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Diverse baleen whale acoustic occurrence around two sub-Antarctic islands: A tale of residents and visitors

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Knowledge on the occurrence and behaviour of baleen whales around sub-Antarctic regions is limited, and usually based on short, seasonal sighting research from shore or research vessels and whaling records, neither of which provide accurate and comprehensive year-round perspectives of these animals' ecology. We investigated the seasonal acoustic occurrence and diel vocalizing pattern of baleen whales around the sub-Antarctic Prince Edward Islands (PEIs) using passive acoustic monitoring data from mid-2021 to mid-2023, detecting six distinct baleen whale songs from Antarctic blue whales, Madagascan pygmy blue whales, fin whales, Antarctic minke whales, humpback whales, and sei whales. Antarctic blue and fin whales were detected year-round whereas the other species' songs were detected seasonally, including a new Antarctic minke whale bio-duck song sub-type described here for the first time. Antarctic minke and sei whales were more vocally active at night-time whereas the other species had no clear diel vocalizing patterns. Random forest models identified month and/or sea surface temperature as the most important predictors of all baleen whale acoustic occurrence. These novel results highlight the PEIs as a useful habitat for baleen whales given the number of species that inhabit or transit through this region.

Keywords Overwintering ground, Stopover spot, Feeding ground, Year-round habitat, Passive acoustic monitoring, Southern Ocean

Baleen whales are distributed widely over a range of oceans spanning from the ice-covered polar zones to the warm tropical regions. These whales play a critical role in the functioning of the Southern Ocean and other marine ecosystems through nutrient recycling and/or transport and can serve as ecosystem health indicators[1,2]. However, their movements between these different regions are understood poorly due to a lack of dedicated research, especially in remote areas. Thus, distributions and seasonal occurrence patterns of baleen whales are usually based on historic whaling records, together with a diverse assortment of data from sightings, strandings, Discovery marks, satellite tagging, species distribution modelling, and passive acoustic monitoring[3–6]. The sub-Antarctic Prince Edward Islands (PEIs; Fig. 1) are remote and isolated, making it logistically challenging to conduct cetacean research in their vicinity. Nonetheless, there has been land-based research studying baleen whales that frequent the PEIs coastal waters, such as southern right whales (*Eubalaena australis)*[7]. Short-term at-sea visual sightings during the annual Marion Island resupply voyages of the South African Department of

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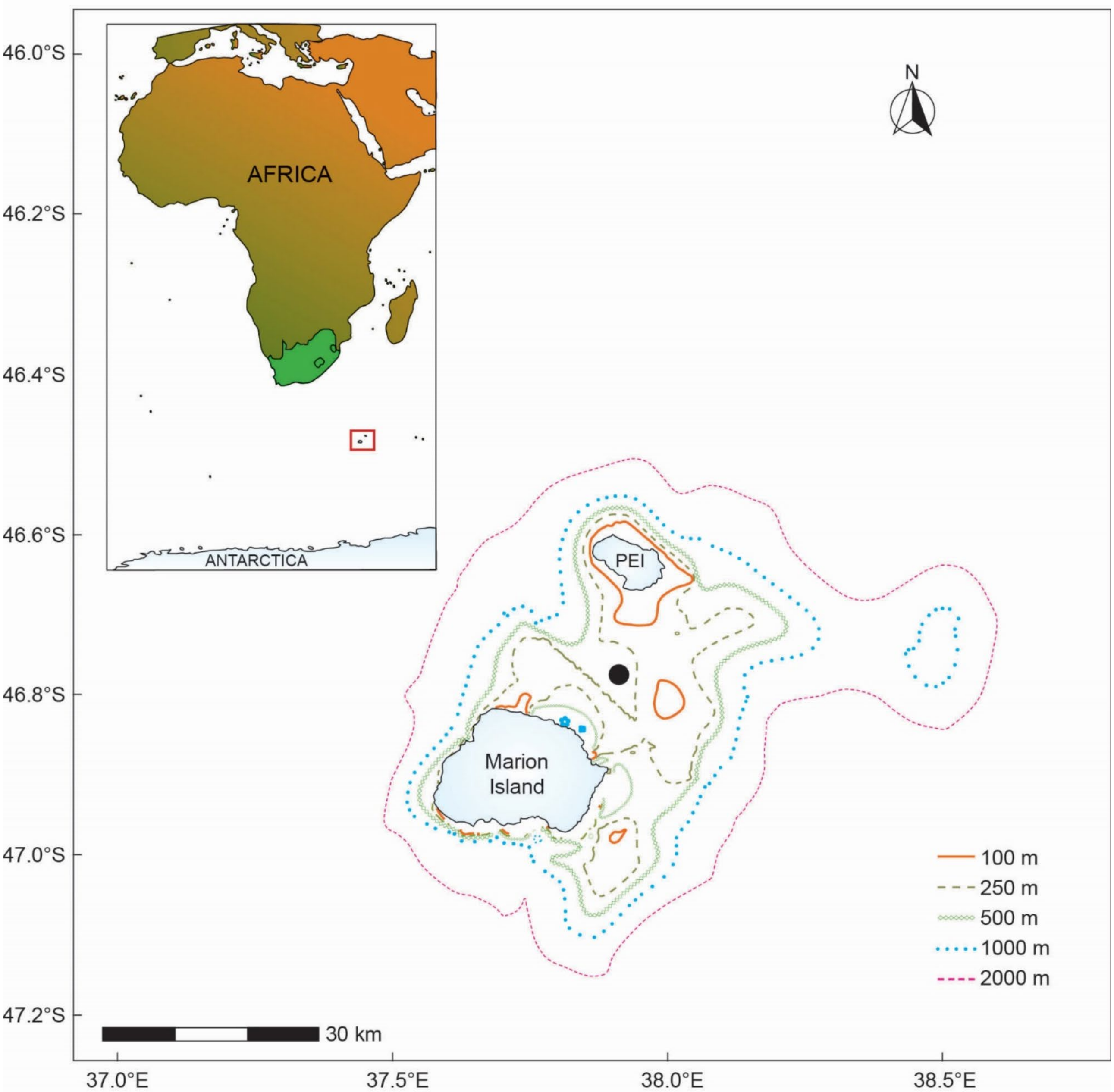

Fig. 1. Location of Marion Island and Prince Edward Island, which comprise the Prince Edward Islands (PEIs), together with location of the oceanographic mooring containing the acoustic recorder (black circle) deployed between the two islands. Bathymetry around the islands is indicated by colour coded lines. Insert map shows the position of the PEIs (small red box) relative to South Africa's mainland (green shading in the African map) and Antarctica. Bathymetry data were obtained from 2023 GEBCO Compilation Group (https://doi.org/10.5285/f98b053b-0cbc-6c23-e053-6c86abc0af7b).

Forestry, Fisheries and the Environment and other dedicated voyages have led to the sighting of blue whales (*Balaenoptera musculus*) near the PEIs[5,8]. The occurrence and behaviour of baleen whales that tend to be found in offshore waters are not properly documented from shore-based observations, but passive acoustic monitoring (PAM) is well suited for detecting their sounds over larger areas underwater[9–11].

Baleen whales produce calls that are specific to a particular geographic region, sex, and population, subspecies, or species[12–17]. These calls can be produced by single or multiple animals in a rhythmic, repetitive, and sometimes predictable or complex hierarchal manner, called a "song"[12,14,15,18]. Antarctic blue whales (ABWs) (*B. m. intermedia*) produce three-unit Z-calls (frequency range: 18–26 Hz, duration: 18–26 s) used for communication[14,19]. In contrast, the songs of Madagascan pygmy blue whales (MPBWs, across the south-western Indian Ocean) (*B. m. brevicauda*) consist of two repeated units: where unit 1 lasts 15–20 s at ~ 13–34 Hz, and unit 2 begins with a 1–2 s long downsweep from 25 to 21 Hz that is followed by a long (15–24 s) slightly modulated tone[14,17]. Males and females of all blue whale populations produce D-calls (frequency range: 22–106 Hz; duration: ~2–6 s) during foraging[19,20] and social interactions[21].

Fin whales (*B. physalus*) produce 20 Hz pulses (frequency range: 15–28 Hz, duration: <1 s) with simultaneous high frequency pulses (peaking at 99 Hz for the Eastern Antarctica Peninsula acoustic population and at 89 Hz for the Western Antarctica Peninsula acoustic population) specific to males that use them for social contact and mating[16,22]. Acoustic population is a "group of detections with rather homogeneous acoustic characteristics"[23], and both Eastern and Western Antarctica fin whale acoustic populations have been concurrently found in some areas such as Cape Leuwin, Australia[24]. In addition, they produce 40 Hz pulses (frequency range: 30–75 Hz; duration: 0.3–1 s) likely produced by both sexes during feeding[25,26]. Male humpback whales (*Megaptera novaeangliae*) sing rhythmic songs primarily in winter months[12,18] and make non-song calls randomly and year-round. The latter are produced by both sexes including calves[27,28]. Antarctic minke whales (AMWs) (*B. bonaerensis*) produce rhythmic bio-duck songs that vary geographically[29–33]. Sei whales (*B. borealis*) are known to produce downsweeps, upsweeps, upsweep-downsweep calls, arch, low and mid-frequency calls[34–36]. PAM research collects data on these vocalizations which characterize the distribution, occurrence, behaviour, and ecology of whales[6,9,10,28,32,37,38].

The objectives of this study were three-fold: (1) establish the seasonal acoustic occurrence and acoustic repertoire of baleen whales around the PEIs; (2) determine whether the acoustic behaviour of baleen whales varies by time of day; and (3) determine which environmental variables influence the seasonal acoustic occurrence of baleen whales around the sub-Antarctic PEIs.

Materials and methods

Study area

The sub-Antarctic PEIs archipelago is in the southern Indian Ocean part of the Southern Ocean and is comprised of Marion Island (296 km^2; 46.5°S, 37.5°E) and 19 km to the north-east the smaller Prince Edward Island (45 km^2; 46.2°S, 37.6°E) (Fig. 1). The PEIs form part of South Africa's territory and are located about 1,800 km from the South African mainland and 2,300 km north of Antarctica (Fig. 1). The PEIs are positioned within the Southern Ocean Polar Frontal Zone, between the sub-Antarctic Front and the Antarctic Polar Front, and these fronts play a critical role in driving ecology, ocean circulation, and nutrient cycling within the region[39–41]. Due to high biological productivity around these islands, the PEIs are an important habitat for numerous seabird and marine mammal species including whales that use them as breeding and feeding grounds[42].

Data collection

Acoustic data were collected using a SoundTrap ST500 STD acoustic recorder (Ocean Instruments NZ, New Zealand) deployed on an oceanographic mooring (Supplementary Fig. S1) during South Africa's South Atlantic Meridional Overturning Circulation (SAMOC) program. The oceanographic mooring consisted of an anchor, two acoustic releases, linking chains, and a float which housed an Acoustic Doppler Current Profiler (ADCP) and the acoustic recorder (Supplementary Fig. S1). Linking chains were interweaved with ropes between the chain links to reduce chain clanking noise. The acoustic recorder was deployed for two years (Table 1) between Marion Island and Prince Edward Island (Fig. 1). To avoid interference from the ADCP that sampled each hour on the clock for five minutes, the acoustic recorder was set to sample the first 14 min of the second half of every hour, 24 h a day (Table 1). Upon recovery, the acoustic recorder was cleaned, batteries replaced, Secure Digital (SD) card replaced, data from internal recorder memory downloaded and deleted, reprogrammed, and re-deployed. From 09 to 26 April 2023, the acoustic recorder recorded haphazardly by skipping some hours and archiving acoustic data with poor quality data masked by white noise, resulting in partially usable data for some hours. This unstable performance was caused by battery depletion according to the instrument manufacturer.

Whale acoustic occurrence determination

Acoustic data were decimated from 96 kHz to 9.6 kHz using the 'PAMmisc' package[43] in R (version 4.3.1)[44], to improve the frequency resolution and the discrete Fourier transform (DFT) length when analysing low frequency calls. Calls of whales were detected visually and reviewed aurally using spectrograms (Fig. 2) in Raven Pro (version 1.6.4)[45]. Spectrograms for analysing calls below the 120 Hz frequency band used the Hann window with a frame size of 1.24 s, 90% overlap, and DFT size of 16,384 samples. For analysing mid-frequency calls (e.g., of AMWs and humpback whales) between 0.12 and 1 kHz frequency, spectrograms used the Hann window with a frame size of 0.56 s, 90% overlap, and DFT size of 8,192 samples. Examples from published literature were used to identify calls and songs of baleen whales: ABW Z-calls[9,14,19]; MPBW calls[14,17]; blue whale D-calls[19]; fin whale 20, 40 and 99 Hz pulses[16,46]; 18–28 Hz blue and fin whale chorus[10,47]; humpback whale songs[48,49]; AMW bio-duck calls[29,30,32,33]; sei whale upsweep calls[35,36,50]. For humpback whales, only the easily discernible and more

Latitude (°S)	Longitude (°E)	Water depth (m)	ST depth (m)	Sampling rate (kHz)	Sampling protocol (min h^{-1})	Duty cycle (%)	Hydrophone sensitivity (dB re 1 V/μPa)	Start recording date	End recording date
46.77	37.91	167	162	96	14	24	− 165	26/04/2021	06/05/2022
46.77	37.91	165	160	96	14	24	− 165	09/05/2022	26/04/2023

Table 1. Summary of deployment details and recording settings of the SoundTrap (ST) autonomous recorder used in this study. Hydrophone sensitivity is from factory calibrations of the HTI-96-MIN (High Tech Inc.) hydrophone.

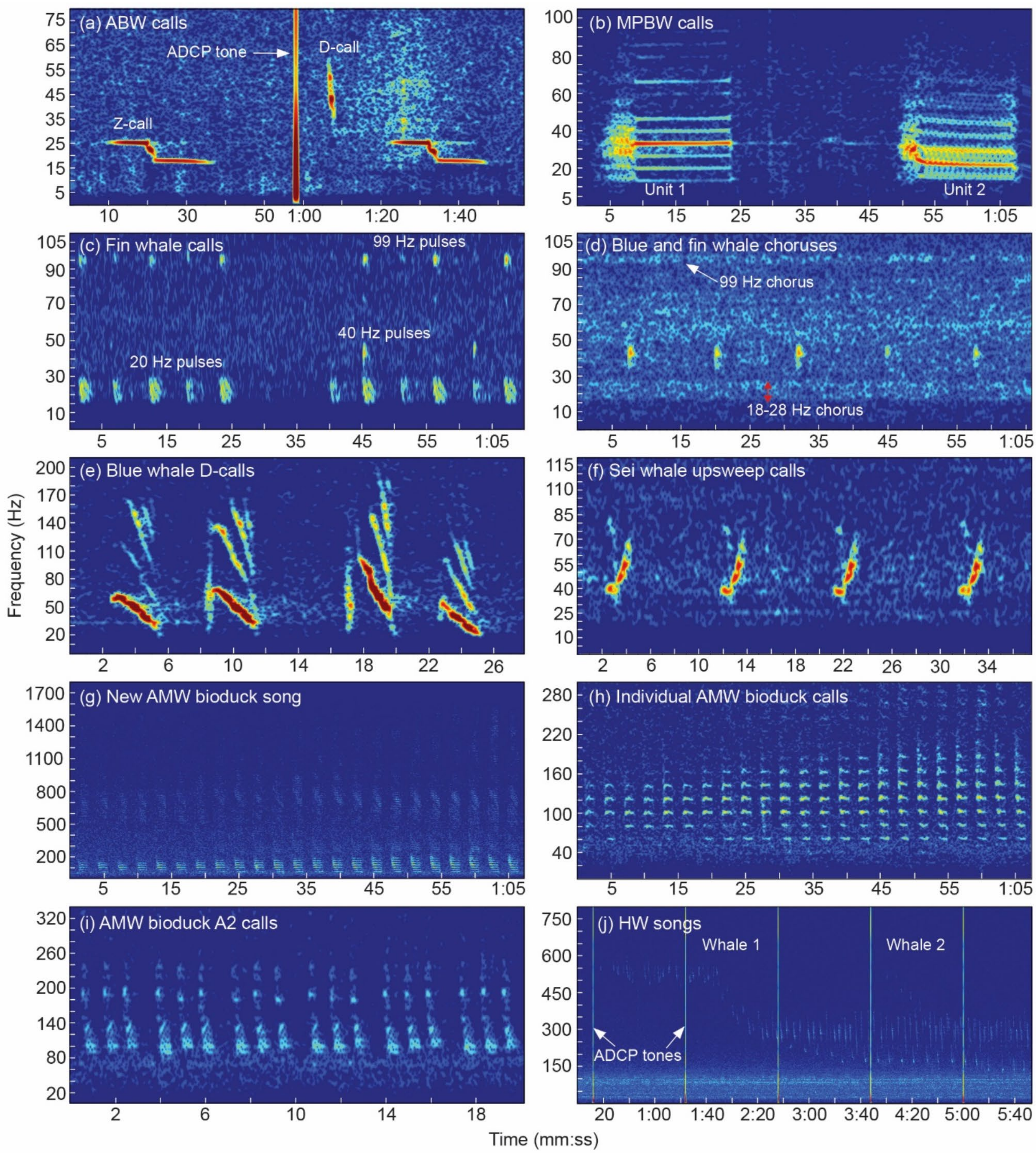

Fig. 2. Spectrograms showing (**a**) Antarctic blue whale (ABW) Z-calls, D-call, and ADCP tone; (**b**) Madagascan pygmy blue whale (MPBW) call units 1 and 2; (**c**) fin whale 20, 40, and 99 Hz pulses; (**d**) blue and fin whale 18–28 Hz chorus, 99 Hz chorus, and 40 Hz pulses; (**e**) blue whale D-calls with harmonics; (**f**) sei whale upsweep calls; (**g**) full frequency range including harmonics of Antarctic minke whale (AMW) bio-duck calls produced in song form; (**h**) zoom in below the 300 Hz range of (**g**) to show the spectral structure of the bio-duck call type described in this study; (**i**) AMW bio-duck A2 song; (**j**) humpback whale (HW) song from two whales singing simultaneously between regular ADCP tones. Note the different y-axes for each spectrogram. Parameters of each spectrogram (Hann window and 90% overlap were used to produce all spectrograms): (**a**) frame size = 1.75 s and discrete Fourier transform (DFT) size = 32,768 samples, (**b**) frame size = 1.24 s and DFT size = 16,384 samples, (**c**) frame size = 0.52 s and DFT size = 8,192 samples, (**d**) frame size = 0.93 s and DFT size = 16,384 samples, (**e**) frame size = 0.56 s and DFT size = 8,192 samples, (**f**) frame size = 0.60 s and DFT size = 8,192 samples, (**g**) frame size = 0.34 s and DFT size = 4,096 samples, (**h**) frame size = 0.70 s and DFT size = 8,192 samples, (**i**) frame size = 0.27 s and DFT size = 4,096 samples, and (**j**) frame size = 0.93 s and DFT size = 16,384 samples.

prevalent songs were detected from our broad analysis but this does not preclude the presence of non-song calls within our acoustic data set.

The Z-calls (Fig. 2a) were used to define the acoustic presence of ABWs, while the presence of either or both unit 1 and/or 2 (Fig. 2b) was used to define the acoustic presence of MPBWs. Since D-calls (Fig. 2e) are produced by both blue whale subspecies[9,37], we did not use this call type to define the acoustic presence of any of the blue whale subspecies but instead used it as an indication of potential foraging[20]. For fin whales, we used the 20 Hz and simultaneous 99 Hz pulses, including the 99 Hz pulse chorus (Fig. 2c, d), to define incidence of social contacts, while the 40 Hz pulse was used to define foraging activities. The 18–28 Hz blue and fin whale chorus (Fig. 3d) was not used to delineate the acoustic presence of either species since it is not possible to differentiate these two species within this band, but can be used to indicate the presence of both species. AMW bio-duck calls and sei whale upsweeps (Fig. 2g-i) were used to determine the acoustic presence of those whales. Humpback whale song units (Fig. 2j) were used to delineate their acoustic presence. These acoustic presences represented and defined the acoustic occurrence of whales at a given hour. From the above acoustic presence defined by the detection of one or more calls or song units within a 14-minute recording session, we calculated the daily number of hours with baleen whale calls as the number of 14-minute recording sessions with calls per day.

To explore diel vocalizing patterns of different whale species, the number of daylight, night, and twilight hours with calls were compared across seasons. Nautical daylight regime (sunrise, sunset, and nautical twilight) for the PEIs was obtained for the oceanographic mooring location (Table 1) using the 'suncalc' package[51] in R. Nautical dawn was defined as the period before sunrise when the centre of the sun was geometrically between 0 and 12° below the horizon. Daytime was the period between sunrise and sunset, and nautical dusk was the period between sunset and the evening when the sun was less than 12° below the horizon. Night-time was the period when the geometric centre of the sun was over 12° below the horizon between dusk and dawn. The austral seasonal cycle was used to describe our data: summer (December through February), autumn (March through May), winter (June through August), and spring (September through October).

For the comparable, but different, AMW bio-duck sub-call type, the minimum frequency, maximum frequency, peak frequency, duration, inter-pulse interval (IPI), and inter-series interval (ISI) were measured for good quality calls with a signal-to-noise ratio greater than 6 dB. Minimum frequency indicated the lowest frequency limit of a call, maximum frequency indicated the highest frequency limit of a call, duration referred to the time difference between the start and end of a call (100% duration), and peak frequency referred to the frequency at which peak power occurs within a call. The ISI was measured as the time from the start of the first pulse in a series to the start of the first pulse in the next series, whereas IPI was measured as the time difference between the start of one pulse and the start of the next pulse within a series.

Acoustic propagation range modelling

A parabolic equation model[52] was used to estimate transmission loss (TL) due to the complicated bathymetry and seasonally dependent sound-speed profiles of the PEIs (Supplementary Fig. S2). This propagation modelling was performed with the aim of determining the approximate detection range for vocalizing ABWs and MPBWs around the PEIs. Estimated propagation ranges are ranges at which the expected received level dropped below 0 dB where the signal level no longer exceeds that of the background noise. Bathymetric data were obtained from the 2023 General Bathymetric Chart of the Oceans Compilation Group (https://doi.org/10.5285/f98b053b-0cbc-6c23-e053-6c86abc0af7b). A sediment grain size value ϕ=4 based on the Wentworth[53] grain size chart was applied to the model for bottom attenuation[54]. Temperature and salinity data from the 2023 World Ocean Atlas[55] were used to calculate sound speed. Based on monthly and climatological average sea surface temperature (SST) patterns from a previous study[56], data from March were used to represent summer and autumn, May to represent winter, and September to represent spring. Propagation modelling was conducted using the procedure detailed in Supplementary Material S2. Resultant average seasonal maximum propagation ranges are presented in Table 2.

Environmental data

Ocean reanalysis and satellite-derived data of daily SST, daily sea surface height (SSH), daily chlorophyll *a*, and hourly wind speed (averaged to daily values to match the temporal scale of other variables) (Table 3) were extracted and spatially averaged across a 2° (222 km latitude) x 2° (156 km longitude) area centred over the mooring system location (46° 46.4′S, 37° 54.7′E) for whale calls with shorter detection ranges than the 2° x 2° quadrant: approximately 30 km for blue whale D-calls[57], 18 km for fin whale 40 Hz pulses[24], 40 km for AMW bio-duck calls[58], up to 45 km for humpback whale songs[48], and up to 20 km for sei whale upsweep calls[34]. We used the above quadrant of 2° x 2° to extract environmental data based on the spatial resolution and correlation between satellite-derived and in situ environmental data as done in Shabangu et al.[56] for the PEIs. This quadrant represents the maximum detection range of the above baleen whale calls around the PIEs since environmental conditions are comparable within the 2° x 2° quadrant[41].

For ABW Z-calls, MPBW calls and fin whale 20 Hz pulses that are known to have greater detection ranges than the 2° x 2° quadrant[10,59], we used the average estimated maximum detection ranges (Table 2) to extrapolate environmental conditions experienced by those whale species. The daily environmental conditions were weighted according to detection ranges for each section to account for bathymetry blocking of sound on the seaward sides of the PEIs (Supplementary Fig. S3 and S4) and to produce daily weighted averages for each environmental variable within a spatial context in the study area. Consequently, environmental data from Sects. 2 and 4 (Table 2) had higher weighting than those from Sects. 1 and 3.

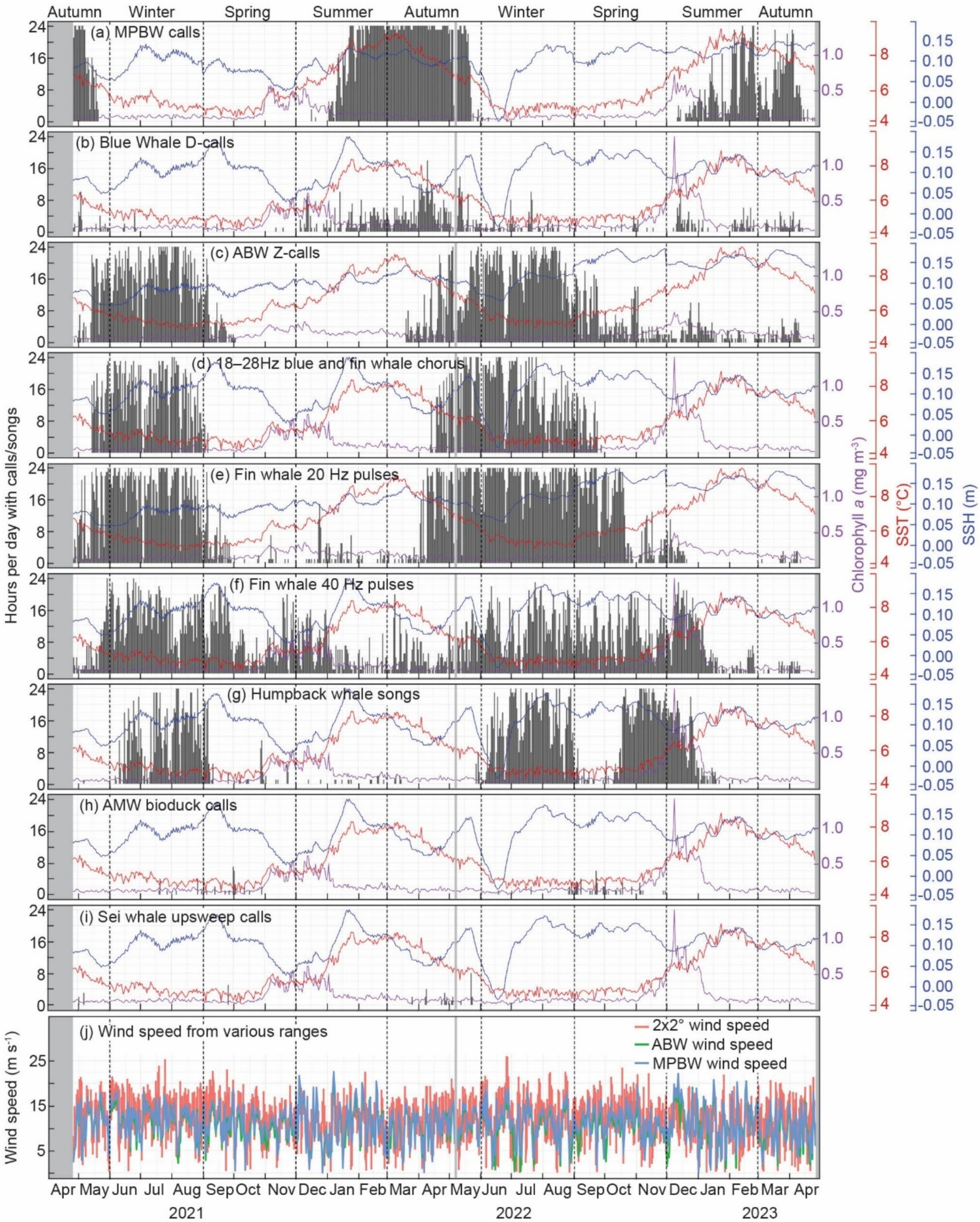

Fig. 3. Daily acoustic occurrence pattern (left y-axes) of all baleen whales (barplots): (**a**) Madagascan pygmy blue whales (MPBWs), (**b**) blue whale D-calls, (**c**) Antarctic blue whales (ABWs), (**d**) 18–28 Hz blue and fin whale chorus, (**e**) fin whale 20 Hz pulse, (**f**) fin whale 40 Hz pulse, (**g**) humpback whales, (**h**) Antarctic minke whales (AMWs), and (**i**) sei whales. Daily environmental variables (line plots) are overlaid for easier interpretation, and their scales are provided on the right y-axes. (**j**) Wind speed from different detection ranges is plotted separately due to its high temporal variability that would have masked other plots. Light grey shadings indicate times without PAM effort.

Whale species	Season (s)	Propagation range per section (km)			
		Section 1	Section 2	Section 3	Section 4
ABW	Summer and autumn	13	440	11	488
	Winter	12	365	11	505
	Spring	13	729	11	599
MPBW	Summer and autumn	12	53	10	224
	Winter	12	50	10	121
	Spring	12	145	10	224

Table 2. Predicted average seasonal maximum propagation ranges for Antarctic blue whale (ABW) Z-calls and Madagascan pygmy blue whale (MPBW) calls for four azimuthal sections (defined in Supplementary Fig. S3) around the PEIs, where Sect. 1 is largely blocked by Prince Edward Island and Sect. 3 is largely blocked by Marion Island.

Variable	Unit	Group: Product	Data repository link	Spatial resolution	Usage
Chlorophyll *a*	mg m^{-3}	CMEMS: GlobColour	http://my.cmems-du.eu/Core/OCEANCOLOUR_GLO_BGC_L4_MY_009_104/cmems_obs-oc_glo_bgc-plankton_my_l4-gapfree-multi-4km_P1D	0.04° x 0.04° (4×3 km)	Proxy for primary production and phytoplankton biomass
Sea surface height (SSH)	m	CMEMS: DUACS	http://nrt.cmems-du.eu/Core/SEALEVEL_GLO_PHY_L4_NRT_OBSERVATIONS_008_046/dataset-duacs-nrt-global-merged-allsat-phy-l4	0.25° x 0.25° (28×19 km)	Locate the position of the Antarctic Circumpolar Current fronts around the PEIs and suitable habitat conditions for animals
Sea surface temperature (SST)	°C	CMEMS: OSTIA	http://nrt.cmems-du.eu/Core/SST_GLO_SST_L4_NRT_OBSERVATIONS_010_001	0.25° x 0.25° (28×19 km)	Indicate changes in physical oceanographic processes which affect primary productivity around the PEIs
Wind speed[a]	m s^{-1}	CMEMS: ERA5	http://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-pressure-levels?tab=form	0.25° x 0.25° (28×19 km)	Proxy of sea state conditions

Table 3. Summary of environmental variables (abbreviations in parentheses) derived from global environmental data repositories. The column "Usage" justifies the use of environmental variables in this study. Group and product abbreviations are defined: CMEMS is Copernicus Marine Environment Monitoring Service, DUACS is Data Unification and Altimeter Combination System, ERA5 is the fifth generation of European Centre for Medium-Range Weather forecasts reanalyses, GlobColour is Global Ocean Colour for Carbon Cycle Research, and OSTIA is operational Sea Surface temperature and sea ice analysis. GlobColour uses merged, gap-free data from multiple satellite sensors which include Sea-viewing-wide field-of-View Sensor (SeaWiFS), the medium resolution imaging spectrometer (MERIS), the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua, the visible infrared imaging Radiometer Suite (VIIRS NPP), and the Ocean and Land Colour Instrument (OLCI-S3A) sensors. [a]Absolute wind speed (ws) was calculated from meridional (v) and zonal (u) wind speed components: $ws = \sqrt{u^2 + v^2}$.

Modelling predictors of whale occurrence

Random forest (RF) models[60] were used to determine if different baleen whale acoustic occurrence responded to variations in environmental conditions around the PEIs. The RF models were chosen for this study as they were found to perform better than generalized additive models and generalized boosted regression trees models for assessing acoustic occurrence of other marine mammals[9,61]. The RF models have high prediction accuracy and non-parametric inferential properties whilst implicitly including variable interaction[60,62,63]. Chlorophyll *a*, SST, SSH, month, hour of day, and wind speed were used as predictor variables. The RF models were fitted using the method described in Supplementary Material S3.

Results

Acoustic effort

In total, 4,024 h of recordings were obtained over 729 days (Table 4) where the first acoustic recorder deployment lasted for 376 days (26 April 2021 and 06 May 2022), and the second deployment lasted for 353 days (09 May 2022 to 26 April 2023). Overall, this acoustic effort covered all months and seasons of the year.

Characteristics of a new minke whale sub-call type

AMW bio-duck song shown in Fig. 2(g, h) as measured from 50 pulses had an average ± standard deviation pulse duration of 1.80 ± 0.11 s (range: 1.58–2.08); minimum frequency of 53.8 ± 4.26 Hz (range: 49–76.4); maximum frequency of 189.68 ± 12.99 Hz (range: 168.4–226.9); peak frequency of 114.84 ± 22.70 Hz (60.94–168.75). These contained an average of 32.60 ± 3.58 pulses per series (range: 28–36, $n = 5$); IPI of 2.90 ± 0.09 s (range: 2.67–3.17, $n = 102$); ISI of 177.81 ± 19.58 s (range: 152.11–213.23, $n = 8$). Given that the pulsed spectral structure of detected calls in this study is comparable to AMW bio-duck B described by other studies, we term this sub-call type bio-duck B10 to follow the alphanumerical order used in previous studies[29,30,32,33].

Occurrence of whale calls

Calls from six baleen whale species were detected from our acoustic recordings spanning over two years: ABWs, MPBWs, fin whales, AMWs, humpback whales, and sei whales (Fig. 3). Other detected sounds included mooring noise and calls from unknown sources (Supplementary Material S4: Other detected sounds; Supplementary Fig. S7). Fin whale 20 and 40 Hz pulses were the most commonly detected calls, followed by calls of MPBWs and ABWs. Sei whale upsweep calls were detected least frequently(Fig. 3). Seasonally, MPBW calls were detected from December to the beginning of June but not at the end of June to November (Fig. 3a). Blue whale D-calls were sporadically detected in all the months of 2022 and 2023 but not in some months in 2021 (Fig. 3b). The peak number of D-call detections corresponded to peak of MPBW calls. ABW Z-calls were detected from April to early October in 2021 and were detected for the whole year from March 2022 to April 2023 with peaks in June to August (Fig. 3c). The 18–28 Hz blue and fin whale chorus was detected from late April to early September and overlaps with blue and fin whale presence although this chorus was sometimes not detected when blue whale Z-calls and fin whale 20 Hz pulses were (Fig. 3).

Year	Month	Hours recorded	Number of days
2021	April	27	5
	May	174	31
	June	168	30
	July	174	31
	August	174	31
	September	168	30
	October	174	31
	November	168	30
	December	174	31
2022	January	174	31
	February	157	28
	March	174	31
	April	168	30
	May	155[a]	29
	June	174	30
	July	174	31
	August	174	31
	September	168	30
	October	174	31
	November	168	30
	December	174	31
2023	January	174	31
	February	157	28
	March	174	31
	April	84[b]	26
	Total	4,024	729

Table 4. Acoustic effort per month over two years between mid-2021 and mid-2023. [a]There was a two-day break in recording between 06 and 09 May 2022 to refurbish the acoustic recorder before redeployment. [b]Only some hours were successfully sampled from 09 to 26 April 2023 due to the malfunctioning of the acoustic recorder.

Fin whale 20 Hz pulses were detected throughout the year, although only intermittently in October to February and with a peak in June through August (Fig. 3e). Similarly, the fin whale 40 Hz pulses were detected throughout the year, with a peak in June to August and December through January (Fig. 3f). There was a temporal separation between the detection peaks of 20 and 40 Hz fin whale pulses in some months (Fig. 3e, f).

Humpback whale songs were detected from May 2021 to March 2022 and from May 2022 to February 2023, where songs were detected continuously from June to mid-September but sporadically from late September to mid-March (Fig. 3g). There was a single humpback whale song peak in June to August of 2021, whereas there were two peaks in 2022/23 with the first peak in June to August and the second in October to December.

AMW bio-duck calls were detected intermittently from July to October in 2021 but from June to November in 2022 (Fig. 3h). Bio-duck A2 and B2 calls were the most detected sub-call types of AMWs (89% of all AMW calls were either A2 or B2 types), and the bio-duck B10 call was detected on several occasions (11% of all AMW calls) in September 2021. On the other hand, bio-duck A2 and B2 calls represented 93% of all AMW calls in 2022 and the B10 call made up the remaining 7%.

Sei whale upsweep calls were detected in May 2021, September 2021, and March to May 2022 (Fig. 3i).

These baleen whale acoustic occurrences seemed to respond differently to changing environmental conditions overlaid on each call detection pattern (Fig. 3a-i), although no trend could be seen for wind speed due to its high temporal variability (Fig. 3j).

Observed diel acoustic occurrence patterns

No diel acoustic patterns were observed in autumn for any species although there were minor hourly changes for some calls (Fig. 4). ABW Z-calls, MPBW calls, and D-calls did not show any diel pattern (Fig. 4a-c). There was no temporal segregation in diel vocalizing pattern between ABWs and MPBWs during periods of call co-occurrence in summer and autumn (Fig. 4a, b). In winter, no diel acoustic occurrence was observed for most whale species except that humpback whale song occurrence was low during the day but high at night and high 18–28 Hz blue and fin whale chorus occurrence during the day (Fig. 4). In spring and summer, fin whale 40 Hz pulse occurrence was higher during daytime than other times of day, whilst fin whale 20 Hz pulse occurrence showed no diel pattern (Fig. 4e, f). Other whale calls did not display diel patterns in spring and summer except that AMWs and sei whales vocalized more at night (Fig. 4h, i).

Whale occurrence predictors

The probability of occurrence of fin whale 40 Hz pulses and humpback whale songs increased with increasing chlorophyll *a* whereas probabilities of occurrence of ABW Z-calls, fin whale 20 Hz pulses, MPBW calls, and sei whale upsweep calls decreased with increasing chlorophyll *a* (Fig. 5a). The probability of occurrence of AMW bio-duck calls first increased, and then decreased before plateauing after chlorophyll *a* increased above 0.5 mg m^{-3}. SSHs above 0.05 m had varying influence on different baleen whale acoustic occurrence. The probability of occurrence of ABW Z-calls, AMW bio-duck calls, fin whale 20 and 40 Hz pulses, and humpback whale songs decreased with increasing SST. On the contrary, the probability of occurrence of blue whale D-calls and MPBW calls increased with increasing SST (Fig. 5a). The probability of occurrence of sei whale upsweep calls was high when SST was between 6 and 7.5 °C. The probability of occurrence of most baleen whale calls decreased with an increase in wind speed; in contrast, MPBW calls and sei whale upsweep calls exhibited no change and increased acoustic occurrence with increase in wind speed, respectively (Fig. 5a).

The following months had the highest influence on whale call detection as a measure of occurrence: May to August for ABW Z-calls, February to May for MPBW calls, February to May for blue whale D-calls, September and October for AMW bio-duck calls, April to August for fin whale 20 Hz pulses, May to December for fin whale 40 Hz pulses, June to August and November for humpback whale songs, and May for sei whale upsweep calls (Fig. 5a). No clear influence of hour of day was observed on ABW Z-calls, fin whale 20 Hz pulses, fin whale 40 Hz, humpback whale song, and MPBW calls (Fig. 5a). However, the probability of occurrence of AMW bio-duck calls and sei whale upsweep calls was high at night-time while probabilities of occurrence D-calls were low at midnight (23:00 and 00:00).

The most important predictors of call occurrence were: month, SST, and chlorophyll *a* for ABW Z-calls and fin whale 20 Hz pulses; month, SST, and wind speed for AMW bio-duck calls; month and SST for blue whale D-calls, MPBW calls and sei whale upsweep calls; SST for fin whale 40 Hz pulses; month for humpback whale songs (Fig. 5b). Moderately important predictors of call occurrence were: SSH for ABW Z-calls, AMW bio-duck calls, fin whale 20 Hz pulses and MPBW calls; chlorophyll *a* and SSH for blue whale D-calls; wind speed for fin whale 40 Hz pulses; SST and SSH for humpback whale songs; chlorophyll *a* for sei whale upsweep calls (Fig. 5b). The least important predictors of call occurrence were: wind speed and hour of day for ABW Z-calls, blue whale D-calls, and fin whale 20 Hz pulses; chlorophyll *a*, SSH and hour of day for AMW bio-duck calls; month, chlorophyll *a*, SSH and hour of day for fin whale 40 Hz pulses; chlorophyll *a*, wind speed and hour of day for humpback whale songs and MPBW calls; SSH, wind speed and hour of day for sei whale upsweep calls (Fig. 5b). Overall, certain predictor variables were found to be significantly important and informative at predicting different baleen whale call occurrence, whereas other variables were non-significantly important and not informative and this also varied by species (Fig. 5b).

Discussion

We provide the first report of the acoustic occurrence for six baleen whale species around the remote sub-Antarctic PEIs, finding a diverse range of species' call occurrence and diel vocalization patterns for some species. We add to previous knowledge by acoustically confirming the presence and importance of this region for humpback whales[42], and by showing that the PEIs are also a useful habitat for at least five other baleen whale species (ABWs, MPBWs, fin whales, AMWs and sei whales) given their diverse acoustic occurrence around this

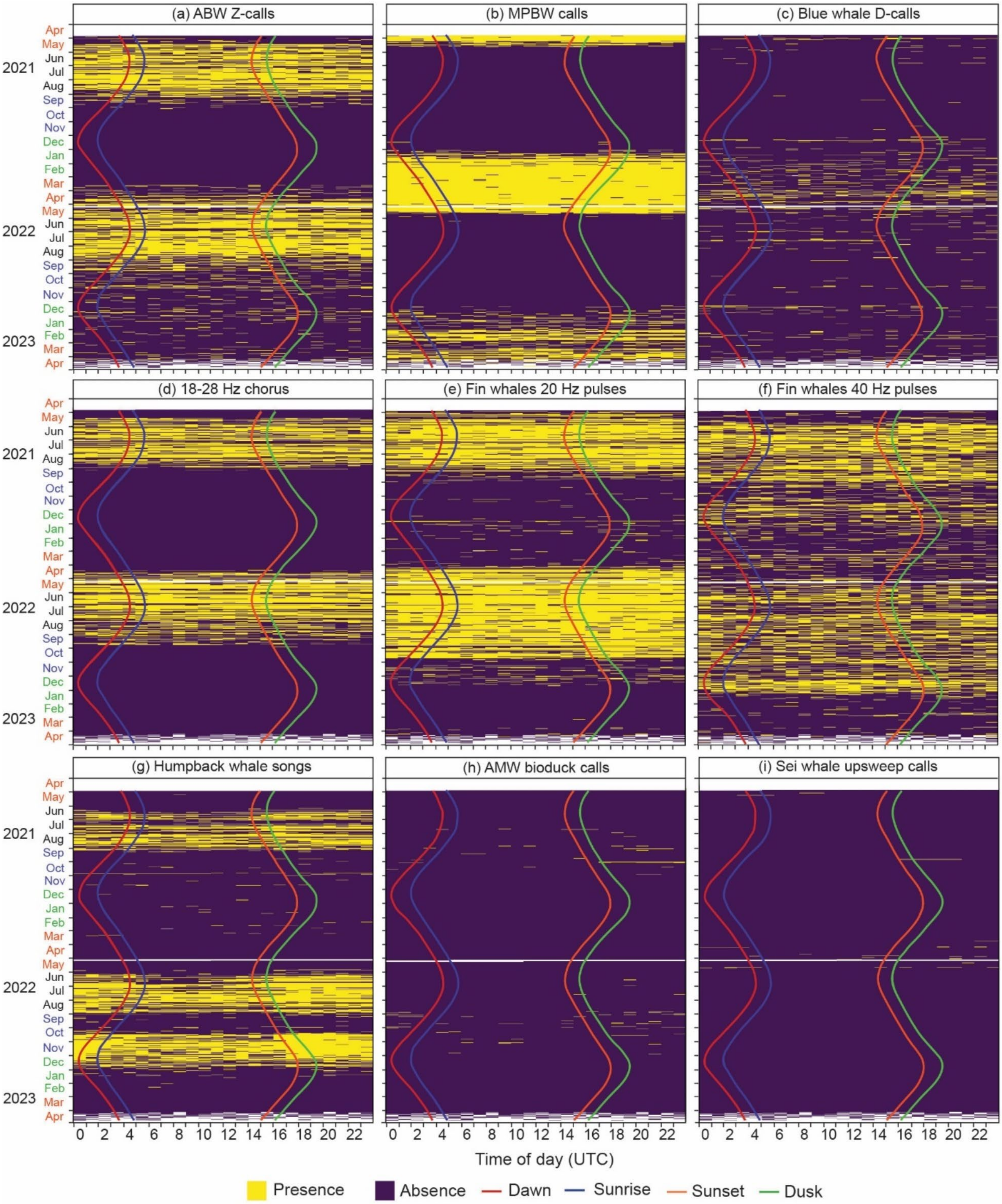

Fig. 4. Diel acoustic occurrence of different whale call types. Acoustic occurrence (i.e. absence/presence of calls) is defined in the key, and daylight regimes are indicated by vertical lines defined in the key. Month font colours represent seasons as defined above: green = summer, orange = autumn, black = winter, and purple = spring. White shading indicates periods without PAM effort, and the period of acoustic recorder malfunction in April 2023.

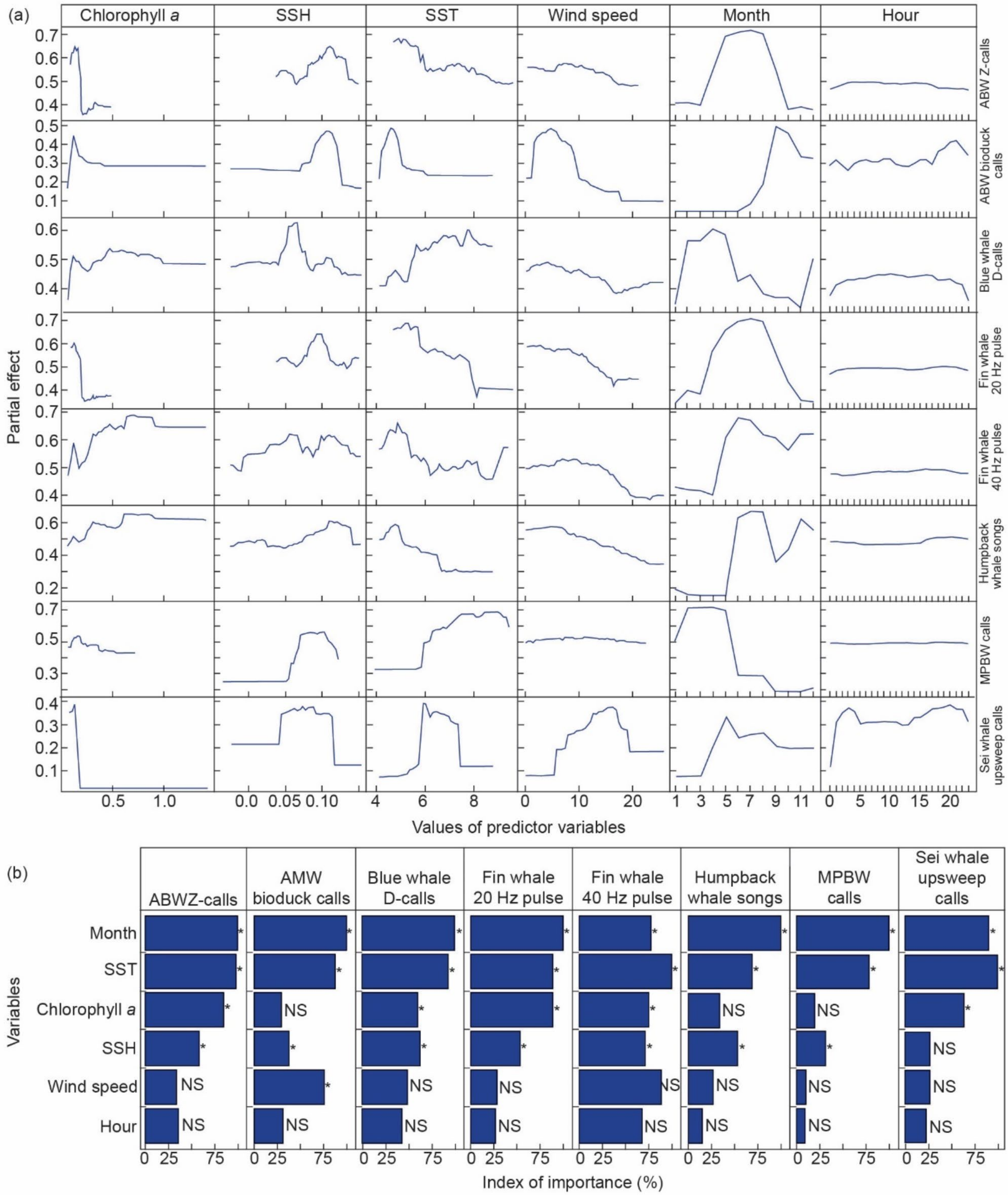

Fig. 5. Random forest (RF) models (**a**) partial effects and (**b**) ranked relative importance of predictor variables on the probability of occurrence of baleen whale calls based on synthetic minority over-sampling technique sample balancing method (Supplementary Material S3). Y-axes scales are different between plots in (a). Asterisks (*) indicate significant importance ($p < 0.05$) and NS indicates non-significant importance ($p > 0.05$) based on the Altmann et al.[64] method.

region. Additionally, characteristics of a relatively different call of AMWs are provided. This study showcases the effectiveness of PAM at detecting sounds from organisms that are sometimes not detected visually and in remote regions of the globe.

Minke whale bio-duck call

The AMW bio-duck B10 sub-call type reported in this study area exhibits a different number of pulses, pulse duration, peak frequency, IPI, and ISI to bio-duck calls reported in previous studies[29,30,32,33], qualifying it as a new sub-call type. The duration of bio-duck B10 pulses is the longest of all AMW bio-duck call types described to date. The differences in acoustic characteristics of this bio-duck sub-call type can potentially be explained by the geographical isolation of AMWs between western Antarctica[29,32], eastern Antarctica[30,32], Brazil[33], and the sub-Antarctic region (this study) which could have led to different acoustic evolution and speciation as understood with fin whales in Western and Eastern Antarctica[16].

Diel acoustic occurrence

ABWs did not exhibit a diel vocalizing pattern which is in contrast to the predominance of daytime vocalizing observed in the southern Indian Ocean[65] and southeast Atlantic Ocean[9,11], and the night-time vocalizing pattern observed in the eastern Weddell Sea[10] and Australia[66]. This diel vocalizing pattern difference between regions might be indicative of region-specific vocalizing behaviour, or because ABWs may be feeding opportunistically in this area and can sing more continuously. The detection of the 18–28 Hz blue and fin whale chorus was high during the day in winter which corresponds to corresponds to previously observed ABW Z-call pattern given their overlapping frequency range[10,11,47,65]. Likewise, MPBW calls did not show any diel pattern, indicating no diel adaptation to daylight regimes in this region, although Leroy et al.[65] found them to be more vocally active during the day in the southern Indian Ocean. Correspondingly, D-calls also did not exhibit a diel pattern as these strongly corresponded to MPBW call occurrence that also lacked a diel vocalising pattern. The lack of temporal segregation between ABW and MPBW calls is different from the temporal segregation found between ABWs and Australian pygmy blue whales in Australian waters[66]. These two subspecies can co-exist without any acoustic competition given the limited frequency range overlap of their calls although the second unit of MPBW calls overlaps in frequency with ABW Z-calls (Fig. 2a, b).

Acoustic occurrence of fin whale 20 Hz pulses showed no diel pattern, which is different from the more daytime vocalizing pattern observed in Antarctica[10,67] and reflect a lack of seasonal adaptation to changes in daylight regime. On the other hand, the acoustic occurrence of fin whale 40 Hz pulses was high during daytime in spring and summer, suggesting that fin whale foraging was adapted to seasonal changes in daylight regimes in response to vertical migration of prey[68]. Humpback whales were more vocally active at night in winter, which corresponds to results from Antarctica and the west coast of South Africa[48]. This behaviour is considered a night-time adaptation to maintain contact with conspecifics when visual contact is reduced or not possible[69]. AMW bio-duck calls and sei whale upsweep calls were detected at night as found by previous studies[30,36]. Overall, the RF models did not support the observed seasonal diel patterns for all the baleen whales except that AMWs and sei whales vocalize more frequently at night.

Whale call occurrence and predictors of call occurrence

The seasonal presence of ABWs around PEIs in 2021/22 versus the year-round presence in the 2022/23 period is comparable to the interannual variability observed off the west coast of South Africa[9,11]. The winter peak in ABW Z-call occurrence around the PEIs is like that observed in the low latitudes[9,11,37,70]; however, this pattern is different to summer/autumn peak occurrence in Antarctica[10,16,71]. Most ABWs likely use this area for overwintering since they feed primarily off the ice edge where their main prey, Antarctic krill (*Euphausia superba)*, is most abundant[4]. But it is possible that opportunistic feeding by ABWs occurred in this area given the simultaneous detection of D- and Z-calls in some instances. Our lower estimated detection ranges for the winter period suggest that calling whales were closer to the PEIs during this time, and this could have affected detection of whale calls between seasons as calls from farther whales would not be detected. The presence of high quality calls and harmonics on calls of ABWs, MPBWs and other baleen whales studied here (Fig. 2) further supports that whales were sometimes very close to the PEIs.

The complete absence of MPBW calls from June to November is consistent with expected feeding patterns in the sub-Antarctic in mid to late summer[72]. The onset of ABW call detections and cessation of MPBW call detections perfectly matches the northward movement (in May, November, and December) and southern position (for the rest of the year) of the southern branch of the sub-Antarctic Front around the PEIs[56]. Peak occurrence of MPBW calls in the Indian Ocean is between June and November[72,73], suggesting that these whales likely migrated north of the PEIs at that time to areas closer to Madagascar and outside the detection range of our acoustic recorder. Unlike off the neighbouring (950 km due east on a similar latitude to the PEIs) Crozet Islands[72], we recorded no calls of the Sri Lanka or the Australian song types, suggesting that the PEIs are out of range for both of those populations of blue whales.

Blue whale D-calls were most often detected in the presence of MPBW calls, suggesting that the PEIs region is a core feeding ground as this call is associated with feeding for this subspecies as hypothesized for the Crozet Islands[72]. The MPBWs are known to feed almost exclusively on *Euphausia vallentini* in the sub-Antarctic region[74]. Historical catch timing in this area also supports this area as a feeding ground of pygmy blue whales[75]. Previous research based on historic whaling catch records indicated that ABWs and pygmy blue whales were geographically isolated at this location as only pygmy blue whales were present[75]. However, our acoustic research shows that both subspecies occur sympatrically for extended periods of time in the region as seen with fin and sei whales, suggesting potential resource partitioning[76]. Similar resource partitioning is postulated for other co-occurring baleen whales in this region[77].

There was an inverse relationship in terms of temporal separation between the fin whale 20 and 40 Hz pulses, suggesting that fin whales only produce the feeding call during foraging and separately produce the socializing and mating song[26]. Like ABWs, the fin whale 20 Hz pulse occurrence peak was in winter, indicating that many of these whales might be overwintering around the PEIs. Additionally, this region might be an important feeding ground for fin whales, given the year-round production of the feeding associated call, the 40 Hz pulse. The fin whale year-round presence around the PEIs could be supported by larger amounts of mesozooplankton prey, the euphausiids (mainly *E. vallentini*, *Thysanoessa vicina* and *Stylocheiron longicorne*), known to be present around the PEIs[78,79].

AMWs and sei whales were previously not reported around the PEIs and therefore this PAM-based study contributes new information about their geographic occurrences in the Southern Ocean[3,4]. The detection of sei whale calls from March to May is consistent with acoustic occurrence in the Ross Sea, Southern Ocean[35], Falkland Islands[36] and Northern Chilean Patagonia[50], but differs from the October/November detection off the Vema Seamount, South Atlantic Ocean[80]. The June to November detection of AMW bio-duck calls around the PEIs is shorter than the April to January detection in the Southern Ocean[29,30,58,71] but overlaps with the detection period in South African waters, August to February[30] indicating dynamic movements between regions.

Our observed humpback whale song occurrence from April to February/March with peaks in June/July and October/November is within the Southern Hemisphere breeding season (June to October)[3] and comparable to the October peak in South African waters[48] but different from the April/May peak reported for in the feeding ground, Antarctica[81]. The bimodal peaks suggest that the PEIs might be used as stopover during the northward humpback migration to breeding grounds in the low latitudes and southward migration to the Southern Ocean. Alternatively, the migration routes and ranges could be changing between years. In addition, the intermittent detection of songs throughout the year suggests that a portion of humpback whales could be using this region year-round.

According to the RF models, the variables month and/or SST were the primary predictors of the occurrence of all baleen whale calls that we analysed, which suggests that the temporal and spatial variation of these variables drive the presence, migration, feeding, and breeding patterns of these six whales around the PEIs marine ecosystem. These variables are also highlighted as important baleen whale occurrence predictors in the low latitudes such as South Africa[9,11,30] and Northern Chilean Patagonia[50], and in the Southern Ocean[6,10,42]. Thus, future changes in the SST regime related to climate change around the PEIs archipelago might influence the acoustic occurrence patterns (i.e., habitat selection) of these baleen whales around this important region, likely through direct impacts on their physiology (by affecting their thermoregulatory costs and metabolic processes) and indirectly through primary productivity of the region[82,83]. The moderately and least important predictor variables not only contribute to the ecology of these baleen whales but also through physical influence on their detection; for example, the negative correlation between wind speed and whale occurrence was due to the reduced detectability of whale calls during elevated underwater noise levels[38].

Conclusions

PAM showed baleen whale species that were not previously known to occur around the PEIs such as AMWs, fin and sei whales. Properties of a new form of the AMW bio-duck call are detailed in this study. ABWs, fin whales, and humpback whales appear to be resident, as calls were detected almost year-around, while MPBWs, AMWs and sei whales were transient likely using the PEIs as an overwintering ground, feeding ground, and/or stop over location during migration. D-calls were most likely produced by MPBWs given the corresponding occurrence of these calls, which highlighted the PEIs as a possible feeding area for MPBWs. AMWs and sei whales were more vocally active at night while other whale species showed no diel vocalizing pattern. Month and/or SST were the most important predictors of all baleen whale acoustic occurrence, suggesting that the seasonal environmental changes around the PEIs drive the ecology of whales around this region. The observed high acoustic diversity of baleen whales supports consideration of the PEIs area as a potential important habitat of baleen whale species. This is the first study of baleen whale acoustic occurrence around this sub-Antarctic region. Therefore, continued monitoring at this region is warranted to better understand the interannual differences in some species' presence, and to inform future conservation and management strategies around the sub-Antarctic region.

Data availability

Data are provided in the form of acoustic .wav file of all exemplar calls illustrated by the spectrograms in the manuscript figure, an MS Excel Spreadsheet file with baleen whale call occurrence and environmental data, and the R code used for fitting the RF models in https://doi.org/10.5281/zenodo.10719537. Links for downloading environmental data are provided in Table 3.

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References

1. Doughty, C. E. *et al.* Global nutrient transport in a world of giants. *PNAS* **113**(4), 868–873. https://doi.org/10.1073/pnas.1502549112 (2016).
2. Fossi, M. C., Baini, M. & Simmonds, M. P. Cetaceans as ocean health indicators of marine litter impact at global scale. *Front. Mar. Sci.* **8**, 586627. https://doi.org/10.3389/fenvs.2020.586627 (2020).
3. Best, P. B. *Whales and dolphins of the Southern African subregion* (Cambridge University Press, 2007).
4. Jefferson, T. A., Webber, M. A. & Pitman, R. L. *Marine mammals of the world: a comprehensive guide to their identification* (Academic, 2015).

5. Branch, T. A. *et al.* Past and present distribution, densities and movements of blue whales (*Balaenoptera musculus*) in the Southern Hemisphere and Northern Indian Ocean. *Mamm. Rev.***37**(2), 116–175. https://doi.org/10.1111/j.1365-2907.2007.00106.x (2007).
6. El-Gabbas, A., van Opzeeland, I., Burkhardt, E. & Boebel, O. Dynamic species distribution models in the marine realm: predicting year-round habitat suitability of baleen whales in the Southern Ocean. *Front. Mar. Sci.* **8**, 802276. https://doi.org/10.3389/fmars.2021.802276 (2021).
7. Postma, M., Wege, M., Bester, M. N., van der Merwe, D. S. & de Bruyn, P. J. N. Inshore occurrence of southern right whales (*Eubalaena australis*) at subantarctic Marion Island. *Afr. Zool.* **46**(1), 188–193 (2011).
8. BirdLife South Africa. Flock to Marion 2022 final species list. (2022). https://www.birdlife.org.za/flock-to-marion-2022/
9. Shabangu, F. W. *et al.* Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa. *J. Mar. Syst.* **190**, 25–39. https://doi.org/10.1016/j.jmarsys.2018.11.002 (2019).
10. Shabangu, F. W., Andrew, R. K., Yemane, D. & Findlay, K. P. Acoustic seasonality, behaviour and detection ranges of Antarctic blue and fin whales under different sea ice conditions off Antarctica. *Endanger. Species Res.* **43**, 21–37. https://doi.org/10.3354/esr01050 (2020).
11. Letsheleha, I. S. *et al.* Year-round acoustic monitoring of Antarctic blue and fin whales in relation to environmental conditions off the west coast of South Africa. *Mar. Biol.* **169**, 41. https://doi.org/10.1007/s00227-022-04026-x (2022).
12. Payne, R. S. & McVay, S. Songs of humpback whales. *Science***173**, 585–597. https://doi.org/10.1126/science.173.3997.585 (1971).
13. Edds-Walton, P. L. Acoustic communication signals of mysticete whales. *Bioacoustics***8**, 47–60. https://doi.org/10.1080/09524622.1997.9753353 (1997).
14. Ljungblad, D. K., Clark, C. W. & Shimada, H. A comparison of sounds attributed to pygmy blue whales (*Balaenoptera musculus brevicauda*) recorded south of the Madagascar Plateau and those attributed to 'true' blue whales (*Balaenoptera musculus*) recorded off Antarctica. *Rep. Int. Whal. Comm.* **48**, 439–442 (1998).
15. McDonald, M. A., Hildebrand, J. A. & Mesnick, S. L. Biogeographic characterization of blue whale song worldwide: using song to identify populations. *J. Cetacean Res. Manage.***8**, 55–65 (2006).
16. Širović, A., Hildebrand, J. A., Wiggins, S. M. & Thiele, D. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. *Mar. Mamm. Sci.* **25**, 125–136. https://doi.org/10.1111/j.1748-7692.2008.00239.x (2009).
17. Leroy, E. C., Royer, J. Y., Alling, A., Maslen, B. & Rogers, T. L. Multiple pygmy blue whale acoustic populations in the Indian Ocean: whale song identifies a possible new population. *Sci. Rep.* **11**, 8762. https://doi.org/10.1038/s41598-021-88062-5 (2021).
18. Guinee, L. N. & Payne, K. B. Rhyme-like repetitions in songs of humpback whales. *Ethol.* **79**, 295–306. https://doi.org/10.1111/j.1439-0310.1988.tb00718.x (1988).
19. Rankin, S., Ljungblad, D., Clark, C. & Kato, H. Vocalisations of Antarctic blue whales, *Balaenoptera musculus intermedia*, recorded during the 2001/2002 and 2002/2003 IWC/SOWER Circumpolar Cruises, Area V, Antarctica. *J. Cetacean Res. Manage.* **7**, 13–20 (2005).
20. Oleson, E. M., Calambokidis, J., Barlow, J. & Hildebrand, J. A. Blue whales visual and acoustic encounter rates in the Southern California Bight. *Mar. Mamm. Sci.* **23**, 574–597. https://doi.org/10.1111/j.1748-7692.2007.02303.x (2007).
21. Schall, E. *et al.* Visual and passive acoustic observations of blue whale trios from two distinct populations. *Mar. Mamm. Sci.***36**, 365–374. https://doi.org/10.1111/mms.12643 (2020).
22. Watkins, W. A., Tyack, P. & Moore, K. E. The 20-Hz signals of finback whales (*Balaenoptera physalus*). *J. Acoust. Soc. Am.***82**(6), 1901–1912. https://doi.org/10.1121/1.395685 (1987).
23. Gerlotto, F. & Marchal, E. The concept of acoustic populations: Its use for analysing the results of acoustic cruises. International Symposium on Fisheries Acoustics, June 22–26, 1987, Seattle, Washington, USA; https://archimer.ifremer.fr/doc/00305/41630/
24. Aulich, M. G. *et al.* Seasonal distribution of the fin whale (*Balaenoptera physalus*) in Antarctic and Australian waters based on passive acoustics. *Front. Mar. Sci.* **9**, 864153. https://doi.org/10.3389/fmars.2022.864153 (2022).
25. Wiggins, S. M. & Hildebrand, J. A. Fin whale 40-Hz calling behavior studied with an acoustic tracking array. *Mar. Mamm. Sci.* **36**, 964–971. https://doi.org/10.1111/mms.12680 (2020).
26. Romagosa, M. *et al.* Food talk: 40-Hz fin whale calls are associated with prey biomass. *Proc. R. Soc. B: Biol. Sci.* **288**, 20211156. https://doi.org/10.1098/rspb.2021.1156 (2021).
27. Zoidis, A. M. *et al.* Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii. *J. Acoust. Soc. Am.* **123**(3), 1737–1746. https://doi.org/10.1121/1.2836750.PMID:18345861 (2008).
28. Videsen, S. K. A., Bejder, L., Johnson, M. & Madsen, P. T. High suckling rates and acoustic crypsis of humpback whale neonates maximise potential for mother-calf energy transfer. *Funct. Ecol.***31**, 1561–1573. https://doi.org/10.1111/1365-2435.12871 (2017).
29. Dominello, T. & Širović, A. Seasonality of Antarctic minke whale (*Balaenoptera bonaerensis*) calls off the Western Antarctic Peninsula. *Mar. Mamm. Sci.* **32**, 826–838. https://doi.org/10.1111/mms.12302 (2016).
30. Shabangu, F. W., Findlay, K. & Stafford, K. M. Seasonal acoustic occurrence, diel-vocalizing patterns and bioduck call-type composition of Antarctic minke whales off the west coast of South Africa and the Maud Rise, Antarctica. *Mar. Mamm. Sci.* **36**, 658–675. https://doi.org/10.1111/mms.12669 (2020).
31. Risch, D. Mysterious minke whales: Acoustic diversity and variability. In *Ethology and behavioral ecology of marine mammals*. 329–348 (eds Clark, C. W. & Garland, E.) (Springer Nature, 2022). https://doi.org/10.1007/978-3-030-98449-6_14
32. Filun, D. & van Opzeeland, I. Spatial and temporal variability of the acoustic repertoire of Antarctic minke whales (*Balaenoptera bonaerensis*) in the Weddell Sea. *Sci. Rep.* 13, 11861; (2023). https://doi.org/10.1038/s41598-023-38793-4 (2023).
33. Rossi-Santos, M. R., Filun, D., Soares-Filho, W., Paro, A. D. & Wedekin, L. L. Playing the beat: occurrence of bio-duck calls in Santos Basin (Brazil) reveals a complex acoustic behaviour for the Antarctic minke whale (*Balaenoptera bonaerensis*). *PLoS ONE* **17**(9), e0255868. https://doi.org/10.1371/journal.pone.0255868 (2022).
34. Baumgartner, M. F. *et al.* Low frequency vocalizations attributed to sei whales (*Balaenoptera borealis*). *J. Acoust. Soc. Am.***124**, 1339–1349. https://doi.org/10.1121/1.2945155 (2008).
35. Calderan, S. *et al.* Low-frequency vocalizations of sei whales (*Balaenoptera borealis*) in the Southern Ocean. *J. Acoust. Soc. Am.***136**(6), EL418–EL423. https://doi.org/10.1121/1.4902422 (2014).
36. Cerchio, S. & Weir, C. R. Mid-frequency song and low-frequency calls of sei whales in the Falkland Islands. *R Soc. Open. Sci.* **9**, 220738. https://doi.org/10.1098/rsos.220738 (2022).
37. Samaran, F. *et al.* Seasonal and geographic variation of southern blue whale subspecies in the Indian Ocean. *PLoS ONE***8**(8), e71561. https://doi.org/10.1371/journal.pone.0071561 (2013).
38. Shabangu, F. W., Yemane, D., Best, G. & Estabrook, B. J. Acoustic detectability of whales amidst underwater noise off the west coast of South Africa. *Mar. Pollut Bull.***184**, 114122. https://doi.org/10.1016/j.marpolbul.2022.114122 (2022).
39. Rintoul, S. R. Antarctic circumpolar current. In *Encyclopedia of ocean sciences* 2nd edn, Vol. 4 (eds Steele, J. H. *et al.*) 178–190 (Academic, London, UK, 2011).
40. Lamont, T., van den Berg, M. A., Tutt, G. C. O. & Ansorge, I. J. Impact of deep-ocean eddies and fronts on the shelf seas of a sub-Antarctic Archipelago: the Prince Edward Islands. *Cont. Shelf Res.* **177**, 1–14. https://doi.org/10.1016/j.csr.2019.03.001 (2019).
41. Toolsee, T. & Lamont, T. Long-term trends and interannual variability of wind forcing, surface circulation, and temperature around the sub-Antarctic Prince Edward Islands. *Remote Sens.* **14**, 1318. https://doi.org/10.3390/rs14061318 (2022).
42. Reisinger, R. R. *et al.* Predator-derived bioregions in the Southern Ocean: characteristics, drivers and representation in marine protected areas. *Biol. Conserv.* **272**, 109630. https://doi.org/10.1016/j.biocon.2022.109630 (2022).

43. Sakai, T. PAMmisc: Miscellaneous functions for passive acoustic analysis. R package version 1.9.2; (2022). https://CRAN.R-project.org/package=PAMmisc
44. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; (2023). https://www.R-project.org/
45. K. Lisa Yang Center for Conservation Bioacoustics. *Raven Pro: Interactive Sound Analysis Software [Computer software]* (The Cornell Lab of Ornithology, 2022). https://ravensoundsoftware.com/
46. Širović, A., Williams, L. N., Kerosky, S. M., Wiggins, S. M. & Hildebrand, J. A. Temporal separation of two fin whale call types across the Eastern North Pacific. *Mar. Biol.* **160**, 47–57. https://doi.org/10.1007/s00227-012-2061-z (2013).
47. Thomisch, K. *et al.* Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea. *Endanger. Species Res.* **30**, 239–253. https://doi.org/10.3354/esr00739 (2016).
48. Shabangu, F. W. & Kowarski, K. A. The beat goes on: humpback whale song seasonality in Antarctic and South African waters. *Front. Mar. Sci.* **9**, 827324. https://doi.org/10.3389/fmars.2022.827324 (2022).
49. Narganes Homfeldt, T., Risch, D., Stevenson, A. & Henry, L. A. Seasonal and diel patterns in singing activity of humpback whales migrating through Bermuda. *Front. Mar. Sci.***9**, 941793. https://doi.org/10.3389/fmars.2022.941793 (2022).
50. Buchan, S. J. *et al.* Distribution of blue and sei whale vocalizations, and temperature – salinity characteristics from glider surveys in the Northern Chilean Patagonia megaestuarine system. *Front. Mar. Sci.* **9**, 903964. https://doi.org/10.3389/fmars.2022.903964 (2022).
51. Thieurmel, B. & Elmarhraoui, A. suncalc: compute sun position, sunlight phases, moon position and lunar phase. R package version 0.5.0. See (2019). https://CRAN.R-project.org/package=suncalc
52. Heaney, K. D. & Campbell, R. L. Three-dimensional parabolic equation modeling of mesoscale eddy deflection. *J. Acoust. Soc. Am.***139**(2), 918–926. https://doi.org/10.1121/1.4942112 (2016).
53. Wentworth, C. K. A scale of grade and class terms for clastic sediments. *J. Geol.* **30**(5), 377–392 (1922).
54. Branch, G. M., Attwood, C. G., Gianakouras, D. & Branch, M. L. Patterns in the benthic communities on the shelf of the sub-Antarctic Prince Edward Islands. *Polar Biol.* **13**, 23–34. https://doi.org/10.1007/BF00236580 (1993).
55. Locarnini, R. A. *et al.* World Ocean Atlas 2023, Volume 1: Temperature. A. Mishonov (Technical Ed.) NOAA Atlas NESDIS NOAA Atlas NESDIS 89, 52 pp. (2024). https://doi.org/10.25923/54bh-1613
56. Shabangu, F. W. *et al.* Killer whale acoustic patterns respond to prey abundance and environmental variability around the Prince Edward Islands, Southern Ocean. *R Soc. Open. Sci.* **10**, 230903. https://doi.org/10.1098/rsos.230903 (2024).
57. Torterotot, M., Samaran, F. & Royer, J. Y. Long-term acoustic monitoring of nonstereotyped blue whale calls in the Southern Indian Ocean. *Mar. Mamm. Sci.***39**(2), 594–610. https://doi.org/10.1111/mms.12998 (2023).
58. Filun, D. *et al.* Frozen verses: Antarctic minke whales (*Balaenoptera bonaerensis*) call predominantly during austral winter. *R Soc. Open. Sci.* **7**, 192112. https://doi.org/10.1098/rsos.192112 (2020).
59. Samaran, F., Adam, O. & Guinet, C. Detection range modeling of blue whale calls in Southwestern Indian Ocean. *Appl. Acoust.* **71**, 1099–1106. https://doi.org/10.1016/j.apacoust.2010.05.014 (2010).
60. Breiman, L. Random forests. *Mach. Learn.***45**, 5–32. https://doi.org/10.1023/A:1010950718922 (2001).
61. Shabangu, F. W., Yemane, D., Stafford, K. M., Ensor, P. & Findlay, K. P. Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales. *PLOS ONE* **12**, e0172705. https://doi.org/10.1371/journal.pone.0172705 (2017).
62. Ziegler, A. & König, I. R. Mining data with random forests: current options for real-world applications. *WIREs Data Min. Knowl. Discov***4**, 55–63. https://doi.org/10.1002/widm.1114 (2014).
63. Hastie, T. J., Tibshirani, R. & Friedman, J. *The elements of statistical learning* (Springer, 2009).
64. Altmann, A., Tolos, L., Sander, O. & Lengauer, T. Permutation importance: a corrected feature importance measure. *Bioinformatics***26**(10), 1340–1347. https://doi.org/10.1093/bioinformatics/btq134 (2010).
65. Leroy, E. C., Samaran, F., Bonnel, J. & Royer, J. Y. Seasonal and diel vocalization patterns of Antarctic blue whale (*Balaenoptera musculus intermedia*) in the Southern Indian Ocean: a multi-year and multi-site study. *PLoS ONE* **11**(11), e0163587. https://doi.org/10.1371/journal.pone.0163587 (2016).
66. Tripovich, J. S. *et al.* Temporal segregation of the Australian and Antarctic blue whale call types (*Balaenoptera musculus* spp). *J. Mammal* **96**, 603–610. https://doi.org/10.1093/jmammal/gyv065 (2015).
67. Aulich, M. G. *et al.* Diel patterns of fin whale 20 Hz acoustic presence in eastern Antarctic waters. *R Soc. Open. Sci.* **10**, 220499. https://doi.org/10.1098/rsos.220499 (2023).
68. Gurney, L. J. Feeding biology of three euphausiid species in the vicinity of the Prince Edward Archipelago (Southern Ocean). Master of Science thesis, Rhodes University, Grahamstown, South Africa (2000).
69. Au, W. W. L., Mobley, J., Burgess, W. C., Lammers, M. O. & Nachtigall, P. E. Seasonal and diurnal trends of chorusing humpback whales wintering in waters off Western Maui. *Mar. Mamm. Sci.* **16**(3), 530–544. https://doi.org/10.1111/j.1748-7692.2000.tb00949.x (2000).
70. Leroy, E. C., Samaran, F., Stafford, K. M., Bonnel, J. & Royer, J. Y. Broad-scale study of the seasonal and geographic occurrence of blue and fin whales in the Southern Indian Ocean. *Endang Species Res.***37**, 289–300. https://doi.org/10.3354/esr00927 (2018).
71. Åsvestad, L. *et al.* Seasonal acoustic presence of marine mammals at the South Orkney Islands, Scotia Sea. *R Soc. Open. Sci.* **11**, 230233. https://doi.org/10.1098/rsos.230233 (2024).
72. Samaran, F., Adam, O. & Guinet, C. Discovery of a mid-latitude sympatric area for two Southern Hemisphere blue whale subspecies. *Endanger. Species Res.* **12**, 157–165. https://doi.org/10.3354/esr00302 (2010).
73. Stafford, K. M., Chapp, E., Bohnenstiel, D. R. & Tolstoy, M. Seasonal detection of three types of pygmy blue whale calls in the Indian Ocean. *Mar. Mamm. Sci.***27**, 828–840. https://doi.org/10.1111/j.1748-7692.2010.00437.x (2011).
74. Ichihara, T. The pygmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic. In Whales, dolphins, and porpoises (ed Norris, K. S.) 79–111 (University of California Press (1966).
75. Branch, T. A. & Monnahan, C. C. Sex ratios in blue whales from conception onward: effects of space, time, and body size. *Mar. Mamm. Sci.***37**, 290–313. https://doi.org/10.1111/mms.12741 (2021).
76. Buss, D. L. *et al.* Evidence of resource partitioning between fin and sei whales during the twentieth-century whaling period. *Mar. Biol.***169**, 150. https://doi.org/10.1007/s00227-022-04131-x (2022).
77. Friedlaender, A. S. *et al.* Sympatry and resource partitioning between the largest krill consumers around the Antarctic Peninsula. *Mar. Ecol. Prog Ser.* **669**, 1–16. https://doi.org/10.3354/meps13771 (2021).
78. Froneman, P. W., Ansorge, I., Pakhomov, E. A. & Lutjeharms, J. R. E. Plankton community structure in the physical environment surrounding the Prince Edward Islands (Southern Ocean). *Polar Biol.* **22**, 145–155. https://doi.org/10.1007/s003000050404 (1999).
79. Hunt, B. P. V. & Pakhomov, E. A. Mesozooplankton interactions with the shelf around the sub-Antarctic Prince Edward Islands Archipelago. *J. Plankton Res.* **25**(8), 885–904. https://doi.org/10.1093/plankt/25.8.885 (2003).
80. Elwen, S. *et al.* Cetacean diversity of the eastern South Atlantic Ocean and Vema Seamount detected during a visual and passive acoustic survey, 2019. *J. Mar. Biol. Assoc. U K* **103**, e41. https://doi.org/10.1017/S0025315423000255 (2023).
81. van Opzeeland, I., van Parijs, S., Kindermann, L., Burkhardt, E. & Boebel, O. Calling in the cold: pervasive acoustic presence of humpback whales (*Megaptera novaeangliae*) in Antarctic coastal waters. *PLoS ONE* **8**(9), e73007. https://doi.org/10.1371/journal.pone.0073007 (2013).
82. Gamliel, I. *et al.* Incorporating physiology into species distribution models moderates the projected impact of warming on selected Mediterranean marine species. *Ecography* **43**, 1090–1106. https://doi.org/10.1111/ecog.04423 (2020).

83. Chambault, P. *et al.* Sea surface temperature predicts the movements of an Arctic cetacean: the bowhead whale. *Sci. Rep.* **8**, 9658. https://doi.org/10.1038/s41598-018-27966-1 (2018).

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Author contributions
F.W.S. conceptualized and designed this study with input from T.M., L.V.U., B.J.E., D.Y., K.M.S., T.A.B., E.V., M.A.v.d.B. and T.L; F.W.S., M.A.v.d.B. and T.L. conducted the passive acoustic monitoring data collection; F.W.S. analysed the acoustic datasets; B.J.E. conducted the underwater noise measurement; T.M. conducted the acoustic propagation modelling with input from F.W.S. and L.V.U.; F.W.S., D.Y. and T.L. acquired and processed environmental data; F.W.S. and D.Y. conducted statistical data analysis; F.W.S., L.V.U., K.M.S., T.A.B., E.V., M.A.v.d.B. and T.L. applied and secured funding to conduct the field work; F.W.S. led the writing of the manuscript with input from T.M., L.V.U., D.Y., B.J.E., K.M.S., T.A.B., E.V., M.A.v.d.B. and T.L. All authors approved the submitted version.

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Declarations

Competing interests
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