Polar Biology (2021) 44:433–450
https://doi.org/10.1007/s00300-021-02804-9

ORIGINAL PAPER

Summer circumpolar acoustic occurrence and call rates of Ross, *Ommatophoca rossii*, and leopard, *Hydrurga leptonyx*, seals in the Southern Ocean

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Received: 5 December 2019 / Revised: 21 December 2020 / Accepted: 23 December 2020 / Published online: 29 January 2021

Abstract

Two of the Antarctic pack ice seals, Ross, *Ommatophoca rossii*, and leopard, *Hydrurga leptonyx,* seals, are extremely difficult to study via traditional visual survey techniques, yet are ideal for an acoustic survey as they are highly vociferous and produce an array of underwater sounds during the austral summer. To determine their acoustic occurrence in the Antarctic pack ice, we use their calls, detected within 680 acoustic recordings made between 1999 and 2009 as part of two multinational programmes. Siren calls of Ross seals were detected mainly in January, and 9.88 calls per minute from low siren calls was the highest call rate for this species. High numbers of Ross seal calls were detected close to the ice edge in areas between 0° and 20° E and 60° and 130° E, suggesting these are important summer habitats. Leopard seal calls were detected mainly in December and January, and December had the highest percentage of calls. Call rate of 11.93 calls per minute from low double trills was the highest call rate for leopard seals. Leopard seal calls were detected throughout the Southern Ocean with more calls detected throughout the pack ice. There was little spatio-temporal overlap in call occurrence of Ross and leopard seals, but both species were more vocally active during the day. Longitude and latitude were the most important predictors of Ross seal occurrence, and month of the year highly predicted leopard seal occurrence. This is the first study to examine the circumpolar acoustic occurrence of Ross and leopard seals in the Southern Ocean pack ice.

Keywords Antarctic pack ice seals · Diel calling behaviour · Animal calls · Antarctic · Passive acoustic survey · Circumpolar occurrence

Introduction

Ross, *Ommatophoca rossii,* and leopard, *Hydrurga leptonyx,* seals have a circumpolar distribution in the Southern Ocean, with Ross seals being the least studied of all the ice-inhabiting phocid seals (i.e. earless seals) due to their dispersed and isolated distribution (Thomas and Rogers 2009; Rogers 2009; Arcalís-Planas et al. 2015). There are four phocid seals in the Southern Ocean: the Ross seal, the leopard seal, the Weddell seal, *Leptonychotes weddellii*, and the crabeater seal, *Lobodon carcinophaga* (Siniff et al. 2008; Southwell et al. 2012). The Ross and leopard seal are particularly difficult to study via traditional visual survey techniques (Southwell et al. 2008a, b, 2012). This was evident from the outcome of the internationally coordinated research programme, the Antarctic Pack Ice Seal (APIS) project, that embarked to determine the distribution and abundance of the Ross (Southwell et al. 2008a, 2012) and leopard seal (Southwell et al. 2008b) by conducting circumpolar aerial and

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Supplementary Information The online version of this article (https://doi.org/10.1007/s00300-021-02804-9) contains supplementary material, which is available to authorized users.

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shipboard surveys, along with quantifying how many seals were missed from the survey by deploying satellite-linked dive recorders to study their haul-out behaviour (Southwell 2003). The authors from the APIS surveys' recognized that the visual surveys likely underestimated the population for the Ross and leopard seals relative to their true populations due to the uncommon or very cryptic nature of these seals (Southwell et al. 2008a, b, 2012). For example, where the Ross seal estimate was ~ 78,500 animals (Southwell et al. 2008a, 2012), genetic studies show that the effective population is likely much larger (i.e. ~ 254,500 individuals; Curtis et al. 2009, 2011). The Ross seal remains one of the least numerous and least studied of the Antarctic seals.

Ross seals are unavailable to traditional surveys because they tend to haul out in areas of dense pack ice during their breeding season (October and November) and these are areas not easily accessed by ships to survey (Southwell et al. 2008b, 2012). Leopard seals, during the austral summer, spend long periods underwater calling (Rogers and Bryden 1997; van Opzeeland et al. 2010; Rogers et al. 2013); while in the water they are unavailable to visual surveys (Southwell et al. 2008b; Rogers et al. 2013). However, as Ross and leopard seals vocalise for many hours underwater (van Opzeeland et al. 2010; Rogers et al. 2013), passive acoustic monitoring (i.e. seal vocalisations as a cue for acoustic presence) is a cost-effective method to identify their spatial distribution and habitat use (Rogers et al. 2013). The use of passive acoustic recording units to survey cryptic animals is an important tool for ecology and conservation biology, and ideal for these two pack ice seal species. Indeed, van Opzeeland et al. (2010), via continuous hydro-acoustic recordings, showed that Ross seals were seasonally present in the Weddell Sea between December 2006 and February 2007, which aligns with the migratory behaviour of satellite-tagged animals (Blix and Nordøy 2007).

Seals are important in the Southern Ocean ecosystem as they transfer nutrients from the primary consumers, at the base of the food chain, to their predator, killer whales, *Orcinus orca*, at the highest trophic level (Trites 1997; Pitman and Ensor 2003; Cherel and Hobson 2007; McMahon et al. 2013; Brault et al. 2019). While Ross seals feed for most of the year north of the pack ice (i.e. in the open ocean) on squid and fish, but also on krill, in low proportions (Rau et al. 1992; Skinner and Klages 1994; Thomas and Rogers 2009; Brault et al. 2019), most leopard seals remain within the Antarctic pack ice (Rogers et al. 2005; Meade et al. 2015). Leopard seals use a wide range of prey, including penguins and other seabirds (Rogers and Bryden 1995; Lowry et al. 1988), Antarctic krill, *Euphausia superba*, fish, squid and juveniles of other seal species (i.e. the Weddell, crabeater, southern elephant, *Mirounga leonina*, and fur seals, *Arctocephalus gazella*) (Hall-Aspland and Rogers 2004; Krause and Rogers 2019). Leopard seals may even switch their diet in response to seasonal and local changes in prey abundance and distribution (Hall-Aspland and Rogers 2004; Guerrero et al. 2016; Botta et al. 2018).

Ross seals, for most of the year, are pelagic and inhabit the open ocean north of the pack ice, but move south into the dense pack ice to pup, breed and moult (Blix and Nordøy 2007; Thomas and Rogers 2009; Southwell et al. 2012) whereas, leopard seals inhabit the Antarctic pack ice year-round (Rogers et al. 2005; Southwell et al. 2008b; Rogers 2009; Meade et al. 2015; Staniland et al. 2018). Compared to leopard seals, Ross seals are more vulnerable to sea ice loss due to climate change, since they are more dependent on the dense consolidated pack ice to rest, pup and avoid predators (Learmonth et al. 2006; Siniff et al. 2008; Bengtson et al. 2011). Although most leopard seals inhabit the Antarctic pack ice year-round (Rogers et al. 2005; Rogers 2009; Meade et al. 2015) some animals move north, out of the pack ice, to sub-Antarctic islands (Rogers 2009; Staniland et al. 2018). Leopard seals are more plastic in their substrate use; where they typically haul-out on the ice floes in the pack ice, they will also use sandy beaches of the sub-Antarctic islands and the southern continents (Rogers 2009).

These seal species produce loud underwater sounds (Stirling and Siniff 1979), with source levels of leopard seals ranging from 153 to 177 dB re 1μPa rms at 1 m (Rogers 2014) while the source levels of Ross seal calls are unknown (Erbe et al. 2017). Passive acoustic monitoring may be used as a cost-effective method to study the acoustic ecology and vocalizing behaviour of seals even in adverse weather conditions and in remote and sometimes inaccessible locations such as Antarctica (Kindermann et al. 2008; van Opzeeland et al. 2010; Rogers et al. 2013). The call detection ranges of both species remain unknown. There are currently 14 defined call types of leopard seals, but we report eight call types that were detected from our datasets: "high double trill", "medium single trill", "medium double trill", "low descending trill", "low ascending trill", "low double trill", "hoot with a single trill" and "hoot" (Stirling and Siniff 1979; Rogers and Bryden 1995; Rogers et al. 1996; van Opzeeland et al. 2010). Trills range in frequency from 150 Hz to 6 kHz and are 2 to 8.1 s in duration (Stirling and Siniff 1979; Rogers and Bryden 1995; Rogers et al. 1996); and lower-frequency burst-pulse sounds range in frequency from 50 Hz to 6 kHz and lasting 0.5–4.3 s (Rogers and Bryden 1995; Rogers et al. 1996). Sounds of leopard seals have been recorded from October through January in the Antarctic (Kindermann et al. 2008; van Opzeeland et al. 2010).

Some of the Ross seals' calls are termed siren calls as they sound like the police siren, and these call types are produced both in air and underwater (Watkins and Ray 1985). To date, five call types have been documented for Ross seals: "high siren call", "mid siren call", "low siren call", "tonal element call", "broadband element call" or "whoosh call"

(Watkins and Ray 1985; Kindermann et al. 2008; van Opzeeland et al. 2010). Very brief downsweeping pulses that range in frequency from 100 Hz to 1 kHz are produced both in air and underwater and can be 0.05–0.1 s per pulse in duration with 5–12 pulses in a sequence (Watkins and Ray 1985). Siren calls range from 100 to 800 Hz and last 1–1.5 s in air (Watkins and Ray 1985), but range from 100 Hz to 8 kHz and last 2–4 s underwater (Seibert 2007). In Antarctica, Ross seal sounds have been detected from December through February (Kindermann et al. 2008; van Opzeeland et al. 2010).

The enormous scale of the Antarctic pack ice makes surveying logistically difficult and expensive to identify the spatial distribution of the cryptic Ross and leopard seals. Here we identify the environmental drivers that best predict the summer acoustic occurrence (as a proxy of seal presence) of Ross and leopard seals across the circumpolar pack ice. We use seal vocalisations detected at up to 680 underwater recording sites, made over nine austral summers, throughout the Southern Ocean and environmental predictors: region (i.e. latitude, longitude, distance to the continent and the ice edge) and the time of day (i.e. diurnal changes in calling rates). We provide the first circumpolar description of the summer acoustic occurrence of the Ross and leopard seal in the Southern Ocean, and this information might be useful towards the establishment of marine protected areas to conserve and protect these species.

Methods

Acoustic data collection

Acoustic data were collected from two multinational programmes, International Whaling Commission's Southern Ocean Whale and Ecosystem Research (IWC-SOWER) Programme and the Scientific Committee on Antarctic Research's Antarctic Pack Ice Seal (SCAR-APIS) Programme, in the Southern Ocean:

IWC-SOWER Cruises

Acoustic datasets from the IWC-SOWER Programme were collected during the austral summer (i.e. December through February) between 1998/1999 and 2008/2009 (Table 1) in the Southern Ocean from 55° S to the ice edge (Table 1; Fig. 1). About 541 Direction Finding and Ranging sonobuoys and 27 towed or deployed hydrophones were used to record the acoustic data, and a total of 1458 h of acoustic files were recorded (Table 1). Ranges of latitudes and longitudes surveyed by each IWC-SOWER cruise are provided in Table 1. Information about hydrophone sensitivities is not available for recorders deployed during IWC-SOWER cruises, as sensitivities of these hydrophones were not provided by their donors. Acoustic data were recorded at a sampling rate of 48 kHz. The sonobuoy system consisted of an antenna, antenna cable, radio receiver, analog-to-digital converter and a recording system; no anti-alias filters were included. Acoustic data were recorded continuously until batteries of sonobuoys were depleted, or until it was time to resume the IWC-SOWER cetacean sighting surveys in the case of towed or deployed hydrophones. Acoustic data were collected at any time of the day (day and night time) but predominantly at night when IWC-SOWER sighting surveys were suspended; acoustic station lasted continuously from few minutes to 15 h.

Further details about the data collection and overview of the IWC-SOWER acoustic data can be found in Shabangu et al. (In press). Data from the 1996/1997 and 1997/1998 IWC-SOWER cruises were not considered in this study as no seal sounds were reported in the cruise reports (Fig. 1; Ensor et al. 1997, 1998). The acoustic component of the IWC-SOWER Programme was introduced to differentiate at sea between the morphological indistinguishable subspecies

Table 1 Summary of acoustic effort from IWC-SOWER cruises

Time of deployment	Latitude range (° S)	Longitude range (° E)	Number of deployments	Number of hours recorded
Jan–Feb 1999	− 65.23 to − 60.28	46.15 to 129.82	109	220.63
Dec 1999–Jan 2000	− 70.47 to − 60.36	− 80.20 to − 57.21	60	198.32
Dec 2001–Jan 2002	− 66.39 to − 60.22	129.95 to 151.88	20	64.30
Dec 2002–Feb 2003	− 68.73 to − 60.02	150.88 to − 170.01	56	165.12
Dec 2003–Feb 2004	− 78.30 to − 60.52	159.78 to − 161.22	63	210.23
Dec 2005–Feb 2006	− 69.66 to − 55.12	0.32 to 19.89	127	231.40
Dec 2006–Feb 2007	− 69.88 to − 55.99	0.03 to 11.62	51	76.32
Dec 2007–Feb 2008	− 65.43 to − 61.09	105.06 to 118.72	59	251.77
Jan–Feb 2009	− 64.98 to − 63.53	82.10 to 92.10	23	40
Total	–	–	568	1458.09

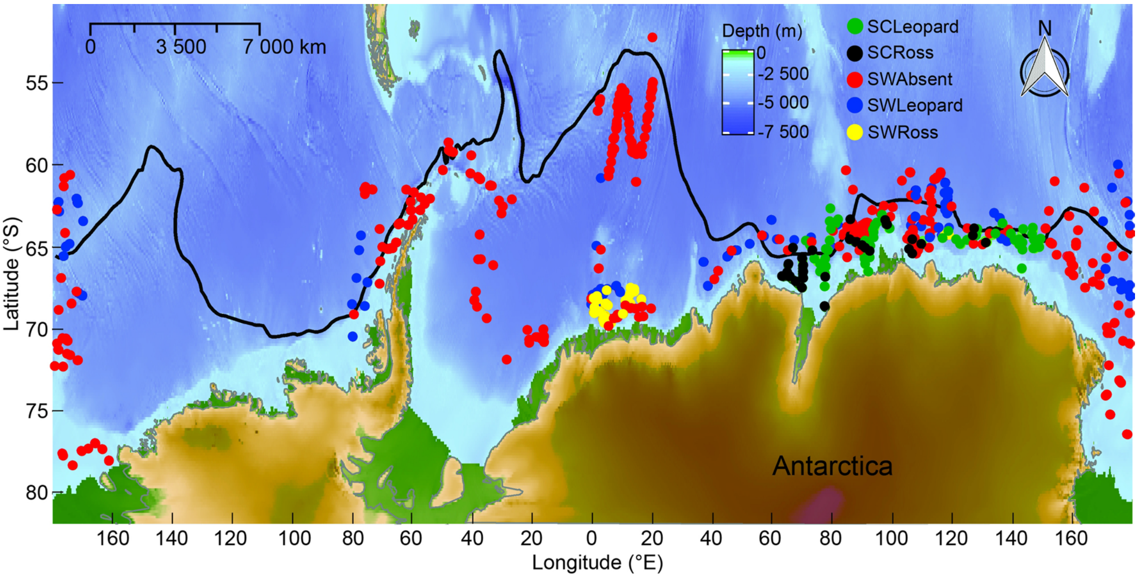

Fig. 1 Acoustic absence and presence of Ross and leopard seals from the IWC-SOWER and SCAR-APIS cruises in the Southern Ocean. The black line represents the Southern Boundary of the Antarctic Circumpolar Current as defined by Orsi et al. (1995). SCRoss is Ross seal presence from the SCAR-APIS cruise, SCLeopard is leopard seal presence from the SCAR-APIS cruise, SWAbsent is acoustic absence of seals from IWC-SOWER cruises, SWLeopard is leopard seal presence from IWC-SOWER cruises, and SWRoss is Ross seal presence from IWC-SOWER cruises. All sonobuoys from the SCAR-APIS cruise produced presence of either species, therefore no SCAbsent. SCRoss indicating acoustic presence of Ross seals are overlaid on top of leopard seal circles where the two species were concurrently detected on the same sonobuoy deployment. Sonobuoy deployments between 16° and 56° W are from 1996/1997 and 1997/1998 IWC-SOWER cruises

of blue whales (Donovan et al. 1996), the Antarctic and pygmy blue whales, *Balaenoptera musculus*. Sonobuoys were deployed either in the presence of whales during the day or blindly without knowledge of the presence of whales at night. Seal calls were incidentally recorded whilst listening for these large baleen whales, and no efforts were made at sea to identify the seal calls to a species level. No acoustic data were collected during the 2000/2001, 2004/2005 and 2009/2010 IWC-SOWER cruises (Ensor et al. 2001, 2005; Sekiguchi et al. 2010).

SCAR-APIS cruise

The acoustic dataset from the SCAR-APIS Programme consisted of 112 underwater passive acoustic recordings made remotely at fixed points using sonobuoys [Sparton Electronics AN/SSQ-57A, mean sensitivity: − 155.20 (range: − 158.50 to − 151.00) dB re 1 V μPa^{-1})] in the Southern Ocean from 4 December 1999 to 12 January 2000 within the pack ice between 64° 31′ S; 62° 42′ E and 67° 17′ S; 149° 31′ E (Rogers et al. 2013; Fig. 1). Sonobuoys sampled over 10 Hz to 22 kHz and had omni-directional hydrophone that had been deployed to a depth of 18 m below the water's surface. Signals were received on the survey platform, the mast of the RSV Aurora Australis, using two, 9-element custom-built stainless steel Yaggi antennas (YH09, RF Industries Pty Ltd) with a series of AR2001 receivers (AOR Ltd, AR 2001). Antennas were secured at a height of 30 m above the sea level. The ship was on survey mode during sonobuoy deployment and kept steaming through the sea ice conducting visual search for seals until the radio signal was lost (Rogers et al. 2013). No anti-aliasing filters were used during data collection. The acoustic signal was recorded using a Sony Digital Audio Tape recorder (DAT TCD-D8) with a frequency response from 10 Hz to 22 kHz ± 3 dB. Recordings were randomly made throughout the day and were from at least 30-min to 2 h in duration depending on the amount of time the ship remained within range of detecting the signal from sonobuoys.

Identification of seal calls

Call occurrence and call rates

Analyses of the acoustic data for calls of Ross and leopard seals were performed on IWC-SOWER cruises from 1998/1999 through 2008/2009, and information on all acoustic stations was derived from cruise reports (Ensor et al. 1999, 2000, 2002, 2003, 2004, 2006, 2007, 2008, 2009). Calls of Ross and leopard seals were visually detected using spectrograms and scrutinized aurally when calls were visually identified in Raven Pro (version 1.5; Bioacoustics

Research Program 2017). For analyses of acoustic data for calls of Ross and leopard seals performed on SCAR-APIS data, the number of calls within at least 30-min recording period was counted by a manual observer using Signal 3.1 (Engineering Design, Belmont, USA) and SpectraPRO 3.32 (Sound Technology Inc., USA). The first 10-15 min of the SCAR-APIS recordings were ignored, as ship noise (propeller cavitation) masked the signal. IWC-SOWER acoustic data collected from 1998/1999 through 2002/2003 cruises were downsampled (i.e. reduce the sample rate) from 48 to 1 kHz to improve the frequency resolution and the fast Fourier transform (FFT) length for the studying of low-frequency sounds of baleen whales, and the non-downsampled acoustic data could not be reconciled as they are likely lost (Shabangu et al. In press). Thus, only sounds below 500 Hz were detected for those earlier years of the IWC-SOWER Programme. As a result of the above Nyquist frequency in earlier years of the IWC-SOWER Programme, high double trills, low ascending trills and medium trills were not detectable while the lower components of the frequency content of low descending trills, low double trills, hoots and hoots with single trills were detected for leopard seals (Fig. 2a). All call types of Ross seals were not detected during IWC-SOWER cruises prior to 2003/2004.

Ross and leopard seal calls were evaluated to a maximum frequency of 5 kHz (Fig. 2) in later years (i.e. 2003/2004 onwards) of the IWC-SOWER Programme, and detected calls were used to determine the acoustic presence of seals. To determine the acoustic presence of Ross seals, we used the low, mid and high siren calls (Fig. 2b), as characterised

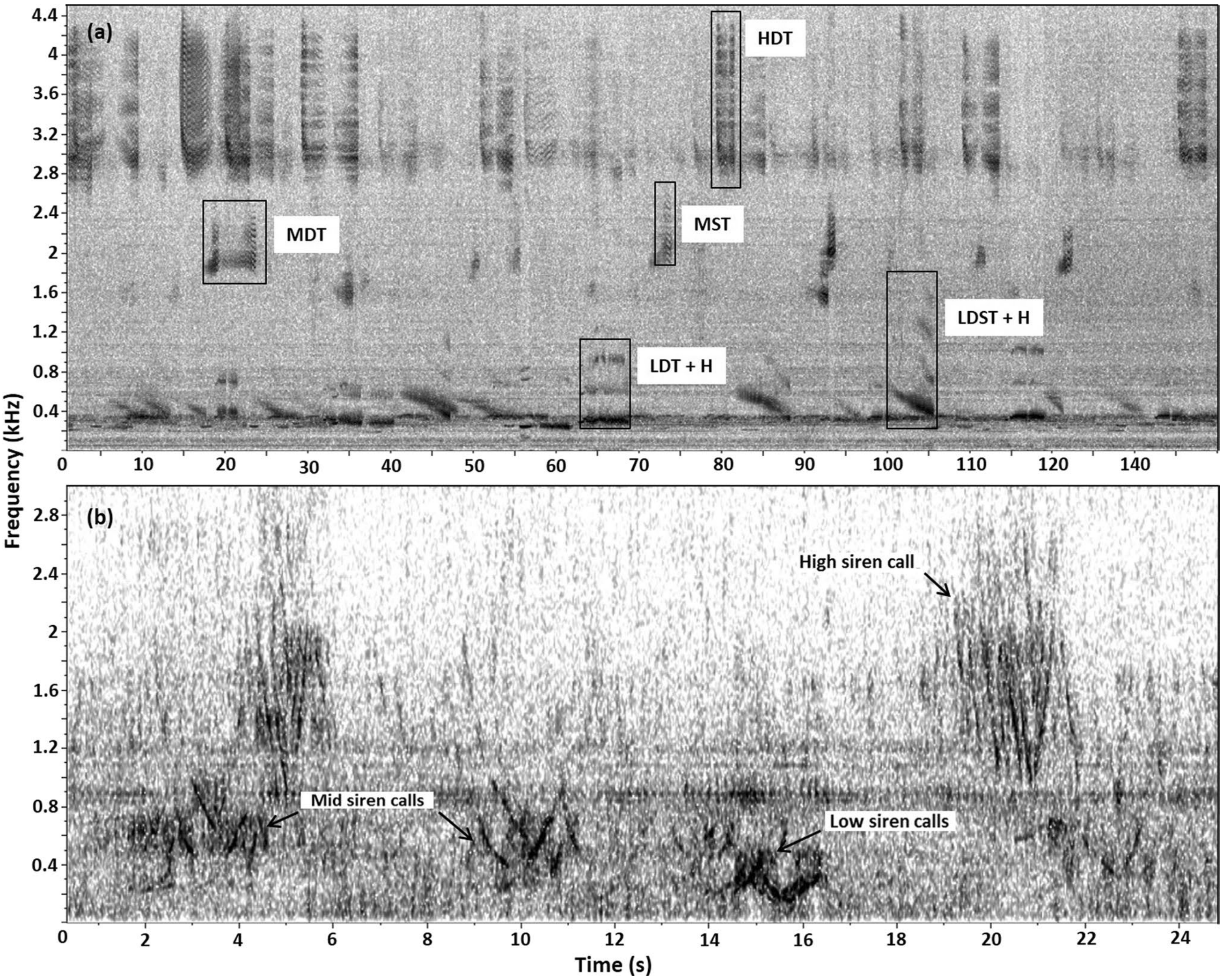

Fig. 2 Exemplary spectrograms showing low descending trills with harmonics (LDST + H), low double trills with harmonics (LDT + H), medium double trill (MDT), medium single trill (MST) and high double trills (HDT) of leopard seals in rectangles (**a**); low, mid and high siren calls of Ross seals (**b**). Note difference in the x- and y-axes scales. Spectrogram parameters: **a** frame size 0.11 s, 50% overlap, FFT size 8192 points, Hann window; **b** frame size 0.07 s, 50% overlap, FFT size 4096 points, Hann window

by Seibert (2007). Low ascending and descending trills, medium single and double trills, hoot and hoot with a single trill, low and high double trills (Fig. 2a) were used to determine the acoustic presence of leopard seals. Overlapping Ross seal siren calls, likely from multiple seals, were sometimes observed (Fig. 2b) and where possible they were differentiated. Thus, it is possible that call numbers were underestimated during periods of call overlap. Likewise, the same issue was faced during instances when there were high rates of leopard seal low double trill calls. Calls of Ross and leopard seals were manually counted to estimate call rates.

Acoustic presence of each seal species was defined as the detection of at least one call type within an acoustic station. Acoustic station refers to the deployment of a sonobuoy at a particular location for a given amount of time, where station duration ranged from minutes to hours. Locations of acoustic stations were used as a proxy for calling seals, taking into account available detection ranges of other phocid seals (see the "Discussion" section for more details). Acoustic absence refers to instances when seal calls were not detected within an acoustic station. Acoustic occurrence of seals was defined by acoustic absence and presence. Percentages of acoustic occurrence of each seal species were calculated as the number of acoustic stations with seal call presences divided by the total number of acoustic stations recorded per month. Call rates were calculated as the number of calls detected in an acoustic station divided by the duration (in minutes) of the acoustic station, to produce call rates as calls per minute.

Digital artefacts

Spurious harmonics together with inverted "reflections" of harmonics of all call types of both leopard and Ross seals were observed in the high-frequency bands of most IWC-SOWER acoustic files (Electronic Supplementary Material Fig. 1), and those were not counted for the calculation of call rates. The frequency band of the spurious harmonics varied between different IWC-SOWER cruises. Spurious harmonics are due to clipped waveform of individual digital sample points that were visible in the amplitude plot where the crests and troughs of waveforms were clipped (Electronic Supplementary Material Fig. 1). Waveform clipping of sound amplitudes occurs when the magnitude of the original waveform from a received sound exceeds the maximum magnitude that a hydrophone digitizer can characterize and record within its bit depth (Charif et al. 2010). Aliasing was observed in IWC-SOWER acoustic files that were downsampled from 48 kHz sample rate to 1 kHz, which resulted in the erroneous appearance of calls at a lower frequency than the frequencies at which those sounds originally occurred (Electronic Supplementary Material Fig. 2). Aliased calls were discounted during the count of calls and calculations of call rates.

Environmental variables

Distance to the sea ice edge and coastline

Distance (km) of sonobuoy locations to the sea ice edge (the outer pack ice sea ice edge) was computed to determine the dependence of seals on sea ice. Shapefiles of positions of monthly averaged sea ice extent from December to February of 1997 through 2009 were obtained from National Snow and Ice Data Center (ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/south/monthly/shapefiles/shp_extent/). We used the "lwgeom" package (Pebesma 2020) in R (version 4.0.1; R Core Team 2020) to calculate the distance (km) of each sonobuoy position to the monthly sea ice edge position for that month and year. We calculated the distance (km) to the nearest Antarctic coastline using custom-developed functions in R to measure the shortest distance to the Antarctic coastline from each sonobuoy deployment location.

Water depth

Water depth (m) for each sonobuoy station was used to indicate how ocean circulation (direction of major ocean currents, bathymetry-induced upwelling and climate change) in the Southern Ocean (Rintoul 2009) might influence the acoustic occurrence of seals. Bathymetry data were attained from the ETOPO1 global relief model (Amante and Eakins 2009) using the "marmap" package (Pante and Simon-Bouhet 2013) in R. Functions of "marmap" were used to process the acquired water depth and merge with the acoustic data.

Daylight regime

Daylight regimes for diel call rate plots and for describing the predictors of acoustic occurrence were obtained from the United States Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil) for the austral summer (December–February) in the Southern Ocean. Daylight regimes were defined according to the altitude of the sun (day and night time) based on averages of hourly altitudes over the austral summer. Nautical twilight (dawn and dusk) does not exist in the Southern Ocean during summer. Daytime hours were defined as when the geometric centre of the sun was less than 12° below the horizon, and night-time hours were when the centre of the sun was greater than 12° below the horizon. Diel mean call rates for each month were smoothed through penalized cyclic cubic regression splines (Wood 2017) in generalized additive model (GAM; Guisan et al. 2002), since time of day is a circular variable.

Modelling the acoustic occurrence

Random forest (RF) modelling approach (Ho 1995; Breiman 2001) was used to investigate the influence of predictor variables (i.e. distance to the sea ice edge, time of day, month of the year, longitude, latitude, distance to nearest Antarctic coastline and water depth) on the summer acoustic occurrence of Ross and leopard seals. We chose the RF model for this study due to its nonparametric inferential parameters (meaning the model does not assume any distribution of the data) and its ability to perform classification functions (Breiman 2001; Hastie et al. 2009). Additionally, previous studies of Shabangu et al. (2017, 2019) found RF models to have higher predictive capabilities than GAM and generalised boosted regression trees model (Ridgeway 1999) for modelling the acoustic occurrence of other marine mammals. Using generalized variance inflation factors (GVIFs; Fox and Monette 1992) to test for multicollinearity between the above predictor variables, we did not eliminate any of our predictor variables as no collinearity was found between our predictor variables prior to fitting the RF models as the highest calculated GVIF value was 1.83 (indicating no or weak correlation).

Optimal parameter settings for each RF model used to investigate the effect and importance of predictors on Ross and leopard seal acoustic occurrence were estimated using the 'ranger' package (Wright and Ziegler 2017) as a computational time-saving method for implementing RF models.

The area under the receiver operating characteristic curve was used to measure the predictive accuracy of each RF model with different combinations of parameter configurations as detailed in Shabangu and Andrew (2020). Optimal parameter configurations for each RF model used in this study are given in Table 2. The 'randomForest' package (Liaw and Wiener 2002) was used to accomplish the RF modelling in R while applying the above estimated optimal parameters. We estimated the relative importance of each of the variables in RF models using the method of permuting the out-of-the-bag data as described in Shabangu et al. (2017, 2019). To allow easier interpretation of our RF models, we tested for significance (p-value) of each feature importance values using the permutation method of Altmann et al. (2010).

Table 2 Optimal RF model settings used for predicting the acoustic occurrence of Ross and leopard seals

RF model for acoustic occurrence	Mtry	Ntree	Node size
Leopard seal occurrence	1	1000	1
Ross seal occurrence	1	500	1

Mtry is the number of acoustic occurrence randomly selected at each tree node; ntree is the number of growing trees; node size is the splitting minimum size of terminal nodes of trees

Results

Observed acoustic occurrence of seals

Detection results of seal sounds from IWC-SOWER cruises are presented together with those of the 1999/2000 SCAR-APIS cruise since both cruises used similar sampling methods. Sounds of leopard seals were detected from the ice edge to the open ocean at 60° S in close association with sub-Antarctic Circumpolar Current, whereas Ross seals were detected more close to the ice edge to the open ocean at 63.35° S and mainly in areas between 0°–20° E and 60°–30° E (Fig. 3). Quantitatively, there was very little spatio-temporal overlap in the acoustic occurrences of Ross and leopard seals as both species were simultaneously recorded only in 46 acoustic stations (out of 680 acoustic stations) in December 1999, and January 2000 and 2006, between 0°–20° E and 60°–130° E (Figs. 3 and Fig. 4). Percentage of acoustic occurrence of leopard seals was highest in December 1999 and 2003; January 2006 had the lowest acoustic occurrence of leopard seals (Fig. 4). Ross seal sounds were detected in December 1999 and Januaries of 2000, 2006, 2007 and 2008; January 2000 had the highest percentage of acoustic occurrence (Fig. 4). Sounds of Ross seals were not detected in February, whereas few leopard seal sounds were detected in February 2000 (Fig. 4). No sounds of both seal species were detected from the 2008/2009 IWC-SOWER cruise (Fig. 4), and this cruise will be excluded in future discussions. There was a poor correlation [Pearson's correlation coefficient $(r) = 0.36$] between the presence and absence reported in the cruise reports and those found during this study's acoustic data analyses. There is a gap in the acoustic data collected between 85° and 160° W (Figs. 1 and 3).

Call numbers and monthly call rates

A total of 44,789 calls of Ross seals were counted, where 18,836 calls were low siren calls, 10,181 calls were mid siren calls, and 15,772 calls were high siren calls (Table 3). For Ross seals, high siren calls were detected in slightly more hours than mid siren calls; low siren calls were detected in slightly fewer hours (Table 3). For December 1999 and January 2000, high siren calls were detected in high percentages > 50% of acoustic occurrence, mid siren calls had the second highest percentage of occurrence in December 1999 while low and mid siren calls had equal percentages in January 2000 (Fig. 5). Low, mid and high siren calls were detected in equal proportions for January 2006 through 2008 (Fig. 5). No Ross seal sounds were detected from earlier years of the IWC-SOWER Programme (Fig. 5).

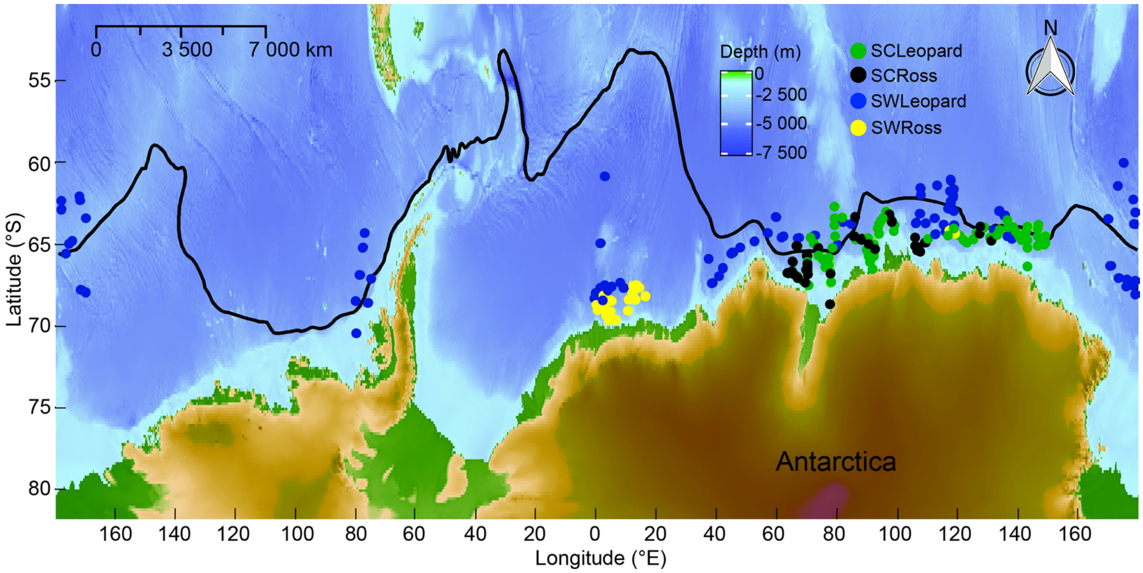

Fig. 3 Acoustic presence only of Ross and leopard seals from IWC-SOWER and SCAR-APIS cruises in the Southern Ocean. Definitions of sound keys in the plot are the same as provided in Fig. 1 caption

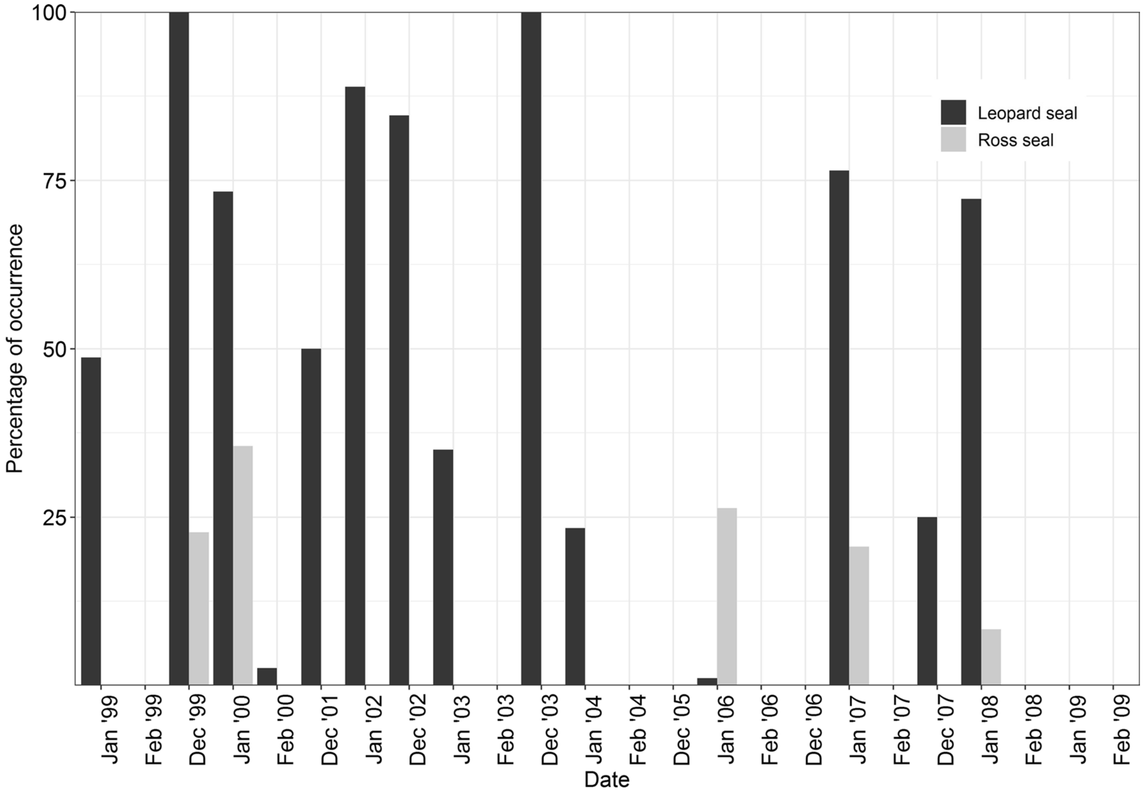

Fig. 4 Percentage of acoustic occurrence of Ross and leopard and seals during summer in the Southern Ocean from 1999 to 2009

A total of 108,245 calls of leopard seals were detected, where low double trills contributed the highest number of calls and medium double trills had the lowest number of calls (Table 3). For leopard seals, low double trills were detected in more hours, low descending trills were detected in the second highest hours, and medium double

Table 3 Total number of detected calls and hours of acoustic data with calls of Ross and leopard seals

Species	Call types	Number of calls	Hours with calls
Leopard seals	Low ascending trills	1616	79
	Low descending trills	7669	491
	Low double trills	81,517	627
	Medium single trills	1156	109
	Medium double trills	231	53
	Hoot	339	219
	Hoot with a low single trill	9292	270
	High double trills	6425	104
Ross seals	Low siren calls	18,836	99
	Mid siren calls	10,181	101
	High siren calls	15,772	112

A total of 1458 h of recordings are from the IWC-SOWER cruises and 79 h of recordings from the 1999/2000 SCAR cruise

trills were detected in fewer hours (Table 3). Low double trills were the most commonly detected call type for leopard seals in most surveys and medium double trills were the least detected (Fig. 5).

For Ross seals, the median call rate of 2.78 calls per minute for low siren calls from January 2006 was the highest median call rate for this species (Fig. 6). Low siren calls yielded the highest call rate of 9.88 calls per minute in January 2006 for Ross seals (Fig. 6). No Ross seal calls were detected from the 2001/2002 through 2003/2004 cruises, thus the median call rate is zero (Fig. 6). For leopard seals, the highest median call rate was 5.21 calls per minute observed for low double trills in January 2007 (Fig. 6). The call rate of 11.93 calls per minute from low double trills in January 1999 was the highest observed call rate for leopard seals (Fig. 6).

Diel calling patterns

Call rates of Ross seal low, mid and high siren calls did not change throughout the day in December (Fig. 7a). During December, call rates of leopard seal low descending trills,

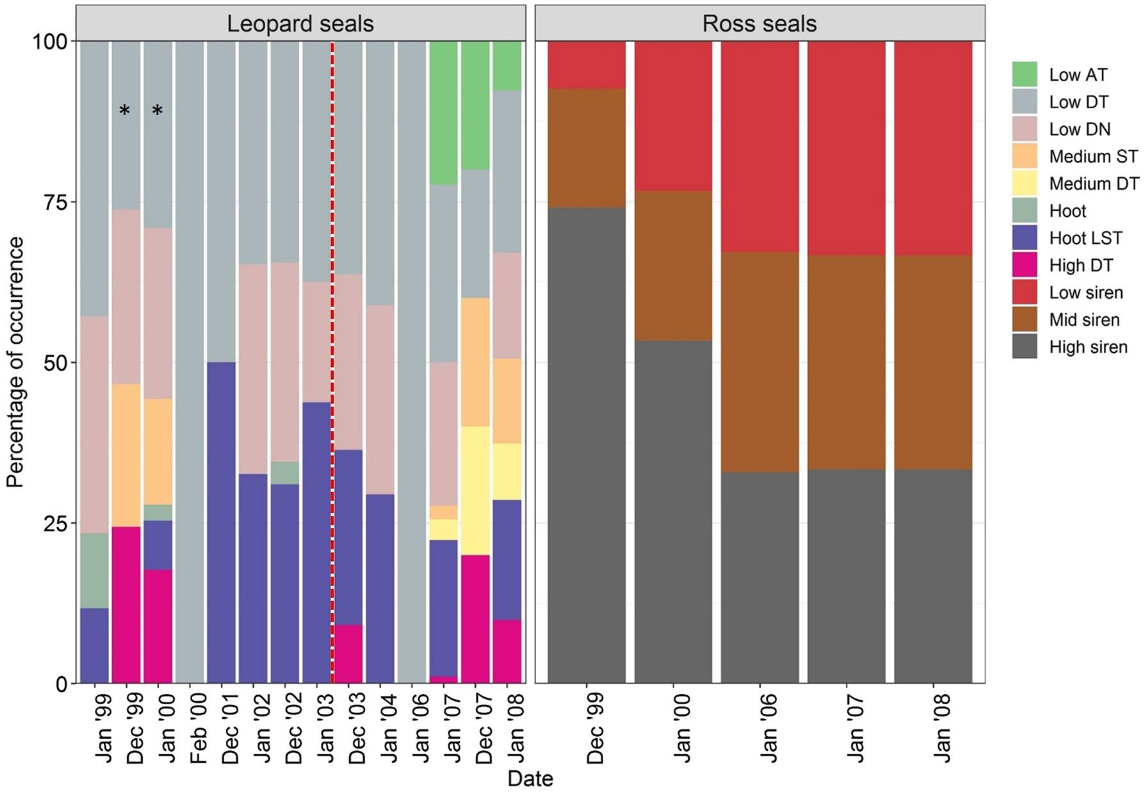

Fig. 5 Monthly percentage of call type occurrence of leopard (left panel) and Ross (right panel) seals per year. The red vertical line indicates the end of years with calls below 500 Hz prior to 2003/2004 due to downsampling of acoustic files to 1 kHz sampling rate, and * represents percentages of call types from the non-downsampled data of the SCAR-APIS cruise. Bar colour shading represents leopard seal call types: LowAT are low ascending trills; Low DT are low double trills; Low DN are low descending trills; Medium ST are medium single trills; Medium DT are medium double trills; Hoot LST are hoot with a low single trill; High DT are high double trills; names of Ross seal call types are given in full on the legend

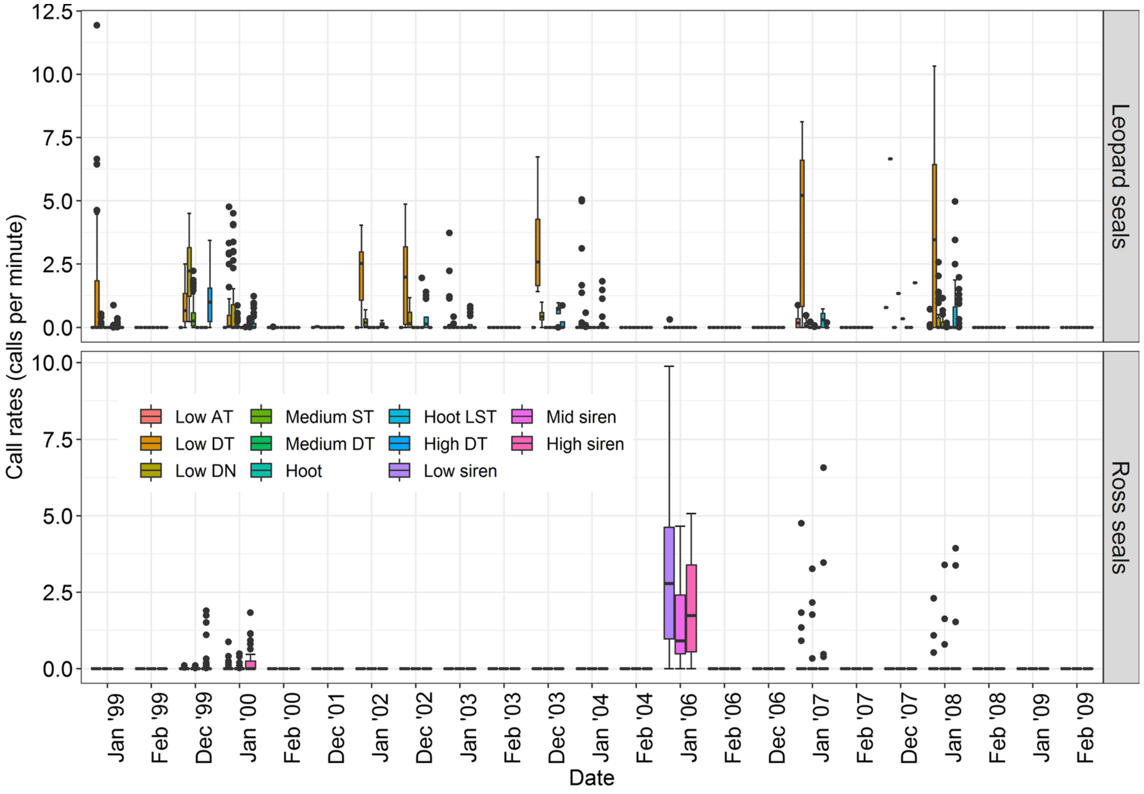

Fig. 6 Box and whisker plots of call rates of leopard (upper panel) and Ross (lower panel) seals per month in summer. Definitions of call type acronyms are the same as in the caption of Fig. 5. Boxes in the box and whisker plot represent the first quartile to the third quartile (the interquartile range), and the black line inside the boxes are medians. Whiskers outline 1.50 times the interquartile width and closed circles are observations that are outside the range covered by the whiskers

high double trills and medium single trills were high at midday, whereas call rates of low ascending trills, medium double trills, hoots, and hoot with single trills were low at midday but high before or at night-time (Fig. 7b). Mean call rates of low double trills were around 1 and remained at that level throughout the day (Fig. 7b). Low descending trills had the highest call rate in December, followed by high double trills and low double trills (Fig. 7b). Low, mid and high siren calls had the same diel calling patterns in January, where they increased from 05:00 to 17:00 (highest call rate) and then decreased until midnight (Fig. 7c). Overall, low siren calls had the highest call rates, followed by high siren calls with the second highest and then mid siren calls with the lowest call rates (Fig. 7c). No diel calling patterns were seen in February for Ross seals, due to little to no samples of calls from that month. In January, low double trills had the highest call rate that was slightly elevated around 17:00, and low descending trills were slightly high during the day (Fig. 7d). Call rates for the other leopard seal call types did not change throughout the day (Fig. 7d). No diel calling patterns were seen in February for leopard seals, due to little to no samples of calls from that month.

Predictors of acoustic occurrence

January and December, longitudes between ~ 15° and 130° E, and latitudes around 68° S, water depth of ~ 2200 m, daytime hours, distances less than 500 km to the nearest coastline and distances less than 200 km to the sea ice edge had the highest effects on Ross sea acoustic occurrence (Fig. 8a–g). Longitude and latitude were the most important predictors of Ross seal acoustic occurrence; water depth and month of the year were moderately important predictors; time of day, distance to the nearest coastline and distance to the sea ice edge were the least important predictors (Fig. 8o). December, latitudes between 64° and 68° S, and longitudes around ~ 50° E and 140° E, distances < 200 km to the sea ice edge, water depths deeper than 4000 m, distances farther than 1000 km from the nearest coastline and daytime hours had the highest effects on leopard seal acoustic occurrence (Fig. 8h–n). Month of the year was the most important predictor of leopard seal acoustic occurrence, whereas latitude, longitude, distance to the sea ice edge, water depth and distance to the nearest coastline were moderately important predictors, and time of day was the least important predictor (Fig. 8p). Contributions of the above variables at predicting

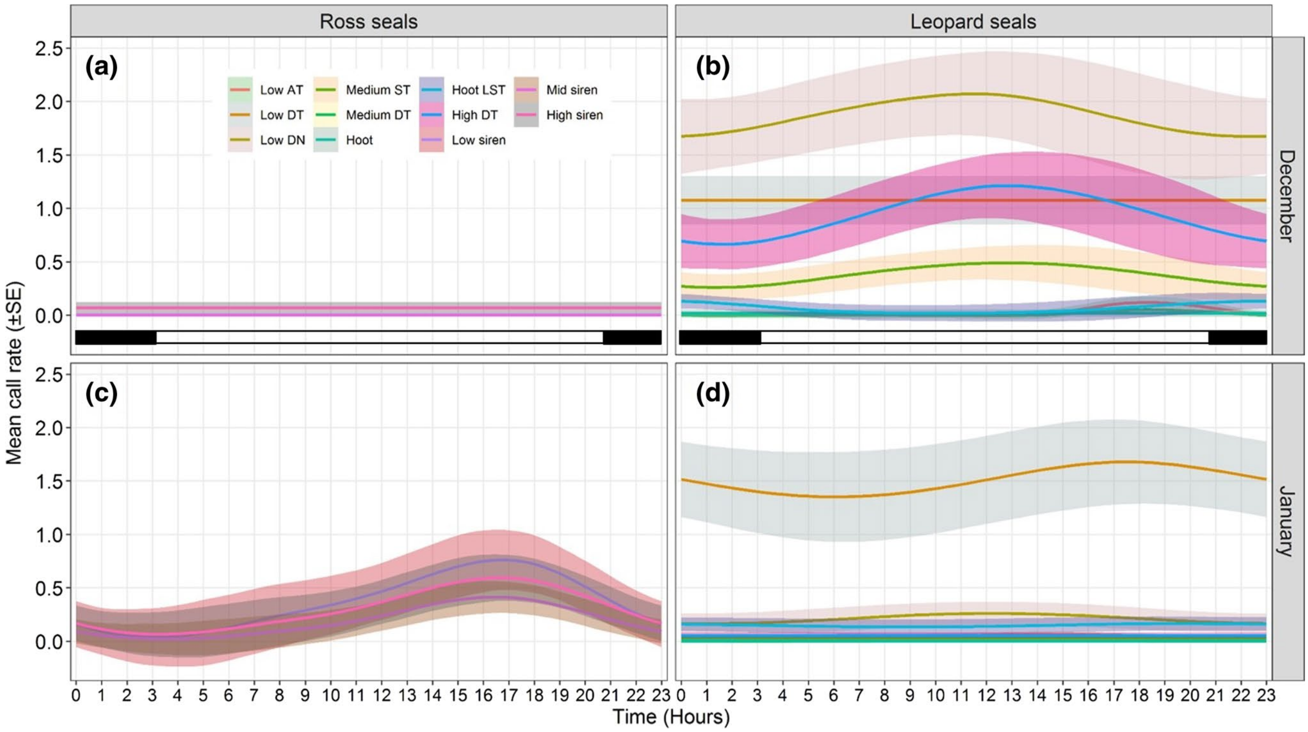

Fig. 7 Monthly circular smoothed mean ± standard error (SE) (lines with different shading colours) diel call rates (calls per minute) for leopard (**a**, **c**) and Ross (**b**, **d**) seals from all years. Definitions of call type acronyms are given in the caption of Fig. 5. Horizontal diel bar shading: black represents average night-time hours; white represents average daytime hours; no twilight hours for summer in Antarctica. Universal Coordinated Time (UTC) zone is used

acoustic occurrence were significant (Fig. 8o and p), indicating that they are informative predictors of Ross and leopard seal acoustic ecology.

Discussion

Acoustic occurrence

Our results indicate little spatio-temporal overlap in the acoustic occurrence of Ross and leopard seals in the circumpolar Antarctic pack ice using 9 years of bioacoustic data collected in austral summers. Ross seal calls were concentrated within restricted regions in the pack ice with high call numbers detected close to the sea ice edge in areas between 0° and 20° E, and between 60° and 130° E. There are more Ross seals seen, particularly off the eastern Weddell Sea, compared to any other region of the Antarctic pack ice, except for the Ross Sea (Bester et al. 2017). From previous visual surveys, Ross seals were abundant in the eastern Weddell Sea, particularly off Dronning Maud Land, during the austral summer/autumn; the seals are generally seen east of 30° W, and rarely venture further south than ~ 73° S (Bester et al. 2019, 2020). This may be why we get more acoustic detections in those later surveys. Similarly, high numbers of Antarctic blue whale calls were detected in those areas of the Southern Ocean (Shabangu et al. 2017). Specifically, areas around the Maud Rise (65° S; 2.5° E), eastern Weddell Sea, were found to be important for other marine mammals such as Antarctic blue and fin, *B. physalus*, whales (Shabangu et al. 2020a), Antarctic minke whales, *B. bonaerensis* (Shabangu et al. 2020b), and crabeater seals (Shabangu and Charif 2020). The acoustic occurrence of these seals and krill-feeding whales in that area suggests that this area is biologically productive enough to support the high concentrations of prey items and has suitable environmental conditions that attract these animals to return to the same area annually (Testa et al. 1991; Learmonth et al. 2006; Arcalís-Planas et al. 2015). RF models indicate that Ross seals inhabit regions characterized by shallow water depths and tend to be closer to the sea ice edge and the Antarctic coastline, whereas leopard seal occurred more offshore, in deep water slightly farther from the sea ice edge and Antarctic coastline.

Locations of acoustic stations were used as proxies of calling animals based on available detection ranges for other phocid seals since there are currently no detection range estimates available for these seals. Detection ranges of underwater trills of Weddell and bearded seals, *Erignathus barbatus*, are estimated to be up to 30 km when using

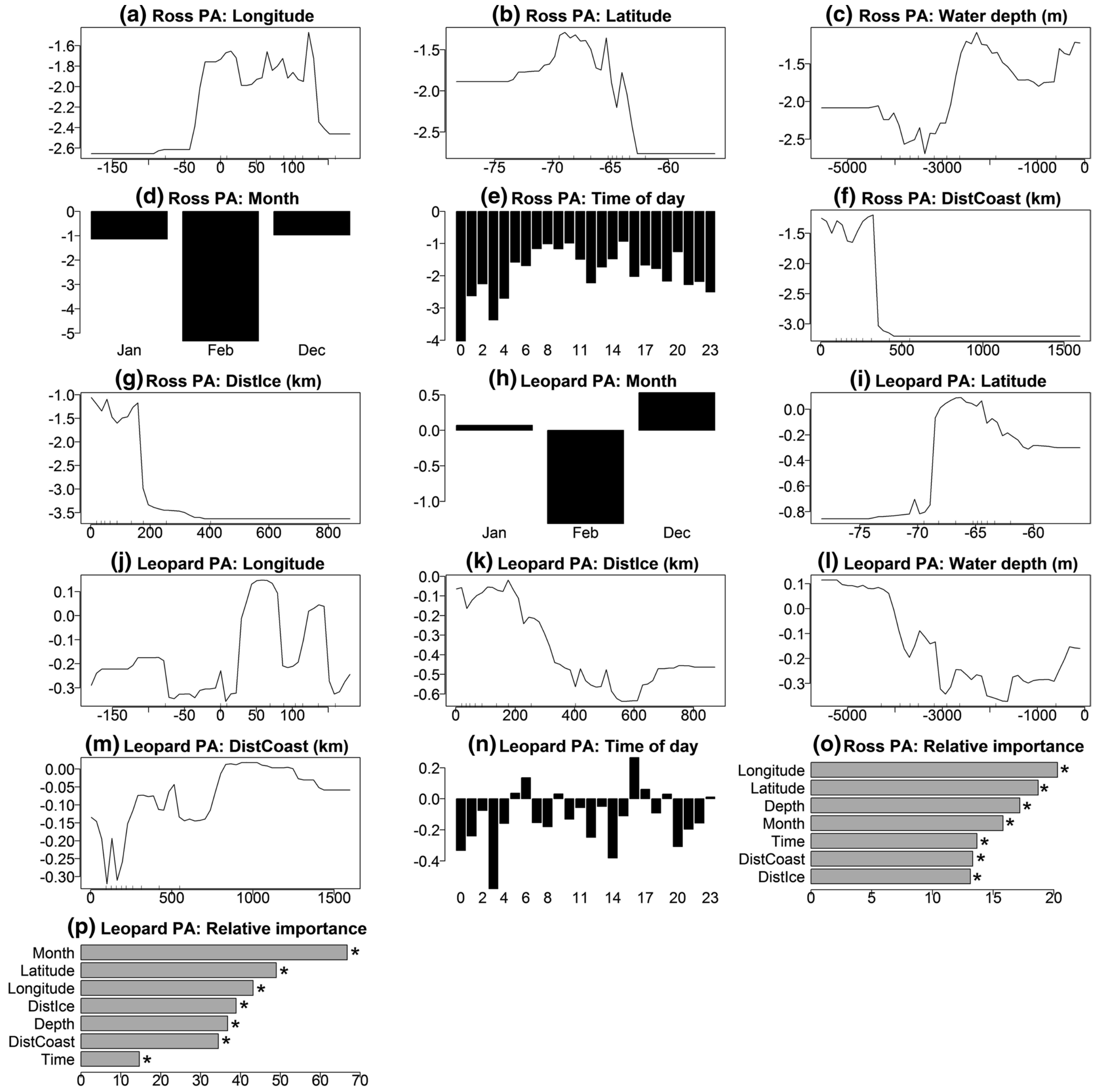

Fig. 8 Relative effects and importance of predictor variables on the acoustic occurrence of Ross (**a**–**g**, **o**) and leopard (**h**–**n**, **p**) seals. *Y*-axes of **a**–**n** are relative effects of predictor variables on call occurrence (Scales are different between plots.). *X*-axes of (**o**) and (**p**) are relative importance of predictor variables on acoustic occurrence. PA is presence/absence to indicate acoustic occurrence, DistIce is distance to the sea ice edge, and DistCoast is distance to the nearest coastline. *highlights variables with significant ($p < 0.05$) importance. Times are referenced to UTC

source levels of 148–193 dB re 1 µPa at 1 m (Thomas and Kuechle 1982) and 100 dB re 1 µPa at 1 m (Cleator et al. 1989), respectively. Given that Ross seals are smaller than Weddell seals in size but comparable to bearded seals in size and that their calls cover overlapping frequency bands; it is conceivable that our sonobuoy detection ranges of siren calls of Ross seals might be similar to detection ranges of those seal species. Since source levels of Ross seal calls are currently unknown, the above detection range is our best approximation of the distance travelled by these calls based on other phocid sound characteristics and anticipated source levels. Source levels of leopard seal calls are estimated to range from 153 to 177 dB re 1 µPa at 1 m (Rogers 2014) and will also likely have a comparable detection range to those of Weddell and bearded seals. Low-frequency calls of these seals potentially experienced less propagation loss in the water column and might consequently have higher detection ranges than high-frequency calls, as the former were detected in high percentages by our study and other studies (e.g. van Opzeeland et al. 2010; Rogers et al. 2013). Thus, the distance of 30 km to acoustic stations serves in this instance as conservative proxy of calling animals. In the future, detection ranges of seal calls derived using sound propagation models are recommended, as this will consider ambient noise levels, sound speeds, source levels, hydrophone depth and bathymetry of hydrophone deployment locations (e.g. Shabangu and Andrew 2020; Shabangu et al. 2020b) to yield more accurate detection range values in relation to the environment around calling animals.

Ross seal siren calls were detected only in late December and January; this timing corresponds well with the detection of their calls in the eastern Weddell Sea (Kindermann et al. 2008). In January, Ross seals haul out in the pack ice to moult on the ice floes (Thomas and Rogers 2009). Through most of the year, Ross seals forage in the open ocean in association with the Antarctic Polar Front (Blix and Nordøy 2007) but in the austral spring (i.e. November), they move south into the pack ice to use the ice floes to give birth and to raise their pups. There is a peak in Ross seal pups born in early to mid-November (Southwell et al. 2003). Pups are weaned after about a month (i.e. in mid-December), at which time the seals mate (Thomas and Rogers 2009), although little is known about their breeding behaviour. Mating is assumed to occur in the water, nevertheless it has not been observed (Thomas and Rogers 2009). No Ross seal calls were detected in February since at this time the seals move north, out of the pack ice, and back into open water (Blix and Nordøy 2007). In comparison, we show that the leopard seal calls were detected widely throughout the pack ice. The acoustic presence of leopard seals from the sea ice edge to the open ocean, close to the polar fronts, is likely due to the their broad (i.e. catholic) diet, allowing them to prey on a wide variety of small to large prey species (i.e. from Antarctic krill, fish, to larger vertebrates; Rogers and Bryden 1995; Hall-Aspland and Rogers 2004; Forcada et al. 2012; Krause and Rogers 2019). The close association of high numbers of leopard seal calls and the sub-Antarctic Circumpolar Current could indicate that these polar front waters provide suitable foraging habitats for this species (Staniland et al. 2018). Such offshore detection of leopard seal sounds in summer could also suggest the southward migration of some seals from the sub-Antarctic islands to the Antarctic pack ice (Nordøy and Blix 2009; Rogers 2009; Staniland et al. 2018). Female southern elephant seals were observed to use the eddy fields of the Antarctic Circumpolar Current to reduce transport energy costs during foraging and migration (Massie et al. 2016), these seals might also follow suit.

Percentages of acoustic occurrence of leopard seals for this study were higher in December than in January, which corresponds with high call rates observed in December in the Davis Sea, eastern Antarctica (Rogers 2017; Rogers et al. 2013) and in the eastern Weddell Sea during peak breeding season (Kindermann et al. 2008; van Opzeeland et al. 2010). Few leopard seal calls were detected in February, although leopard seals remain in the pack ice (Rogers et al. 2005; Meade et al. 2015), their calls are no longer recorded in large numbers. This is possibly due to behavioural changes with the end of the breeding season as captive leopard seals have been shown to cease calling with the drop in their reproductive hormones (Rogers et al. 1996). The acoustic absence of seals in the majority of IWC-SOWER survey locations maybe because sonobuoys were deployed in open water, as these recordings were aimed at detecting the sounds of baleen whales, which tend to use open water habitat. The SCAR-APIS recordings were targeting the detection of seal calls, so that the sonobuoys were deployed within the pack ice, the habitat of seals and not in the open water.

High call rates for leopard than Ross seals were detected in later years of the IWC-SOWER Programme; this is likely due to the difference in survey locations between years; where the earlier surveys were conducted in the south western Pacific sector of the Southern Ocean, in later years, the surveys were further west in the Atlantic and Indian Ocean sectors (Table 1; Fig. 1). This is why our RF models show that acoustic occurrence of the Ross seal was more likely to be within regions surveyed in later years, in the eastern Atlantic and the Indian Ocean sectors of the Southern Ocean (i.e. between longitudes ~ 15° and ~ 130° E).

It is unlikely that the downsampling of the recordings from earlier surveys removed Ross seal vocalisations and this is why they were not detected in the earlier years of the IWC-SOWER cruises. The downsampled acoustic data (i.e. IWC-SOWER recordings made prior to 2003/2004) had been downsampled (i.e. resampled by a factor of 10); thus, only every tenth sample within the signal was retained. Consequently, if the seal calls were very short, they may have been removed from the recordings via the subsampling. However, as the Ross seal siren calls are 2 to 4 s (Seibert 2007) and the leopard seal trills and hoots are 4 to 6 s (Rogers 2007), they are very long sounds so that the downsampling process would have removed samples from within the calls, rather than removing entire calls. This meant that our ability to detect the calls was not impacted. Downsampling, however, has a second impact upon the recordings; the highest frequencies retained within the resampled recordings will be half the sampling rate; thus, for our study (i.e. resampled at 1 kHz), only energy below 500 Hz was retained in the subset of downsampled recordings. This meant that although none of the energy in the Ross seal high siren calls (i.e. between ~ 600 Hz and 8 kHz; Seibert 2007) remained in the post-downsampled recordings, all the energy of the low siren calls (~ 130 and 450 Hz; Seibert 2007) and a significant proportion of the mid siren calls (~ 168.42 Hz to 2.01 kHz; Seibert 2007) were well within the frequency bandwidth retained in the resampled recordings. Thus, the absence of Ross seal calls in the downsampled recordings is not due to subsampling, as the frequency bandwidth of the Ross seals' low siren calls was entirely within the downsampled recordings. In addition, leopard seal low-frequency calls were detected in these recordings and they have a similar frequency range as Ross seal calls. Instead, the absence of Ross seal calls in these recordings indicates that they were not calling, potentially absent, from these survey locations.

Low double trills were the most commonly detected call type for leopard seals and low siren calls were the most commonly detected call type for Ross seals. van Opzeeland et al. (2010) also reported similar proportion of seal call types off the Ekström Iceshelf, eastern Weddell Sea, further indicating the behavioural context of these breeding related sounds in summer. Furthermore, the detection of these low-frequency calls indicates that the downsampled data from earlier years of the IWC-SOWER Programme is effective at describing the low-frequency vocal repertoire and acoustic occurrence of these seals. The high call rates of low double trills for leopard and low siren calls for Ross seal may indicate the escalation of vocal sexual advertisement and/or territorial signalling between seals during the breeding season (Rogers and Cato 2002; Rogers 2007, 2017; van Opzeeland et al. 2010; Rogers et al. 1996, 2013). Alternatively, the increase in seal densities as the ice floe's become concentrated with the contraction of the sea ice through the summer (Rogers et al. 2013). Diel call rates indicate that both Ross and leopard seals are more vocally active during the day, suggesting that most acoustic interaction with conspecifics took place during the day. Off the Ekström Iceshelf, eastern Weddell Sea, van Opzeeland et al. (2010) detected less leopard seal calls during the day in December and January. Differences in the leopard seal behaviour between this study (offshore) and van Opzeeland et al. (2010; on the iceshelf) could be due to differences in region-specific behaviour, where most seals could have been resting in small groups on the pack ice during the day but vocalize at night to communicate with conspecifics underwater, whereas animals are likely scattered on floating ice in the offshore regions, hence the need to vocalize more even during the day.

Diel calling pattern of Ross seals observed in this study is comparable to van Opzeeland et al. (2010), since both studies found increased vocal activity in the late afternoon, 16:00 for van Opzeeland et al. (2010) and 17:00 for this study. Furthermore, Ross seal call rates were low in December but higher in January for both studies (this study and van Opzeeland et al. 2010). Our highest call rates for leopard and Ross seals were lower than those documented by van Opzeeland et al. (2010). Our recordings were made from sonobuoys deployed from ships; thus, a great deal of ship noise masked the signals in our recordings and reduced our survey range relative to that of the hydrophones recording under the iceshelf close to the sea floor in the van Opzeeland et al. (2010) study. Alternatively, there were fewer animals in our study area, as we conducted recordings offshore in the pack ice while van Opzeeland et al. (2010) were recording continuously on the iceshelf, potentially in the presence of a higher number of animals. Additionally, our results indicate that leopard seal sounds are detectable in February, as yet undocumented in previous studies (e.g. Kindermann et al. 2008; van Opzeeland et al. 2010).

The weak correlation between the seal acoustic presences reported in the IWC-SOWER cruise reports and the ones observed in this study likely indicates that less effort was dedicated to observing seals as the IWC-SOWER Programme focussed on studying baleen whales. Thus, a relatively high correlation ($r = 0.62$) was found between the acoustic presence of Antarctic blue whales in the IWC-SOWER cruise reports and those in Shabangu et al. (2017, In press). Given that the SCAR-APIS cruise was a marine science cruise, it presented higher detections of seal sounds and allows for a fine resolution study of seal acoustic occurrence and behaviour.

Impact of clipping

The digital artefacts, due to waveform clipping and aliasing, did not hinder the detection of the seal calls in the recordings. Although spurious harmonics and erroneous signals were introduced into recordings, they were above and below the frequencies of the seal vocalisations. The likely cause of the waveform clipping was that the gain was too high on the preamplifier, which resulted in the maximum voltage of the digitizer being exceeded (Russell Charif, personal communication). Stirling and Siniff (1979) noted that leopard seal sounds were very loud at close range and they had to set the record level control (i.e. preamplifier gain) to the lowest value to avoid the signal distortion due to waveform clipping. Although the source levels of the Ross seal calls are yet to be measured, at close range to a vocalising individual, their vocalisations are very loud (TLR, unpublished data). Future pack ice acoustic surveys that use sonobuoys should ensure that the gain of the preamplifier is appropriately set to accommodate the loud vocalisations of the pack ice seals. In addition, we recommend that, in order to reduce aliasing issues, anti-aliasing filters should be incorporated.

Conclusion

Ross and leopard seal vocalisations collected during IWC-SOWER whale surveys and SCAR-APIS seal survey were successfully used here to study the acoustic occurrence and behaviour of these Antarctic pack ice seals during summer in the Southern Ocean. Little spatial overlap was found between the two species. Acoustic occurrence of Ross seals can be easily predicted by latitude and longitude, whereas leopard seals show complex but flexible acoustic occurrence must be predicted by a suit of variables. Ross seals were detected mainly in January with few calls in December, while leopard seals were detected in December and January with fewer calls in February. Predictors used in this study were informative given their significant importance at predicting acoustic occurrence of the Ross and leopard seals. Call types, acoustic occurrence and call rates of Ross and leopard seals were successfully documented in this study, supporting the use of opportunistic data to study other non-target animals. This passive acoustic monitoring study indicates the circumpolar areas inhabited by these two species in summer, which might be informative and useful for the establishment of marine protected areas for these species in the Southern Ocean. This study contributes knowledge important towards improving our understanding of the summer circumpolar acoustic occurrence and behaviour of Ross and leopard seals in the Southern Ocean.

Acknowledgements We are grateful to all participants of the IWC-SOWER cruises for collecting and providing this valuable acoustic dataset. Special thanks to Holger Klinck for his kind assistance with the identification of seal sounds. We thank the IWC for granting us permission to use the SOWER acoustic data for studying calls of seals. Dinah Mukhari is acknowledged for "pushing" FWS to design this study as a short project that grew into this paper. Ilse van Opzeeland, Caroline Casey and an anonymous reviewer are acknowledged for their helpful comments and suggestions on the manuscript.

Author contributions FWS and TLR participated in the design of the study and drafted the manuscript, performed the acoustic data analyses and wrote the manuscript; FWS analysed the environmental data and carried out the statistical analyses; and TLR collected SCAR-APIS field data. All authors read and approved the manuscript.

Funding International Whaling Commission's Southern Ocean Whale and Ecosystem Research cruises were conducted by the International Whaling Commission, and the Scientific Committee on Antarctic Research cruise was funded by the Antarctic Scientific Advisory Committee (ASAC 552 and 1140), the Sea World Research and Rescue Foundation Inc. and the Scott Foundation.

Data availability The full dataset from the Scientific Committee on Antarctic Research cruise is available on the Dryad data repository (https://doi.org/10.5061/dryad.rr4xgxd79). Acoustic data from International Whaling Commission's Southern Ocean Whale and Ecosystem Research cruises are available upon request from the International Whaling Commission's offices.

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

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Informed consent The International Whaling Commission and Scientific Committee on Antarctic Research granted permission to publish data.

References

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

Amante C, Eakins BW (2009) ETOPO1 1 arc-minute global relief model: procedures, data sources and analysis. NOAA Technical Memorandum NESDIS NGDC-24:1−19

Arcalís-Planas A, Sveegaard S, Karlsson O, Harding KC, Wåhlin A, Harkonen T, Teilmann J (2015) Limited use of sea ice by the Ross seal (*Ommatophoca rossii*), in Amundsen Sea, Antarctica, using telemetry and remote sensing data. Polar Biol 38:445–461

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

Bester MN, Bornemann H, McIntyre T (2017) Antarctic marine mammals and sea ice. In: Thomas DN (ed) Sea Ice, 3rd edn. Wiley, Hoboken, pp 534–555

Bester MN, Wege M, Lübcker N, Postma M, Syndercombe G (2019) Opportunistic ship-based census of pack ice seals in eastern Weddell Sea, Antarctica. Polar Biol 42:225–229. https://doi.org/10.1007/s00300-018-2401-7

Bester MN, Wege M, Oosthuizen WC, Bornemann H (2020) Ross seal distribution in the Weddell Sea: fact and fallacy. Polar Biol 43:35–41. https://doi.org/10.1007/s00300-019-02610-4

Bioacoustics Research Program (2017) Raven Pro: interactive sound analysis software (version 1.5) [Computer Software]. Ithaca, NY: The Cornell Lab of Ornithology. http://www.birds.cornell.edu/raven. Accessed 26 June 2019

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

Blix AS, Nordøy ES (2007) Ross seal (*Ommatophoca rossii*) annual distribution, diving behaviour, breeding and moulting, off Queen Maud Land, Antarctica. Polar Biol 30:1449–1458

Brault EK, Koch PL, Costa DP, McCarthy MD, Hückstädt LA, Goetz KT, McMahon KW, Goebel ME, Karlsson O, Teilmann

J, Harkonen T, Harding KC (2019) Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. Mar Ecol Prog Ser 611:1–18

Breiman L (2001) Random forests. Mach Learn 45:5–32

Charif RA, Waack AM, Strickman LM (2010) Raven Pro 1.4 user's manual. Cornell Lab of Ornithology, Ithaca

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287

Cleator HJ, Stirling I, Smith TG (1989) Underwater vocalizations of the bearded seal (*Erignathus barbatus*). Can J Zool 67:1900–1910

Curtis C, Stewart BS, Karl SA (2009) Pleistocene population expansions of Antarctic pack-ice seals. Mol Ecol 18:2112–2121

Curtis C, Stewart BS, Karl SA (2011) Genetically effective population sizes of Antarctic seals estimated from nuclear genes. Conserv Genet 12:1435–1446

Donovan GP, Hammond PS, Larsen F, Reilly SB, Kato H, Clark CW, Brownell RL (1996) Report of the scientific committee, annex E. Report of the sub-committee on Southern Hemisphere baleen whales. Appendix 2. An approach for responding to the Commission's resolution. Rep Int Whal Comm 46:126–127

Ensor P, Findlay K, Hara T, Hedley S, Pitman R, Sekiguchi K, Tsurui T, Yamagiwa D (1997) 1996–97 IWC—Southern Ocean Whale and Ecosystem Research (IWC – SOWER) Antarctic cruise, Area II. Paper SC/49/SH7 presented to the IWC Scientific Committee

Ensor P, Pastene LA, Cawthorn M, Findlay K, Hedley S, Iwakami H, Kleivane L, Pitman R, Tsurui T, Sakai K (1998) 1997–98 IWC Southern Ocean Whale and Ecosystem Research (IWC – SOWER) Antarctic cruise, Area II. Paper SC/50/Rep1 presented to the IWC Scientific Committee

Ensor P, Sekiguchi K, Doherty J, Kleivane L, Ljungblad D, Marques F, Matsuoka K, Narita H, Pitman R, Sakai K (1999) 1998–99 IWC-Southern Ocean Whale and Ecosystem Research (IWC SOWER) Antarctic cruise, Areas III and IV. Paper SC/51/Caws6 presented to the IWC Scientific Committee

Ensor P, Findlay KP, Hucke-Gaete R, Kleivane L, Komiya H, Ljungblad D, Marques F, Muira T, Sekiguchi K, Shimade H (2000) 1999–2000 IWC-Southern Ocean Whale and Ecosystem research (IWC SOWER) Antarctic cruise, Areas I and II. Paper SC/52/IA1 presented to the IWC Scientific Committee

Ensor P, Matsuoka K, Marques F, Miura T, Murase H, Pitman R, Sakai K, Van Waerebeek K (2001) 2000–2001 International Whaling Commission – Southern Ocean Whale and Ecosystem Research (IWC – SOWER) circumpolar cruise, Area V, VI and I. Paper SC/53/IA5 presented to the IWC Scientific Committee

Ensor P, Sekiguchi K, Cotton J, Hucke-Gaete R, Kariya T, Komiya H, Ljungblad D, Narita H, Olson P, Rankin S (2002) 2001–2002 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) circumpolar cruise, Area V. Paper SC/54/IA2 presented to the IWC Scientific Committee

Ensor P, Matsuoka K, Hirose K, Ljungblad D, Minami K, Olson P, Rankin S, Stevick P, Tsunekawa M, Ugarte F (2003) 2002–2003 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) circumpolar cruise, Area V. Paper SC/55/IA1 presented to the IWC Scientific Committee

Ensor P, Matsuoka K, Komiya H, Ljungblad D, Miura T, Morse L, Olson P, Olavarria C, Mori M, Sekiguchi K (2004) 2003–2004 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) circumpolar cruise, Area V. Paper SC/56/IA13 presented to the IWC Scientific Committee

Ensor P, Findlay K, Friedrichsen G, Hirose K, Komiya H, Morse L, Olson P, Sekiguchi K, Van Waerebeek K, Yoshimura I (2005) 2004–2005 International Whaling Commission – Southern Ocean Whale and Ecosystem Research (IWC – SOWER) cruise, Area III. Paper SC/57/IA1 presented to the IWC Scientific Committee

Ensor P, Komiya H, Olson P, Sekiguchi K, Stafford K (2006) 2005–2006 International Whaling Commission- Southern Ocean Whale and Ecosystem Research (IWC SOWER) cruise. Paper SC/58/IA1 presented to the IWC Scientific Committee

Ensor P, Komiya H, Beasley I, Fukutome K, Olson P, Tsuda Y (2007) 2006–2007 International Whaling Commission—Southern Ocean Whale and Ecosystem Research (IWC- SOWER) cruise. Paper SC/59/IA1 presented to the IWC Scientific Committee

Ensor P, Minami K, Morse L, Olson P, Sekiguchi K (2008) 2007–2008 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC SOWER) cruise. Paper SC/60/IA1 presented to the IWC Scientific Committee

Ensor P, Komiya H, Kumagai S, Kuningas S, Olson P, Tsuda Y (2009) 2008–2009 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC- SOWER) cruise. Paper SC/61/IA19 presented to the IWC Scientific Committee

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

Forcada J, Trathan PN, Boveng PL, Boyd IL, Burns JM, Costa DP, Fedak M, Rogers TL, Southwell CJ (2012) Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. Biol Conserv 149(1):40–50

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

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

Guerrero AI, Negrete J, Márquez MEI, Mennucci J, Zaman K, Rogers TL (2016) Vertical fatty acid composition in the blubber of leopard seals and the implications for dietary analysis. J Exp Mar Biol 478:54–61. https://doi.org/10.1016/j.jembe.2016.02.004

Hall-Aspland SA, Rogers TL (2004) Summer diet of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. Polar Biol 27:729–734

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

Ho TK (1995) Random decision forests. In: Kavavaugh M, Storms P (eds) Proc 3rd int conf document analysis and recognition, montreal, 14–16 August 1995. IEEE Computer Society Press, Los Alamitos, pp 278–282

Kindermann L, Boebel O, Bornemann H, Burkhardt E, Klinck H, Van Opzeeland I, Plötz J, Seibert M (2008) A Perennial acoustic observatory in the Antarctic Ocean, computational bioacoustics for assessing biodiversity. Bundesamt Nat Skr 234:15–28

Krause DJ, Rogers TL (2019) Food caching by a marine apex predator, the leopard seal (*Hydrurga leptonyx*). Can J Zool 97(6):573–578. https://doi.org/10.1139/cjz-2018-0203

Learmonth JA, Macleod CD, Santos MB, Pierce GJ, Crick HQP, Robinson RA (2006) Potential effects of climate change on marine mammals. Oceanogr Mar Biol 44:431–464

Liaw A, Wiener M (2002) Classification and regression by RandomForest. R News 2:18–22

Lowry L, Testa JW, Calvert W (1988) Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. Polar Biol 8:475–478

Massie PP, McIntyre T, Ryan PG, Bester MN, Bornemann H, Ansorge IJ (2016) The role of eddies in the diving behaviour of female southern elephant seals. Polar Biol 39:297–307

Meade J, Ciaglia MB, Slip DJ, Negrete J, Márquez MEI, Mennucci J, Rogers TL (2015) Spatial patterns in activity of leopard seals *Hydrurga leptonyx* in relation to sea ice. Mar Ecol Prog Ser 521:265–275. https://doi.org/10.3354/meps11120

McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58:697–714

Nordøy ES, Blix AS (2009) Movements and dive behaviour of two leopard seals (*Hydrurga leptonyx*) off Queen Maud Land, Antarctica. Polar Biol 32:263–270

Orsi AH, Whitworth T III, Nowlin WD Jr (1995) On the meridional extent and fronts of the Antarctic circumpolar current. Deep-Sea Res I 42(5):641–673

Pante E, Simon-Bouhet B (2013) marmap: a package for importing, plotting and analyzing bathymetric and topographic data in R. PLoS ONE 8(9):e73051

Pebesma E (2020) lwgeom: bindings to selected 'liblwgeom' functions for simple features. R package version 0.2–5. https://CRAN.R-project.org/package=lwgeom. Accessed 13 Aug 2020

Pitman RL, Ensor P (2003) Three forms of killer whales in Antarctic waters. J Cetacean Res Manag 5:131–139

R Core Team (2020) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/. 8 July 2020

Rau GH, Ainley DG, Bengtson JL, Torres JJ, Hopkins TL (1992) $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Mar Ecol Prog Ser 23:1–8

Ridgeway G (1999) The state of boosting. Comput Sci Stat 31:172–181

Rintoul SR (2009) Antarctic circumpolar current. In: Steele JH, Thorpe SA, Turekian KK (eds) Encyclopedia of ocean sciences, vol 1, 2nd edn. Academic Press, London, pp 178–190

Rogers TL (2007) Age-related differences in the acoustic characteristics of male leopard seals, *Hydrurga leptonyx*. J Acoust Soc Am 122(1):596–605. https://doi.org/10.1121/1.2736976

Rogers TL (2009) Leopard seal *Hydrurga leptonyx*. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic Press, New York, pp 673–674. https://doi.org/10.1016/B978-0-12-373553-9.00155-3

Rogers TL (2014) Source levels of the underwater calls of a male leopard seal. J Acoust Soc Am 136(4):1495–1498. https://doi.org/10.1121/1.4895685

Rogers TL (2017) Calling underwater is a costly signal: size-related differences in the call rates of Antarctic leopard seals. Curr Zool. https://doi.org/10.1093/cz/zox028

Rogers T, Bryden MM (1995) Predation of Adélie penguins (*Pygoscelis adeliae*) by leopard seals (*Hydrurga leptonyx*) in Prydz Bay. Antarctica. Can J Zool 73(5):1001–1004. https://doi.org/10.1139/z95-119

Rogers TL, Cato DH, Bryden MM (1996) Behavioral significance of underwater vocalizations of captive leopard seals *Hydurga leptonyx*. Mar Mamm Sci 12:414–427. https://doi.org/10.1111/j.1748-7692.1996.tb00593.x

Rogers T, Bryden MM (1997) Density and haul-out behavior of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. Mar Mamm Sci 13:293–302. https://doi.org/10.1111/j.1748-7692.1997.tb00632.x

Rogers TL, Cato DH (2002) Individual variation in the acoustic behaviour of the adult male leopard seal, *Hydrurga leptonyx*. Behaviour 139:1267–1286. https://doi.org/10.1163/156853902321104154

Rogers TL, Hogg CJ, Irvine A (2005) Spatial movement of adult leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. Polar Biol 28(6):456–463. https://doi.org/10.1007/s00300-004-0703-4

Rogers TL, Ciaglia MB, Klinck H, Southwell C (2013) Density can be misleading for low-density species: Benefits of passive acoustic monitoring. PLoS ONE 8(1):e52542. https://doi.org/10.1371/journal.pone.0052542

Seibert AM (2007) The Ross seal and its underwater vocalizations. MSc thesis, University of Munich

Sekiguchi K, Fukotome K, Morse L, Shinyashiki Y, Oedekoven C (2010) 2009–2010 International Whaling Commission—Southern Ocean Whale and Ecosystem Research (IWC SOWER) cruise. Paper SC/62/IA1 presented to the IWC Scientific Committee

Shabangu FW, Andrew RK (2020) Clicking throughout the year: sperm whale clicks in relation to environmental conditions off the west coast of South Africa. Endanger Species Res 43:475–494. https://doi.org/10.3354/esr01089

Shabangu FW, Charif RA (2020) Short moan call reveals seasonal occurrence and diel-calling pattern of crabeater seals in the Weddell Sea, Antarctica. Bioacoustics. https://doi.org/10.1080/09524622.2020.1819877

Shabangu FW, Yemane D, Stafford KM, Ensor P, Findlay KP (2017) Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales. PLoS ONE 12(2):e0172705. https://doi.org/10.1371/journal.pone.0172705

Shabangu FW, Findlay KP, Yemane D, Stafford KM, van den Berg M, Blows B, Andrew RK (2019) Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa. Journal of Marine Systems 190:25–39. https://doi.org/10.1016/j.jmarsys.2018.11.002

Shabangu FW, Findlay K, Stafford KM (2020a) Seasonal acoustic occurrence, diel-vocalizing patterns and bioduck call-type composition of Antarctic minke whales off the west coast of South Africa and the Maud Rise, Antarctica. Mar Mam Sci 36:658–675. https://doi.org/10.1111/mms.12669

Shabangu FW, Andrew RK, Yemane D, Findlay KP (2020b) Acoustic seasonality, behaviour and detection ranges of Antarctic blue and fin whales under different sea ice conditions off Antarctica. Endanger Species Res 43:21–37. https://doi.org/10.3354/esr01050

Shabangu FW, Stafford KM, Findlay KP, Rankin S, Ljungblad D, Tsuda Y, Morse L, Clark CW, Kato H, Ensor P (In press) Overview of the IWC SOWER cruise circumpolar acoustic survey data and analyses of Antarctic blue whale calls. J Cetacean Res Manag's IWC SOWER Special Issue

Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Opinion: projecting the effects of environmental change on Antarctic seals. Antarct Sci 20:425–435

Skinner JD, Klages NT (1994) On some aspects of the biology of the Ross seal *Ommatophoca rossii* from King Haakon VII Sea, Antarctica. Polar Biol 14:467–472

Southwell C (2003) Haul-out behaviour of two Ross seals off eastern Antarctica. Antarct Sci 15:257

Southwell C, Kerry K, Ensor P, Woehler EJ, Rogers T (2003) The timing of pupping by pack-ice seals in East Antarctica. Polar Biol 26:648–652. https://doi.org/10.1007/s00300-003-0534-8

Southwell C, Paxton CGM, Borchers D, Boveng P, Nordøy ES, Blix ES (2008a) Estimating population status under conditions of uncertainty: the Ross seal in east Antarctica. Antarct Sci 20:123–133

Southwell C, Paxton CG, Borchers D, Boveng P, Rogers T, William K (2008b) Uncommon or cryptic? Challenges in estimating leopard seal abundance by conventional but state-of-the-art methods. Deep-Sea Res I 55(4):519–531. https://doi.org/10.1016/j.dsr.2008.01.005

Southwell C, Bengtson J, Bester M, Blix AS, Bornemann H, Boveng P, Cameron M, Forcada J, Laake J, Nordøy E, Plötz J, Rogers T, Southwell D, Steinhage D, Stewart BS, Trathan P (2012) A review of data on abundance, trends in abundance, habitat use and diet of ice-breeding seals in the Southern Ocean. CCAMLR Sci 19:49–74

Staniland IJ, Ratcliffe N, Trathan PN, Forcada J (2018) Long term movements and activity patterns of an Antarctic marine apex predator: the leopard seal. PLoS ONE 13(6):e0197767. https://doi.org/10.1371/journal.pone.0197767

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

Testa JW, Oehlert R, Bengston J, Laws R, Ainley D, Siniff D (1991) Temporal variability in Antarctic marine ecosystems: a possibility. J Fish Aquat Sci 48(4):631–639

Thomas JA, Kuechle VB (1982) Quantitative analysis of Weddell seal (Leptonychotes weddelli) underwater vocalizations in McMurdo Sound, Antarctica. J Acoust Soc Am 72:1730–1738

Thomas JA, Rogers TL (2009) Ross seal *Ommatophoca rossii*. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals. Academic Press, New York, pp 988–990

Trites AW (1997) The role of pinnipeds in the ecosystem. In: Stone G, Goebel J, Webster S (eds) Pinniped populations, eastern north Pacific: status, trends and issues. A symposium of the 127th Annual Meeting of the American Fisheries Society, New England Aquarium, Conservation Department, Central Wharf, Boston, MA 02110, pp 31–39

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

Watkins WA, Ray GC (1985) In-air and underwater soundso f the Ross seal, *Ommatophoca rossii*. J Acoust Soc Am 77(4):1598–1600

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

Wright MN, Ziegler A (2017) ranger: a fast implementation of random forests for high dimensional data in C++ and R. J Stat Softw 77:1–17