South African west coast. This could possibly be due to upwelling being more intense during austral summer when trade winds are upwelling-favourable (Hutchings et al. 2009). Higher offshore wind speeds contribute significantly to faster net movement of surface waters offshore which resultantly push deep nutrient water to the surface, thereby enhancing primary productivity at a shorter time scale (Hutchings et al. 2009; Shannon et al. 1985). Temporal and spatial lags have been observed between blue whale acoustic occurrence, wind and coastal upwelling, were blue whales appear to lag annual blooms in primary production due to upwelling events (Barlow et al. 2021).

Varying wind speeds (which drives upwelling) in the vicinity of AAR3, could have possibly indirectly caused a lag in acoustic occurrence of blue whales. Hence, a small increase in December. SSTA was increasing (warmer) in winter around both AARs, suggesting that the presence of blue and fin whale calls in the vicinity of AAR3 might have coincided with this temperature, hence the peaks in call occurrence in July and June respectively. Shabangu et al. (2019) also observed peak blue whale Z-calls with higher SSTA during winter (Z-calls most abundant) around shallower water depth of AAR2 suggesting that the presence of these animals' calls might coincide with higher SSTA. Similarly, Gill et al. (2011) observed higher blue whales with higher SSTA using whale sightings in a regional upwelling system off southern Australia. However, around AAR4, peaks of blue and fin whale call occurrence coincided with lower temperatures in May. Z-call acoustic occurrence decreased in May in the vicinity of AAR4 followed by a peak in July in the vicinity of AAR3 that could possibly suggest that the presence of blue whales might coincide with warmer SSTA around AAR3. The RF model classified month of the year as the most important predictor of blue whale acoustic occurrence and behaviour for both AARs, and of fin whale acoustic occurrence and behaviour from AAR3. Whereas wind speed and month of the year, lchl-a and SSTA were the most important predictors of fin whale acoustic occurrence and behaviour from AAR4, respectively. The observed peak fin whale acoustic occurrence in September for AAR4 coincided with those changing environmental conditions.

There was an overall lesser number of blue whale calls recorded by AAR4 than AAR3, likely indicating water depths around 1100 m that are associated with biological productive conditions could be important for blue whales, given that areas around AAR3 were characterised by higher overall lchl-a concentration than around AAR4 (Fig. 3). Shabangu et al. (2019) also seasonally detected more calls (no occurrence of calls in the summers of 2014 and 2015) at 1100 m water depth than at 850 m, further supporting this water depth to be important for blue whales. Fin whale 20 Hz pulses showed a seasonal acoustic occurrence at both AARs, with the highest number of calls within the AAR3 (28,697) recordings than in the AAR4 (23,403) recordings. Shabangu et al. (2019) also seasonally detected higher fin whale 20 Hz pulses (53,964) in waters at 1118 m. Similarly, more sounds of Antarctic minke whales *B. bonaerensis* and sperm whales *Physeter macrocephalus* were also detected in the AAR3 recordings (Shabangu et al. 2020b; Shabangu and Andrew 2020), further supporting the idea of the importance of this water depth for various whale species.

The blue whale 27 Hz chorus, and blue and fin whale 18–28 Hz chorus were higher within recordings from AAR3 than AAR4, further supporting the importance of the continental slope waters (AAR3) than the more offshore waters (AAR4) to these animals. These choruses have also been recently described in both high latitudes off Antarctica (Shabangu et al. 2020a; Miller et al. 2021) and low latitudes off the Namibian coast (Thomisch et al. 2019), the Equator in the Atlantic Ocean (Samaran et al. 2018) and Indian Ocean (Leroy et al. 2016). Shabangu et al. (2019) did not detect any choruses off the west coast of South Africa, suggesting that the presence of these chorus varies with changes in occurrence of blue and fin whale calls since both choruses generally follow a similar trend as the seasonal variations of individual calls (Leroy et al. 2016; Thomisch et al. 2016; Shabangu et al. 2020a).

The lack of sympatric acoustic occurrence of blue and fin whales between the two AAR locations is supported by detection ranges for most seasons except for spring when detection ranges from both AARs exceed 240 km and would have allowed for simultaneous detection of calls. Overall, AAR3 had higher detection ranges than AAR4 especially in spring where ranges were almost twice that of the latter (i.e. 800 vs 460 km), due to variations in ambient noise between the two locations. This high detection range supports the significantly higher Z-calls, 27 Hz chorus, 18–28 Hz chorus and 20 Hz pulses detected around AAR3. Shabangu et al. (2019) found significantly shorter detection ranges of 35–60 km from AAR2 deployed at the same location as AAR3, since 2015 (AAR2) seems to be have been characterized with higher ambient noise compared to 2016 (AAR3).

In the central Benguela ecosystem, Thomisch et al. (2019) found a maximum detection range of 200 km off the Namibian coast with higher detection in spring. However, the estimated maximum detection range of 800 km in spring for AAR3 does not allow detection of whales off Namibia,

implying that the detected whales were in South African waters. The variation in detection ranges in our study compared to other studies could possibly be due to multiple factors including but not limited to used background noise, sea state conditions, the sound propagation model, bathymetric properties, recorder types and source levels (Širović et al. 2007; Thomisch et al. 2016, 2019; Shabangu et al. 2019, 2020a). Low detection ranges in autumn and winter when the blue and fin whale calls were at the highest, coincided with high ambient noise suggests that most animals may have been possibly calling closer to the recorder since there is a negative correlation between noise level and detection range. The higher ambient noise detected in the AAR4 is due to fast ocean current speeds associated with this depth (Shabangu et al. Unpublished data).

Previous understandings of blue whale migrations and seasonal abundances have been heavily based on historic catch data. Prior to 1913, Olsen (1914) found blue whales to be present off the Cape Province from May to June. Catches from the Saldanha Bay stations on the west coast of South Africa between 1922 and 1928 showed bimodal seasonality centred on May to July and August to October peaks (Harmer 1931; Best 2007). Off both Namibia and Angola, catches (1924–1927) showed a single unimodal seasonality in July and August respectively (Harmer 1931; Best 2007). Our results show a similar pattern to historic catch data as AAR3 indicates a strong peak across May–August and AAR4 indicate a single unimodal distribution centred in May.

The peak in monthly acoustic occurrence of Antarctic blue whale Z-calls, 27 Hz chorus, 18–28 Hz chorus and fin whale 20 Hz pulses occurred in May 2016 in the AAR4 recordings, a month earlier than the June peak reported for AAR3. The seasonal offset in peak acoustic occurrence between the two recording locations suggests different arrival time of whales at these locations. It should be emphasised that an absence of acoustic detections does not essentially mean that whales are not present, just that they are not vocalizing.

Thomisch et al. (2019) detected Antarctic blue whale Z-calls from November 2011 to August 2012 and from November 2012 to May 2013 with significant increase of calls from autumn through winter off the Namibian coast, which corresponds to arrival of these whale species in South African waters. Shabangu et al. (2019) also detected an increase in blue whale acoustic occurrence off the west coast of South Africa from late autumn through winter with a peak in winter. Similar peaks have also been observed in the Indian Ocean in autumn and winter (Samaran et al. 2010, 2013; Leroy et al. 2016). In contrast, Širović et al. (2009) detected a peak in call numbers in the Southern Ocean from late summer through autumn followed by a decrease in call numbers in winter; then call numbers increasing yet again during late spring. However, Shabangu et al. (2020a) found increased proportion of blue whale acoustic occurrence above 81% off the Maud Rise, Antarctica, from mid-January to mid-September indicating that some of these animals might not migrate to the low latitudes possibly to conserve energy expenditure associated with this long migration.

Decreased acoustic occurrence in spring and summer possibly mean that most of the vocalising individuals leave these grounds to go north or south, while some individuals choose to remain in this area. Blue whale sightings have been observed to occur in spring off Angolan waters (Figueiredo and Weir 2014). Mackintosh and Wheeler (1929) suggested that non-migratory whales could be juvenile individuals. Off Namibia, juveniles with impoverished body states prevailed in winter catches, suggesting that juveniles might possibly have not undertaken a southward migration during the previous summer but chose to overstay in wintering areas (Mackintosh and Wheeler 1929). In the Southern Ocean, some adult whales are hypothesized to not undertake in the annual winter migration but rather stay in these high-latitude areas to feed (Širović et al. 2004, 2009). Shabangu et al. (2019) detected fin whale calls off the South African west coast from late autumn (May) until end of spring (November) with a peak occurrence in winter (July). Historical whale catch data also show abundance of fin whales from May to November (Best 1998, 2007). This peak in winter is consistent with this study; however, the absence of fin whales in spring and summer within the AAR3 recordings could mean that the population could have already migrated to the south or offshore where a concurrent peak was observed within the AAR4 recordings, whereas some of the blue whale population were present year-round.

Širović et al. (2009) and Shabangu et al. (2020a) recorded a small number of fin whale calls in the Antarctic from late summer through autumn (with peaks in autumn) and no calls were detected for the remainder of the year. These complementary patterns are consistent with the notion that the vocalizing blue and fin whales that make up the majority of acoustic detections are migrating between summer feeding grounds off the Antarctic in summer and overwintering grounds off the low latitudes in winter. However, some animals also maintain year-round presence in both latitudes. Furthermore, the intermittent acoustic occurrence of blue whale and fin whales is consistent with suggestions that blue and fin whale migration are defined by gradual movement of animals from Antarctic waters, as opposed to a bulk movement (Širović et al. 2004, 2009). In addition to the detection of the key species of this study, a call from an unknown source, M-call, was detected seasonally in the recordings of both AARs. In AAR3, the M-call occurred intermittently in April, July, October and November of 2016. In AAR4, M-calls occurred intermittently in December 2015 and May 2016. The occurrence of M-calls off the South African west

coast and Namibia (Thomisch et al. 2019), suggests that the source of this call likely inhabits the Indian and Atlantic Oceans and likely follow similar migration patterns as these baleen whales.

Blue whale Z-calls have been reported to follow a Diel trend with increased calls produced during the day than at night (Stafford et al. 2004; Oleson et al. 2007a, b; Leroy et al. 2016). This study's results are consistent with this trend as rates of Z-calls and 20 Hz pulses recorded by both AARs increased during the day in autumn and winter, while Z-call rates from AAR3 decreased during the day in summer and spring. Shabangu et al. (2019) also found an increase in rates of Z-calls and 20 Hz pulses during the day in South African waters. This Diel calling pattern change with seasons shows that variability in Diel behaviour of animals might be an adaptation to different seasonal ecological functions. For both AARs, time of day was eliminated from RF models for both blue and fin whale acoustic occurrence and behaviour due to its non-essentiality, with an exception of AAR3 blue whale acoustic occurrence where the RF model ranked time of the day as a least important predictor. Although diurnal patterns of blue and fin whale acoustic occurrences and behaviour were found during certain seasons, the RF model suggests that time of day is not a reliable predictor of these whales' acoustic occurrence and behaviour.

The continued acoustic occurrence of blue and fin whales in both stations extends our knowledge of the ecological importance of the southern Benguela ecosystem not only as an overwintering ground, but also as a potential year-round habitat of some blue whales. Protection of this region from growing blue economy activities might protect these animals from fatal interaction with humans, such as recent (April 2021) blue whale ship strikes observed in Namibia. These whales utilize these areas for similar purposes at times, even though some blue whales remained much longer particularly around AAR3.

Conclusion

Passive acoustic monitoring allowed us to continue to monitor the seasonal acoustic occurrence and behaviour of the rarely sighted blue and fin whales off the west coast of South Africa. The acoustic occurrence of blue whales in the vicinity of AAR3, suggests that the southern Benguela ecosystem may be a potential year-round habitat. On the other hand, the seasonal acoustic occurrence of blue whales around AAR4 and of fin whales around AARs 3 and 4 indicates that that region is a seasonal habitat used for overwintering/breeding/calving ground and/or migratory route. Blue and fin whale acoustic occurrence was high in autumn and winter suggesting this as a period when a high number of these whales arrive in the Benguela ecosystem given the existing relationship between call rates and number of Antarctic blue whales. Call rates of both whale species were high during the day for most seasons as most whales were vocally active during the day, but time of day was a non-informative predictor of acoustic occurrence and behaviour of these whales according to RF models. BELLHOP modelled detection ranges were longer for AAR3 than AAR4 due to ambient noise fluctuations, and those detection ranges indicated that detected calls are from whales within South African waters. RF models indicated environmental conditions influenced the acoustic occurrence and behaviour of blue and fin whale whales, reflecting the importance of the environment in driving the ecological interaction and adaptation of these whales in Benguela ecosystem. This study highlights the ecological importance of the South African west coast as a potential year-round and seasonal habitat/migration corridor of Antarctic blue whales and fin whales. Lastly, this study like others, further confirms that these Antarctic baleen whales can be monitored effectively through bioacoustics in the low latitudes such as the west coast of South Africa.

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Author contributions ISL, FWS, PLG and KF participated in the conception, design, and management of the study; ISL analysed acoustic data; DF and RKA performed the sound propagation modelling; FWS analysed environmental data; ISL and FWS carried out the statistical analyses; ISL and FWS wrote the first draft of the manuscript. All authors read and approved the final manuscript.

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Data availability All data are presented in results of the manuscript. Raw acoustic data are available upon request.

Code availability Software R codes used for environmental data extraction and statistical data analyses are available upon request.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

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