Southern right whale vocalizations on foraging grounds in South Georgia

Cite as: JASA Express Lett. 1, 061202 (2021); https://doi.org/10.1121/10.0005433
Submitted: 08 March 2021 . Accepted: 03 June 2021 . Published Online: 23 June 2021

Susannah V. Calderan, Russell C. Leaper, Brian S. Miller, Artur Andriolo, Danielle L. Buss, Emma L. Carroll, Amy S. Kennedy, Emilie N. Stepie, and Jennifer A. Jackson
Southern right whale vocalizations on foraging grounds in South Georgia

Susannah V. Calderan,1,7 Russell C. Leaper,3 Brian S. Miller,1 Artur Andriolo,1 Danielle L. Buss,5 Emma L. Carroll,6 Amy S. Kennedy, Emilie N. Stepien,8 and Jennifer A. Jackson1

1Scottish Association for Marine Science (SAMS), Argyll PA37 1QA, United Kingdom
2International Fund for Animal Welfare, London SE1 8NL, United Kingdom
3Australian Antarctic Division, Department of Agriculture, Water and the Environment, Kingston, Tasmania 7950, Australia
4Instituto de Ciências Biológicas, Universidade Federal de Juiz de Fora, Juiz de Fora, Minas Gerais, Brasil
5British Antarctic Survey, NERC, High Cross, Cambridge CB3 0ET, United Kingdom
6School of Biological Sciences, University of Auckland, Auckland, New Zealand
7Cooperative Institute for Climate, Ocean, and Ecosystem Studies (CICOES), University of Washington, Seattle, Washington 98105, USA
8Department of Bioscience, Aarhus University, Aarhus, Denmark

susannah.calderan@sams.ac.uk, russell@rcleaper.com, brian.miller@awe.gov.au, artur.andriolo@ufjf.edu.br, danss36@bas.ac.uk, e.carroll@auckland.ac.nz, amy.kennedy@noaa.gov, emilie.stepien@gmail.com, jeck@bas.ac.uk

Abstract: Southern right whale vocalizations were recorded concurrently with visual observations off the sub-Antarctic Island of South Georgia, and the characteristics of these calls were described. Calls were also compared to those of humpback whales at South Georgia, to determine how the two species might reliably be distinguished acoustically. The southern right whale calls measured (which were all upcalls) had lower frequency with peak energy and were mostly shorter in duration than the calls measured from humpback whales. The frequency upsweep and the lack of harmonics of southern right whale calls were also diagnostic characteristics. © 2021 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).

[Editor: Laura N. Kloepper] https://doi.org/10.1121/10.0005433

Received: 8 March 2021 Accepted: 3 June 2021 Published Online: 23 June 2021

1. Introduction

All species of right whale are known to produce a range of low frequency sounds; the vocalizations of North Atlantic (Eubalaena glacialis), North Pacific (E. japonica), and southern right whales (E. australis) have all been previously described (Clark, 1982; McDonald and Moore, 2002; Mellinger et al., 2004; Parks and Tyack, 2005; Parks et al., 2011; Webster et al., 2016; Dombroski et al., 2020; Shabangu et al., 2020). However, whilst southern right whale vocalizations have been described on their breeding grounds (Clark, 1982; Webster et al., 2016), on high latitude feeding grounds southern right whales have only been visually and acoustically detected during the same time period when other species of whales were also sighted in the vicinity (Sirovic et al., 2006). Here, we describe vocalizations of southern right whales which can directly be linked to visual sightings. These were recorded on their austral summer foraging grounds around South Georgia, an island in the Atlantic Sector of the Southern Ocean to the south of the Polar Front.

Right whale vocalizations comprise low frequency sounds, mostly with call energy <1000 Hz, including upcalls, downcalls, moans, and screams/high calls (Clark, 1982; McDonald and Moore, 2002; Mellinger et al., 2004; Parks and Tyack, 2005; Parks et al., 2011; Webster et al., 2016). Of these calls, the most commonly detected sound, believed to be a contact call used by all age and sex classes, is the upcall. This is a stereotyped tonal call rising in frequency from a mean low frequency of around 80 Hz to a mean high frequency of around 200 Hz, lasting 1–2 s, and is the call most often used in passive acoustic monitoring to detect right whales (McDonald and Moore, 2002; Sirovic et al., 2006; Parks et al., 2007; Webster et al., 2016; Davis et al., 2017). Right whales also produce a high-intensity (185 dB re 1 µPa p-p), short-duration (<0.02 s), broadband call (20 Hz to 20 kHz)—the gunshot—which is thought to be primarily part of mating behaviour (Parks et al., 2005; Parks and Tyack, 2005; Matthews et al., 2014; Crance et al., 2017). Gunshots have also been recorded as part of song (typically defined as a series of stereotyped sound units that are repeated with regular sequences of units and regular inter-unit intervals) in eastern North Pacific right whale males (Crance et al., 2019). Call rate and call type of individual whales can be highly variable, depending on individual or group behaviour and age/sex composition of groups (Parks et al., 2011).

a1Author to whom correspondence should be addressed.
Southern right whale vocalizations were recorded using directional frequency analysis and recording (DIFAR) sonobuoys as part of the "South Georgia Right Whale Project," initiated to study southern right whales on their feeding grounds in South Georgia (Jackson et al., 2020). The project included two years of boat-based, multi-disciplinary field work in South Georgia waters to collect data on distribution, genetics, fine-scale movements, foraging ecology, and body condition. Passive acoustic tracking using DIFAR sonobuoys was used to assist in locating southern right whales and to record their vocalizations. Other vocalizing whale species such as blue whales (Balaenoptera musculus), fin whales (Balaenoptera physalus), humpback whales (Megaptera novaeangliae), and sperm whales (Physeter macrocephalus) were also recorded during recording operations. Whilst these species' vocalizations are generally straightforward to identify (Goold and Jones, 1995; Sirović et al., 2004; Rankin et al., 2005; Sirović et al., 2009; Van Opzeeland et al., 2013a), difficulties can be experienced distinguishing right whale calls from those of humpback whales, in particular upcalls (Gillespie, 2004). We therefore also describe a sample of the humpback whale calls which we recorded to identify characteristics which could be used to distinguish between the two species where they co-occur. This is of particular relevance given the increasing use of long-term passive acoustic monitoring in the Southern Hemisphere, for example in the International Whaling Commission Southern Ocean Research Partnership (IWC-SORP) Acoustic Trends Project (Van Opzeeland et al., 2013b). Improving the capacity of acoustic researchers to distinguish between species across their foraging ranges will be useful for understanding the spatiotemporal distribution and migration patterns of these recovering species. For example, humpback whales are steadily recovering from whaling and are increasingly abundant in many Southern Hemisphere areas (Zerbini et al., 2019), whilst southern right whale recovery is more patchy (Harcourt et al., 2019). Southern right whale feeding ground distribution is particularly poorly known, and mostly inferred from whaling records (Smith et al., 2012; Torres et al., 2013; González Carman et al., 2019) and isotope data (Valenzuela et al., 2018; van den Berg et al., 2020).

2. Methods

Acoustic data were collected in South Georgia waters in January and February of 2018 and 2020 by deploying DIFAR sonobuoys from a vessel to monitor for, record and where possible, track vocalizing southern right whales. Acoustic data collection in 2018 was conducted onboard RV Song of the Whale, a 23 m research sailing vessel, and in 2020 from MV Braveheart, a 36 m motor vessel. Data collection was carried out under permits RAP/2017/017 and RAP/2019/031 issued by the Government of South Georgia and the South Sandwich Islands following approval of data collection approaches by the British Antarctic Survey Animal Welfare and Ethics Review Board (review #1040).

The equipment (sonobuoys, receiving hardware, and software) and real-time whale call detection and processing protocol for these surveys largely followed the methodology developed to track Antarctic blue whales, as described by Miller et al. (2015), using AN/SSQ-955-HIDAR sonobuoys (Ultra Electronics Sonar Systems). However, whilst Miller et al. (2015) prioritised the use of passive acoustics to detect, track and locate Antarctic blue whales in real time, during the 2018 and 2020 research cruises this approach was taken for some sonobuoy deployments, but other deployments were more opportunistic due to survey constraints.

The details of the recording system have been described in detail elsewhere (Miller et al., 2015; Miller et al., 2016; Calderan et al., 2020; Jackson et al., 2020). Briefly, sonobuoy signals were received by VHF radio onboard the research vessel, digitized, recorded, and processed using PAMGUARD (Gillespie et al., 2008). Continuous recordings were made at a sample rate of 48,000 samples per second, and all buoys were monitored continuously by an experienced analyst (S.V.C. or R.C.L.), who viewed scrolling spectrograms of calls and listened through headphones. The analyst drew a box around a detection on the spectrogram to define a sound clip. All calls detected in real time were clipped by the analyst, classified to species/call type, and their bearings resolved using the PAMGUARD DIFAR module described by Miller et al. (2016). These clips were stored as PAMGUARD "binary" files for later post-processing and analysis. Although automated detectors have been developed for North Atlantic right whale upcalls (Gillespie, 2004; Baumgartner and Mussoline, 2011; Soklevilla et al., 2014), a detector was not used due to the presence of the analyst.

During research operations, DIFAR sonobuoys were deployed either to assist in locating whales (primarily over-night to allow the vessel to move to areas where right whales had been acoustically detected by the commencement of visual observations in the morning), or in response to a sighting to enable the acoustic tracking and recording of right whale vocalizations. To ensure that we were able to reliably differentiate right whale calls from humpback whale calls, where possible we followed acoustic bearings until vocalizing animals were located visually, or matched bearings to received calls with known whale locations during a sighting. All the acoustic detections which were measured to describe call characteristics were made during periods when a team of visual observers was on watch and all whales sighted were recorded.

The clips of calls which had been detected and classified to species/call type in PAMGUARD were post-processed, and a series of call parameters (high and low frequency, frequency with peak energy, frequency sweep, duration) was measured to allow comparison with other studies. Regardless of the classification to species/call type, the same parameters were measured for all the calls described here. Future studies involving building automated detectors and classifiers could be informed by describing the relationship between parameters measured from calls, so some of these (duration, high and low frequency) were investigated using simple regressions. The analyst marked a box on the spectrogram indicating the precise start and stop times, and lower and upper frequency limits of the call within each clip. Duration and frequency
limits of each call were measured from these precise, post-processed data. Frequency of peak energy was measured from
the spectrogram after correcting for the sonobuoy shaped filter to allow for variation of sensitivity with frequency, follow-
ing methods described by Rankin et al. (2019). All measurements were from spectrograms using an 8000 Hz sample rate
and 2048 sample fast Fourier transform (FFT), with 90% overlap (1843 sample), and a Hamming window.

Calls from non-target species which could be easily identified and classified such as blue, fin, and sperm whales
were excluded from analysis. In relation to humpback and right whale calls, we only measured those which could be tem-
porally and spatially linked with visual sightings. Further, we only selected calls for measurement if they were high quality
with both a clean start and finish, and signal-to-noise ratio (SNR) > 3 dB. SNR was calculated for the duration and fre-
quency band defined by the analyst’s box as the ratio of signal to noise power. For the SNR measurements, the “signal”
was measured over the detection box, and the “noise” was measured for the same duration and frequency band as the
detection, but for the period immediately before and after the detection. The occurrence of possible or likely gunshots was
also noted during monitoring. However, it was difficult to reliably differentiate these sounds from the broadband sounds
of calving glaciers and other ice noise at South Georgia, and as impulsive sounds such gunshots are not long enough in
duration to allow the DIFAR beamforming algorithms to derive a bearing and enable call localization, we did not carry
out further analysis on these vocalizations.

3. Results

In 2018, 26 sonobuoys were deployed between 25 January and 17 February in the western approaches to South Georgia
and in locations around the northern coastline and shelf, comprising 83 h of recordings. In 2020, 31 sonobuoys were
deployed all around the island between 9 January and 3 February comprising 114 h of recordings. In 2018, there were 15
southern right whale visual encounters comprising 31 individuals; in 2020 there were 10 southern right whale visual
encounters comprising 11 individuals (Jackson et al., 2020; Kennedy et al., 2020).

In 2018, there were five acoustic encounters which we were confident were associated with sightings of southern
right whales and during which no sightings of other species were made (32.7 h of recordings, seven sonobuoys). These
were encounters where acoustic bearings either matched to a concurrent visual sighting or to an area where southern right
whales only were sighted within approximately two hours before or after the detection. In 2020 there were two of these
events (9.9 h of recordings, two sonobuoys). All the tonal calls determined to be from southern right whales during these
encounters were simple upcalls sweeping monotonically from a low frequency (L) to a high frequency (H) over the dura-
tion of the call (t) with no harmonics [Fig. 1(a)], or gunshot-type calls. In total, 73 upcalls from southern right whales
were measured from the five encounters in 2018 and 76 upcalls from the two encounters in 2020 (Table 1). Likely gun-
shots were heard on three out of five encounters in 2018 and one out of two encounters in 2020.

A total of 85 humpback whale calls was measured from two encounters in 2018 and five encounters in 2020,
where we were confident of association with humpback whale sightings (using the same criteria as for southern right
whales) (Table 1). An example of a humpback whale call during a visually confirmed encounter is given in Fig. 1(b). There
were no upcalls amongst these visually confirmed calls. Rather, call repertoire comprised simple tonal calls with little
variation in frequency during the call, and harmonics apparent in most.

The distribution of measurements of L, H, and the frequency with peak energy from the southern right whale
upcalls is shown in Fig. 2. The peak energy generally occurred towards the end of the call. The median of the length of
time from the start of the call to the time of peak energy as a fraction of the total duration of the call, was 0.75 [range
0.32–0.99].

Fig. 1. Examples of visually confirmed whale calls recorded off South Georgia [note that ranges are different for (a) and (b)]. (a) Southern
right whale upcall. For production of this figure, recording was down-sampled to a sample rate of 500 Hz. Spectrogram generated using a 128
sample FFT and Hamming window with 90% overlap between slices. (b) Humpback whale call. For production of this figure, recording was
down-sampled to a sample rate of 4000 Hz. Spectrogram generated using a 512 sample FFT and Hamming window with 90% overlap between
slices.
In all cases humpback whale simple tonal calls had higher frequency with peak energy, and in most cases they were longer duration than those of southern right whales (Fig. 3). The shorter duration humpback whale calls of 0.5–1.5 s duration were mainly higher frequency (median Hz) than the longer duration calls (median Hz). The separation shown in Fig. 3 demonstrates that the southern right whale upcalls detected around South Georgia could be distinguished from the simple tonal calls of humpback whales based on frequency of peak energy. In addition, the frequency upsweep and the lack of harmonics in southern right whale upcalls were diagnostic characteristics.

Further investigation of the frequency characteristics of the southern right whale upcalls indicated that \( L \) appeared to be normally distributed with mean (87 Hz) and sd (11 Hz) and no correlation with the duration of the call. \( H \) was correlated with the duration of the call with longer calls resulting in higher frequencies. Our best model for \( H \) was

\[
H = L + 62.8 \times L^{0.652}.
\]

A linear regression of the predicted \( H \) based on \( L \) and \( t \) [Eq. (1)] gave an \( R^2 \) value of 0.38, showing that there is also considerable variation in \( H \) that is not explained by \( L \) or \( t \).

A comparison of our measured characteristics of southern right whale upcalls with those from other areas, and also upcalls from other right whale species is given in Table 2. North Atlantic right whale upcalls had both the broadest frequency range and also the longest duration. Duration, start frequency, and peak frequency of calls from this study were similar to the equivalent mean values reported by Webster et al. (2016) from the Auckland Islands and not appreciably different from those reported by Sirović et al. (2006). However, the average sweep rate measured by Sirović et al. (2006), which involves a combination of these measurements, was substantially greater than we observed.

| Call Characteristics | Min | Median | Max |
|----------------------|-----|--------|-----|
| **149 measured southern right whale upcalls** | | | |
| Duration (s) | 0.43 | 0.8 | 1.87 |
| Low frequency (Hz) | 63 | 86 | 114 |
| High frequency (Hz) | 82 | 142 | 223 |
| Frequency with peak energy (Hz) | 79 | 128 | 207 |
| Frequency sweep (Hz) | 19 | 57 | 118 |
| Frequency sweep rate Hz.s\(^{-1}\) | 22 | 86 | 159 |
| **78 measured humpback whale calls (<400 Hz)** | | | |
| Duration (s) | 0.7 | 3.5 | 5.9 |
| Low frequency (Hz) | 215 | 324 | 360 |
| High frequency (Hz) | 228 | 333 | 372 |
| Frequency with peak energy (Hz) | 228 | 329 | 368 |
| Frequency sweep (Hz) | 0 | 9 | 25 |
| **7 measured humpback whale calls (>400 Hz)** | | | |
| Duration (s) | 0.52 | 0.96 | 1.35 |
| Low frequency (Hz) | 486 | 803 | 1038 |
| High frequency (Hz) | 552 | 812 | 1045 |
| Frequency with peak energy (Hz) | 526 | 809 | 1045 |
| Frequency sweep (Hz) | 4 | 9 | 66 |

In all cases humpback whale simple tonal calls had higher frequency with peak energy, and in most cases they were longer duration than those of southern right whales (Fig. 3). The shorter duration humpback whale calls of 0.5–1.5 s duration were mainly higher frequency (median Hz) than the longer duration calls (median Hz). The separation shown in Fig. 3 demonstrates that the southern right whale upcalls detected around South Georgia could be distinguished from the simple tonal calls of humpback whales based on frequency of peak energy. In addition, the frequency upsweep and the lack of harmonics in southern right whale upcalls were diagnostic characteristics.

Further investigation of the frequency characteristics of the southern right whale upcalls indicated that \( L \) appeared to be normally distributed with mean (87 Hz) and sd (11 Hz) and no correlation with the duration of the call. \( H \) was correlated with the duration of the call with longer calls resulting in higher frequencies. Our best model for \( H \) was

\[
H = L + 62.8 \times L^{0.652}.
\]

A linear regression of the predicted \( H \) based on \( L \) and \( t \) [Eq. (1)] gave an \( R^2 \) value of 0.38, showing that there is also considerable variation in \( H \) that is not explained by \( L \) or \( t \).

A comparison of our measured characteristics of southern right whale upcalls with those from other areas, and also upcalls from other right whale species is given in Table 2. North Atlantic right whale upcalls had both the broadest frequency range and also the longest duration. Duration, start frequency, and peak frequency of calls from this study were similar to the equivalent mean values reported by Webster et al. (2016) from the Auckland Islands and not appreciably different from those reported by Sirović et al. (2006). However, the average sweep rate measured by Sirović et al. (2006), which involves a combination of these measurements, was substantially greater than we observed.

---

**Table 1. Measured call characteristics of southern right and humpback whales from automated measurement with SNR>3 dB.**

| Call Characteristics | Min | Median | Max |
|----------------------|-----|--------|-----|
| **149 measured southern right whale upcalls** | | | |
| Duration (s) | 0.43 | 0.8 | 1.87 |
| Low frequency (Hz) | 63 | 86 | 114 |
| High frequency (Hz) | 82 | 142 | 223 |
| Frequency with peak energy (Hz) | 79 | 128 | 207 |
| Frequency sweep (Hz) | 19 | 57 | 118 |
| Frequency sweep rate Hz.s\(^{-1}\) | 22 | 86 | 159 |
| **78 measured humpback whale calls (<400 Hz)** | | | |
| Duration (s) | 0.7 | 3.5 | 5.9 |
| Low frequency (Hz) | 215 | 324 | 360 |
| High frequency (Hz) | 228 | 333 | 372 |
| Frequency with peak energy (Hz) | 228 | 329 | 368 |
| Frequency sweep (Hz) | 0 | 9 | 25 |
| **7 measured humpback whale calls (>400 Hz)** | | | |
| Duration (s) | 0.52 | 0.96 | 1.35 |
| Low frequency (Hz) | 486 | 803 | 1038 |
| High frequency (Hz) | 552 | 812 | 1045 |
| Frequency with peak energy (Hz) | 526 | 809 | 1045 |
| Frequency sweep (Hz) | 4 | 9 | 66 |
4. Discussion

We recorded southern right whale vocalizations on their summer foraging grounds at South Georgia using DIFAR sonobuoys, classified them, and successfully differentiated them from humpback whale calls. A notable feature of the southern right whale vocalizations recorded in both 2018 and 2020 was the lack of variation in call type. Of tonal calls, only upcalls were recorded. Sirović et al. (2006) also only recorded upcalls in association with areas in South Georgia waters where southern right whales were seen. Although the majority of tonal calls by right whales in other areas also comprise upcalls, they also include other call types (Clark, 1982; Webster et al., 2016).

We neither observed large aggregations of right whales (the maximum aggregation size was seven individuals but these were spread over too large an area to be considered a group), nor extensive surface-active group behaviours in either year of our study. No calves were observed. As right whale behavioural state is thought to strongly affect call rate and type, and many right whale vocalizations are reported to be associated with group and surface behaviours (Parks et al., 2011), the low densities and small groups of right whales seen during our study might partly explain the lack of variation in call-type. Other right whale studies have demonstrated a correlation between group size and calling rate (Matthews et al., 2001; Parks et al., 2011).

The measured average start frequency, end frequency, and duration of the southern right whale upcalls at South Georgia were broadly similar to those previously attributed to southern right whales from South Georgia and the Scotia Sea (Sirović et al., 2006), to those recorded at southern right whale breeding areas in Argentina (to which there is genetic association with South Georgia (Clark, 1982; Carroll et al., 2020)), and to those recorded at the Auckland Islands (Webster et al., 2016). However, Parks et al. (2007) noted a significant increase in the start frequency of southern right whale upcalls in Argentina between 1977 and 2000 from 69 to 78 Hz. Our study (with a start frequency of 86 Hz) and other recent studies (Sirović et al., 2006; Webster et al., 2016) also show higher mean starting frequencies than those reported by Parks et al. (2007) for 1977 to 2000. Whilst our measured parameters are also somewhat similar to those of North Pacific right whale (McDonald and Moore, 2002) and North Atlantic right whale upcalls (Parks et al., 2007) on feeding grounds, the mean start and end frequencies for North Atlantic right whale upcalls recorded on the east coast of the US and Canada between 2000 and 2004 by Parks et al. (2007) were 101 and 195 Hz, respectively. Both the increase in start frequency over time of southern right whale upcalls and the higher frequency of North Atlantic right whale upcalls might support the hypothesis of Parks et al. (2007) that upcall frequency increases in response to anthropogenic noise, although Parks et al. (2009) also note that habitat area and noise levels are not in themselves sufficient to predict call parameter variability.

For the measured calls which were associated with visual sightings of right or humpback whales, we were able to clearly separate the two species based on frequency characteristics. The right whale calls had a lower maximum frequency

![Figure 3. Frequency of peak energy against call duration for southern right whale upcalls (red) and humpback whale simple tonal calls (blue). Each line shows the frequency range within a call with a dot to indicate the peak frequency for each call.](Fig. 3. Frequency of peak energy against call duration for southern right whale upcalls (red) and humpback whale simple tonal calls (blue). Each line shows the frequency range within a call with a dot to indicate the peak frequency for each call.)

Table 2. Measured characteristics of upcalls from the three right whale species (values in parentheses are standard deviations where available).

| Area (and habitat type) | Species | This study | Sirović et al., 2006 | Webster et al., 2016 | McDonald and Moore, 2002 | Parks et al., 2007 |
|-------------------------|---------|------------|----------------------|----------------------|------------------------|-------------------|
|                         | E. australis | South Georgia (Feeding) | South Georgia and Scotia Sea (Feeding) | Auckland Islands (Nursery/breeding) | North Pacific (Feeding) | E. glacialis | South Pacific and US (Feeding) |
| Number of calls measured |         | 149 | 31 | 701 | 436 | 929 |
| Mean Duration (s)       | 0.8 (0.27) | 0.7 (0.1) | 0.9 | 0.7 | 0.87 (0.27) | 0.87 (0.27) |
| Mean Low frequency (Hz)  | 86 (10) | 92 (11) | 87 | 89 | 101 (22) | 101 (22) |
| Mean High frequency (Hz) | 145 (23) | 173 (11) | 143 | 153 | 195 (38) | 195 (38) |
| Mean frequency of peak energy (Hz) | 115 (25) | 121 | | | | |
| Mean sweep rate          | 72 (25) | 125 (24) | | | | |
with peak energy than the minimum frequency of the humpback whale calls. There was also little overlap in frequency sweep, with right whale calls monotonically increasing with a median increase of 57 Hz compared to largely tonal calls of humpbacks with little change in frequency. The average duration of humpback whale calls was also considerably longer than the upcalls of right whales. Whilst humpback whale non-song call repertoire is extensive and variable (Recalde-Salas et al., 2020), Sirović et al. (2006) recorded calls with similar characteristics to the humpback whale calls detected in this study, which they attributed to humpbacks. In another high latitude study, Cerchio and Dahlheim (2001) recorded humpback feeding vocalizations in southeast Alaska, which also shared characteristics with our observations, with calls ranging in fundamental frequency from 360 Hz to 988 Hz (median = 553 Hz), and a frequency oscillation of 16–65 Hz. No harmonics were observed from the right whale calls we recorded, but these were observed in most humpback whale calls. Taken together, these characteristics were fully diagnostic for the calls that we recorded. However, this separation may not be so straightforward in areas such as the North Atlantic, where humpback vocalizations can be more similar to right whale upcalls; the presence of harmonics can also be variable, such as in situations when calls from distant animals are recorded, and any harmonics present might not be detected (Mellinger et al., 2007).

Nevertheless, the ability to reliably detect upcalls from southern right whales at South Georgia indicates the potential for long-term acoustic studies of this species on their sub-Antarctic and Antarctic feeding grounds using moored acoustic recorders. Such studies could improve information about the temporal occupancy of southern right whales at known feeding grounds such as South Georgia, as well as at other recording sites where data have already been collected, for example Southern Ocean Hydrophone Network sites (Van Opzeeland et al., 2013b). Such information could potentially be useful for ecosystem-based-management of Antarctic fisheries (Constable et al., 2000). Additional in situ acoustic and visual surveys could further improve estimates of the proportion of animals calling, provide measures of individual call rates and associated variability, allowing investigation of the wider context of call production on feeding grounds.

**Acknowledgments**

It is a pleasure to acknowledge the dedication and enthusiasm of the crew and management of RV Song of the Whale and MV Braveheart, and of our fellow scientists on the two voyages. Denise Risch and two anonymous reviewers provided helpful input to improve this manuscript. This work was supported by funding from a DARWIN PLUS Award No. DPLUS057, an EU BEST 2.0 Medium Grant No. 1594, South Georgia Heritage Trust, Friends of South Georgia Island, and WWF. This study forms part of the Ecosystems component of the British Antarctic Survey Polar Science for Planet Earth Programme, funded by The Natural Environment Research Council. We thank the Government of South Georgia and the South Sandwich Islands for providing logistical support for these expeditions.

**References and links**

1See supplementary material at https://www.scitation.org/doi/suppl/10.1121/10.0005433 for audio files of southern right whale upcall and humpback whale call.

Baumgartner, M. F., and Mussoline, S. E. (2011). “A generalized baleen whale call detection and classification system,” J. Acoust. Soc. Am. 129, 2889–2902.

Calderan, S. V., Black, A., Branch, T. A., Collins, M. A., Kelly, N., Leaper, R., Lurcock, S., Miller, B. S., Moore, M., Olson, P. A., Sirović, A., Wood, A. G., and Jackson, J. A. (2020). “South Georgia blue whales five decades after the end of whaling,” Endangered Species Res. 43, 359–373.

Carroll, E. L., Ott, P. H., McMillan, L. F., Galletti Vernazzani, B., Neveceralova, P., Vermeulen, E., Gaggiotti, O. E., Andriolo, A., Baker, C. S., Bamford, C., Best, P., Cabrera, E., Calderan, S., Chirife, A., Fewster, R. M., Flores, P. A. C., Freasier, T., Freitas, T. R. O., Groch, K., Hulva, P., Kennedy, A., Leaper, R., Leslie, M. S., Moore, M., Oliveira, L., Seger, J., Stepien, E. N., Valenzuela, L. O., Zerbini, A., and Jackson, J. A. (2020). “Genetic diversity and connectivity of southern right whales (Eubalaena australis) found in the Brazil and Chile–Peru wintering grounds and the South Georgia (Islas Georgias del Sur) feeding ground,” J. Heredity 111, 263–276.

Cerchio, S., and Dalheim, M. (2001). “Variation in feeding vocalizations of humpback whales Megaptera novaeangliae from southeast Alaska,” Bioscience 51, 277–295.

Clark, C. W. (1982). “The acoustic repertoire of the southern right whale, a quantitative analysis,” Animal Behaviour 30, 1060–1071.

Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I., and Miller, D. (2000). “Managing fisheries to conserve the Antarctic marine ecosystem: Practical implementation of the Convention of the Conservation of Antarctic Marine Living Resources (CCAMLR),” ICES J. Mar. Sci. 57, 778–791.

Crance, J. L., Berchok, C. L., and Keating, J. L. (2017). “Gunshot call production by the North Pacific right whale Eubalaena japonica in the southeastern Bering Sea,” Endangered Species Res. 34, 251–267.

Crance, J. L., Berchok, C. L., Wright, D. L., Brewer, A. M., and Woodrich, D. F. (2019). “Song production by the North Pacific right whale, Eubalaena japonica,” J. Acoust. Soc. Am. 145, 3467–3479.

Davis, G. E., Baumgartner, M. F., Bonnell, J. M., Bell, J., Berchok, C., Bort Thornton, J., Brault, S., Buchanan, G., Charif, R. A., Cholewiak, D., Clark, C. W., Corkeron, P., Delarue, J., Dudzinski, K., Hatch, L., Hildebrand, J., Hodge, L., Klinck, H., Kraus, S., Martin, B., Mellinger, D. K., Moors-Murphy, H., Nieuwirk, S., Nowacek, D. P., Parks, S., Read, A. J., Rice, A. N., Risch, D., Sirović, A., Soldevilla, M., Stafford, K., Stanisstreet, J. E., Summers, E., Todd, S., Warde, A., and Van Parijs, S. M. (2017). “Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (Eubalaena glacialis) from 2004 to 2014,” Sci. Rep. 7, 13460.
Dombroski, J. R. G., Parks, S. E., Flores, P. A. C., López, L. M. M., Shorter, K. A., and Groch, K. R. (2020). “Animal-borne tags provide insights into the acoustic communication of southern right whales (Eubalaena australis) on the calving grounds,” J. Acoust. Soc. Am. 147, EL498–EL503.

Gillespie, D. (2004). “Detection and classification of right whale calls using an ‘edge’ detector operating on a smoothed spectrogram,” Can. Acoust. 32, 39–47, available at https://jca.aac-acca.ca/index.php/jca/article/view/1586.

Gillespie, D., Gordon, J., McHugh, R., McLaren, D., Mellinger, D., Redmond, P., Thode, A., Trinder, P., and Deng, X. Y. (2008). “PAMGUARD: Semi-automated, open source software for real-time acoustic detection and localisation of cetaceans,” Proceedings of the Institute of Acoustics, Vol. 30.

González Carman, V., Piola, A., O’Brien, T. D., Tormosov, D. D., and Acha, E. M. (2019). “Circumpolar frontal systems as potential feeding grounds of Southern Right whales,” Prog. Oceanogr. 176, 102123.

Goold, J. C., and Jones, S. E. (1995). “Time and frequency domain characteristics of sperm whale clicks,” J. Acoust. Soc. Am. 98, 1279–1291.

Harcourt, R., van der Hoop, J., Kraus, S., and Carroll, E. L. (2019). “Future directions in Eubalaena spp.: Comparative research to inform conservation,” Front. Mar. Sci. 5, 530.

Jackson, J. A., Kennedy, A., Moore, M., Andriolo, A., Bamford, C. C. G., Calderon, S., Cheeseman, T., Gittins, G., Groch, K., Kelly, N., Leaper, R., Leslie, M. S., Lurcock, S., Miller, B. S., Richardson, J., Rowntree, V., Smith, P., Stepien, E., Stowasser, G., Trathan, P., Vermeulen, E., Zerbini, A. N., and Carroll, E. L. (2020). “Have whales returned to a historical hotspot of industrial whaling? The pattern of southern right whale Eubalaena australis recovery at South Georgia,” Endangered Species Res. 43, 323–339.

Kennedy, A. S., Carroll, E. L., Baker, S., Bassoi, M., Buss, D., Collins, M. A., Calderon, S., Ensror, S., Fielding, S., Leaper, R., MacDonald, D., Olson, P., Cheeseman, T., Groch, K., Hall, A., Kelly, N., Miller, B. S., Moore, M., Rowntree, V. J., Stowasser, G., Trathan, P., Valenzuela, L. O., Vermeulen, E., Zerbini, A. N., and Jackson, J. A. (2020). “Whales return to the epicentre of whaling? Pre-liminary results from the 2020 cetacean survey at South Georgia (Islas Georgias del Sur)” in IWC Scientific Committee 2020, Virtual Meeting, available at https://archive.iwc.int/pages/search.php?search¼collection29934&bc_from¼themes.

Matthews, L. P., McCordic, J. A., and Parks, S. E. (2014). “Remote acoustic monitoring of North Atlantic right whales (Eubalaena glacialis) reveals seasonal and diel variations in acoustic behavior,” PLoS One 9, e91367.

McDonald, M. A., and Moore, S. E. (2002). “Calls recorded from North Pacific right whales (Eubalaena japonica) in the eastern Bering Sea,” J. Cetacean Res. Manage. 4, 261–266.

Mellinger, D. K., Stafford, K. M., Moore, S. E., Munger, L., and Fox, C. G. (2004). “Detection of North Pacific right whale (Eubalaena japonica) calls in the Gulf of Alaska,” Mar. Mammal Sci. 20, 872–879.

Mellinger, D. K., Nieuwirk, S. L., Matsumoto, H., Heimlich, S. L., Dziak, R. P., Haxel, J., Fowler, M., Meinig, C., and Miller, H. V. (2007). “Seasonal occurrence of North Atlantic right whale (eubalaena glacialis) vocalizations at two sites on the Scotian shelf,” Mar. Mamm. 25, 856–867.

Miller, B. S., Barlow, J., Calderon, S., Collins, K., Leaper, R., Olson, P., Ensror, P., Peel, D., Donnelly, D., Andrews-Goff, V., Olavarria, C., Owen, K., Redkahl, M., Schmitt, N., Wedley, V., Gedamke, J., Gales, N., and Double, M. C. (2015). “Validating the reliability of passive acoustic localization: A novel method for encountering rare and remote Antarctic blue whales,” Endangered Species Res. 26, 257–269.

Miller, B. S., Calderon, S., Gillespie, D., Weatherup, G., Leaper, R., Collins, K., and Double, M. C. (2016). “Software for real-time localization of baleen whale calls using directional sonobuoys: A case study on Antarctic blue whales,” J. Acoust. Soc. Am. 139, EL83–EL89.

Parks, S. E., Clark, C. W., and Tyack, P. L. (2007). “Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication,” J. Acoust. Soc. Am. 122, 3725–3731.

Parks, S. E., Hamilton, P. K., Kraus, S. D., and Tyack, P. L. (2005). “The gunshot sound produced by male North Atlantic right whales (Eubalaena glacialis) and its potential function in reproductive advertisement,” Mar. Mammal Sci. 21, 458–475.

Parks, S. E., Searby, A., Célérié, A., Johnson, M. P., Nowacek, D. P., and Tyack, P. L. (2011). “Sound production behavior of individual North Atlantic right whales: Implications for passive acoustic monitoring,” Endangered Species Res. 15, 63–76.

Parks, S. E., and Tyack, P. L. (2005). “Sound production by North Atlantic right whales (Eubalaena glacialis) in surface active groups,” J. Acoust. Soc. Am. 117, 3297–3306.

Parks, S. E., Urazghildiev, I., and Clark, C. W. (2009). “Variability in ambient noise levels and call parameters of North Atlantic right whales in three habitat areas,” J. Acoust. Soc. Am. 125, 1230–1239.

Rankin, S., Liu, J., Clark, C., and Kato, H. (2005). “Vocalizations of Antarctic blue whales, Balaenoptera intermedia, recorded during the 2001–2002 and 2002–2003 IWC-SOWER circumpolar cruises, Area V, Antarctica,” J. Cetacean Res. Manage. 7, 13–20.

Rankin, S., Miller, B., Crane, J., Sakai, T., and Keating, J. L. (2019). “Distribution, sonobuoy acoustic data collection during cetacean surveys,” U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC614.

Recalde-Salas, A., Erbe, C., Salgado Kent, C., and Parsons, M. (2020). “Non-song vocalizations of humpback whales in western Australia,” Front. Mar. Sci. 7, 141.

Shabangu, F. W., Andrew, R. K., and Findlay, K. (2020). “Acoustic occurrence, diel-vocalizing pattern, and detection ranges of southern right whale gunshot sounds off South Africa’s west coast,” Mar. Mammal Sci. 36, 658–675.

Širović, A., Hildebrand, J. A., and Thiele, D. (2006). “Baleen whales in the Scotia Sea during January and February 2003,” J. Cetacean Res. Manage. 8, 161–171.

Širović, A., Hildebrand, J. A., Wiggins, S. M., McDonald, M. A., Moore, S. E., and Thiele, D. (2004). “Seasonality of blue and fin whale calls west of the Antarctic Peninsula,” Deep Sea Res. II 51, 2327–2344.

Širović, A., Hildebrand, J. A., Wiggins, S. M., and Thiele, D. (2009). “Blue and fin acoustic presence around Antarctica during 2003 and 2004,” Mar. Mammal Sci. 25, 125–136.
Smith, T. D., Reeves, R. R., Josephson, E. A., and Lund, J. N. (2012). “Spatial and seasonal distribution of American whaling and whales in the age of sail,” PLoS One 7, e34905.
Soldevilla, M. S., Rice, A. N., Clark, C. W., and Garrison, L. P. (2014). “Passive acoustic monitoring on the North Atlantic right whale calving grounds,” Endangered Species Res. 25, 115–140.
Torres, L. G., Smith, T. D., Sutton, P., MacDiarmid, A., Bannister, J., and Miyashita, T. (2013). “From exploitation to conservation: Habitat models using whaling data predict distribution patterns and threat exposure of an endangered whale,” Diversity Distributions 19, 1138–1152.
Valenzuela, L. O., Rowntree, V. J., Sironi, M., and Seger, J. (2018). “Stable isotopes in skin reveal diverse food sources used by southern right whales (Eubalaena australis),” Mar Ecol. Prog Ser. 603, 243–255.
Van den Berg, G. L., Vermuelen, E., Valenzuela, L. O., Berubé, M., Ganswindt, A., Gröcke, D. R., Hall, G., Hulva, P., Nevecralova, P., Palsbøll, P., and Carroll, E. L. (2021). “Decadal shift in foraging strategy of a migratory southern ocean predator,” Global Change Biol. 27, 1052–1067.
Van Opzeeland, I., Van Parijs, S., Kindermann, L., Burkhardt, E., and Boebel, O. (2013a). “Calling in the cold: Pervasive acoustic presence of humpback whales (Megaptera novaeangliae) in Antarctic coastal waters,” PLoS One 8, e73007.
Van Opzeeland, I. C., Samaran, F., Staffort, K. M., Findlay, K., Gedamke, J., Harris, D. J., and Miller, B. (2013b). “Towards collective circum-Antarctic passive acoustic monitoring: The Southern Ocean Hydrophone Network (SOHN),” Polarforschung 83, 47–61, available at https://epic.awi.de/id/eprint/36703.
Webster, T. A., Dawson, S. M., Rayment, W. J., Parks, S. E., and Parijs, S. M. V. (2016). “Quantitative analysis of the acoustic repertoire of southern right whales in New Zealand,” J. Acoust. Soc. Am. 140, 322–333.
Zerbini, A. N., Adams, G., Best, J., Clapham, P. J., Jackson, J. A., and Punt, A. E. (2019). “Assessing the recovery of an Antarctic predator from historical exploitation,” R. Soc. Open Sci. 6, 190368.