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

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Highlights
• Whale calls were detected from May to November but peaked in July.

• First acoustic records of sympatric whale occurrence off the west coast of South Africa.

• Acoustic evidence of Antarctic blue whales feeding in the Benguela ecosystem

• Call occurrences indicate the west coast of South Africa as an overwintering ground and migration route.

• Environmental conditions influenced whale call occurrence and diel acoustic behaviour.

Abstract

Passive acoustic monitoring was used to detect the sounds of rarely sighted Antarctic blue and fin whales to investigate their seasonal occurrence (as presence or absence of whale calls) and behaviour (as determined from call rates) in the Benguela ecosystem. Data were collected using autonomous acoustic recorders deployed on oceanographic moorings for 16.26 months off the west coast of South Africa in 2014 and 2015. Satellite derived environmental variables were used as predictors of whale acoustic occurrence and behaviour. Migratory Antarctic blue and fin whales were acoustically present in South African waters between May and August with call occurrence peaks in July whereas some fin whales extended their presence to November. No whale calls were recorded in summer for either species, suggesting whales use the Benguela ecosystem as an overwintering ground and migration route. Antarctic blue whales produced both their characteristic Z-call and their feeding associated D-call. Fin whales produced calls characteristic of animals from the eastern Antarctic fin whale acoustic population. Random forest models identified environmental variables such as sea surface temperature anomaly, sea surface height, wind speed, months of the year, Ekman upwelling index and log-transformed chlorophyll-a as the most important predictors of call occurrence and call rates of blue and fin whales. Here we present the first acoustic recordings of Antarctic blue and fin whales in the Benguela ecosystem, and provide preliminary information to investigate seasonal abundance and distribution of these large baleen whale populations. This work demonstrates the feasibility of cost-effectively monitoring Antarctic top-consumer baleen whales in the Benguela ecosystem.

Keywords: Seasonal occurrence, blue whale, fin whale, acoustic monitoring, behaviour, Benguela ecosystem, environmental conditions

Introduction

Antarctic blue whales *Balaenoptera musculus intermedia* and fin whales *B. physalus* are rarely sighted off the coasts of South Africa (with fewer than 10 confirmed Antarctic blue whale sightings since 1975) due to lack of search effort and monitoring in the offshore environment. As a result of their large size, they yielded more oil than any other whale species, and both species were therefore harvested to near-extinction in the Southern Hemisphere before modern whaling ceased in the 1960s (Hilborn et al., 2003; Branch et al., 2004, 2007; Best, 2007). Operating from 1909 onwards, the modern whaling stations at Saldanha Bay and Cape Hangklip (South Africa), as well as stations at Lüderitz and Walvis Bay (Namibia), were the main whaling stations to target blue and fin whales in the southern African west coast region (Best, 1994, 1998, 2007), although catches were also made from Angolan land stations to the north.

By the time illegal whaling ceased in the mid-1970s, only 0.7% (95% confidence interval: 0.3%-1.3%) of the pre-exploitation blue whale population remained (Branch et al., 2004). At present, the Antarctic blue whale population remains low; the 1996 Southern Hemisphere estimate was 1,700 individuals (860-2,900) and the population was estimated to be increasing at 8.2% (1.7-15.3%) per annum (Branch et al., 2004). There are fewer data available for fin whales but some evidence suggests that they, too, may be recovering although the current rate of increase is unknown (Branch and Butterworth, 2006). The International Union for the Conservation of Nature (IUCN) currently classifies Antarctic blue and fin whales as Critically Endangered and Endangered respectively (Reilly et al., 2013).

Both blue and fin whales produce low-frequency calls (< 120 Hz) with high intensities (~189±4 dB re: 1 μPa at 1 m) that can travel great distances underwater (Širović et al., 2007); and such calls

are believed to be whale population specific (McDonald et al., 2006; Širović et al., 2009). Antarctic blue whales produce two kinds of calls, a D-call (McDonald et al., 2001; Rankin et al., 2005; Oleson et al., 2007a,b) and a Z-call (Ljungblad et al., 1998). D-calls are frequency modulated (FM) and downsweep from about 106 to 22 Hz lasting 0.7-7.5 s (Rankin et al., 2005). D-calls are not population specific as they have been record in the California Current (McDonald et al., 2001; Oleson et al., 2007a,b), Indian Ocean (Samaran et al., 2010), Southern Ocean (Rankin et al., 2005; Shabangu et al., 2017) and southeastern Atlantic Ocean (this study). Males and females have been observed to produce D-calls during lunge feeding and also used this call for group communication (McDonald et al., 2001; Oleson et al., 2007a,b). Although much of what is known about feeding associations of this call type originates from the California Current; it is very unlikely that other blue whale populations produce this call type in a different behavioural context. The characteristic Z-call (termed so due to its Z-shaped spectrogram signature) is a low frequency, stereotyped three-unit sequence of tonal sounds that lasts from 18 s to ~26 s (Ljungblad et al. 1998; Rankin et al. 2005). The first unit of the Z-call is a tone at ~27 Hz followed by a second unit that frequency modulates and downsweeps from ~27 to 20 Hz and third unit slightly frequency modulates from 20 to ~18 Hz. Like blue whale songs in other regions, the Z-call is believed to be produced in song sequences by Antarctic blue whale males only as a long-distance contact call for sexual advertisement and likely other communication purposes (McDonald et al., 2001, 2009; Oleson et al., 2007a,b). A decrease has been observed in the vocalization frequency of the Z-call song from ~28 to ~26 Hz over the past 16 years and a wide variety of reasons have been suggested for this decrease including cultural conformity, sex, body size, climate change and many others (McDonald et al. 2009; Gavrillov et al. 2012; Ward et al. 2017).

Antarctic fin whales produce short (1 s) FM downsweeps from ~28 Hz to 15 Hz (also known as the 20 Hz pulse), and a second, simultaneously produced higher frequency pulse. These signals are repeated at 13 s intercall intervals (Širović et al., 2004). The higher frequency pulse has been used to delineate between two acoustic populations of fin whales in the Antarctic: the eastern Antarctic acoustic population with a secondary frequency peak at 99 Hz and the western Antarctic acoustic population with a peak at 89 Hz (Širović et al., 2009). Fin whales also make irregular and short (usually under 1 s) pulses that tend to downsweep from 70 to 40 Hz, termed hereafter the 40 Hz pulses. Unlike the 20 Hz pulses, the fin whale 40 Hz pulses are not repeated regularly and are sometimes confused with blue whale D-calls as they both cover a similar frequency band. However, the D-call is longer in duration and slightly slanted to the right as it downsweeps whereas the 40 Hz pulse in shorter in duration and downsweeps vertically without such slanting. Both male blue and fin whales produce calls in repeated sequences at regular intervals, these repeated stereotyped sequences of calls are considered songs (McDonald et al. 2001, 2006; Croll et al. 2002; Oleson et al. 2007c, 2014; Širović et al., 2017). Songs can last from minutes to hours, days or even weeks with only slight breaks, which have been attributed to a whale surfacing to breathe (Cummings and Thompson 1971; McDonald et al. 2001, 2006).

The Benguela ecosystem, also referred to as Benguela Current Large Marine Ecosystem, extends from east of the Cape of Good Hope (South Africa) equatorwards to near the southern border of Angola (Figure 1) and is generally characterized by its nutrient-rich upwelling regime (Shannon, 2006). Northwestward winds in the Benguela ecosystem induce the movement of cold nutrient-rich bottom waters to the sea surface which results in upwelling (Andrews and Hutchings, 1980; Lutjeharms and Meeuwis 1987; Jury and Bundrit, 1992; Grodsky et al., 2008; Goubanova et al., 2013). Such nutrient-rich water movement into the photic zone drives phytoplankton blooms and

the productive food webs within the Benguela ecosystem. This productivity drives high zooplankton biomass, which are prey for some economically important South African pelagic fisheries species including anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi*. Both these and the large zooplankton are consumed by marine mammals, piscivorous fish and seabirds. Faecal matter from feeding whales and other top predators fertilises the Benguela ecosystem and presumably enhances the growth of phytoplankton as identified elsewhere in the world's oceans (Lavery et al., 2010; Roman et al., 2014; Doughty et al., 2016). Hence, large baleen whales may potentially play an important role in the Benguela ecosystem functioning if they feed within the system.
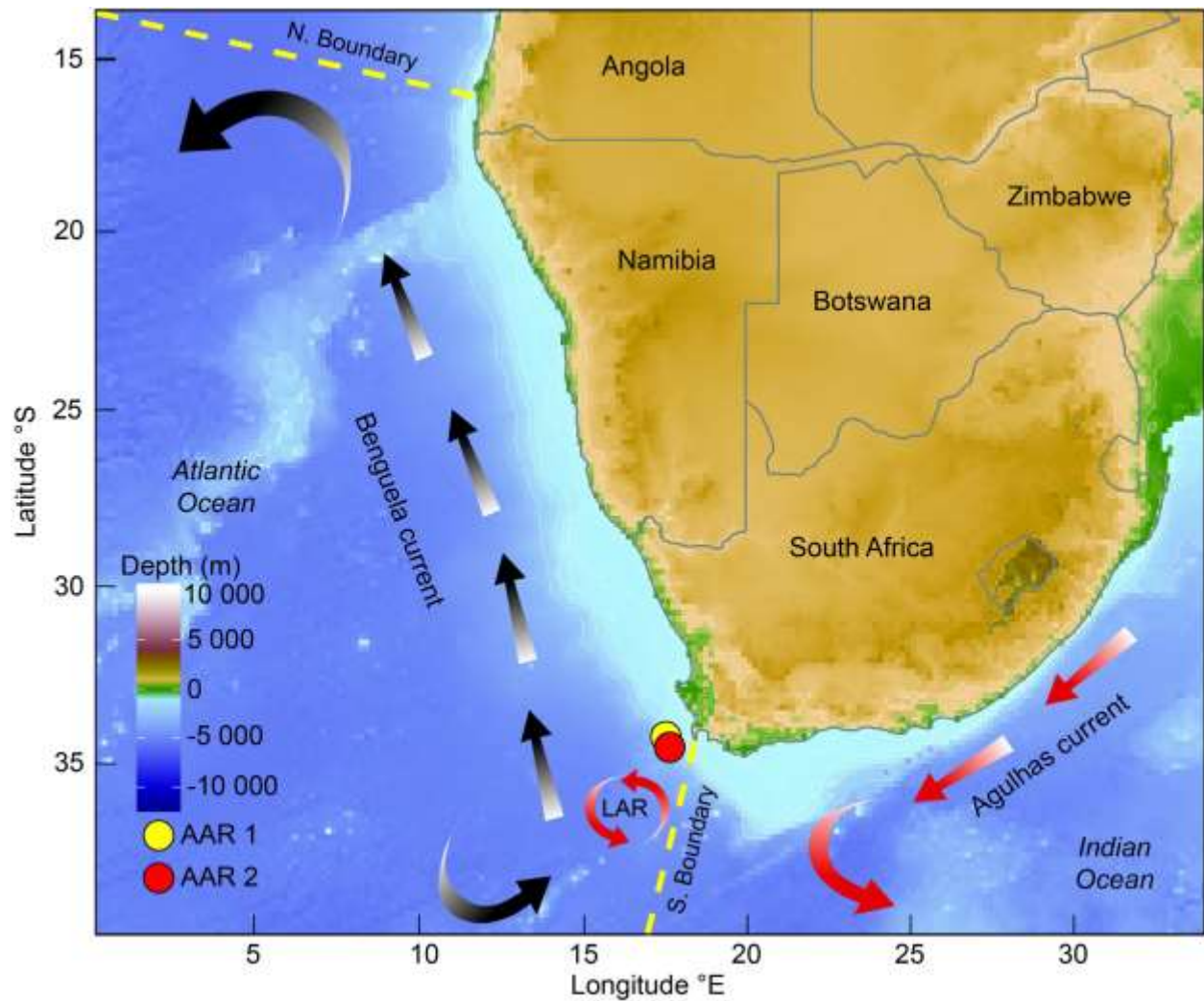
Fig. 1. Location of AAR1 (●) and AAR2 (●) off the west coast of South Africa in the Benguela ecosystem, Atlantic Ocean. The flow direction of the cold Benguela Current is shown by black arrows and the flow direction of the warm Agulhas Current is shown by red arrows. The dashed yellow lines are the northern and southern boundaries of the Benguela Current respectively. LAR is the Agulhas Current leakage via Agulhas Rings introducing warm waters to the Bengulea ecosystem. Bathymetry data were obtained from the ETOPO1 dataset (Amante and Eakins, 2009).

The aim of our study was to determine the seasonal occurrence and calling behaviour of blue and fin whales in the Benguela ecosystem using passive acoustic monitoring. Such acoustic monitoring of large baleen whales from the Antarctic in low latitude regions is potentially the most economical and reliable method of monitoring and tracking these whales. This study establishes the acoustic

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seasonal occurrence and acoustic behaviour of Antarctic blue and fin whales in the Benguela ecosystem, which are important for the conservation and management strategies of these species.

Materials and Methods

Acoustic data collection

Acoustic data were collected off the west coast of South Africa in the southern Benguela ecosystem in the southeast Atlantic Ocean (Figure 1). We used two passive acoustic monitoring stations each equipped with an Autonomous Acoustic Recorder (AAR) AURAL-M2 instrument (Autonomous Underwater Recorder for Acoustic Listening-Model 2 version 04.1.3 manufactured by Multi-Electronique Inc., Canada) to record the acoustic data (Supplementary Figure S1). The first AAR (hereafter AAR1) was deployed at 34° 22.21'S, 17° 37.69'E from 24 July 2014 to 1 December 2014 in water depth of 855 m (Figure 1). The second AAR (hereafter AAR2) was deployed at 34° 23.64'S, 17° 35.66'E from 16 September 2014 to 1 December 2015 in water depth of 1,118 m (Figure 1). Both AARs (Supplementary Figure S1) were deployed on the South Atlantic Meridional Overturning Circulation Basin-wide Array (SAMBA) of oceanographic moorings (Ansorge et al., 2014) and situated approximately 70 km from the coast (Figure 1). The SAMBA transect is a hydrographic transect that falls under the South Atlantic Meridional Overturning Circulation (SAMOC) global project. AAR1 recorded the first 30 minutes of every hour of each day, whereas AAR2 only recorded the first 20 minutes of every hour of each day to maximize battery lifespan. AAR1 was positioned at 200 m below the sea surface whereas AAR2 was slightly deeper at 300 m below the sea surface. Both AARs sampled at 4,096 Hz for an effective monitored bandwidth range of 10 Hz to 2,048 Hz (i.e. the Nyquist frequency) and had receiving sensitivities of -169 dB re 1V/μPa when applying a AAR gain of 22 dB.

A total of 5,057 hours were recorded from both listening stations: 1,567 hours from AAR1 and 3,489.75 hours from AAR2. Here we use Southern (austral) Hemisphere seasons of the year to parse our data into seasons: summer (December to February), autumn (March to May), winter (June to August), and spring (September to November). Classification of different light regimes over different seasons for diel call rates plots and smoothing methods of diel call rates are described in Supplementary Material B.

Whale call detections

Acoustic data were analysed using the eXtensible Bio-Acoustic Tool (XBAT) software (Figueroa, 2006) implemented as a MATLAB routine (MathWorks Inc, 2014). We used automated detection templates (developed from the 2014-15 data and applied in XBAT) as a time-effective method to detect fin whale calls, and Antarctic blue whale D- and Z-calls. . The D-call downsweeps from 70 to 30 Hz (Figure 2a) and a complete (all the three units) Z-call (Figure 2b) were used as detection templates for Antarctic blue whales because they contained most of the energy of the calls. The 20 Hz pulse with a short downsweep from 28 to 15 Hz tone (Figure 2b) was used for automated detection of fin whale calls as it is the most abundant and reliable sound of fin whales. The 40 Hz pulse of fin whales was absent from our acoustic recordings. The template detector method operates on an acoustic time series of spectrograms by constructing a correlation kernel for the vocalization (Mellinger and Clark, 2000). Calls were recognized from spectrograms by cross-correlating with the template kernel based on a similarity level above a set threshold (i.e. the lowest detectable similarity percentage between a template and call). We used high signal-to-noise ratio calls to construct templates. In order to estimate the number of false negative calls (incorrectly missed blue or fin whale calls), the entire acoustic dataset was assessed visually, whilst visually identified detections of false positive calls (detections that were not blue or fin whale calls) were

manually excluded from further data analyses without quantifying their prevalence rate. Visually identified false negative detections were manually incorporated into the calculations of final total call number and rates but considered true negatives (correctly missed blue or fin whale calls) during the below detector accuracy test on the entire acoustic dataset.

We tested seven different thresholds from 10% to 70% by increments of 10% on randomly selected 5% of the acoustic data and implemented the results on the entire acoustic dataset to determine optimal thresholds for our analyses of Antarctic blue whale Z-calls from AARs 1 and 2, D-calls from AAR2, and for fin whale calls from AAR1 (Figure 3). However, only six different thresholds (from 20% to 70% by increments of 10%) in randomly selected 5% of the acoustic data were tested for fin whale calls from AAR2 dataset (Figure 3). The 10% threshold was not used for fin whale calls from AAR2 because it produced many false positives during threshold-testing. The 10% detection threshold was optimal for detections of Z-calls from both AARs, for D-calls from AA2 and for fin whale call detections from AAR1 as it produced the fewest false negatives and positives. The 20% detection threshold was best suited for detecting fin whale calls from AAR2 (Figure 3). Detection templates for AAR1 produced false negative errors of 13% and 1% for the fin whale and Z-calls respectively; hence 87% and 99% true positives (correctly identified blue or fin whale calls) for fin whale calls and Z-calls correspondingly (Figure 3). Detection templates from AAR2 produced false negative error rates of 13% and 11% for D- and Z-calls respectively; hence true positives of 87% and 89% for D- and Z-calls respectively. Fin whale detection template from AAR2 produced 2% false negatives and 98% true positives e (Figure 3).

Acoustic presence of blue and fin whales is defined herein as instances when calls of either whale species were detected within a sampling interval. The Z-call and 20 Hz pulse were used to

determine acoustic occurrence of blue and fin whale respectively, since these were the most prevalent call types in our data. Acoustic absence refers to instances when neither blue nor fin whale calls were detected by AARs within a sampling interval.
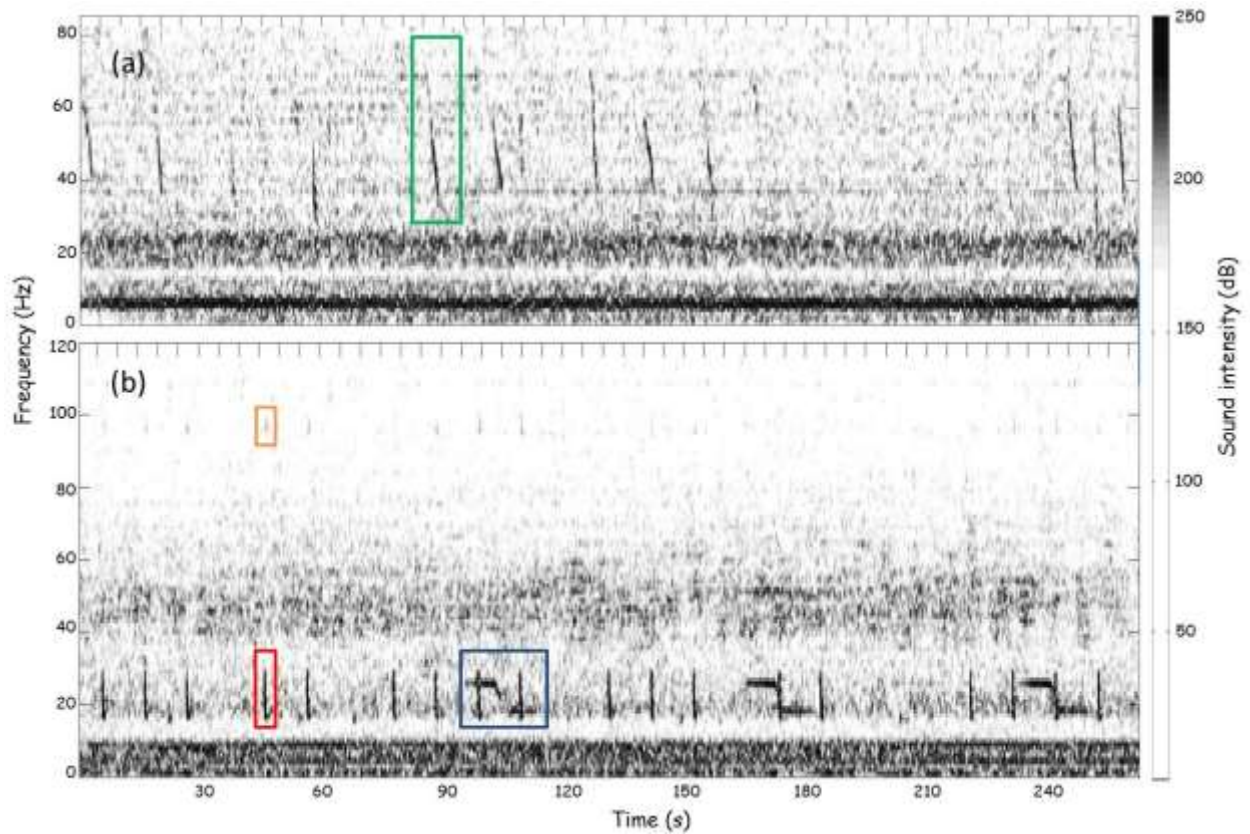

Figure 2. Spectrograms showing a) Antarctic blue whale D-calls (green box) and b) low frequency downsweeping ~28-15 Hz tone (red box) and high frequency 99 Hz tone (orange rectangle) of eastern Antarctic fin whale acoustic population and Z-calls (blue box) of Antarctic blue whales including co-occurring fin whale calls. Spectrogram parameters: frame size 1.28 s, 25% overlap, FFT size 4,096 points, Hanning window.
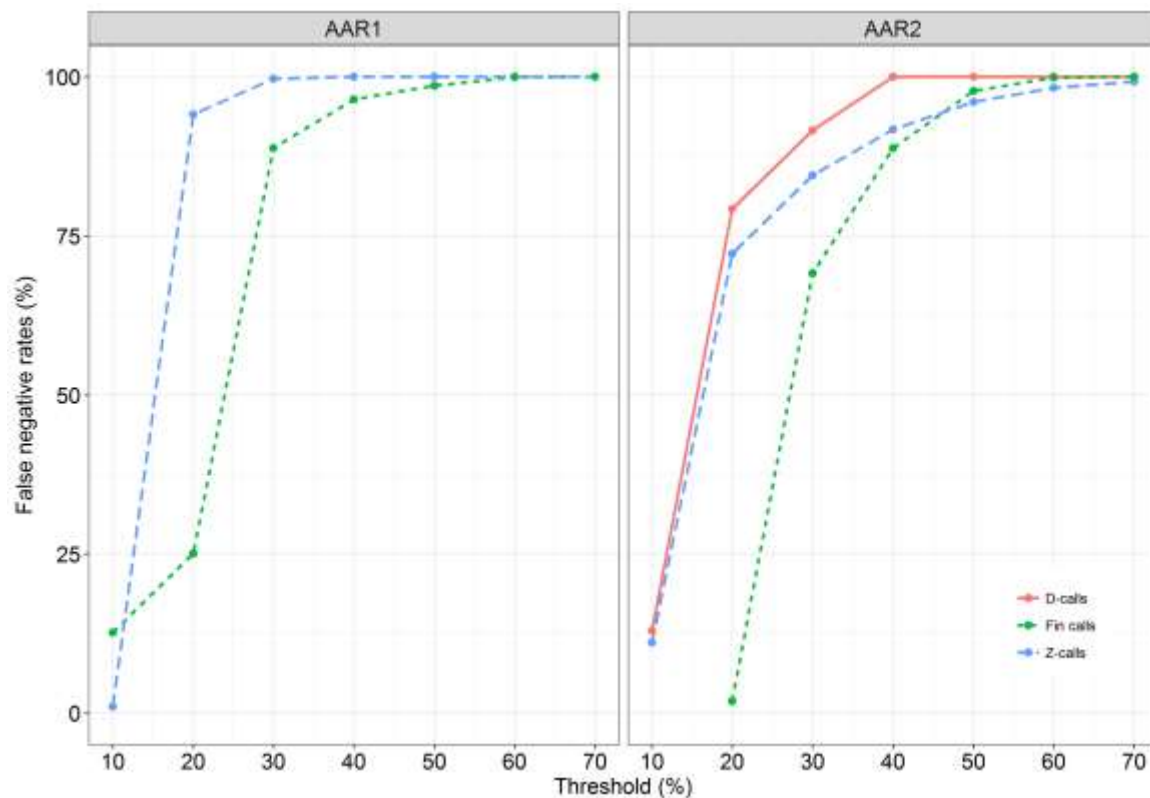
Figure 3. Overall false negative rates at different thresholds for 28 Hz fin whale calls and Antarctic blue whale Z- and D-calls recorded from AAR1 (left) and AAR2 (right). No D-calls were recorded from AAR1.

Calculation of call rates

Call rates (expressed as calls detected per hour) of Antarctic blue and fin whales were calculated as the total number of calls recorded within a sampling interval divided by the duration of duty cycle (0.50 h for AAR1 and 0.33 h for AAR2). Total hours with Z-, D-, and fin whales calls were calculated as the sum of sampling periods with detections multiplied by the sampling intervals. Whale call rates refer to the overall call detection rate per unit time, and not the number of calls per individual, which is unknown. Call rates reflected the acoustic behaviour of these whales off the west coast of South Africa as they indicated the detection rate of whale calls by our AARs, whereby call detection rate can be assumed to be correlated with call production rate within the AAR detection range. Proportion of species call occurrence as percentages was calculated as the

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number of instances with call presences of each species divided by the total number of samples recorded over time (month or season). We use call rates detected from one-third to two-third of autumn and spring to describe a full season as those are the only available representative samples off the west coast of South Africa for those seasons.

Detection distance estimation

Following the approach of Širović et al. (2007), we used BELLHOP beam tracing model (Porter, 2011) to compute seasonal transmission loss of a signal with a source level of 189 dB re 1 µPa @ 1 m and source depth of 30 m at each AAR where the hydrophones are at 200 m for AAR1 or 300 m for AAR2. We also assumed signals could be detected just above local ambient noise (SNR + 0).

The Smith-Sandwell database (Smith and Sandwell, 1997) was used for bathymetry as it has depths every minute of latitude and longitude in the region of the Benguela ecosystem. Seafloor depth at intermediate points was computed via bilinear interpolation. Seafloor depth along radials out from the receivers along geodesic paths was extracted from roughly every 1 km out to a maximum range of 100 km. Sound speed profiles were derived using the Thermal Equation of Seawater (TEOS-1) using temperature and salinity data at location 34° S, 15° E from the Autumn 2013 World Ocean Database (Boyer et al., 2013).

Representative ambient noise levels in the 15-30 Hz band (the frequency band that overlaps with both blue and fin whale calls) were estimated for each instrument for data files that did not contain calls from either species, using PAMGuide (Merchant et al., 2015). We used the manufacturer's specifications of -149 dB re 1 µPa for the end-to-end sensitivity of the instrument. This resulted in

normalized ambient noise levels of 105.9 dB re 1 μPa^2 in 1 Hz band for AAR1 and 95.1 dB re 1 μPa^2 in 1 Hz band for AAR2.

The above parameters were used in BELLHOP model to produce detection coverage maps for 32 bearings around each AAR location for the seasons with acoustic data (only winter and spring seasons were used for AAR1; all seasons of the year were used for AAR2).

Environmental variables

Sea surface temperature anomaly

We used daily sea surface temperature anomaly (SST anomaly) from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) data downloaded from the Copernicus Marine Environment Monitoring Service (ftp://cmems.isac.cnr.it/Core/SST _GLO_SST_L4_ NRT_OBSERVATIONS_010_001/METOFFICE-GLO-SST-L4-NRT-OBS-ANOM-V2/). OSTIA uses satellite data provided by the Group for High Resolution Sea Surface Temperature project (Donlon et al., 2012). SST anomaly was used to indicate changes in biological, physical, and chemical process that influence productivity and animal behaviour around the moorings.

Chlorophyll-a

Daily weighted average chlorophyll-a (chl-a) measurements of the GlobColour project (http://globcolour.info) were obtained from GlobColour developer, validator and distributor: ACRI-ST, France (ftp://ftp.hermes.acri.fr). Globally blended and binned high-resolution level-3 mapped grid, case-1 water GlobColour project merges the remotely sensed ocean colour (i.e. phytoplankton pigment concentration) measurements from two satellite data sources (Maritorena et al., 2010). About 90% of the records (dates) contained chl-a concentrations; for missing data,

we used chl-a concentrations from the previous available record as there is a known spatial and temporal autocorrelation of daily chlorophyll-a within a time series (e.g., Mackas, 1984; Jutla et al., 2012). The replacement was done using the 'zoo' library (Zeileis and Grothendieck, 2005). Chl-a concentration data were log-transformed for further analyses due to skewness of their distribution.

Wind speed

Data on daily blended vector sea surface wind speed (at 10 m above sea level) were downloaded from the National Climatic Data Center (ftp://eclipse.ncdc.noaa.gov/pub/seawinds/SI/). These sea wind speeds were blended from multiple satellites on a global 0.25 degree spatial grid and a 6-hourly temporal resolution (see Zhang et al., 2006). Wind speed was used as a proxy of circulation around our moorings and was not used as a proxy of ambient noise since previous studies found insignificant effect of wind-induced noise on sounds below 100 Hz (e.g., Wenz, 1962; Menze et al., 2017).

Sea surface height

Daily sea surface height (SSH) information were obtained from Archiving, Validation and Interpretation of Satellite Oceanographic (ftp.aviso.altimetry.fr) that uses level 4 absolute dynamic topography. SSH indicated sea state conditions around the mooring.

Wind stress curl and Ekman upwelling index

Daily data on wind stress curl and Ekman upwelling index was measured by the meteorological operation's advanced scatterometer that globally sampled at a 0.25 degree spatial grid (Bentamy and Croize-Fillon, 2012). Such data were obtained from Environmental Research Division's Data

Access Program (http://coastwatch.pfeg.noaa.gov/erddap/griddap/erdQMstress1day.html) of the United States National Oceanic and Atmospheric Administration. Wind stress and Ekman upwelling index were used as indices of nutrient transport around the moorings.

Processing of all environmental variables, data processing and model fitting were performed in R (R Core Team, 2016). All the above environmental data were processed and analysed using 'ndcf4' library (Pierce, 2015). To determine the oceanographic conditions around the AAR1 mooring, the above variables were averaged by 0.18° grid where the values of four 0.18° blocks adjacent to the AAR1 mooring were averaged. For AAR2 mooring, the above variables were averaged by 0.45° grid where the values of four 0.45° blocks adjacent to the AAR2 mooring were averaged. Grids of 0.18° (i.e. 0.24° longitude) and 0.45° (i.e. 0.59° longitude) of latitude closer to 40° south are approximately 20 km and 50 km respectively, which are equivalent to the detection ranges of around 20 km for AAR1 and 50 km for AAR2 that we estimated for Antarctic blue and fin whale calls off the South African west coast. All whales from which calls were detected by the AARs would fall within the gridded areas making environmental variables directly comparable. The above grids also fall within the meso-spatial scale (5 to 100 km) for foraging baleen whales (Torres, 2017).

Seasonal occurrence and behaviour modelling

Data processing

Although our two AARs were very close (4.8 km apart), we treated the data from these as two separate listening stations because they produced different seasonal detection ranges (20 km for AAR1 vs 50 km for AAR2; Supplementary Figure S2). Furthermore, there were significant

differences (Welch Two Sample t-test, p-values <0.05, n= 1828) between Z-call rates and fin whale call rates recorded by the two AARs during the period of overlap (16 September to 1 December 2014). AAR2 recorded fin whale calls during overlapping period whereas AAR1 recorded none, however, both AARs did not record D-calls during overlapping period. Since environmental data from AAR1 were collected within the second half of the year, smoothed means of environmental variables for plots were calculated by the locally weighted polynomial regression (i.e., non-circular smoothing) using the function 'loess' (Cleveland et al., 1992). As AAR2 contained year-round data, smoothed means of environmental variables for plots were calculated through penalized cyclic cubic regression splines (Wood, 2017) in generalised additive models (GAMs; Guisan et al., 2002).

We investigated correlations between predictor variables (time of the day, months of the year, SST anomaly, SSH, wind speed, wind stress curl, Ekman upwelling index and log transformed chl-a) prior to modelling to determine the effects of multi-collinearity using generalised variance inflation factors (GVIF; Fox and Monette, 1992). We implemented GVIF through the 'car' library (Fox and Weisberg, 2011). GVIF quantified how much variance of the estimated regression coefficients was amplified because of collinearity. Low GVIF values (around one) indicate weak or no correlations, GVIF values around five indicate moderate correlations, and high GVIF values around 10 or more indicate strong correlations (Fox and Monette, 1992; O'Brien, 2007; Hair et al., 2009). Wind stress curl was eliminated from further analysis due to strong collinearity with the log transformed chl-a, Ekman upwelling index, SSH and SST anomaly. Highest values around 47115.85 GVIF were obtained when wind stress curl was included in the GVIF model and GVIF dropped to 4.13 for AAR1 and 3.75 for AAR2 when this variable was excluded.

Model features

We used random forest (RF) modelling (Ho, 1995; Breiman, 2001) to investigate the influence of different environmental variables (time of the day, months of the year, SST anomaly, SSH, wind speed, Ekman upwelling index and log transformed chl-a) on the acoustic seasonal occurrence (i.e. presence and absence of species calls) and behaviour (i.e. species call rates) of Antarctic blue and fin whales. The RF model is an ensemble modelling approach to model wide range of problems but mostly classification, regression and survival with non-parametric inferential properties (Breiman, 2001; Hastie et al., 2009). As a machine learning method, RF modelling provides higher performance and has considerable benefits over standard regression methods such as GAM (Elith et al., 2008; James et al., 2013). RF modelling uses a set of unpruned decision trees in the forest that are bootstrapped as they grow with trained sample data, and rely on randomly chosen subsets of the predictor variables as candidate splitting tree nodes (Hastie et al., 2009; James et al., 2013).

Unlike generalised boosted regression trees model (GBM; Friedman et al., 2000), RF does not completely ignore some variables and its candidate split-variable selection increases the probability of any solitary variable being included in the final model output (Hastie et al., 2009; James et al., 2013). The RF model is generally built to avoid overfitting of growing trees in the training data (e.g. Hastie et al., 2009). The RF model is furthermore known to be immune to autocorrelation and is also better at dealing with zero-inflated data from count data (Hastie et al., 2009; Mascaro et al., 2014).

The relative importance of predictor variables in the RF model was assessed by computing the influence of each of the variables on the prediction error of the model. The relative importance of each of the variables in the model was computed by permuting the out of the bag (OOB) data

where for each tree the prediction error is recorded. Then prediction error on the OOB was computed, for each tree, after permuting each predictor variable. The difference between the two, prediction errors with and without permutation of predictor variables, are then averaged over all the trees and scaled by the standard deviation of the difference. In a situation when the standard deviation of the difference is zero for some variables then the difference will not be divided by zero, and just the difference in prediction error will just be presented (Hastie et al., 2009). This scaled index was calculated for each of the variables and used as an index of relative importance (see Supplementary Material C for a comparison of RF model with GAM and GBM).

Model fitting

The RF models for the two AARs were fitted using the optimal configuration values in Supplementary Table S3. The RF modelling was performed using the 'randomForest' library (Liaw and Wiener, 2002), whilst the optimal parameter configuration values were determined using the 'ranger' library as a computational-time-saving method for the implementation of RF model (Wright and Ziegler, 2016). To improve the performance prediction of RF model, variables in Table 1 were eliminated from the RF model because their index of relative importance was negative. Negative relative importance generally indicates that variables are not important at all as they do not have a role in the prediction (Perrier, 2015).

Table 1. List of variables eliminated from RF models of AAR1 and AAR2.

RF model	Eliminated variable(s)
AAR1 Blue whale call occurrence	Time of the day, SST anomaly and chl-a
AAR1 Fin whale call occurrence	Time of the day
AAR2 Blue whale call occurrence	Time of the day
AAR2 Fin whale call occurrence	Time of the day
AAR1 Fin whale call rate	Months of the year
AAR1 Z-call rates	None
AAR2 D-call rates	Ekman upwelling index, chl-a and wind speed
AAR2 Fin whale call rates	Time of the day

Results

Transmission loss

Detection ranges for Antarctic blue and fin whale calls differed between the two instruments according to bearings around each AAR location. For AAR1, which had higher noise levels, the transmission loss indicated a statistical mode of about 20 km detection range but a maximum of 60 km for the two seasons with data (Supplementary Figure S2). It should be noted that to the north and east of this instrument is the continental shelf and BELLHOP is not particularly robust where there are interactions of the transmitted signal with the seafloor. For AAR2, the detection range around all seasons ranged from 35 km (to the north) to 60 km with a mode of 50 km in the south and west directions, which are bearings into open water (Supplementary Figure S2). Detection ranges did not vary between seasons for both AARs (Supplementary Figure S2).

Benguela environment and call detections

Mean environmental conditions showed strong variation by season (Figures 4 and 5). Around AAR1 location, lower values for Ekman upwelling index and log transformed chl-a were observed in winter whilst the highest values of those variables were observed in spring through summer (Figure 4a and b). Wind speed decreased in winter but increased mid-spring and SSH was high towards the end of winter but low in spring (Figure 4c and d). SST anomaly around AAR1 was positive in winter through spring and was negative in December (Figure 4e). Raw data distributions of environmental variables around AAR1 are shown in Supplementary Figure S3. Around AAR2 location, SSH was high at the beginning of winter but low in summer (Figure 5a). Lower values

for log transformed chl-a, wind speed, Ekman upwelling index and SST anomaly were observed from autumn to winter whilst highest values of those variables were observed in spring through summer around AAR2 (Figure 5b-e). There was a general inverse relationship between SSH and wind speed, and there was lag in the decrease of log transformed chl-a after the decrease in Ekman upwelling index (Figures 4 and 5). According to SST anomaly, 2014 winter (Figure 4) was generally warmer than the 2015 winter (Figure 5). Raw data distributions of environmental variables around AAR2 are shown in Supplementary Figure S4.

Of the 1,567 total hours of acoustic data recorded by AAR1 from 30-minute sampling intervals, only 14 hours contained fin whale calls and 79.5 hours contained Antarctic blue whale calls. The total numbers of post-processed and operator verified calls for the two species from AAR1 were 2,539 fin whale 20 Hz pulse signals; 2,602 Antarctic blue whale Z-calls and no Antarctic blue whale D-calls. Out of the 3,489.75 total hours recorded by the AAR2 from 20-minute sampling intervals, 211.86 hours contained fin whale sounds whilst 156.09 hours contained Antarctic blue whale calls. The total numbers of post-processed and operator verified calls for the two species from AAR2 were 53,964 fin whale 20 Hz pulse signals; 6,114 Antarctic blue whale Z-calls and 176 Antarctic blue whale D-calls. All recorded fin whale sounds were those of the eastern Antarctic fin whale acoustic population (Figure 2b; Širović et al., 2009). There were temporal segregation between the peaks of diel call rates of blue and fin whales in autumn and winter, however, spring had no strong temporal segregation of diel call rate peaks (Supplementary Figures S5 and S6). Summary of the results of diel call occurrence and call rates is given in Supplementary D.

Antarctic blue whale calls were detected within detection radii of our hydrophones in 29 days for 2014 and 48 days for 2015, whereas fin whales were detected in 11 days for 2014 and 50 days for

2015. No calls of either species were recorded in summer from both AARs and no choruses (i.e., indiscernible bands of continuous calls) of either whale species were recorded throughout the deployment period of our AARs. No recordings were conducted in summer and autumn from AAR1. No pygmy blue whale calls were detected from these recordings. Both Antarctic blue and fin whale calls occurred between July and October in 2014 and May through November in 2015 (Figure 6). In 2014, the peaks of monthly call occurrences of blue and fin whale from AAR1 were in July (austral winter) with a proportion of occurrence of 16% and 3% respectively (Figure 6). There were second peaks in call proportion of occurrence for AAR1 blue (6%) and fin whale (5%) in October and September respectively (Figure 6). Blue whale calls were only recorded in September for AAR2 in 2014, corresponding to the late deployment of the AAR. In 2015, peak monthly call occurrences of both species (32% of the time for Antarctic blue whale and 40% of the time for fin whale) were recorded in July (austral winter) for both AARs (Figure 6). Blue whale calls disappeared quite earlier in 2015 (August) than in 2014 (September), whereas fin whale calls disappeared earlier in 2014 (October) than in 2015 (November).
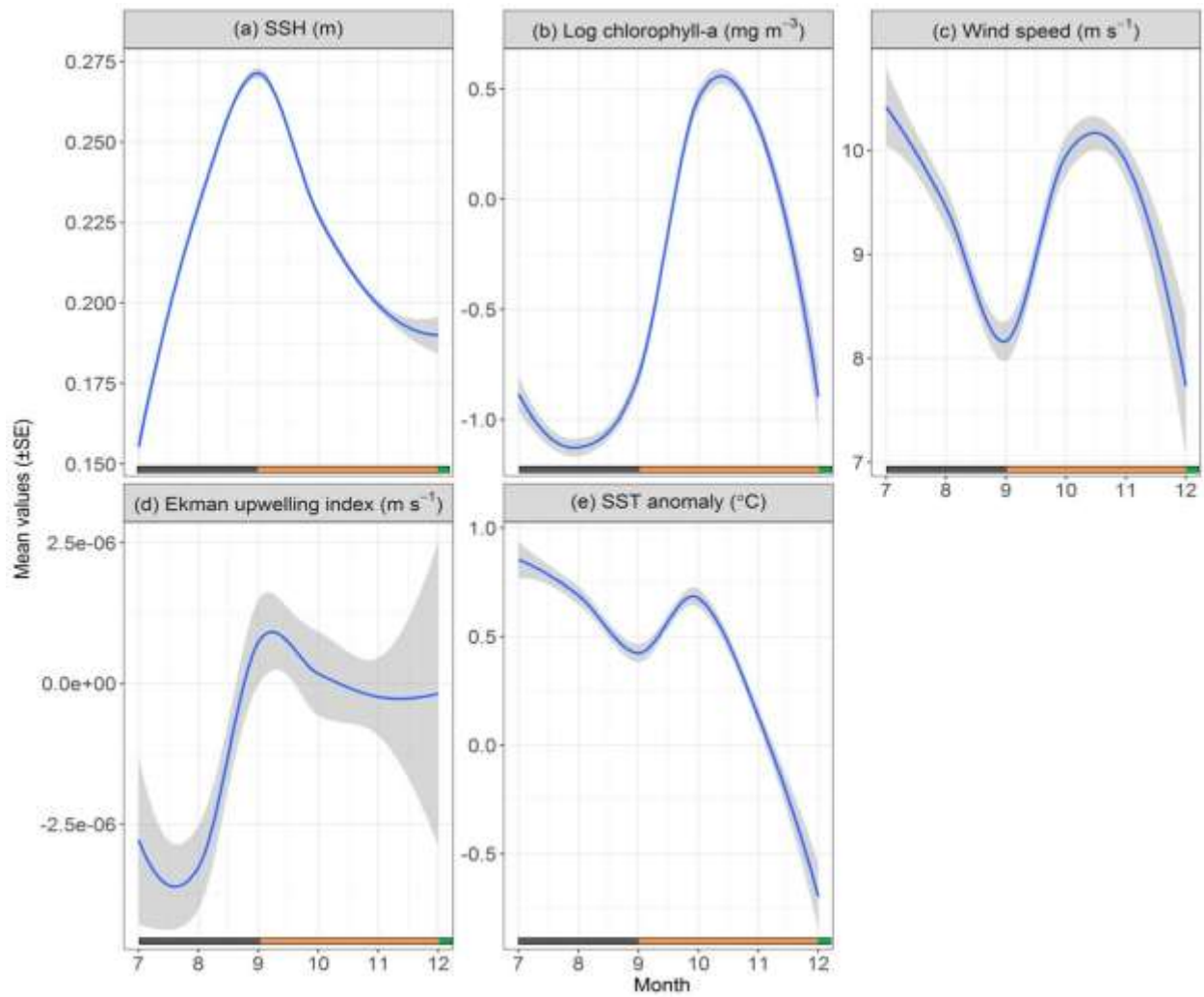
Figure 4. Non-circular smoothed monthly means of different environmental variables around AAR1 location. The grey shaded areas indicate the standard error (SE) of the smoothed mean (line). Horizontal seasonal bar shading: green represents summer, black represents winter, and orange represents spring.
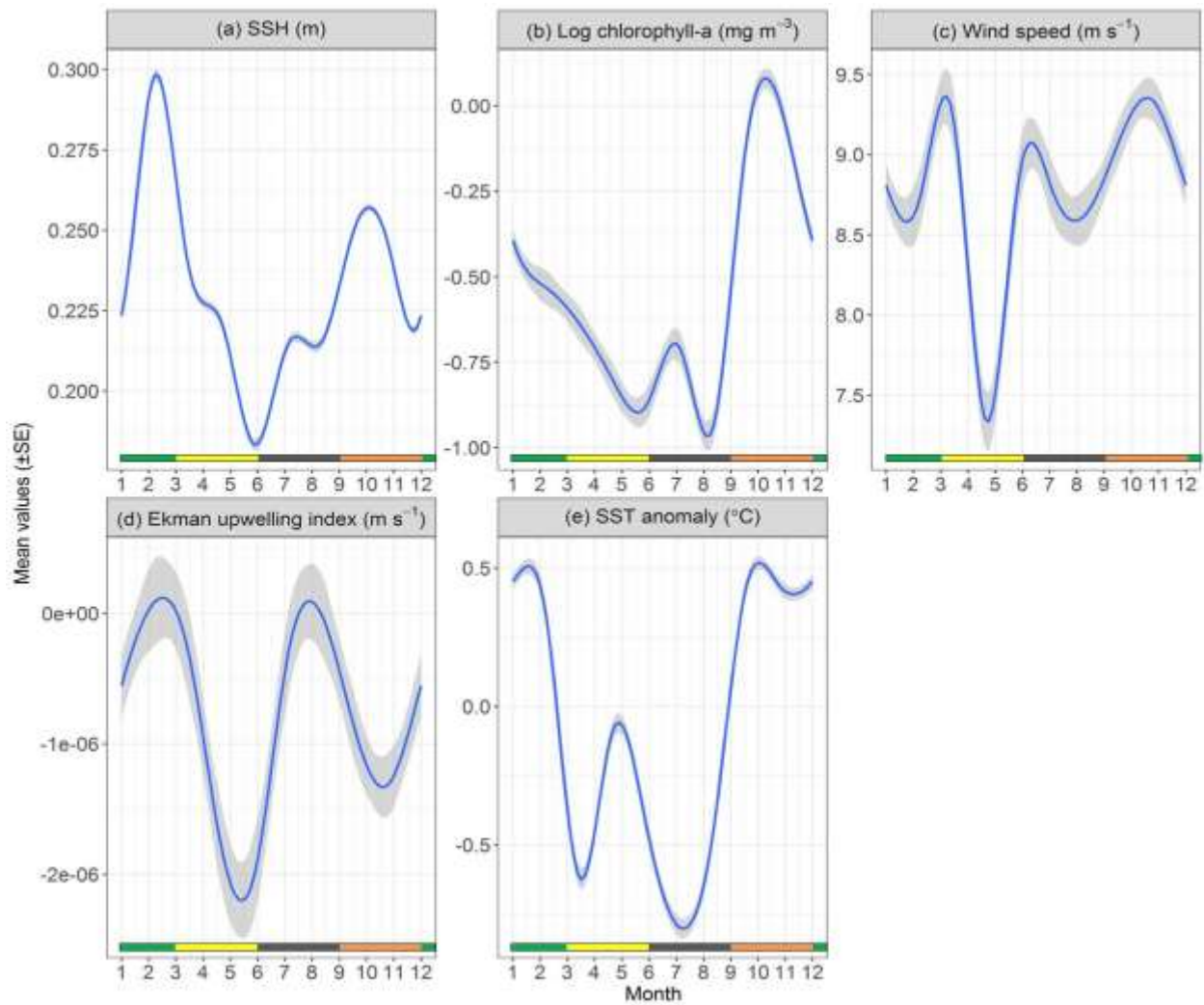
Figure 5. Circular smoothed monthly means of different environmental variables around AAR2 location. The grey shaded areas indicate the standard error (SE) of the smoothed mean (line). Horizontal seasonal bar shading: green represents summer, yellow represents autumn, black represents winter, and orange represents spring.
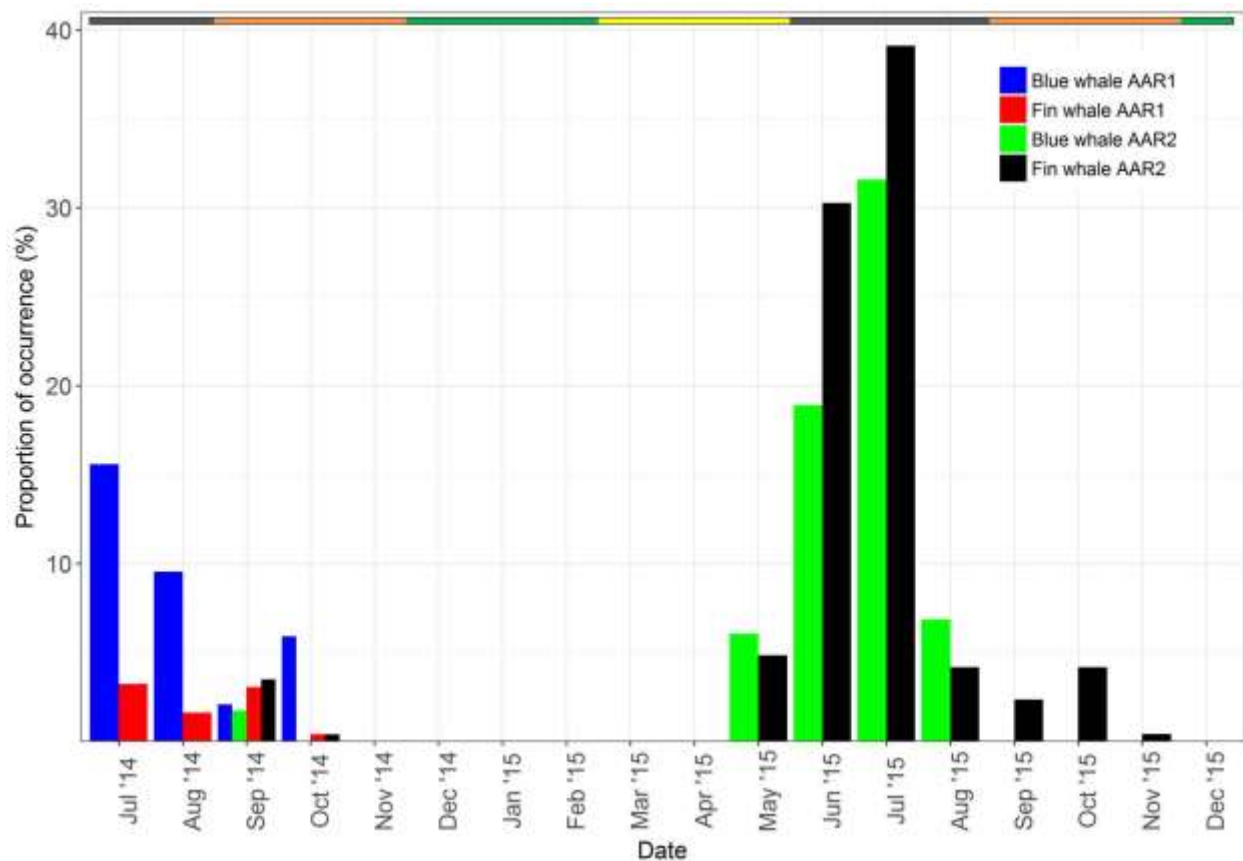
Figure 6. Monthly proportion of call occurrence of Antarctic blue and fin whales off the west coast of South Africa according to AAR system. Only seven days were sampled in July 2014 and one day was sampled in December 2015. Horizontal seasonal bar shading: green represents summer, yellow represents autumn, black represents winter, and orange represents spring. Legend shows arrangement of call types in the plot.

Seasonal call occurrences and acoustic behaviour

Months of the year (July, August and October), low wind speeds (0 to 4 m s^{-1}), low Ekman upwelling index (-5 to -0.5 x 10^{-5} m s^{-1}), but high SSH (0.17-0.19 m) had the highest effect on Antarctic blue whale call occurrence from AAR1 (Figure 7a-d). Months of the year (June and July) had the highest effect on Antarctic blue whale call occurrence from AAR2 (Figure 7e). Low log transformed chl-a (-2 to 1.3 mg m^{-3}), low wind speeds (<8 m s^{-1}), low SST anomaly (-2 to -0.5 °C) but high Ekman upwelling index (1.2 to 5 x 10^{-5} m s^{-1}) and high SSH (0.15 to 0.25 m) had the highest effect on Antarctic blue whale call occurrence from AAR2 (Figure 7f-j). The RF model

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identified months of the year and SSH as the most important predictors of Antarctic blue whale call occurrence from AAR1 (Figure 7k). Wind speed was a moderately important predictor, whilst Ekman upwelling index was the least important predictor of overall Antarctic blue whale call occurrence from AAR1 (Figure 7k). Months of the year was the most important predictor of Antarctic blue whale call occurrence from AAR2 (Figure 7l). Wind speed, SST anomaly, SSH and Ekman upwelling index were moderately, whereas log transformed chl-a was the least important predictors of Antarctic blue whale occurrence from AAR2 (Figure 7l).

High SSH (0.15-0.18 m), months of the year (July and October), low log transformed chl-a (-1.6 to -0.5 mg m^{-3}), low wind speed (below 4 m s^{-1}), high and low Ekman upwelling index (-4 to 3 x 10^{-5} m s^{-1}), positive SST anomaly (1.3-4°C) and daytime were highly influential on Z-call rates from AAR1 (Figure 8a-g). Low log transformed chl-a (-2 to -0.3 mg m^{-3}), low wind speed (below 8 m s^{-1}), negative SST anomaly (-2 to -0.3 °C), high Ekman upwelling index (1 to 5 x 10^{-5} m s^{-1}), months of the year (June and July) and high SSH (0.15-0.24 m) were highly influential on Z-call rates from AAR2 (Figure 8h-m). SSH and months of the year were the most important predictors of Z-call rates from AAR1; log transformed chl-a and wind speed were the most important predictors of Z-call rates from AAR2 (Figure 8n and o). Log transformed chl-a and wind speed were moderately important predictors, whilst Ekman upwelling index, SST anomaly and time of the day were the least important predictors of the Z-calls rates from AAR1 (Figure 8n). SST anomaly, Ekman upwelling index and months of the year were moderately important predictors of Z-call rates, whereas SSH was the least important predictor of Z-call rates from AAR2 (Figure 8o). Positive SST anomaly (0.9-2°C), high SSH (above 0.20 m), month of the year (June) and nighttime positively influenced D-call rates from AAR2 (Figure 9a-d). SST anomaly was the most

important predictor of D-call rates; SSH and months of the year were moderately important; time of the day was the least important predictor of D-call rates from AAR2 (Figure 9e).

High Ekman upwelling index (around 1 x 10^{-5} m s^{-1}) and positive SST anomaly (above 1°C) were highly influential on fin whale call occurrence from AAR1 (Figure 10a and b). Months of the year (July to September), low log transformed chl-a (below 0.6 mg m^{-3}), low wind speed (below 12 m s^{-1}), and varying SSH values had the highest effects on fin whale call occurrence from AAR1 (Figure 10c-f). Months of the year (June and July), varying wind speeds, varying Ekman upwelling index, varying log transformed chl-a, negative SST anomaly (below -0.9 °C) and varying SSH were highly influential on fin whale call occurrence from AAR2 (Figure 10g-l). Ekman upwelling index was the most important predictor of fin whale call occurrence, whereas SST anomaly and months of the year were moderately important predictors of fin whale call occurrence from AAR1 (Figure 10m). Log transformed chl-a, wind speed and SSH were the least important predictors of fin whale call occurrence from AAR1 (Figure 10m). Months of the year was the most important predictor of fin whale call occurrence, whereas wind speed and Ekman upwelling index were moderately important predictors of fin whale call occurrence from AAR2 (Figure 10n). Log transformed chl-a, SST anomaly and SSH were the least important predictors of fin whale call occurrence from AAR2 (Figure 10n).

Low wind speed (below 1 m s^{-1}), low SSH (around 0.28 m), and low log transformed chl-a (below -1.5 mg m^{-3}) but high Ekman upwelling index (above 0.5 x 10^{-5} m s^{-1}), positive SST anomaly (above 0.9°C), and time of the day (nighttime, dawn and dusk) were influential on fin whale call rate from AAR1 (Figure 11a-f). Months of the year (June and July), low SSH (0.23-0.32 m) but high wind speeds, positive SST anomaly, high Ekman upwelling index and high log transformed

chl-a were highly influential on fin whale call rate from AAR2 (Figure 11g-l). Wind speed was the most important predictor; SSH and time of the day were moderately important predictors; and Ekman upwelling index, log transformed chl-a and SST anomaly were the least important predictors of fin whale call occurrences from AAR1 (Figure 11m). Months of the year was the most important predictor of fin whale call rates; SSH, wind speed, SST anomaly and Ekman upwelling index were moderately important predictors of fin whale call rates; whereas log transformed chl-a was the least important predictor of fin whale call rates from AAR2 (Figure 11n).
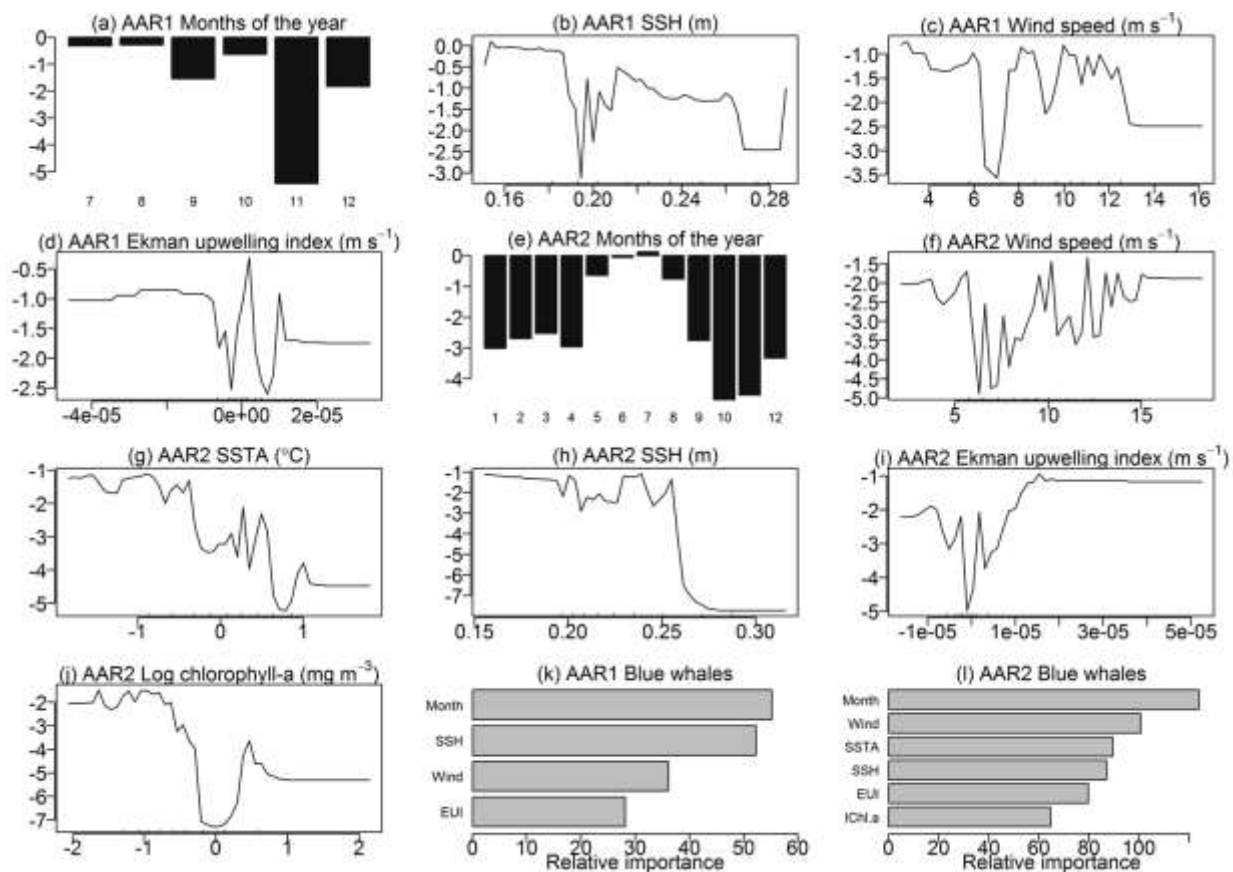

Figure 7. Marginal effects (a-j) and ranked relative importance (k and l) of different variables on Antarctic blue whale call occurrences from AAR1 (a-d, k) and AAR2 (e-j, l). Y-axis (a-j) is the partial effect of each predictor on occurrence (in logit-scale). Barplots are for factor variable (i.e. non-continuous variable). lChl.a is log transformed chl-a, EUI is Ekman upwelling index, SSTA is SST anomaly and Wind is wind speed.
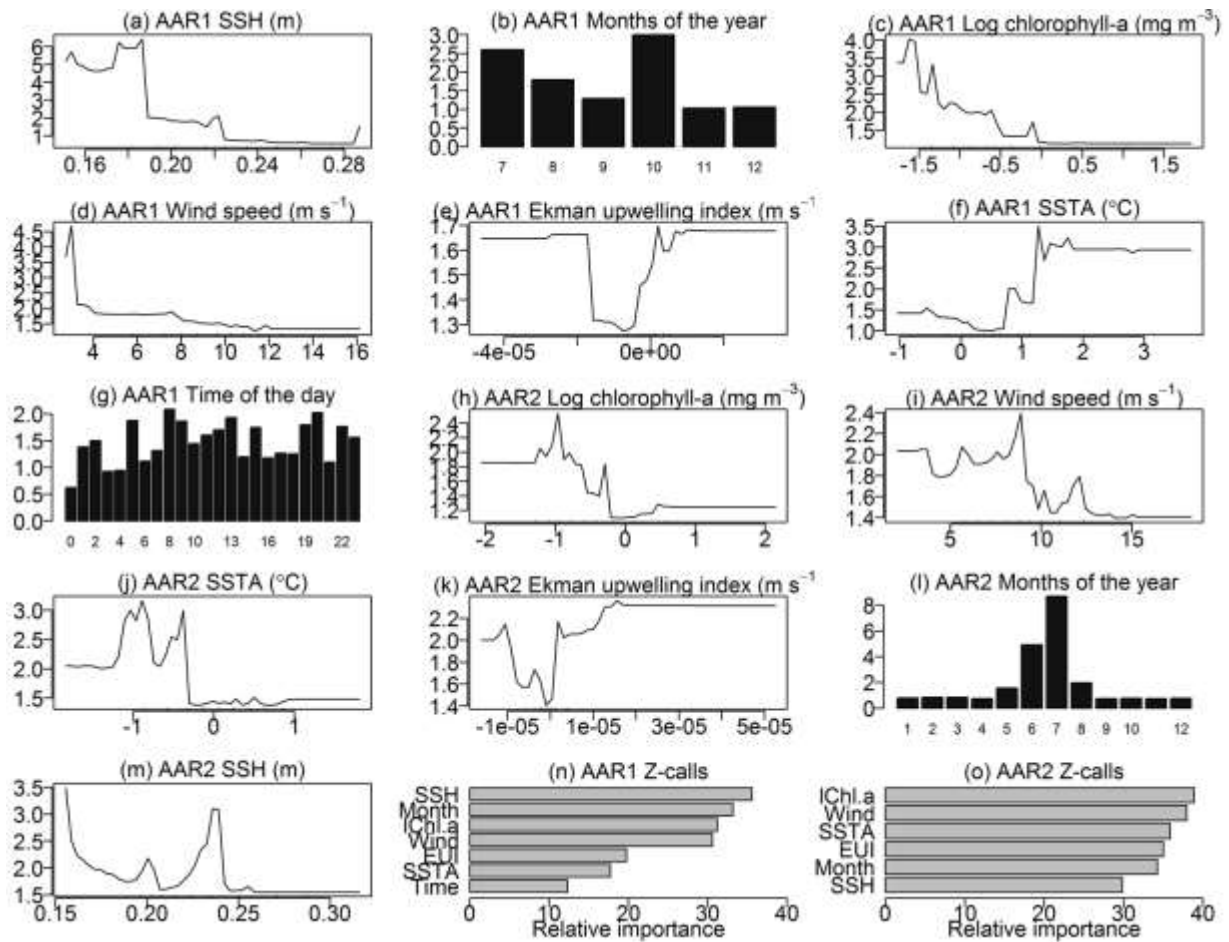
Figure 8. Marginal effects (a-m) and ranked relative importance (n and o) of different variables on Antarctic blue whale Z-call rates from AAR1 (a-g, n) and AAR2 (h-m, o). Y-axis (a-m) is the partial effect of each predictor on acoustic behaviour. Barplots are for factor variable (i.e. non-continuous variable). lChl.a is log transformed chl-a, EUI is Ekman upwelling index, SSTA is SST anomaly and Wind is wind speed.
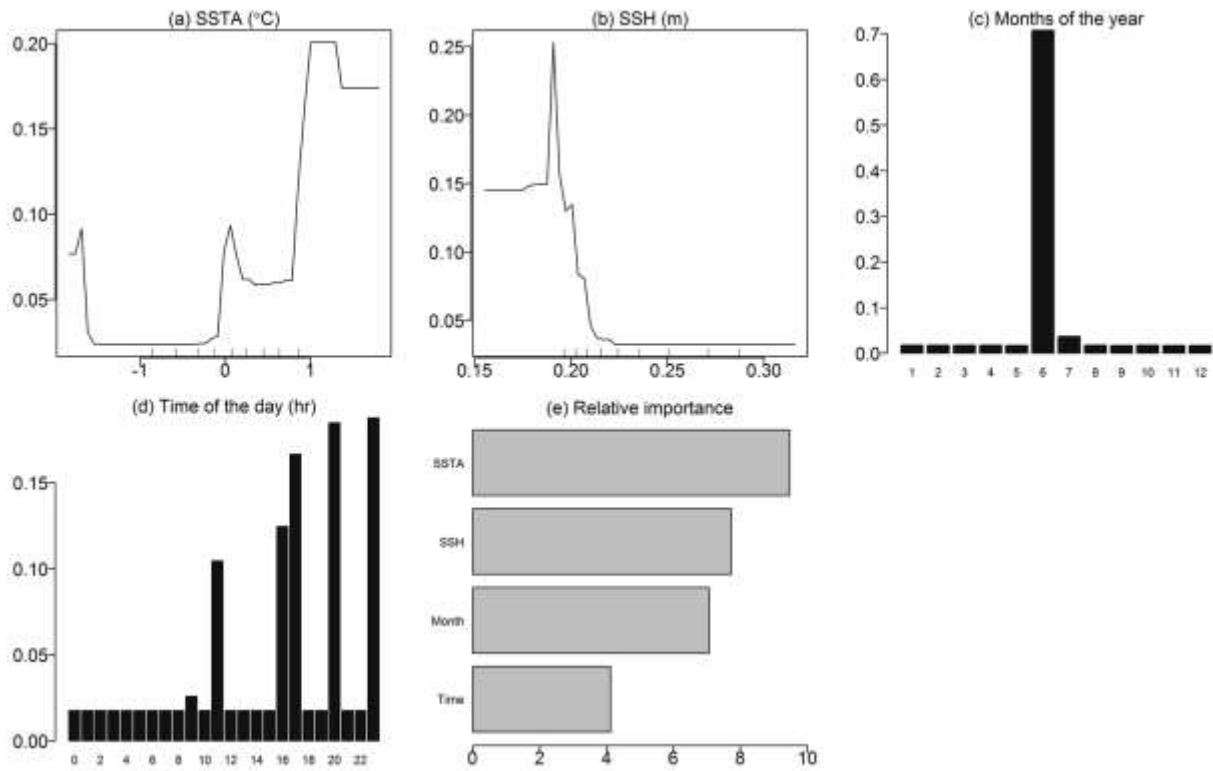
Figure 9. Marginal effects (a-d) and ranked relative importance (e) of different variables on Antarctic blue whale D-call rates from AAR2. Y-axis (a-d) is the partial effect of each predictor on acoustic behaviour. Barplots are for factor variable (i.e. non-continuous variable). lChl.a is log transformed chl-a, EUI is Ekman upwelling index, SSTA is SST anomaly and Wind is wind speed.

Figure 10. Marginal effects (a-l) and ranked relative importance (m and n) of different variables on Antarctic fin whale call occurrences from AAR1 (a-f, m) and AAR2 (g-j, n). Y-axis (a-l) is the partial effect of each predictor on occurrence (in logit-scale). Barplots are for factor variable (i.e. non-continuous variable). lChl.a is log transformed chl-a, EUI is Ekman upwelling index, SSTA is SST anomaly and Wind is wind speed.
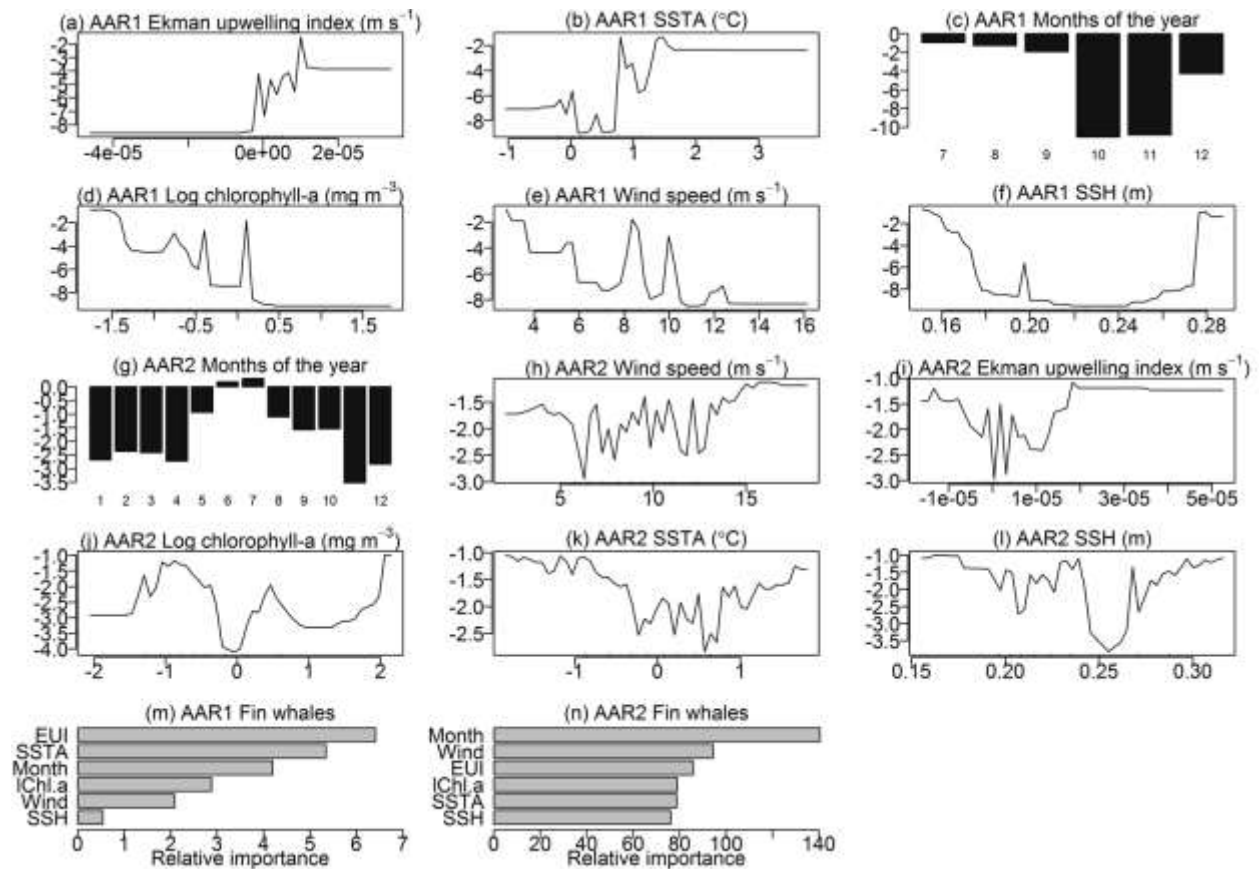
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Figure 11. Marginal effects (a-l) and ranked relative importance (m and n) of different variables on fin whale call rates from AAR1 (a-f, m) and AAR2 (g-l, n). Y-axis (a-l) is the partial effect of each predictor on acoustic behaviour. Barplots is for factor variable (i.e. non-continuous variable). lChl.a is log transformed chl-a, EUI is Ekman upwelling index, SSTA is SST anomaly and Wind is wind speed.
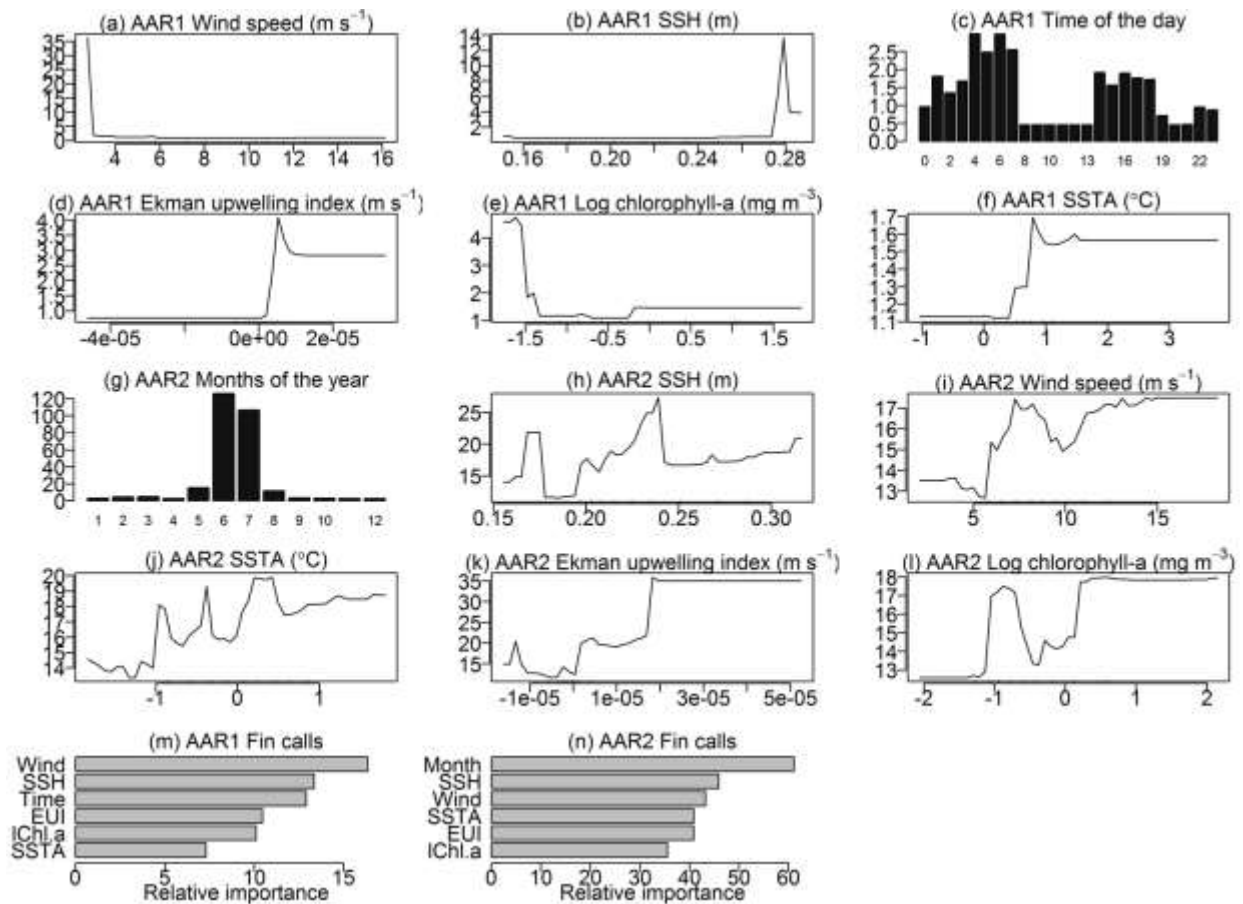
Discussion

Detection ranges of our AARs for Antarctic blue and fin whale calls off the west coast of South Africa are significantly lower than those estimated in other regions such as the southwestern Indian Ocean where Samaran et al. (2010a) estimated a maximum of 200 km; North Pacific where Stafford et al. (1998) estimated 400-600 km. Other regions include Western Antarctic Peninsula where Širović et al. (2007) estimated a maximum of 1300 km and Weddell Sea where Thomisch et al. (2016) estimated a maximum of 700 km. Such differences in call detection ranges could be due to varying transmission loss, oceanographic conditions, noise levels, recorder types, recorder

depth, sound propagation model used and bathymetric properties of different regions (Stafford et al., 1998; Širović et al., 2007; Samaran et al., 2010a; Thomisch et al., 2016). For instance, AAR1 deployed at shallower depth than AAR2 had high noise levels, which resulted in lower detection ranges from AAR1 than AAR2. Such variation in noise levels could also illustrate that animals found at these closely spaced locations might be affected differently by background noise. Sources of these noises around AARs are unknown to authors but we suspect they originate from ship propellers and possibly mooring movement.

Environmental and oceanographic conditions are excellent depicters of productivity and climate variability and/or change because they are influenced by changes in climate on both seasonal and inter-annual scales (Moore et al., 2008; Goubanova et al., 2013; Sydeman and Thompson, 2013). For example, wind speeds, log transformed chl-a, and Ekman upwelling index were observed to be high in summer of this study, which indicate the upwelling regime on the wide shelf in the southern Benguela (Jury and Bundrit, 1992; Veitch et al., 2010; Goubanova et al., 2013). Likewise, Brown (1992) noted high log transformed chl-a concentrations in summer and low concentrations of log transformed chl-a in winter in the southern Benguela ecosystem. Marine animals living in the Benguela ecosystem adapt to such environmental changes by varying their distribution and behaviour (Ekau et al., 2001). The remotely sensed environmental conditions (SST anomaly, SSH, wind speed, log transformed chl-a, and Ekman upwelling index) derived for our study showed seasonal trends that coincided with the seasonal acoustic occurrence of whales. For instance, winter had the lowest values of Ekman upwelling index and log transformed chl-a but the highest occurrences of both whale species from both AARs. A similar relationship was observed during summer in Antarctic between Antarctic blue whale acoustic occurrences and environmental conditions (Shabangu et al., 2017). Relationships between call occurrences and call rates with

environmental conditions are sometimes spiky due to varying levels of interactions between predictor environmental variables within the RF models.

The observed SST anomaly cooling from 0.6°C in summer to -0.7°C in winter (i.e., 21-15°C decrease in sea surface temperature) around AAR2 could be due to weaker solar radiation (caused by cloud cover) and mean wind stress in winter (Goubanova et al., 2013) and the intrusions of cold sub-Antarctic surface waters (Lutjeharms and Meeuwis, 1987). Environmental conditions such as SSH, wind speed, SST anomaly, Ekman upwelling index and chl-a were the most important predictors of blue and fin whale acoustic occurrence and call rates (i.e., behaviour), suggesting that environmental conditions drive other ecological processes that are beneficial to these whales. For example, fin whale prey such as sardine and anchovy are known to prefer cold SST (17-20°C) in the Benguela ecosystem (Checkley et al., 2009; Mhlongo et al., 2015). SST was the strongest predictor of fin whale acoustic occurrence in the North Pacific (Stafford et al., 2009) and data from Antarctic whaling grounds suggested that fin whales were most abundant in frontal zones with relatively colder water (Nasu, 1966). North-directed winds along the southern Benguela coast reinforce the Ekman transport offshore and upwelling of nutrient-rich, cold water to the euphotic zones (Lutjeharms and Stockton, 1991; Jury and Bundrit, 1992). Future changes in these environmental conditions might be influential to the occurrence and behaviour of these whales in the Benguela ecosystem.

Months of the year, SSH, log transformed chl-a and wind speed were the most important predictors of Antarctic blue whale call occurrence and Z-call rates because they describe seasonal upwelling events; it is well known that Antarctic blue whales are often reliant on upwelling regimes (Branch et al., 2007; Stafford et al., 2009; Shabangu et al., 2017). Ekman upwelling index was ranked by

the RF model as the most, moderately and least important predictor of both whale call occurrence and call rates, likely indicating that nutrient recycling was well captured by variations in this variable than phytoplankton pigment concentration from the transformed chl-a measurements. The lack of temporal segregation between the peaks of diel call rates of blue and fin whales in spring is indicative that blue and fin whales are not only sympatrically but vocalise at similar times during this season. The observed temporal segregation between peaks of diel call rates of blue and fin whales in autumn and winter could be to avoid vocal competition between these two species during those seasons when the two species are most abundant in the Benguela ecosystem.

Blue and fin whales were previously thought to feed mainly in the Antarctic and fast in the lower latitudes during overwintering (Mackintosh and Wheeler, 1929; Best, 2007). Our detections of Antarctic blue whale feeding associated D-call in the Benguela ecosystem might indicate that these animals could be foraging on their overwintering ground. While this has been hypothesized in the Indian Ocean (Samaran et al., 2013), to the best of our knowledge, this is the first acoustic indication that Antarctic blue whales might be feeding in the Benguela ecosystem. SST anomaly was the most important predictor of the Antarctic blue whale feeding associated D-call rates, indicating that biological processes controlled by seasonal environmental changes might have influenced whale feeding. There is little evidence of Antarctic blue whale prey in the Benguela ecosystem, although Best (1967) found megalopa larvae in stomachs of few Antarctic blue whales caught in the southern African region during the whaling era. We therefore hypothesize that Antarctic blue whales might have been feeding on the local species of krill that form large enough swarms to be suitable prey. *Nematoscelis megalops* is the most abundant local krill species found in the outer-shelf waters of the Cape Peninsula while other krill species that also occur in the outer-shelf area do so in low numbers; these include *Euphausia recurva* and *Thysanoessa gregaria*

(Pillar et al., 1992). Werner and Buchholz (2013) found low biomass but bigger sizes of *N. megalops* in winter on the Northern Benguela that corresponded well with changes in environmental conditions.

Barange et al. (1991) showed that *N. megalops* performs nocturnal vertical migrations from the deep sea to just below the thermocline positioned at around 20 to 40 m; the timing of this migration to near the surface corresponds well with the slight increase in the call rates of the Antarctic blue whale D-calls that we observed from dusk to midnight. The low numbers of D-calls (i.e. 176 calls) demonstrate that compared to Z-calls (with 6,114 calls detected), this call type was rarely detected in the Benguela ecosystem since it is not a feeding ground. The Z-call rates were higher during the day than at night in winter for both AARs, which is similar acoustic behaviour to that observed in summer in the Southern Ocean (Shabangu et al., 2017). This inverse relationship between detection of D-calls and Z-calls in Antarctic blue whales might be an energy saving behaviour whereby animals socialize when their prey are at depth but forage when the prey are easily accessible close to the sea surface (Stafford et al., 2005).

Similarly, Leroy et al. (2016) observed Antarctic blue whales in the Indian Ocean to be more vocally active during the day. Although diurnal pattern in Antarctic blue and fin whale call rates were found during certain seasons, the RF model ranked the time of the day as moderately to least important predictor of rates of Z-call and fin whale calls from AAR1. For AAR2, time of the day was eliminated from the RF models of Z-call rates and fin whale call rates due non-essentialness but predicted as least important predictor of D-call rates. Such ranking corresponds well with the smoothed diel call rate patterns that was flat in some instances and also indicates that time of the day cannot be reliably used to determine when whales will vocalise. This ranking is further

explained by the observed non-importance of time of the day on whale call occurrence for both AARs.

In contrast to the Indian Ocean, where Antarctic blue whales were detected acoustically year-round (Samaran et al., 2010b, 2013; Leroy et al., 2016), in the Benguela ecosystem (i.e., southeast Atlantic Ocean) we detected Antarctic blue and fin whales only seasonally, most likely due to food limitations that influenced the migratory behaviour of these species in this region. Local krill species are not as abundant as *E. superba* is in the Antarctic and could not sustain a commercial fishery (Shabangu et al., 2016). Samaran et al. (2013) postulated that Antarctic blue whales could forage and move regionally and seasonally to utilize food resources available within the Indian Ocean. It is currently unknown whether fin whales were also feeding in the Benguela ecosystem as there has not been a feeding associated call yet documented for this species, but we suspect that they may have similar behaviour patterns to blue whales.

Seasonal changes in the call occurrences of Antarctic blue and fin whales might indicate a difference in the number of vocally active animals within recording radii of our AARs, an asynchronous whale migration, or they might be due to seasonal changes in calling rates. Peaks observed in Antarctic blue whale call occurrences and rates by this study are as expected the inverse of the seasonal peak observed by Širović et al. (2009) in the Southern Ocean. Širović et al. (2009) observed a peak in call numbers from late summer through autumn but low numbers in winter; with call numbers increasing again towards the end of spring. We observed an increase in Antarctic blue whale calls towards the end of autumn through winter and peaks in winter. Širović et al. (2009) also detected few fin whale calls by the late summer through autumn with the peak in autumn and no calls for the remainder of the year; however, we detected fin whale calls from late

autumn until end of spring. Antarctic blue whale calls also peaked between the austral autumn and winter (May–September) in the Indian Ocean (Stafford et al., 2004; Samaran et al., 2010b, 2013; Leroy et al., 2016).

These complementary patterns between high and low latitudes supports the idea that both species migrate between these regions annually and that the Benguela ecosystem forms an important migratory route, overwintering, mating and calving ground for them (True, 1904; Best, 2007). The west coast of South Africa is likely used as a migration corridor to locations further north by Antarctic blue and fin whales because we did record dual peaks in the acoustic presence of these species from AAR1, where one peak might indicate a northward migration and a second peak might indicate a return southward migration to the Antarctica. Our results confirm the observation by Best (1998, 2007), based on whale catches in the northern and southern Benguela ecosystem, that Antarctic blue and fin whales use the Benguela ecosystem as an overwintering ground since they are most abundant in winter between May and August and fin whales between May and November.

Antarctic blue whale calls detected here could be from any of the three recently genetically differentiated Antarctic blue whale populations that feed sympatrically in Antarctica but do not breed in the same Southern Hemisphere grounds (Attard et al., 2016). Acoustic presence of only eastern Antarctic fin whale acoustic population (Širović et al., 2009) in the southern Benguela ecosystem suggests that eastern and western Antarctic fin whale acoustic populations do not migrate sympatrically, and that western Antarctic fin whale acoustic population does not use the Benguela ecosystem for overwintering, probably due to the long distance from their feeding grounds.

Passive acoustic data collection did not interfere with any oceanographic instruments on the moorings nor did such instruments interfere with the acoustic recordings, illustrating the value and efficacy of oceanographic moorings as acoustic platforms (Shabangu and Findlay, 2014). Acoustic monitoring of these large Antarctic baleen whales off the west coast of South Africa can be considered the most economical and reliable method of monitoring these offshore marine mammals. We recommend continuous recording of acoustic data in an array series of moorings to track individual whales, estimate seasonal whale densities and identify whale migration corridors. Such recordings would also help to evaluate the effects of anthropogenic noise on the health of marine mammals in the Benguela ecosystem.

The results of this work have improved our understanding of the Benguela ecosystem by quantitatively describing the relationship between Antarctic blue and fin whale occurrence and behaviour in relation to environmental conditions off the west coast of South Africa. Antarctic blue whales were believed to have largely been extirpated from the system due to whaling but our study indicate this species is present again in the system for at least six months of the year. Sounds of humpback *Megaptera novaeangliae* and other whales were also observed from our acoustic recordings, expanding the efficacy of these systems for offshore large whale acoustic monitoring. Recent (i.e. July 2017) offshore sighting research efforts conducted along the SAMBA line during the SEAmester cruise, South Africa's Class Afloat programme (Ansorge et al., 2016), resulted in the sighting of fin, sperm *Physeter macrocephalus*, sei *B. borealis*, minke *B. bonaerensis*, and humpback whales but not Antarctic blue whales.

Conclusion

This study provides the first acoustic records of sympatric occurrence of Antarctic blue and fin whales off the west coast of South Africa and the first acoustic evidence of Antarctic blue whales possibly feeding in the Benguela ecosystem. The detection of the feeding associated D-calls of Antarctic blue whales might suggest that these whales do not necessarily fast while overwintering but may feed opportunistically on available prey, contrary to earlier assumptions (e.g. Mackintosh and Wheeler, 1929). Based on call occurrences, our study confirms the west coast of South Africa as an overwintering ground and migration route of Antarctic blue and fin whales. Both the call occurrences and diel acoustic behaviour of these whales in the southern Benguela ecosystem varied with seasons, and the peak in occurrence and call rates for both species was in winter (mainly July). This suggests a link with seasonal variation in environmental conditions. Using oceanographic moorings to collect passive acoustic data at the low latitude locations, a cost-effective method of monitoring whales was demonstrated. We recommend further research effort in the Benguela ecosystem to investigate abundance, and distribution of populations of these large Antarctic baleen whales over extended periods of time. The information produced here is vital for the management and conservation of these world's largest animals through the identification of essential overwintering grounds and migration routes.

Acknowledgements

for his help with access to the AVISO SSH data. We are sincerely indebted to Prof Isabelle Ansorge and other SAMOC oceanographers for permitting our AARs to "hitchhike" on their oceanographic moorings. We thank everyone who helped in the deployment and recovery of the AARs including captains and crew of RV *Algoa*. Catherine Boucher is thanked for graphic assistance. We are grateful to Dr Sheldon Dudley for his invaluable comments and suggestions on the earlier draft of this manuscript.

Competing interests

The authors have no competing interests.

Author contributions

FWS KPF DY KMS MVDB BB RKA participated in the design of the study and drafted the manuscript; FWS DY carried out the statistical analyses; RKA KMS conducted sound propagation modelling; MVDB BB collected field data; FWS KPF DY KMS RKA wrote the manuscript. All authors gave final approval for publication.

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