



MASTER THESIS

Exploring and verifying

the acoustic presence of southern right whales

off Elephant Island, Antarctica.

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Abstract

The upcall is the most commonly detected and prevalent vocalization of the southern right whales' (*Eubalaena australis*) vocal repertoire. This vocalization is similar among populations, is used by all sexes and age classes, as well as over a range of behavioural contexts, and thus, it is commonly used as a basis for passive acoustic monitoring (PAM) studies on this species. Efficiency of PAM methods depends on the ability to detect and correctly interpret acoustic signals, but previous studies report difficulties to distinguish between southern right whale upcalls and similar humpback whale (*Megaptera novaeangliae*) vocalizations. Recently, vocalizations similar to southern right whale upcalls were detected off Elephant Island, Antarctica, which forms an important feeding ground also for other baleen whales including humpback whales which are also acoustically present in the data. The similarity between southern right whale upcalls and humpback whale vocalizations complicates distinguishing between the two with certainty, as has also been reported by previous studies. In this study, we structurally analysed these vocalizations and compared call characteristics to a) confirmed southern right whale vocalizations recorded off Argentina and b) confirmed humpback whale vocalizations recorded in the Atlantic Sector of the Southern Ocean.

Based on call features, detected upcalls off Elephant Island could be attributed to southern right whales. Apart from a similar mean duration, southern right whale upcalls had a notably lower frequency range compared to humpback whale vocalizations. Measurements describing slope and bandwidth were identified as the main differences in call characteristics between species. Moreover, vocalization parameters of analysed southern right whale upcalls were broadly similar to mean values of previous studies on southern right whale vocalizations. Surprisingly, compared to the upcalls from Argentina and from other previous studies, a shift in low frequency limits to higher frequencies was observed in the detected upcalls off Elephant Island. Potential drivers of this shift, such as anthropogenic noise and acoustic niche development in regard of sympatric species, are discussed. An acoustic energy analysis suggests fin whale (Balaenoptera physalus) acoustic activity off Elephant Island as a cause of high levels of low frequency background noise, potentially functioning as a driver for the shift of low frequency limits in southern right whales off Elephant Island. Confirming the acoustic presence of southern right whales in waters off Elephant Island, provides further support that these waters form an important foraging ground for multiple species. With the newly gained knowledge from this study, additional data can be analysed and provide insights in temporal occurrence and migratory behaviour of southern right whales in Antarctic waters.

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1. Introduction

Southern right whales (*Eubalaena australis*; hereafter referred to as SRW) were extensively depleted over several centuries of historical and modern whaling. Although the species is legally protected since 1935, illegal whaling by the Soviet Union in the 20th century slowed down the population recovery (Cooke and Zerbini, 2018). Presently, SRWs are steadily recovering throughout their whole distributional range, but differences in recovery success between populations, and even rapid changes in habitat use have been reported (Weir and Stanworth, 2020). These differences in recovery rate and occurrence patterns require an understanding and monitoring of their spatio-temporal distribution to provide further information for conservation approaches.

Having a circumpolar distribution of around 12°S to 65°S (Figure 1; Cooke and Zerbini, 2018; Harcourt et al., 2019), this species' seasonal migration covers thousands of kilometres. SRWs migrate from low to mid latitude coastal breeding grounds in austral winter to mid to high latitude off-shore foraging grounds in summer (Tormosov et al., 1998; Zerbini et al., 2018). Major current, and well-studied breeding grounds are located off Argentina and Brazil, South Africa and Namibia, as well as off southern Australia and New Zealand (Cooke and Zerbini, 2018). Feeding grounds have been identified in the waters off southwestern Australia and off South Georgia in the southwestern Atlantic (Patenaude et al., 2007), where SRWs are thought to feed on copepods (north of 40°S) or on Antarctic krill (Euphausia superba - south of 50°S; Cooke and Zerbini, 2018; Zerbini et al., 2018). Based on historical whaling data, and the National Marine Fisheries Service report (Austin, 2021), additional feeding grounds have been suggested in the south western Atlantic and the Southern Ocean (Tormosov et al., 1998; Zerbini et al., 2018), but comprehensive knowledge on main summer feeding grounds in sub-Antarctic and Antarctic waters is scarce. A recent study by Kanda et al., (2014) suggested that SRWs operate longerdistance migration than previously thought, reporting whales from the Indo-Pacific and Indo-Atlantic basins migrating to feeding grounds in Antarctic management Area IV. Additionally, Best et al., (2003) showed long range movements from Brazil to South Georgia. Presence of SRWs was not only reported at South Georgia (e.g., Carroll et al., 2020; Calderan et al., 2021), but also north of the Weddell Sea (Zerbini et al., 2018) and around the Antarctic Peninsula during austral summer (Vermeulen et al., 2021). The identification of feeding habitats could lead to an improved understanding on foraging and spatio-temporal distribution. Additionally, to enhanced knowledge on environmental factors, which may affect the reproductive success of SRWs, and, thus, improvement of conservation approaches (Jackson et al., 2020; Vermeulen et al., 2021).



Figure 1. World map providing an approximate representation over southern right whales' circumpolar distribution, indicated by blue shade. Orange shading on the map indicates well-known breeding (Cooke and Zerbini, 2018). Suggested feeding grounds are indicated by yellow shading (Tormosov *et al.*, 1998; Kanda *et al.*, 2014; Zerbini *et al.*, 2018; Austin, 2021). The black arrows represent simplified migratory routes (Best *et al.*, 1993; Childerhouse *et al.*, 2010; Kanda *et al.*, 2014; Zerbini *et al.*, 2018; Mackay *et al.*, 2020).

Based on sighting data (Vermeulen *et al.*, 2021), one possible foraging ground could be located in close vicinity to the Antarctic Peninsula. The waters off Elephant Island (hereafter EI, 61°S 55°W), which is part of the South Shetland Islands and located at the tip of the Antarctic Peninsula (Orsi *et al.*, 1995), are an important foraging ground for other baleen whales, such as humpback whales (*Megaptera novaeangliae;* hereafter referred to as HW) and fin whales (*Balaenoptera physalus*; Santora *et al.*, 2010; Santora and Veit, 2013; Burkhardt *et al.*, 2021). As these waters are known for their high krill densities, including Antarctic krill (Siegel, 2005), a main prey species of SRWs (Cooke and Zerbini, 2018), the waters off EI might also represent an important foraging ground for SRWs. Due to weather and sea ice conditions and general logistical effort, the majority of available sighting data south of 55°S are from the austral summer and autumn and only represent limited point-estimates (Vermeulen *et al.*, 2021). Alternative monitoring methods such as passive acoustic monitoring (PAM) could be advantageous to investigate acoustic presence of SRWs on Antarctic feeding grounds during all seasons (Kimura *et al.*, 2009).

Since acoustic signals play a major role in cetacean ecology (Verfuß *et al.*, 2005; Sayigh, 2014), PAM methods can be used to monitor underwater vocalizations of cetaceans and even help to investigate related behaviours (Clark, 1982; Van Parijs *et al.*, 2009). Over the last decade, continuously improving technologies increased the possibility of passive acoustic data collection over large spatial and temporal

scales (Van Parijs et al., 2009), providing continuous, long-term, and seasonally unbiased data of soundproducing marine fauna from different types of marine environments (Mellinger et al., 2007). In coral reefs and other ecosystems PAM can, for example, be used to investigate acoustic behaviour of invertebrates such as crustaceans, or fish (Bouwma and Herrnkind, 2009; Kasumyan, 2009; Radford et al., 2014; Lammers and Munger, 2016). PAM is used to record long-term acoustic data of species producing high-frequency clicks, such as harbour porpoise in scottish waters (Brookes et al., 2013) as well as calls of low frequency baleen whales (Burkhardt et al., 2021). It can cover tropical species (Xu et al., 2020) as well as narwhales in remote high-latitude areas like the Western Fram Strait, as this method is not affected by weather, ice, temperature or light conditions (Kimura et al., 2009; Ahonen et al., 2019). These features make PAM invaluable for (acoustic) data collection on baleen whales migrating to offshore and logistically challenging areas (Ahonen et al., 2019; Calderan et al., 2021). The development of effective management and conservation strategies for migratory baleen whales, including successful implementations of marine protected areas (MPAs), is based on a detailed understanding of key habitats and migratory corridors (Hooker et al., 2011). Thus the knowledge on large-scale spatio-temporal patterns in occurrence and possible human-induced changes of these patterns is crucial (Hammond et al., 2013; Rowntree et al., 2020). Previous studies have shown that the investigation of small- and large-scale distribution patterns, migratory behaviour, habitat-use, and also variation of sound production in response to changes in ambient noise conditions of marine mammals is possible with PAM methods (e.g., Širović et al., 2006; Parks et al., 2007, 2010; Postma et al., 2011; Van Opzeeland et al., 2013; Schall et al., 2021b). Therefore, PAM can help to investigate the ecological importance of areas for sound-producing marine species (Van Parijs et al., 2009) and in the case of this study, for SRWs to better understand spatio-temporal habitat use on sub-Antarctic and Antarctic feeding grounds.

The efficiency of PAM methods depends on the ability to detect and correctly interpret acoustic signals, relying on baseline information on the focal species' acoustic features and behaviour (Mellinger *et al.*, 2007; Van Parijs *et al.*, 2009). Baleen whales have diverse vocal repertoires including unpatterned social vocalizations and patterned song sequences (Payne and McVay, 1971; Dunlop *et al.*, 2007). Based on variations in terms of duration, frequency range and bandwidth, spectrographic image, and visio-aural inspection, vocalizations cannot only be distinguished between different species, but in some cases also between different populations (Mellinger *et al.*, 2007). Right whales (*Eubalaena spp.*), including SRWs, are known to produce social vocalizations, and have one of the most intensively studied vocal repertoires among mysticetes. They produce a wide-range of low-frequency signals with energy below 1000 Hz, including stereotyped and variable vocalizations (Clark, 1982). Although the vocalization rates and types are highly variable depending on the individual or group behaviour, the vocal repertoire of right whales is very similar among regions (Clark, 1982; Parks and Tyack, 2005). Clark (1982) described six vocalization types of SRWs, including the upcall. Being the most commonly detected sound in acoustic studies of right whales (e.g., Clark, 1982; Parks and Tyack, 2005; Urazghildiiev *et al.*, 2009; Calderan

et al., 2021), the upcall, produced by all age classes and both sexes, on both breeding and foraging grounds, is believed to be a contact call (Clark, 1982; Dombroski et al., 2016; Calderan et al., 2021). Single SRWs producing upcalls were observed to be joined by other SRWs while also producing upcalls (Clark, 1982). Further, the upcall is not only essential for mothercalf communication (Dombroski et al., 2016), but also for individual whales believed to announce their presence in SRWs surface active groups (Parks and Tyack, 2005). Strong diurnal patterns of call rates also suggest the upcall as a primary contact call, as its call rate was highest in dusk and night times, when visual contact among whales is thought to be reduced (Webster *et al.*, 2019) The SRW upcall is a tonal vocalization rising in frequency from a mean low of 50 Hz, to a mean high frequency of 200 Hz, lasting 0.5 to 1.5 seconds as described by Clark (1982). However, recent studies indicate variation in the total frequency range and bandwidth of upcalls, between and within right whale species, probably due to demographic features, such as individual identity and age (McCordic et al., 2016), or changes in ambient noise, such as vessel noise (Parks et al., 2007, 2010, 2016). Gillespie (2004) indicates difficulties to distinguish between right whale upcalls and similar vocalizations of HWs. HWs produce songs, consisting of long, complex, stereotyped and repetitive acoustic signals (Payne and McVay, 1971). Only produced by males, HW song is most commonly produced during migration and on breeding grounds, but was also recorded on feeding grounds (Vu et al., 2012). So called non-song social sounds are produced for social interactions by both male and female whales, and are common at breeding (Silber, 1986) and feeding (D'Vincent et al., 1985) grounds, but were also found in migrating HW whales (Dunlop et al., 2007). Some social sounds can be part of songs as song units, which are highly variable and range from 30 Hz up to 2.5 kHz (Dunlop et al., 2007). One specific HW vocalization, in the literature described as 'whoop', 'wop' or 'upsweep' (hereafter also referred to as upcall; Dunlop et al., 2007; Wild and Gabriele, 2014) is often as social sounds (Dunlop et al., 2007), but is also found in HW song (Payne and McVay, 1971). As the HW upcall is used in a broad range of contexts it is also believed to be a contact call (Wild and Gabriele, 2014). It represents a tonal signal rising in frequency over a mean duration of 0.2 seconds with mean low and high frequency limits of 52 and 743 Hz, respectively, overlapping with the acoustic characteristics of right whale upcalls (Gillespie, 2004; Wild and Gabriele, 2014). Similarities in SRW and HW upcalls are problematic for PAM studies covering areas of overlapping distribution of the two species, as this may cause difficulties in correct species-classification of upcalls and thus, probably affect interpretations of species-specific spatio-temporal distribution patterns (Gillespie, 2004).

The Hybrid Antarctic Float Observation System (HAFOS) is an oceanographic observing network providing the infrastructure for a PAM network in the Atlantic Sector of the Southern Ocean (hereafter ASSO; Rettig *et al.*, 2013) also covering EI where presence of both SRWs and HWs was reported (Schall *et al.*, 2020; Vermeulen *et al.*, 2021). A previous analysis of passive acoustic data from EI from 2013 using the 'low frequency detection and classification system', LFDCS (Baumgartner and Mussoline, 2011) and a custom-made acoustic-context filter to detect HW vocalizations, identified unknown vocalizations off EI, which were falsely classified by LFDCS as HW acoustic signals (Schall *et al.*, 202).

2020). These unknown vocalizations were similar to known SRW vocalizations, more precisely SRW upcalls (Clark, 1982; Urazghildiiev *et al.*, 2009; Webster *et al.*, 2016; Calderan *et al.*, 2021), but not further examined at the time since the focus was on HW acoustic behaviour. Therefore, the aim of this study was to confirm and to investigate these data for potential acoustic presence of SRWs off EI. To date, SRWs and HWs are the only species known to produce vocalizations similar to upcalls in the Southern Hemisphere. Consequently upcalls of these two species were included in this studies' comparison, aiming to develop a decision structure for future reference to distinguish these species acoustically. As SRW upcalls are similar among regions and produced in both foraging and breeding areas, passive acoustic recordings from SRWs gatherings confirmed through on-site visual observations on an Argentinian winter breeding ground (Goldwater *et al.*, 2021) were analysed for comparison. HW upcalls detected in passive acoustic recordings from the ASSO extracted from HW song were added to the comparative analyses (Schall *et al.*, 2020). This comparison aims to confirm the acoustic presence of SRWs off EI and provides the vocalization parameters needed to differentiate acoustic signals between species for further PAM studies, facilitating the correct detection of SRW acoustic presence and behaviour.

2. Material and Methods

2.1 Study area and sampling

Passive acoustic data from Elephant Island (EI) were obtained using SonoVault autonomous recorders (Develogic GmbH, Hamburg, Reson TC4037-3 hydrophone, -193 dB re1 V μ Pa⁻¹ hydrophone sensitivity, 48 dB amplification gain, 24 bit resolution), which continuously recorded at a sampling frequency of 5,333 Hz as parts of oceanographic moorings (Figure 2 and Table 1). For vocalization comparisons passive acoustic recordings from SRWs gathering in Bahía San Antonio (BSA), Argentina, were analysed. Data were recorded using an array of six SoundTrap 202 STD recorders (Ocean Instruments NZ, -205 dBV re 1 μ Pa sensitivity, max level before clipping of 186 dB re 1 μ Pa gain, 16 bit successive approximation resolution) at a 4,000 Hz sampling frequency, for 14 days from 24 August to 6 September 2015. In addition, similar upcalls were analysed from HW songs (HWs are the only baleen whale species known to produce complex song within the target frequencies in the Southern Hemisphere, therefore these upcalls are confidently attributed to HWs; Payne and McVay, 1971; Clark, 1990) recorded in the Southern Ocean along the Greenwich Meridian (GM1, GM2 and GM3, summarized as GM) in 2011. Data from GM were obtained using the same recording set-up as off EI.



Figure 2. Bathymetric map of the southern Atlantic and the Southern Ocean including the geographical locations of the five acoustic recorders used in this study. (EI - Elephant Island, BSA - Bahía San Antonio, GM1, GM2, GM3 summarized as GM - Greenwich Meridian). Bathymetry data from Aamante and Eakins (2009).

Table 1. Deployment information on passive acoustic recordings. (EI - Elephant Island, BSA - Bahía San Antonio, GM	1,
GM2, GM3 summarized as GM – Greenwich Meridian).	

Recording ID	Latitude	Longitude	Sampling frequency	Deployment
			(Hz)	depth (m)
EI - AWI251-01_SV1008	61 0.88 °S	55 58.53 °W	5,333	212
BSA - Argentina	40 48.46 °S	65 58.20 °W	4,000	10 - 25
GM1 - AWI227-11_SV0002	59 3.02 °S	000 6.63 °E	5,333	1007
GM2 - AWI230-07_SV1001	66 1.9 °S	000 3.25 °E	5,333	934
GM3 - AWI231-09_SV1002	66 30.71 °S	000 1.51 °W	5,333	1083

2.2 Data analysis

2.2.1 Data selection

Information on acoustic presence of upcalls was available for EI through previous work within the Ocean Acoustics Group (Schall et al., 2020). Only even hours of the full dataset of EI recordings were previously analysed, therefore even hours with confirmed upcalls, and adjacent odd hours were considered in this study. A total of 102h of data comprisiong 1125 upcalls were logged and measured. The multi-channel sound recordings from BSA were originally used for the tracking of individual whale positions. To avoid logging the same individual whale vocalizations multiple times, only one of the six

channels was used for analysis in this study. Of the 14 recorded days, only ten days (i.e., from 25 August to 05 September.) were considered to avoid effects of noise pollution from the deployment as well as behavioural alterations of the whales caused by deployment and retrieval of equipment. Thus, 226.5h of in total 279.5h were manually analysed and 348 upcalls logged. The passive acoustic data of GM recorders in the ASSO had also been pre-processed for song structure analysis of HW songs in a previous study of Schall *et al.* (2021b). Seven days of song recordings with the known presence of confirmed HW song units (see explanation under 2.1, why HW song units are confidently attributed to HWs; Clark, 1990) in the Southern Ocean, were chosen for this study. The recordings are of different HW individuals (Schall *et al.*, 2021b) and song units include vocalizations which can be described as upcalls. A total of 168h of these recordings were reanalysed and 348 HW upcalls were logged and measured.

2.2.2 Spectrographic analysis

All passive acoustic recordings were analysed using the sound analysis software Raven Pro 1.6 (The Cornell Lab of Ornithology, Center for Conservation Bioacoustics, Ithaca, NY), with which spectrograms were calculated and visually scanned for upcalls.

To allow for a precise comparison of acoustic measurements from spectrograms between the different sampling rates at EI and GM, window sizes for spectrogram calculation were adjusted for each recording position. By means of vocalization duration and bandwidth of randomly chosen SRW and HW upcalls, the time analysis resolution error (TAR error) and the frequency analysis resolution error (FAR error) were calculated for each recording setup:

$$TAR_{error} = \frac{100}{\Delta t * TAR}$$
 with $TAR = \frac{fs}{ws}$,
and $FAR_{error} = \frac{100}{\Delta f * FAR}$ with $FAR = \frac{ws}{fs}$,

where Δt is the duration of a vocalization, Δf is the vocalizations' bandwidth, *ws* represents the window size and *fs* the sampling frequency. Creating spectrograms with similarly low error values ensures a similar trade-off between time and frequency resolution for all recording sites and with this the comparability of results is optimized (Table 2).

Recording	Sample	Window	Time analysis	Frequency analysis	TAR error	FAR error (%)
sites	frequency	size	resolution (s)	resolution (Hz)	(%)	
BSA	4000	560	0.14	7.143	10.769	10.504
GM	5333	350	0.065	15.237	10.938	7.619
EI	5333	740	0.141	7.111	10.818	10.457

Table 2. Raven Pro 1.6 settings for acoustic data analysis, and calculated time (TAR) and frequency analysis resolution (FAR).

Only vocalizations without overlapping signals (e.g., boat noise, other whale vocalizations etc.) were selected for analysis. For the characterization of vocalizations, selection boxes were drawn around

encountered upcalls according to the temporal and spectral limits of the respective vocalization. Within these boxes, a series of acoustic parameters were automatically extracted using available measurements in Raven Pro 1.6, to allow for numeric comparisons among vocalizations and with other studies (Table 3 and Figure 3). All measurements were performed using smoothed spectrograms in a Hanning window, with 50% overlap.

In addition to upcalls described in the literature (Clark, 1982), vocalizations with an alternation in their time-frequency pattern, namely a short additional frequency down-sweep at the end of the vocalization were detected off EI. As these visually represent a hook, vocalizations were annotated as 'hook'-calls to be able to check for the statistical similarity of the two types of upcalls encountered at EI.

Table 3. Quantitative measurements to describe detected upcalls of southern right and humpback whales in Argentina and the ASSO. Parameters were calculated according to the temporal and spectral limits of the respective vocalizations by drawing selection boxes around detected vocalizations. Details on measurements based on the Raven Pro 1.4 User's Manual (Charif *et al.*, 2010).

Measurement	Description
Low Frequency	Lower frequency limit of the selection box in Hz.
High Frequency	Upper frequency limit of the selection box in Hz.
Delta Frequency	The difference between the upper and lower frequency limits of the
	selection box in Hz.
Center Frequency	The frequency that divides the selection into two frequency intervals of
	equal energy in Hz.
1st Quartile Frequency	The frequency that divides the selection into two frequency intervals
	containing 25% and 75% of the energy in Hz.
3rd Quartile Frequency	The frequency that divides the selection into two frequency intervals
	containing 75% and 25% of the energy in Hz.
Frequency 5%	The frequency that divides the selection into two frequency intervals
	containing 5% and 95% of the energy in Hz.
Frequency 95%	The frequency that divides the selection into two frequency intervals
	containing 95% and 5% of the energy in Hz.
Delta Time	The difference between begin time and end time of the selection in
	S.
Duration 90%	The difference between the point in time that divides the selection into two time intervals
	containing 5% and 95% of the energy (Time 5%) and the point in time that divides the
	selection into two time intervals containing 95% and 5% of the energy in the selection in s.
Slope	The slope of the selection, calculated as delta frequency divided by delta time in Hz/s.



Figure 3. Visualization of performed measurements in Raven Pro 1.6. (a) Spectrogram of a southern right whale upcall (recorded on 25 August 2013 at 11:07:54 pm) showing low and high frequency limits (Low F and High F), bandwidth (Δ F) and duration (Δ Time), (b) waveform of the same upcall displaying the selected duration (Δ Time) and the duration 90% (Dur 90) measurements, and (c) associated frequency spectrum showing low and high frequency limits (Low F and High F), s and the division into frequency intervals of 5%, 25% (1st quartile), 50% (Center F), 75% (3rd quartile) and 95% of the energy contained in the signal. Spectrogram and frequency spectrum calculated with a FFT of 740 in Hanning window.

2.2.3 Statistical analysis

Selection tables containing quantitative acoustic measurements were exported from Raven Pro 1.6 and imported into RStudio Version 2021.09.02 (RStudio Team 2020) for statistical analysis.

For all quantitative acoustic measurements, descriptive statistics (minimum value, maximum value, mean and standard deviation) were calculated with the R package 'stats' (R Core Team, 2017). As an explorative method a principal component analysis (PCA) was performed to visually determine the degree of similarity/dissimilarity between 'hook-calls' and upcalls from EI. The PCA presented 'hook-calls' and upcalls from EI as a homogenous group, hence all logged vocalizations from EI were treated as 'normal upcalls' (Appendix, Figure A1). Boxplots representing descriptive statistics were created for all quantitative acoustic measurements.

To decide on suitable tests for further statistical analysis, the Shapiro-Wilk test using the function 'shapiro.test' within the R package 'stats version 3.6.2' (R Core Team, 2017) was used to test for normal distribution of the data. Moreover, an analysis of homogeneity of multivariate dispersion (PERMDISP) within the R package 'vegan' (Oksanen et al., 2020) was applied to the data (Appendix, Table A1). These tests indicated that the data were neither normally distributed nor homogenous. Nevertheless, to attempt to statistically verify the influence of the factor 'group' (the different upcall classes detected off EI, BSA and GM, respectively) on the variability of acoustic measurements, two non-parametric statistical approaches within the R package 'vegan' were implemented (Oksanen et al., 2020). An analysis of similarities (ANOSIM) based on the rank order of dissimilarities using the function 'anosim' and a permutational analysis of variance (PERMANOVA) using the function 'adonis' were performed. Both tests were performed with 10,000 permutations, using the Bray-Curtis and the Euclidean distance as distance measures (Appendix, Table A1). Further, a pairwise comparison using the packages 'vegan' and 'pairwiseAdonis' (function 'pairwise.comparison') was conducted to determine which groups' vocalizations were different based on their acoustic characterization (Martinez Arbizu, 2020). Additionally, to avoid biased results through an un-balanced design, all three tests were also performed with ten random subsets of 350 samples each from the EI dataset, using the original dataset-sizes from BSA and GM (i.e., $n_{BSA} = 348$, $n_{GM} = 354$).

Furthermore, a Similarity Percentage (SIMPER) analysis within the package 'vegan' was applied (function 'simper') using the Bray-Curtis distance measure to determine the contribution of each acoustic measurement to the dissimilarities between groups (Appendix, Table A1). To visualize groupings of samples based on the quantitative acoustic measurements, non-metric multidimensional scaling (NMDS) was used to reduce the multiple dimensions of conducted measurements to two dimensions within the R package 'vegan'.

3. Results

In the total amount of 496.5 analysed hours of acoustic recordings 1,827 upcalls were logged and analysed. Off EI, 1,125 upcalls were logged of which 620 were 'hook'-calls. For comparison, 348 and 354 upcalls from SRWs and HWs were logged in the BSA and at GM, respectively (Figure 4). The PCA showed 'hook'- and upcalls from EI as almost completely overlapping clusters, so that both vocalization types from EI were pooled to be upcalls (Appendix, Figure A1). During the 2013 collection period upcalls were detected on 27 days, with data available only for parts of January and November and no data available for December (Table 4 and Appendix, Figure A2). Upcall vocalizations were detected from January to May and in August. April shows a peak in vocalization numbers with 448 upcalls being detected on a single day, 22 April 2013. While 1,120 upcalls were detected in austral summer and autumn, only 5 were detected in austral winter (August).

Table 4. Temporal distribution of detected upcalls off Elephant Island (EI). In total 1125 upcalls were detected on 27 days. Recordings took place from 15 January to 9 November 2013, lighter grey shading of cells indicates that data are available for only parts of the months. White fields indicate no data available.

Month	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Recordings												
Number of detected vocalizations	46	80	145	775	74			5				

The mean frequency of the vocalizations recorded at EI varied from 113 Hz to 181 Hz. Vocalization frequency in some cases did range from a minimum low frequency of around 44 Hz to a maximum high frequency value of around 401 Hz. EI upcalls had a mean bandwidth of around 67 Hz and an average duration of 0.56 s. The detected vocalizations were characterized by a mean slope of around 137 Hz/s. Vocalizations detected in the BSA had a mean low frequency around 75 Hz and a mean high frequency around 162 Hz. The slope of the vocalization averages to 104 Hz/s with a mean bandwidth of around 86 Hz and a mean duration of 0.89s. Frequencies of the HW vocalizations detected at GM ranged on average from 116 Hz to 568 Hz, while the mean duration was 0.51s. The mean bandwidth was 452.27 Hz resulting in a mean slope of around 1024 Hz/s (Table 5).



Figure 4. Spectrograms of analysed upcalls. (a) southern right whale upcall detected off Bahía San Antonio (BSA), (b) humpback whale upcall detected at the Greenwich Meridian (GM, (c) upcall and (D) 'hook-call' detected off Elephant Island (EI). Spectrograms calculated with FFT 740 (a + b), and FFT 850 (c + d) and a Hanning window.

Table 5. Summary statistics of measured upcall vocalization characteristics: minimum (min), mean, maximum (ma	ax) values
and standard deviation (sd). Explanations on how the different measurements were conducted can be found in Tab	le 3.

Group	measurement	min	mean	max	sd
	Low Freq (Hz)	44	113.97	353.4	24.26
	High Freq (Hz)	103.6	181.94	401.2	21.34
	Delta Freq (Hz)	23.59	67.97	154.8	19.25
	Duration (s)	0.18	0.56	2.42	0.27
	Center Freq (Hz)	72.91	146.43	374.98	25.14
EI	Freq 25 (Hz)	62.49	134.26	369.77	25.89
	Freq 75 (Hz)	83.33	159.03	380.19	23.09
	Freq 5 (Hz)	46.87	121.21	364.56	25.2
	Freq 95 (Hz)	93.74	172.23	390.6	21.57
	Dur 90 (s)	0.07	0.39	20.16	0.23
	Slope (Hz/s)	34.59	137.27	418.58	51.32
	Low Freq (Hz)	42.43	75.67	321.53	38.28
	High Freq (Hz)	98.99	162.3	442.94	46.71
	Delta Freq (Hz)	35.99	86.63	177.81	24.33
	Duration (s)	0.33	0.89	1.70	0.26
	Center Freq (Hz)	66.41	103.75	371.09	42.04
BSA	Freq 25 (Hz)	62.5	93.04	339.84	40.15
	Freq 75 (Hz)	70.31	116.97	382.81	43.64
	Freq 5 (Hz)	50.78	83.59	332.03	39.03
	Freq 95 (Hz)	82.03	137.54	410.16	44.71
	Dur 90 (s)	0.14	0.56	1.26	0.2
	Slope (Hz/s)	33.85	104.36	370.28	41.72
	Low Freq (Hz)	30.24	116.57	464.93	55.48
	High Freq (Hz)	238.36	568.84	1.006.56	147.42
	Delta Freq (Hz)	109.72	452.27	910.5	139.65
	Duration (s)	0.13	0.51	0.92	0.2
	Center Freq (Hz)	72.91	252.22	593.71	76.46
GM	Freq 25 (Hz)	52.08	198.67	531.22	65.88
	Freq 75 (Hz)	104.16	317.1	677.04	87.00
	Freq 5 (Hz)	31.25	146.32	510.39	59.37
	Freq 95 (Hz)	187.49	434.44	812.45	112.83
	Dur 90 (s)	0.33	0.31	0.72	0.13
	Slope (Hz/s)	336.47	1024.48	3.090.58	508.42

For consistency, only the results based on the Bray-Curtis distance measures will be reported here, since statistics using comparative distance measures resulted in similar outputs. The results based on the Euclidean distance measure are provided in the Appendix (Tables A2, A4, A6 and A8) and lead to the same conclusions as the statistical results presented here. Both the ANOSIM applied to the complete data set (R-value = 0.8174 and p-value = $9.999e^{-05}$, Appendix, Table A2), and the ANOSIMs applied to multiple subsamples (mean R-value = 0.5847 and p-values = $9.999e^{-05}$, Appendix, Table A3) suggested

greater dissimilarities between than within groups, with high significance levels. F-values of the performed PERMANOVAs on the complete dataset (F-value = 3148.1, p-value = $9.999e^{-05}$ and R² = 0.77537, Appendix, Table A5) and on the subsamples (mean F-value = 1168.36, p-value = $9.999e^{-05}$ and R² = 0.690164, Appendix, Table A7) demonstrate a significant group separation, while the determination coefficient values indicate a good fit for the variation in distances explained by groups. Since the assumption of homogeneity was violated when conducting the above listed tests, the reported statistical results have to be interpreted with caution.

When scaling the various acoustic measurements with the NMDS method, two dimensions were chosen to collapse information, since the stress value of 0.037 indicates a good fit of ordination. All analyzed vocalizations are clearly split into two groups, namely the EI and BSA vocalizations as a single group and the GM vocalizations as a separate group (Figure 5).



Figure 5. NMDS plot representing the two-dimensional grouping of analysed vocalizations. Stress value = 0.037. (GM – Humpback whale, BSA – southern Right Whale and EI – Unknown).

Examining medians and value ranges of conducted acoustic measurements can reveal drivers of similarities and dissimilarities between groups, while it also shows that there are actual differences in means between groups supporting the statistical results (Figure 6). Low frequency measurements of upcalls from EI had similar overall ranges compared to BSA, but with a higher median and interquartile range at EI. In comparison to EI, the low frequency limits of vocalizations recorded at GM had a greater overall range. High frequency limits of EI vocalizations resulted in a relatively small interquartile range, also similar to BSA vocalizations, where slightly lower high frequencies were recorded. GM upcalls

were characterized by a far greater overall and interquartile range of the high frequency limits than EI and BSA upcalls. The bandwidths of EI vocalizations resulted in a relatively small interquartile range similar to BSA measurements, but had slightly lower values compared to vocalizations from BSA. However, bandwidths of GM vocalizations were spanning a larger overall and interquartile range. The remaining robust frequency measurements (center frequency, 1st quartile frequency, 3rd quartile frequency, 5% frequency, 95% frequency) all indicated a very similar pattern. Robust frequency measurements of upcalls detected at EI had a comparable range to BSA vocalizations, while GM upcalls were characterized by a much greater range, including a greater and higher interquartile range, as well as a higher median. However, EI vocalizations had a higher and greater interquartile range than BSA vocalizations. The slope of analysed vocalizations showed very similar and small ranges of EI and BSA upcalls, all located below 500 Hz/s, while the overall range of GM vocalizations was considerably different. Analysed upcalls spanned from around 400 Hz/s up to over 3000 Hz/s, with a median around 900 Hz/s. These median and range differences in frequency measurements are reflected in the performed pairwise comparison, which also indicated greater, but similar differences between GM vocalizations and detected vocalizations at EI and BSA, respectively (GM - EI SumOfSqs = 38.776119 and p-value = 0.001, GM - BSA SumOfSqs = 38.5435545 and p-value = 0.001, Appendix, Table A9), and the analysis applied on the subsets showed comparable results (GM - EI mean SumOfSqs = 39.6827625 and p-value = 0.001, GM – BSA mean SumOfSqs = 55.6936864 and p-value = 0.001, Appendix, Table A10). Temporal measurements of the vocalization (duration and duration 90%) showed similar patterns with respect to parameter ranges of groups. The overall range for EI upcalls was comparable to BSA upcalls, but the median and height of the interquartile range was more similar to GM upcalls. These variations are reflected in the pairwise comparison between EI and BSA applied to the whole dataset (SumOfSqs = 6.143 and p-value = 0.001, Appendix, Table A9) and the subsets (mean SumOfSqs = 4.5717328 and p-value = 0.001, Appendix, Table A10), which indicated small dissimilarities between EI and BSA upcalls. Consistent with these results are the outcomes of the performed SIMPER analyses, which indicated that the measurements slope, delta frequency and high frequency mainly drove differences between GM and EI, and GM and BSA (Appendix, Table A11). According to this analysis, the minor differences between EI and BSA were driven by slope, 3rd quartile frequency and center frequency.



Figure 6. Boxplots representing quantitative acoustic measurements for the three groups GM - Humpback Whale, BSA - southern Right Whale and EI - Unknown.

4. Discussion

4.1 Southern right whale vocalizations

Vocalizations recorded at EI in 2013 were characterized and successfully attributed to SRWs. The measured mean start frequency of the EI vocalizations was 113 Hz monotonically increasing to a mean end frequency of 181 Hz, with a mean slope of 137 Hz/s. These upcall characteristics are broadly similar to the measured characteristics of SRW vocalizations at BSA. Apart from a similar mean duration (EI: 0.56 s and GM: 0.52 s), EI vocalizations were notably different from HW vocalizations recorded at GM, with a mean slope of 1,024 Hz/s and a mean bandwidth of 452 Hz as the main contributors to differences between groups, allowing to successfully differentiate SRW upcalls from HW vocalizations (Tables 5 and 6). I can exclude the possibility that the acoustic measurements are biased by the analyst's manual logging of individual vocalizations; this method of acoustic analysis is widely used in the literature to investigate call parameters (e.g., Dombroski *et al.*, 2016; Webster *et al.*, 2016; Calderan *et al.*, 2021). I extracted robust measurements (center frequency, 1st quartile and 3rd quartile frequency, frequency 5%

and 95%, duration 90%) that do not entirely rely on time and frequency endpoints, but on the energy distribution within the selection. Thus, small changes in borders of the selection should have little influence on the resulting measures (Charif et al., 2010). As these robust measurements were also included in this studies' acoustic analysis and show clear differences between species as well, the results of more subjective selection-based comparison of acoustic parameters are substantiated. Nevertheless, future studies should also include a more robust and less time-consuming method for upcall detection, since the manual acoustic analysis used in this study is subjective. Standardized acoustic metrics can provide an objective alternative solution to analyse large passive acoustic datasets (Schall et al., 2021a). Besides describing general acoustic diversity in an ecosystem and distinguishing species-specific vocalizations from natural ambient noise (Roca and Van Opzeeland, 2020), acoustic metrics are also used for intraspecies call classification (Schall et al., 2021a). Therefore, acoustic metrics could probably be used for realiable automated SRW upcall classification. Measurements describing bandwidth and slope were identified as the main contributors to differences in upcall characteristics between SRWs and HWs. Results of this study could also help to generally improve automated detection of right whale upcalls in PAM approaches, and probably also provide some additional information for near-real-time detection of (North Atlantic right whale) upcalls for ship strike mitigation (Spaulding et al., 2009). The Identified main differences in call characteristics, describing bandwidth and slope, of SRW and HW upcalls could further improve this approach and might decrease false detection rates.

The measured means of vocalization parameters of SRWs at EI and BSA are also within the time and frequency ranges of right whale vocalizations described by Clark (1982). The EI vocalizations' bandwidths are broadly similar to approximated bandwidths of SRW vocalizations detected off South Georgia (Calderan et al., 2021), off the Auckland Islands (Webster et al., 2016), and on breeding grounds off Brazil (Dombroski et al., 2016). The measured mean of the upper frequency limit of EI upcalls is more similar to upcalls recorded by Širović et al. (2006) off South Georgia (Table 6). However, the mean duration of analysed EI upcalls is relatively short, compared to previously mentioned studies. Only Dombroski et al. (2016) describe SRW upcalls off Brazil with similar durations (0.6 s) compared to the upcalls attributed to SRWs in this study (0.56 s). Likewise, the measured means of HW vocalization parameters at GM are within frequency limits of non-song vocalizations obtained in previous studies from the Southern Hemisphere (Dunlop et al., 2007). The mean low and high frequencies for comparable 'upsweeps' recorded at a southeastern Alaska feeding ground were 52 and 743.4 Hz, respectively, spanning an even greater mean bandwidth (691 Hz; Wild and Gabriele, 2014) than detected HW vocalizations in this study (452.27 Hz). In contrast, detected vocalizations at GM have a longer mean duration (0.52 s) than analysed upsweeps in Wild and Gabriele (2014; 0.2 s). Since the upcall-similar non-song vocalizations of HWs in Wild and Gabriele (2014), the so called 'whup'calls, were analysed in two selections (growl and upsweep), the measured mean upsweep duration might be shorter in time, than in analysed HW vocalizations in this study, where no such two-part selection was performed.

	right whale								humpho	ak wholo
				right w	nare				numpouch what	
	This Study	This	Calderan	Webster	Širović <i>et</i>	Dombros	Parks et al.	2007	This Study -	Wild and
	- EI	Study -	et al. 2021	et al. 2016	al. 2006	ki <i>et al</i> .			GM	Gabriele
		BSA				2016				2014
Species	Е.	Е.	Е.	Е.	Е.	Е.	Е.	Е.	М.	М.
	australis	australis	australis	australis	australis	australis	australis	glacialis	novaeangliae	novaeangliae
Area	Elephant	Bahía San	South	Auckland	South	Brazil	Argentina	Bay of	Greenwich	Southeastern
	Island	Antonio	Georgia	Islands	Georgia			Fundy	Meridian,	Alaska
					and Scotia				ASSO	
					Sea					
Mean	0.56 (0.27)	0.89 (0.26)	0.8 (0.27)	0.9	0.7 (0.1)	0.6 (0.2)	0.82 (0.23)	0.87	0.51 (0.2)	0.2 (0.1)
Duration								(0.27)		
Mean Low	113.97	76.67	86 (10)	87	92 (11)	58 (22)	78 (15)	101 (22)	116.57	52 (13)
Frequency	(24.26)	(38.28)							(55.48)	
Mean High	181.94	162.3	145 (23)	143	173 (11)	138 (38)	156 (29)	195 (38)	568.84	743.4 (169)
Frequency	(21.34)	(46.71)							(147.42)	
Delta	67.97	86.63				71 (35)			452.27	691 (172)
Frequency	(19.25)	(24.33)							(139.65)	
Slope	137.27	104.36							1024.48	
	(51.32)	(41.72)							(508.42)	
N° Calls	1125	348	149	701	31	769	78	929	354	248

Table 6. Selected acoustic characteristics of vocalizations of two right whale species and humpback whales from different studies. (Values in parentheses are standard deviations, not available for Webster *et al.* 2016).

4.1.1 Shifts in vocalization parameters

Compared to the SRW vocalizations recorded at BSA and vocalizations analysed in other studies, the detected EI upcalls have higher mean low frequency limits. An increase of the start frequency (69 to 78 Hz) of SRW upcalls between 1977 and 2000 off Argentina was shown by Parks et al. (2007), and the latter value corresponds to the mean low frequency limit of BSA upcalls measured in this study. I found a remarkable difference of on average 21 Hz for the low frequency limit of EI upcalls compared to SRW upcalls from other regions. Comparable low frequency limits were only measured in North Atlantic right whale upcalls detected in the northwest Atlantic (Parks *et al.*, 2007), an area characterized by high levels of anthropogenic noise, such as noise caused by shipping and fishing (Parks et al., 2009, 2010). Changes in background noise conditions are known to not only be possible drivers for changes in vocalization amplitudes, also known as the Lombard-effect (Scheifele et al., 2005; Helble et al., 2020), but also for changes in frequency limits of vocalizations, as well as their duration (Parks et al., 2010, 2016). Parks et al., 2016 found that the low frequency limit of SRW vocalizations shifted to higher frequencies compared to baseline conditions, when dominant background noise at lower frequencies than SRW vocalizations was present. This phenomenon has also been studied in urban song of great tits (Parus major; (Slabbekoorn and den Boer-Visser, 2006) and in striped dolphins (Stenella coeruleoalba), which increase their low-frequency limits with increasing levels of environmental noise occurring in frequencies of social communication (Papale et al., 2015). Background noise conditions are not only influenced by anthropogenic noise, but also biological noise (e.g., fish chorus). To avoid acoustic competition among species that share the same acoustic environment, many animal species are thought to adapt and develop specific acoustic niches (i.e., timespans or frequency bands with comparatively little overlap from other species). This niche can be be extended through frequency modulation, for example, when an acoustic invasion of another species occurs (Mossbridge and Thomas, 1999). Likewise to changes in spectral properties of signals of white-banded tree frogs (*Hypsiboas albomarginatus*) caused by an acoustic invasion of another species (Both and Grant, 2012), also Orcas (*Orcinus orca*) were observed to adapt frequency ranges when leopard seals (*Hydrurga leptonyx*) were acoustically present (Mossbridge and Thomas, 1999).

Fin whales are known to produce a variety of low-frequency, but high-intensity vocalizations (Watkins, 1981; McDonald and Fox, 1999; Širović et al., 2004). Off EI, fin whale low-frequency vocalizations, the so called 20 Hz-pulses with frequency limits of 15-28 Hz are often accompanied by a higher frequency component at 85-89 Hz (Širović et al., 2004; Burkhardt et al., 2021). As fin whales aggregate in great numbers off EI, resulting in high amplitude levels of the frequency bands used by local fin whales at EI (Burkhardt et al. 2021), they may compete for acoustic space with the SRWs off EI, possibly leading to shifts in SRW vocalization parameters. An acoustic energy analysis in the typical fin whale frequency bands of 13-28 and 84-89 Hz for the analysed recording snippets from this study shows different energy levels in background noise for the three different locations (Figure 7). The fin whale energy at EI was characterized by a greater overall range compared to BSA and GM recordings and moreover, the median of the fin whale energy of the EI recordings was considerably higher than at BSA and GM. Maximum energy levels in fin whale vocalization frequencies at BSA were even lower than the energy level median energy level of EI recordings. These results suggest that fin whales are a considerable source of background noise at EI, which potentially is the cause for a shift of the low frequency limit of SRW upcalls. As right whales are long-lived animals and adaptations to noise conditions occur within the life-times of individual whales within a population (Tennessen and Parks, 2016), the ability of vocal learning might allow SRWs to adapt to high-intensity vocalizations produced by fin whales in regard of communication within the species. In this context, SRWs might also have the ability to exploit their acoustic niche in presence of anthropogenic noise (Dombroski et al., 2016). Although, compared to the Arctic only limited marine traffic and industrial acitivties are present, sporadic cruise ships and research vessels emit low frequency sounds in the Southern Ocean (Riley and Hollich, 2018; Morley et al., 2020). Hydroacoustic instrumentation, either autonomous or installed on survey vessels, also represent a considerable source of ambient noise that overlap in frequencies with the frequency bands actively used by SRWs (Van Opzeeland and Boebel, 2018). If SRWs could adapt to anthropogenic noise in respect to intra-species communication, as they do to high-intensity vocalizations of fin whales, the acoustic adaptation probably improves the resilience of SRWs in a rapid changing ocean. Nevertheless, when ambient noise levels exceed the compensation abilities of SRWs, either the whales' communication range will be reduced (Parks et al., 2010), or as it was shown in terrestrial species, the acoustic environment potentially drives the site occupancy (Kleist et al., 2017), or even affects the receivers' responses to the adjusted signals, with the potential of maladaptive mating behaviours (Senzaki *et al.*, 2018; Schou *et al.*, 2021).



Figure 7. Analysis of fin whale vocalization energy, (a) displaying boxplots representing the mean energy within frequency limits of 13 - 28 and 85 - 89 Hz. Energy was calculated from frequency spectra of sound snippets from all detected upcalls. Representative spectrogram snippets showing detected upcalls and background noise off (b) BSA – Bahía San Antonio, (c) EI – Elephant Island, and (d) GM – Greenwich Meridian, were calculated with FFT 560 (b), FFT 740 (c), FFT 850 (d) and a Hanning window.

4.2 Potentials of PAM

Altogether, the conducted comparative analyses and comparisons with published vocalization characteristics clearly indicate that the upcalls recorded at EI can be attributed to SRWs with high

certainty. The upcall is the most well-known and prevalent vocalization of the SRW's vocal repertoire, thought to be used as a contact call between individuals (Clark, 1982), and based on its prevalence is also most commonly used for passive acoustic detection (Urazghildiiev et al., 2009). As these vocalizations are used by both sexes, all age classes and during a range of behavioural contexts (Parks et al., 2011), detection of these calls (e.g., through evaluation and comparison of vocalization rates and amplitudes of single vocalizations) could also be used as an indicator for social context or group composition. For example, the upcall is the most frequently detected vocalization in mother-calf pair aggregations on wintering grounds, probably associated with both intra-pair and inter-pair signalling. Upcalls are also detected during socializing activities of right whales at the water's surface, known as surface active groups (SAG), but not as frequent as in mother-calf pairs (Dombroski et al., 2016). The automated detection of upcalls can also be used as an indicator for the presence of other vocalizations in the SRW vocal repertoire (which can be identified and analyzed in more detail subsequently), which could give additional information on group composition, breeding, feeding or social behaviour (McDonald and Moore, 2002). For instance, the most common detected vocalizations in SAGs are gunshots and moans. Gunshots are brief, broadband sounds thought to be produced by males, which may function as sexual advertisement (Parks and Tyack, 2005), as these vocalizations are commonly detected in SAGs including sexual behaviour and are not detected at breeding grounds with high abundance of mother-calf pairs (Dombroski et al., 2016). Besides behavioural insights, detections of right whale upcalls can provide information on single whale identity and age class, which are mainly dependent on spectral entropy and duration (McCordic et al., 2016). Further, acoustic cue counting using upcall detections has been shown to be successful for estimating right whale density in the northern Pacific (Marques et al., 2011). In the northwest Atlantic, PAM is used for the real-time detection of North Atlantic right whale (Eubalaena glacialis) upcalls (Van Parijs et al., 2009) not only for information on their distribution, but also for collision mitigation, as ship strikes are a major mortality cause for the highly endangered North Atlantic right whale (Campbell-Malone et al., 2008). For all these applications of PAM, the ability to correctly detect vocalizations and distinguish between co-occurring species is essential. This study shows that especially frequency related measurements such as slope, delta and high frequency could help to distinguish between SRW and HW upcalls in future acoustic studies.

4.3 SRW distribution and importance of environmental factors

The correct detection of SRWs is also important to understand the spatio-temporal distribution and migration patterns. In this study, SRW presence off EI was detected in austral summer (January and February), austral autumn (March to May) and in austral winter (August; Table 5 and Appendix, Figure A2), with a peak of 775 detected upcalls on a total of 11 days in April. This observation is in broad agreement with post-whaling sighting data collected between 1982 - 2020 around the Antarctic

Peninsula and in the Weddell Sea (Vermeulen *et al.*, 2021). The majority of sightings were registered in austral summer (December to February) spread around the Antarctic Peninsula, with fewer individuals observed in austral autumn but closer inshore. This inshore movement could explain the considerably increased number of upcall detections in EI recordings in April. While five upcalls were detected in August in this study, Vermeulen *et al.* (2021) did not list any sightings in austral winter. This is likely caused by a lack of data since no sighting data were collected south of 55°S in austral winter months, probably due to weather conditions and less reseach effort. Here PAM with autonomous devices is advantageous in comparison to visual sighting survey. As this method is less affected by weather, and not affected by ice-cover and light conditions (Kimura *et al.*, 2009), PAM data are extremely valuable to close the knowledge gap on SRW winter distribution, especially in Antarctic regions.

The temporal occurence of SRWs off EI presented in this study, however, needs to be interpreted with caution, as all analysed upcalls were a byproduct of HW occurrence from Schall *et al.* (2020). Therefore, there is a high possibility that some SRW vocalizations were missed in the EI recordings of 2013 by the detector which was tuned for HW vocalization detection. The repeated analysis of these and of all available recording data of EI since 2012 (Rettig *et al.*, 2013), using automated detection searching for SRW upcalls specifically, would most likely yield further insights into the temporal occurrence of SRWs.

The combined investigation of environmental factors, anthropogenic impacts, and soundscapes including the specific identification of SRWs' and other species' vocalizations is of high interested to understand the future of Southern Ocean ecosystems and should be the focus in future research projects. In order to protect and conserve species or populations as effectively as possible, the identification of areas of importance for the species or population is crucial. While current SRW breeding grounds are well-studied, contemporary data on feeding ground locations south of 40°S are sparse. The identification of offshore feeding grounds could lead not only to an improved understanding of SRWs spatio-temporal distribution, but also to a better knowledge on environmental variables which may be relevant for links to reproductive success. Thus, identification of possible offshore feeding grounds is a key part of the International Whaling Comission - Southern Ocean Research Programme (IWC-SORP) research theme 6 (Vermeulen et al., 2021). As the SRWs' temporal acoustic presence is accompanied by phytoplankton blooms from January to March, and the waters are characterized by high krill densities, including Antarctic krill, a main foraging source of SRWs and other baleen whales (Siegel, 2005), EI could not only be a key habitat for fin whales (Burkhardt et al., 2021) and HWs (Schall et al., 2020), but presumably also for SRWs. Compared to South Georgia, where SRW occurrence was confirmed through whaling records for the first time in 1905 (Townsend, 1935; Tønnessen and Johnsen, 1982), no whaling records on SRWs around the Antarctic Peninsula, but only recent sightings through opportunistic and direct efforts (Best et al., 2001) exist to my knowledge. Accordingly, it is not possible to conclude whether SRW occurrence is historical or has been shifted into these waters in recent years. Nevertheless,

the general importance of EI for baleen whales requires special protection of this ecosystem (Schall et al., 2020; Burkhardt et al., 2021; IUCN-Marine Mammal Protected Areas, 2021). In recent years touristic activities increased in certain areas around the Antarctic Peninsula (Bender et al., 2016), probably causing a variety of impacts such as acoustic disturbance, increase in stress levels for the animals or even ship strikes (Rolland et al., 2012; Halliday et al., 2018). Additionally, krill fisheries using advanced technology concentrated around the Antarctic Peninsula in recent years increasing catch rates of Antarctic krill (Krüger, 2019), leading to increased pressure on this important prey species, especially in the light of onging climate change. The Antarctic Peninsula has one of the fastest rates of regional warming on Earth, which is reflected in the retreat of glaciers and collapsing ice shelves (Clarke et al., 2007; Rogers et al., 2020), which particularly affects organisms that rely on a regional winter sea ice coverage (Atkinson et al., 2004; Clarke et al., 2007). Our preliminary results on the temporal occurrence of SRWs off EI suggest that SRWs do not occupy the area around EI when sea ice concentration is high, although more and reliable data than presented by this study would be needed to draw firm conclusions. Sea ice coverage changes can directly and indirectly impact cetaceans (Nicol et al., 2008). According to Burkhardt et al. (2021) sea ice was present to up to 80% coverage off EI during July to October 2013 (while coverage in summer and autumn was below 5%), when only five SRW upcalls were detected in August. Yet, no vocalizations were detected in June when no sea ice was present, suggesting that sea ice coverage might not be the cause for SRWs to be acoustically absent (however, as already mentioned, acoustic absences could be influenced by the way vocalizations were detected in this study). Sea ice coverage could also indirectly affect SRWs as their reproductive success is dependent on body condition and thus foraging success (Seyboth et al., 2016), as this is shown to be the case for North Atlantic right whales (Greene et al., 2003). Since Antarctic krill is clearly influenced by sea ice coverage, annual fluctuations in sea ice concentration can be linked to fluctuations in krill abundance (Atkinson et al., 2004). Sea ice coverage is important for the krills' survival during austral winter, because the underside of sea ice provides refugee from predators and food for larval krill. Through its' movement, sea ice can even influence the dispersal of larval krill (Nicol, 2006). Moreover, as the ice seasonally melts it facilitates the spring bloom increasing post-winter larval survival and positively impacts spawning success (Siegel and Loeb, 1995; Wiedenmann et al., 2009). Thus, a high reproductive output of Antarctic krill is generally favoured by a large sea ice area and a long duration for this large sea ice area in winter (Atkinson et al., 2004; Siegel, 2005). Sea ice data is often used as a proxy for E. superba abundance and, for example, a relationship has been found between body condition in HWs in west Australian waters and sea ice presence on Antarctic feeding grounds (Braithwaite et al., 2015). Body conditions of SRWs could therefore also be indirectly linked to the local sea ice coverage off EI. Loeb and Santora, (2015) suggest that climate variabilities like the El Niño Southern Oscillation events (ENSO) and the Southern Annular Mode (SAM), increasing water temperatures and facilitating sea ice melting, also influence Antarctic krill abundance in the Southern Ocean. This has been shown to affect the spatio-temporal distribution of HWs in the ASSO (Schall et al., 2021b) and probably also affects the distribution of SRWs. Climate variabilities were also linked to the reproductive success of female SRWs (Seyboth *et al.*, 2016). Further, Agrelo *et al.*, (2021)found reduced survival in female SRWs that have calves in the season before a strong El Niño event. Low prey availability following El Niño events affect the blubber recovery in female right whales after spending energy to gestate, nurse and wean a calf, and therefore, the events are likely to affect the recovery rate of SRWs (Agrelo *et al.*, 2021).

5. Conclusions and outlook

Detected unknown vocalizations off EI were successfully attributed to SRWs, confirming acoustic presence of SRWs in the waters off EI in 2013. As the present analysis only provides first insights into the spatio-temporal distribution of SRWs in the ASSO, and confirmed sightings are located not only around the Antarctic Peninsula, but also in other sub-Antarctic and Antarctic areas (Vermeulen *et al.*, 2021), there is potential for future PAM studies.

Since acoustic presence of SRWs was confirmed off EI, all available acoustic data of the HAFOS EI recorders since 2012, spanning nine years of recordings (Rettig et al., 2013), should be analysed for presence of SRW upcalls. Additionally, the recorder located on the Greenwich Meridian in the northeastern Weddell Sea (59 2.82 °S, 000 5.78 °E), could be considered for further analyses, as a South African data source reported a sighting close to this location. For future PAM studies, new recorder positions should preferably overlap with sighting data from Vermeulen et al., (2021), and extend in a transect around 60°S from EI towards the east. This would give a year-round (acoustic) insight for an area between locations of confirmed visual presence of SRWs. Analysis approaches including multiyear and multi-location data for long-term and large-scale studies conducting more comprehensive analyses of acoustic recordings would help to understand SRW spatio-temporal distribution and their migration patterns. Since marine species' distribution patterns are driven by environmental parameters (such as sea surface temperature (SST) or sea ice coverage; e.g., Smith et al., 2007; Abrahamsen et al., 2020) that drive biological productivity (net primary production; Séférian et al., 2014), joint analyses of environmental conditions and SRWs' distribution data can help to identify drivers of distribution patterns and habitat choice (Payne et al., 2017). These analyses together with ecological knowledge on trophic relationships and a quantitative understanding of spatial and temporal lags between physical drivers and ecological response can be used to calculate forecasts on weekly, annual or even decadal scales (Barlow and Torres, 2021). Spatial predictions of SRW distribution are potentially vital for effective management implementations (Williams et al., 2006; Barlow and Torres, 2021), such as MPAs, especially in a region like the Antarctic Peninsula facing one of the fastest regional warming rates on earth (Vaughan et al., 2003; Rogers et al., 2020) and rising anthropogenic pressure (Morley et al., 2020), while representing an important feeding ground for SRWs and other baleen whales in the Southern Ocean.

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Appendix



Figure A1. Comparison of the two types of vocalizations recorded at EI. Spectrogram displays of (a) an upcall and (b) a 'hookcall' with an alternation in their time-frequency pattern detected off Elephant Island. The PCA (c) shows the scattering of all vocalizations analysed in this study on two dimensions.

Table A1. Overview of the R functions used for the statistical testing. com = community matrix, df = data frame and G = Groups of the different upcall classes used in this study.

Test	Function	Parameter
ANOSIM	'anosim'	(com, df\$G, distance = "bray", permutations = 10000)
PERMANOVA	'adonis'	(com~G, data = df, permutations = 10000)
Pairwise Comparison	'pairwise.adonis'	(com, factors = df G)
SIMPER	'simper'	(df, simper (com, G))



Figure A2. Temporal distribution of detected upcall vocalizations at Elephant Island (EI). In total 1125 upcalls were detected on 27 days in 2013 (15.01.2013 - 09.11.2013). The bar plot shows the number of analysed upcalls by the days of detected vocalizations.

Table A2. Results of the ANOSIMs using the Bray-Curtis and the Euclidean distance for the factor Species. The R-value comparing the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups, and the significance level (p-value) are given for both analyses performed.

Factor tested	Permutation	Distance	R value	p value
Groups	10000	Bray-Curtis	0.8174	9.999e-05
Groups	10000	Euclidean	0.71	1e-04

Table A3. Results of the ANOSIM using the Bray-Curtis distance, performed on ten random subsets of the EI vocalizations (n = 350) and the complete datasets of BSA-SRW (n = 348) and GM-HW (n = 354) upcalls. The R-value comparing the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups, and the significance level (p-value) are given for all analyses performed.

Run	R Value	p value
1	0.57885	9.999e-05
2	0.5800254	9.999e-05
3	0.5802777	9.999e-05
4	0.5883798	9.999e-05
5	0.5863917	9.999e-05
6	0.5834296	9.999e-05
7	0.5880759	9.999e-05
8	0.5857662	9.999e-05
9	0.5935087	9.999e-05
10	0.5823958	9.999e-05

Table A4. Results of the ANOSIM using the Euclidean distance, performed on ten random subsets of the EI vocalizations (n = 350) and the complete datasets of BSA-SRW (n = 348) and GM-HW (n = 354) upcalls. The R-value comparing the mean of ranked dissimilarities between groups to the mean of ranked dissimilarities within groups, and the significance level (p-value) are given for all analyses performed.

Run	R Value	p value
1	0.787	1e-04
2	0.793	1e-04
3	0.79	1e-04
4	0.79	1e-04
5	0.795	1e-04
6	0.788	1e-04
7	0.797	1e-04
8	0.783	1e-04
9	0.786	1e-04
10	0.792	1e-04

Table A5. Results of the PERMANOVA using the Bray-Curtis distance. Df: Degrees of freedom, SumsOfSqs: Sums of Squares, MeanSqs: Mean of Squares, F.Model: Pseudo-F value, R2: determination coefficient and p-value are given for all combinations (EI – Elephant Island, BSA – Bahía San Antonio, GM – Greenwich Meridian).

	Df	SumOfSqs	MeanSqs	F.Model	R2	p value
Species	2	71.633	35.817	3148.1	0.77537	9.999e ⁻⁰⁵
Residuals	1824	20.752	0.011		0.22463	
Total	1826	92.385			1.00000	

Table A6. Results of the PERMANOVA using Euclidean distance. Df: Degrees of freedom, SumsOfSqs: Sums of Squares, MeanSqs: Mean of Squares, F.Model: Pseudo-F value, R2: determination coefficient and p-value are given for all combinations (EI – Elephant Island, BSA – Bahía San Antonio, GM – Greenwich Meridian).

	Df	SumOfSqs	MeanSqs	F.Model	R2	p value
Species	2	351227962	175613981	2429	0.72702	9.999e ⁻⁰⁵
Residuals	1824	131875553	72300		0.27298	
Total	1826	483103514			1.00000	

Table A7. Results of the PERMANOVA using the Bray-Curtis distance, performed on ten random subsets of the EI vocalizations (n = 350) and the complete dataset of BSA-SRW and GM-HW upcalls. Df: Degrees of freedom, SumsOfSqs: Sums of Squares, MeanSqs: Mean of Squares, F.Model: Pseudo-F value, R2: determination coefficient and p-value are given for all combinations (EI – Elephant Island, BSA – Bahía San Antonio, GM – Greenwich Meridian).

Run		Df	SumsOfSqs	MeanSqs	F.Model	R2	p value
	Species	2	258707145	129353572	1168.2	0.69014	9.999e-05
	Residuals	1049	116156548	110731		0.30986	
1	Total	1051	374863693			1.00000	
	Species	2	258757791	129378896	1169.9	0.69045	9.999e-05
	Residuals	1049	116006788	110588		0.30955	
2	Total	1051	374764579			1.00000	
	Species	2	258424643	129212322	1167.6	0.69003	9.999e-05
	Residuals	1049	116088740	110666		0.30997	
3	Total	1051	374513383			1.00000	
	Species	2	258550172	129275086	1167.4	0.68999	9.999e-05
	Residuals	1049	116167296	110741		0.31001	
4	Total	1051	374717468			1.00000	
	Species	2	257932604	128966302	1167.9	0.69008	9.999e-05
	Residuals	1049	115838172	110427		0.30992	
5	Total	1051	373770776			1.00000	
	Species	2	257487765	128743883	1166.2	0.68976	9.999e-05
	Residuals	1049	115810391	110401		0.31024	
6	Total	1051	373298156			1.00000	
	Species	2	258535609	129267804	1169.1	0.6903	9.999e-05
	Residuals	1049	115992569	110574		0.3097	
7	Total	1051	374528178			1.00000	
	Species	2	258993247	129496624	1172.9	0.69099	9.999e-05
	Residuals	1049	115821509	110411		0.30901	
8	Total	1051	374814756			1.00000	
	Species	2	258515426	129257713	1169.3	0.69034	9.999e-05
	Residuals	1049	115960026	110543		0.30966	
9	Total	1051	374475452			1.00000	
	Species	2	257729744	128864872	1165.1	0.68956	9.999e-05
	Residuals	1049	116027634	110608		0.31044	
10	Total	1051	373757378			1.00000	

Table A8. Results of the PERMANOVA using the Euclidean distance, performed on ten random subsets of the EI vocalizations (n = 350) and the complete dataset of BSA-SRW and GM-HW upcalls. Df: Degrees of freedom, SumsOfSqs: Sums of Squares, MeanSqs: Mean of Squares, F.Model: Pseudo-F value, R2: determination coefficient and p-value are given for all combinations (EI – Elephant Island, BSA – Bahía San Antonio, GM – Greenwich Meridian).

Run		Df	SumsOfSqs	MeanSqs	F.Model	R2	p value
	Species	2	257727284	128863642	1162.7	0.68913	9.999e-05
	Residuals	1049	116261079	110830		0.31087	
1	Total	1051	373988363			1.00000	
	Species	2	258621128	129310564	1168	0.6901	9.999e-05
	Residuals	1049	116136874	110712		0.3099	
2	Total	1051	374758002			1.00000	
	Species	2	258451354	129225677	1167.2	0.68995	9.999e-05
	Residuals	1049	116140429	110715		0.31005	
3	Total	1051	374591783			1.00000	
	Species	2	258536784	129268392	1167	0.68992	9.999e-05
	Residuals	1049	116198961	110771		0.31008	
4	Total	1051	374735744				
	Species	2	258163577	129081789	1167.3	0.68998	9.999e-05
	Residuals	1049	116000067	110582		0.31002	
5	Total	1051	374163644			1.00000	
	Species	2	258898775	129449387	1170.8	0.69062	9.999e-05
	Residuals	1049	115982334	110565		0.30938	
6	Total	1051	374881109			1.00000	
	Species	2	257597287	128798644	1164.3	0.68942	9.999e-05
	Residuals	1049	116044664	110624		0.31058	
7	Total	1051	373641951			1.00000	
	Species	2	258131775	129065888	1163.9	0.68934	9.999e-05
	Residuals	1049	116329007	110895		0.31066	
8	Total	1051	374460783			1.00000	
	Species	2	257646380	128823190	1163.8	0.68934	9.999e-05
	Residuals	1049	116111622	110688		0.31066	
9	Total	1051	373758002			1.00000	
	Species	2	258345253	129172627	1169.6	0.69039	9.999e-05
	Residuals	1049	115856677	110445		0.30961	
10	Total	1051	374201931			1.00000	

Table A9. Results of the pairwise comparison using the function 'pairwise.adonis'. Df: Degrees of freedom, SumsOfSqs: Sums
of Squares, F.Model: Pseudo-F value, R2: determination coefficient and p-value are given for all combinations (EI - Elephant
Island, BSA – Bahía San Antonio, GM – Greenwich Meridian).

pairs	Df	SumOfSqs	F.Model	R2	p value
BSA - GM	1	38.543554	2444.6800	0.7774018	0.001
BSA - EI	1	6.143399	769.9299	0.3435761	0.001
GM - EI	1	38.776119	4392.5074	0.7483605	0.001

Table A10. Results of the pairwise comparison of detected vocalizations. Performed on ten random subsets of the EI vocalizations (n = 350) and the complete dataset of BSA-SRW and GM-HW upcalls. Df: Degrees of freedom, SumsOfSqs: Sums of Squares, F.Model: Pseudo-F value, R2: determination coefficient and p-value are given for all combinations (EI – Elephant Island, BSA – Bahía San Antonio, GM – Greenwich Meridian).

Run	Pairs	Df	SumsOfSqs	F.Model	R2	p value
	BSA - GM	1	55.69369	2901.641	0.8056442	0.001
	BSA - EI	1	4.50416	383.0559	0.3549917	0.001
1	GM - EI	1	39.53030	2516.7120	0.7819003	0.001
	BSA - GM	1	55.693686	2901.6416	0.8056442	0.001
	BSA – EI	1	4.577088	388.9455	0.3584931	0.001
2	GM - EI	1	39.743750	2528.7932	0.7827159	0.001
	BSA - GM	1	55.693686	2901.6416	0.8056442	0.001
	BSA – EI	1	4.641076	393.6976	0.3612907	0.001
3	GM - EI	1	39.653172	2519.7735	0.7821076	0.001
	BSA - GM	1	55.693686	2901.6416	0.8056442	0.001
	BSA – EI	1	4.444691	375.6602	0.3505404	0.001
4	GM - EI	1	39.934089	2530.7280	0.7828459	0.001
	BSA - GM	1	55.693686	2901.6416	0.8056442	0.001
	BSA – EI	1	4.611556	398.422	0.3640481	0.001
5	GM - EI	1	39.525749	2545.9840	0.7838659	0.001
	BSA - GM	1	55.693686	2901.6416	0.8056442	0.001
	BSA – EI	1	4.671484	408.4861	0.3698427	0.001
6	GM - EI	1	39.745176	2582.9560	0.7862985	0.001
	BSA - GM	1	55.693686	2901.6416	0.8056442	0.001
	BSA – EI	1	4.834772	421.1334	0.3769768	0.001
7	GM - EI	1	39.316917	2547.8537	0.7839903	0.001
	BSA - GM	1	55.693686	2901.642	0.8056442	0.001
	BSA – EI	1	4.607747	380.617	0.3535306	0.001
8	GM - EI	1	39.535004	2462.987	0.7781981	0.001
	BSA - GM	1	55.693686	2901.6416	0.8056442	0.001
	BSA – EI	1	4.395826	371.3333	0.3479075	0.001
9	GM - EI	1	39.784239	2520.2386	0.7821390	0.001
	BSA - GM	1	55.693686	2901.6416	0.8056442	0.001
	BSA – EI	1	4.428928	391.6708	0.3601005	0.001
10	GM - EI	1	40.059229	2625.0681	0.7890034	0.001

Table A11. Results of the SIMPER analysis, determining the contribution of each acoustic measurement to dissimilarities between groups. The measurements' contribution to average in between-group dissimilarity (average), the standard deviation of contribution (sd), average per group (ava, avb) and the ordered cumulative contribution are given for all contrast groups.

	Cont	rast BSA - GM			
Measurement	average	sd	ava	avb	cumsum
Slope (Hz/s)	1.997e-01	8.224e-02	104.362	1024.4793	0.3515
High Frequency (Hz)	8.996e-02	2.561e-02	162.299	568.8417	0.5099
Delta Frequency (Hz)	8.087e-02	2.476e-02	86.626	452.2725	0.6522
Frequency 95 (Hz)	6.588e-02	2.001e-02	137.538	434.4421	0.7681
Frequency 75 (Hz)	4.502e-02	1.644e-02	116.974	317.0999	0.8473
Center Frequency (Hz)	3.388e-02	1.451e-02	103.751	252.2203	0.9070
Frequency 25 (Hz)	2.484e-02	1.272e-02	93.046	198.6690	0.9507
Frequency 5 (Hz)	1.599e-02	1.131e-02	83.591	146.3242	0.9788
Low Frequency (Hz)	1.186e-02	1.054e-02	75.673	116.5692	0.9997
Delta Time (s)	9.662e-05	6.827e-05	0.891	0.5079	0.9999
Duration 90 (s)	6.595e-05	4.863e-05	0.560	0.3060	1.0000
	Cont	trast BSA - EI	L	L	
Measurement	average	sd	ava	avb	cumsum
Slope (Hz/s)	0.0258299	2.010e-02	104.362	137.2667	0.1326
Frequency 75 (Hz)	0.0245744	1.245e-02	116.974	159.0269	0.2587
Center Frequency (Hz)	0.0245471	1.269e-02	103.751	146.4304	0.3847
Frequency 25 (Hz)	0.0236377	1.235e-02	93.043	134.2599	0.5060
Low Frequency (Hz)	0.0220506	1.147e-02	75.673	113.9690	0.6191
Frequency 5 (Hz)	0.0220002	1.178e-02	83.591	121.2098	0.7320
Frequency 95 (Hz)	0.0217432	1.232e-02	137.538	172.2251	0.8436
High Frequency (Hz)	0.0173033	1.255e-02	162.299	181.9383	0.9324
Delta Frequency (Hz)	0.0128438	9.666e-03	86.626	67.9694	0.9981
Delta Time (s)	0.0001915	1.263e-04	0.891	0.5643	0.9993
Duration 90 (s)	0.0001302	9.447e-05	0.560	0.3907	1.000
	Con	trast GM - EI			
Measurement	average	sd	ava	avb	cumsum
Slope (Hz/s)	1.805e-01	7.863e-02	1024.4793	137.2667	0.3736
Delta Frequency (Hz)	7.992e-02	2.248e-02	452.2725	67.9694	0.5390
High Frequency (Hz)	7.979e-02	2.266e-02	568.8417	181.9383	0.7041
Frequency 95 (Hz)	5.383e-02	1.800e-02	434.4421	172.2251	0.8155
Frequency 75 (Hz)	3.252e-02	1.514e-02	317.0999	159.0269	0.8828
Center Frequency (Hz)	2.215e-02	1.353e-02	252.2203	146.4303	0.9286
Frequency 25 (Hz)	1.518e-02	1.087e-02	198.6690	134.2599	0.9600
Frequency 5 (Hz)	1.006e-02	8.749e-03	146.3242	121.2098	0.9809
Low Frequency (Hz)	9.141e-03	7.614e-03	116.5692	113.9690	0.9998
Delta Time (s)	5.640e-05	4.927e-05	0.5079	0.5643	0.9999
Duration 90 (s)	4.454e-05	4.226e-05	0.3060	0.3907	1.0000

Selbstständigkeitserklärung

Hiermit versichere ich an Eides statt. Dass ich diese Arbeit selbstständig verfasst und keine anderen Quellen als die angegebenen Quellen und Hilfsmittel benutzt habe. Außerdem versichere ich, dass ich die allgemeinen Prinzipien wissenschaftlicher Arbeit und Veröffentlichungen, wie sie in den Leitlinien guter wissenschaftlicher Praxis der Carl von Ossietzky Universität Oldenburg festgehalten sind, befolgt habe.

Strew

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