Weddell seals produce ultrasonic vocalizations

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ABSTRACT

Seals (phocids) are generally not thought to produce vocalizations having ultrasonic fundamental frequencies (≥ 20 kHz), though previous studies could have been biased by sampling limitations. This study characterizes common, yet previously undescribed, ultrasonic Weddell seal (*Leptonychotes weddellii*) vocalizations. They were identified in > 1 year (2017-2018) of broadband acoustic data obtained by a continuously recording underwater observatory in McMurdo Sound, Antarctica. Nine recurrent call types were identified that were composed of single or multiple vocal elements whose fundamental frequencies spanned the ultrasonic range to nearly 50 kHz. Eleven vocal elements had ultrasonic center frequencies (≥ 20 kHz), including chirps, whistles and trills, with two elements at > 30 kHz. Six elements had fundamental frequencies always > 21 kHz. The fundamental frequency of one repetitive U-shaped whistle element reached 44.2 kHz and descending chirps (≥ 3.6 ms duration) commenced at ≤ 49.8 kHz. The source amplitude of one fully ultrasonic chirp element (29.5 kHz center frequency) was 137 dB re 1 μPa-m. Harmonics of some vocalizations exceeded 200 kHz. Ultrasonic vocalizations occurred throughout the year, with the usage of repetitive ultrasonic chirp-based calls appearing to dominate in winter darkness. The functional significance of these high-frequency vocalizations is unknown.

I. INTRODUCTION

A. Weddell seals and their known underwater vocalizations

The Weddell seal (*Leptonychotes weddellii*) is a large and relatively abundant true seal (f. Phocidae) with a circumpolar distribution around Antarctica, including the highest-latitude coastal regions (Reeves *et al*., 2002). In contrast to the other seals of the Antarctic clade, they prefer expanses of heavy pack ice or thick shore-fast sea ice, using their teeth to maintain access holes in the ice. They dive to at least 600 m and for up to 82 min in search of fish and invertebrate prey year-round (Thomas and Terhune, 2009). Weddell seals have been extensively studied, owing to their prevalence near several research stations, their aggregation on the sea ice for pupping and breeding in the austral spring (Oct. – Dec.), and their approachability when hauled out on the sea ice surface.

The Weddell seal's extensive and relatively high amplitude (to 193 dB re 1 μPa-m) repertoire of multiple-element frequency- and amplitude-modulated underwater chirps, whistles, buzzes and chugs, among other sounds, forms a major component of the underwater soundscape in areas where they are abundant (Terhune, 2019; Thomas and Kuechle, 1982). Thomas and Kuechle (1982) provided the first comprehensive quantification of the species' underwater vocalizations. They described 34 sonic call types (< 20 kHz, human-audible) plus 9 accessory sounds recorded in McMurdo Sound in the southwestern Ross Sea. Studies have now described repertoires consisting of 14 to 50 sonic call types from populations around Antarctica, with the variation in repertoire size estimations likely due to geographic and temporal differences and inconsistent definitions of call types. Weddell seals have the most diverse vocal repertoire of any phocid (Pahl *et al.*,1997; Terhune, 2019; Thomas and Kuechle, 1982).

It is likely that the full diversity of Weddell seal underwater vocalizations remains to be described. Indeed, most studies have been limited to short-term recordings (hours to days) from near the surface beneath shore-fast sea ice, and typically detected only calls at ≤ 15 kHz (see **Fig. 1**). Long-duration recordings appear to be limited to those from the multi-year Perennial Acoustic Observatory in the Antarctic Ocean (PALAOA) effort in the Weddell Sea. In that study most analyses were conducted at ≤ 15 kHz at a coarse subsampling, and the recording site was beneath an ice shelf, 1 km from the edge (Klinck *et al.*, 2016; van Opzeeland *et al.*, 2010).

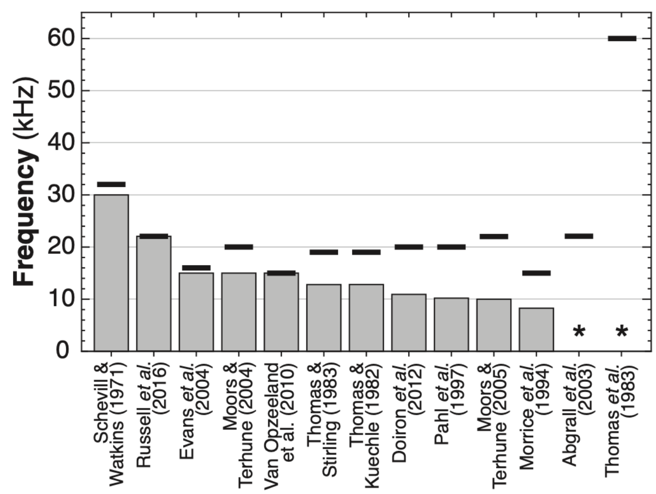

Fig. 1. Maximum reported fundamental frequencies of Weddell seal vocalizations. **Bars**: Mean or maximum of highest-frequency fundamentals reported in the cited studies. **Lines**: Upper limit of recording/analysis equipment frequency response (FR). Ultrasonic fundamental frequencies (≥ 20 kHz) have been presented in two prior studies (in a trill and a sequence of chirps; Russell *et al.*, 2016; Schevill and Watkins, 1971); Most others reported sounds to ≤ 15 kHz despite higher equipment capabilities. Two studies (asterisks) did not report maximum frequencies of vocalizations. Details of each study are available in supplementary material online[1]. The present study (not shown) is based on recordings with an upper FR limit of 256 kHz.

Weddell seal sonic underwater vocalizations are thought to be used primarily for mediating social interactions (Russell *et al*., 2016; Terhune, 2019). Social functions are supported given that the seals respond with specific vocalizations when presented with playbacks of their recorded calls (Thomas *et al*., 1983; Watkins and Schevill, 1968), by behavioral observations (Evans *et al*., 2004; Russell *et al*., 2016), and since most vocalizations appear to occur when the seals are near the surface (Evans *et al*., 2004; Moors and Terhune, 2005).

B. Ultrasonic underwater vocalizations

Weddell seals are typically not thought to produce vocalizations having ultrasonic fundamental frequencies (F0 ≥ 20 kHz, above the human hearing range; Terhune, 2019; Thomas and Kuechle, 1982), though studies could have been biased by sampling limitations. Thomas and Kuechle (1982) stated they "found no vocalizations above 20 kHz" and therefore recorded data at ≤ 19 kHz. Likewise, the majority of other studies used an effective upper frequency response (FR) of 15 to 20 kHz (see **Fig. 1**). However, two studies have presented limited evidence of ultrasonic vocalizations in Weddell seals: Schevill and Watkins (1971) reported a series of short-duration descending chirps with fundamentals to ≤ 30 kHz, and Russell *et al*. (2016) recorded a trill-type vocalization reaching to 22 kHz. These findings are not widely recognized and it remains unknown whether Weddell seals regularly use vocalizations originating at ultrasonic frequencies.

Other than the two recordings from Weddell seals, there exists only scant evidence for pinniped (seals, eared seals and walrus) vocalizations having fundamental frequencies ≥ 20 kHz. In one study of a single captive leopard seal (*Hydrurga leptonyx*), ultrasonic frequency-modulated (FM) sweeps, buzzes and pulses were recorded underwater (max. frequency 164 kHz, peak energy typically from 50 to 60 kHz; Awbrey *et al*., 2004; Thomas and Awbrey, 1983). However, field studies have only reported leopard seal vocalizations in the sonic range (≤ 6 kHz; Erbe *et al*., 2017). Several other seal species may produce broad-bandwidth roars, hisses, moans and short-duration clicks with some energy ≥ 20 kHz (reviewed in Southall *et al.,* 2019). Yet, these appear to be based on sonic-range fundamentals (< 20 kHz). Vocalizations with ultrasonic fundamental frequencies have not been reported from eared seals (f. Otariidae) or walrus (f. Odobenidae; reviewed in Southall *et al*., 2019).

Ultrasonic vocalizations are, however, produced by a number of aquatic and terrestrial animals for communication and other functions (Sales and Pye, 1974). Perhaps best known are those used in the highly-evolved echolocation (active biosonar) abilities of toothed whales (odontocetes) and bats (chiropterans). In these, the reflections of their pulsatile ultrasonic vocalizations permit obstacle avoidance and locating prey with high accuracy, given that short durations and increased sound frequency improve precision (Au, 1993). A primary indicator that vocalizations are being used for echolocation is the emission of a series of pulsed sounds ("click trains") whose interval varies directly as a function of distance to a target in order to avoid overlapping emissions and returns (Au, 1993).

Longer-duration ultrasonic vocalizations are also known from some toothed whales, in which the functions are typically attributed to intraspecific communication.

Several dolphins produce whistles whose fundamental frequencies extend into the ultrasonic range (e.g., to 25, 27 and 34 kHz for *Stenella longirostris*, *S. frontalis,* and *Lagenorhynchus albirostris,* respectively; Lammers *et al*., 2003; Rasmussen and Miller, 2002). In addition, some killer whales (*Orcinus orca*) produce high-frequency sweeping whistles with fundamentals to 75 kHz and durations of ten to a few-hundred ms, the functions of which are unknown (e.g., Samarra *et al*., 2010).

The present study characterizes a variety of previously undescribed, yet commonly occurring, ultrasonic underwater vocalizations produced by Weddell seals identified in a long-term dataset of high-frequency recordings (to 256 kHz FR) from McMurdo Sound, Antarctica.

II. METHODS

A. Data collection

Year-round digital recordings of Weddell seal underwater vocalizations were collected by passive acoustic monitoring over two years (Nov. 2017 – Nov. 2019) in southeastern McMurdo Sound, Ross Sea, Antarctica (**Fig. 2**). The recording equipment was integrated into the shore-cabled McMurdo Oceanographic Observatory (MOO) mooring, which also included a self-cleaning pan-tilt-zoom camera (Octopus, View into the Blue, Boulder, CO) and ocean condition sensors (CTD; SBE37-SMP, SeaBird Electronics, Bellevue, WA). The mooring was installed by divers at a bottom depth of 21 m at the base of the seaward terminus of the McMurdo Station seawater intake jetty (S 77.8510°, E 166.6645°). Recordings were collected continuously throughout the deployment (> 90% coverage, with occasional short gaps from network and power outages, and software bugs), yet the present study focuses on only the first 13 months of the dataset (Nov. 2017 – Nov. 2018).

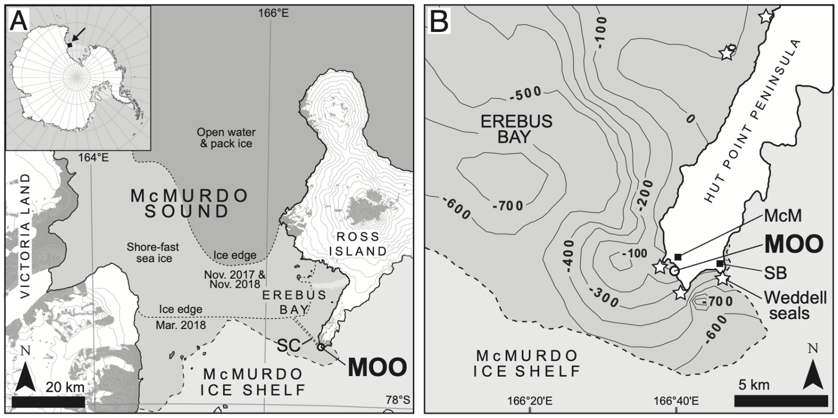

Fig. 2. Geographic location, bathymetry, and local distribution of seals. **(A)** The hydrophone was deployed as part of the McMurdo Oceanographic Observatory (MOO) mooring at 21 m deep in southeastern McMurdo Sound, Antarctica. Excepting January to early April 2018 when the ship's channel (SC) was open, thick shore-fast sea ice likely precluded most penguins and marine mammals other than Weddell seals from diving within 10 to 30 km of the recording site (see Methods, Results). **(B)** Detail of MOO environs. Weddell seals are common in Erebus Bay, where they aggregate around predictable access holes in the sea ice (stars). Bathymetry (m) is estimated based on relatively few data points (Davey and Nitsche, 2013), though it largely matches field observations (PAC, personal observations). McM, McMurdo Station (USA); SB, Scott Base (New Zealand).

The calibrated broadband omnidirectional digital hydrophone (icListen HF-SB2-ETH, Ocean Sonics, Nova Scotia, Canada; ethernet-connected, GeoSpectrum M24-205 transducer ; 118 dB dynamic range, sensitivity –170.8 ± 3.4 dBV re 1 μPa for 10 Hz to 200 kHz) was mounted vertically on a stainless-steel strut-channel attached to a 150-kg concrete block, holding the transducer 70 cm off the mud/gravel seabed. Data were recorded at 512 kSs^{-1} (256 kHz Nyquist frequency), 24 bits and written as 10-min WAV files (c. 900 MB each, with UTC-based timestamps) to a storage array in a heated structure on shore, then losslessly compressed using the Free Lossless Audio Codec (FLAC, Xiph.org Foundation). A software pipeline computed three audio spectrograms (upper limits of 2.5, 25 and 256 kHz) per file and combined those into timestamped PNG images (see example in supplementary material online[1]).

B. Seal distribution, environmental factors and interfering noises

Erebus Bay in southeastern McMurdo Sound (**Fig. 2**) is one of the most populous haul-out areas for Weddell seals, annually hosting up to 2000 individuals (Smith, 1965; Testa and Siniff, 1987). The largest concentrations of individuals occur at major sea ice breeding sites in austral spring (Oct. – Dec.), 10 to 20 km north of the MOO, where over 400 pups are born in most years (Ainley *et al*., 2015; Cameron *et al*., 2007). Weddell seals are also common around the southern end of Hut Point Peninsula (Stirling, 1969) in the MOO's immediate vicinity. From October to December in 2017 and 2018 (when project personnel were present), daily maxima of 5 to 30 Weddell seals were observed hauled out on the sea ice near crack features emanating from Hut Point, < 1 km north of the MOO, with smaller aggregations near the tip of Cape Armitage, 1 km to the south. Weddell seals occasionally hauled out at cracks < 100 m from the MOO. No other species of marine mammals were noted during these observations. Following the breeding season (Oct. – Dec.), the seals disperse more widely throughout McMurdo Sound and northward into the Ross Sea (Goetz, 2015), with only 250 individuals estimated to remain throughout the austral winter (Smith, 1965).

During the majority of the project’s first year, southern McMurdo Sound was covered with 2 to 3 m of solid shore-fast sea ice and the water column was essentially isothermal (−1.9°C; slight upward refraction of sound). In 2017-18 the natural fast-ice edge was from 30 (Nov. 2017 and Nov. 2018) to 10 km (Mar. 2018) from the MOO (NASA EOSDIS Worldview, https://worldview.earthdata.nasa.gov; **Fig. 2A**). In January 2018 an icebreaker created an open water channel from the ice edge to about 0.5 km north of the MOO, and near-surface temperatures rose slightly (max. −0.4°C recorded by the MOO at 21 m in late Jan. 2018) before the channel refroze by late March or early April.

Weddell seals are the only mammals that routinely inhabit and dive beneath the thick, shore-fast sea ice of southern McMurdo Sound (see Results). Other potentially soniferous marine mammals and diving birds may transiently visit the area, but typically only when open water exists in the austral summer (Jan. – April; Kim *et al*., 2018; Thomas *et al*., 1987; Thomas and Kuechle, 1982). These most commonly include leopard and crabeater seals (*Lobodon carcinophaga*), killer and Antarctic minke (*Balaenoptera bonaerensis*) whales, and Adelie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) penguins (PAC personal observations). Nevertheless, aside from the sounds attributed to Weddell seals, only those of killer whales (Wellard *et al.*, 2020) were noted in the year-round recordings, and on only about five total days throughout February 2018. Some penguin species may produce brief sounds underwater at ≤ 7 kHz (Thiebault, 2019). However, the nearest rookery, of Adelie penguins at Cape Royds, is 35 km north of the recording site, and no similar vocalizations were noted in the dataset. Various notothenioid fishes (≤ 30 cm) were continuously present at the recording site, but no sounds could be attributed to them.

Natural and anthropogenic interfering sounds were relatively common throughout the dataset. Identifiable sounds included irregular low-intensity, broad-spectrum clicks and cracks from the sea ice cover, occasional wind noise, a 1.5-s gurgle with components to 200 kHz every 90 s from the CTD's pump, a broad-spectrum mechanical sound for 3 min every 4 h from the camera's cleaning system, low-intensity whines (c. 18, 58, 83 and 130 kHz) thought to be from the station seawater pumps (> 100 m away, within the jetty's well casing) and intermittent noises from tracked-vehicles and helicopters (Sep. – Feb.), SCUBA divers (Oct. – Dec.), and ships (Jan.). Given the overlying ice cover, overall background noise levels from sources other than Weddell seals and the observatory itself were generally very low. Aside from a thin layer of diatoms, neither biofouling nor anchor ice were observed on the hydrophone.

C. Data analysis

Ultrasonic vocalizations of Weddell seals were identified by browsing archived spectrogram images and by watching the real-time spectrogram display at McMurdo Station or remotely over the internet. Signals of interest were further investigated using sound analysis software. In this way, a search set of discrete sounds was compiled from a relatively exhaustive review of an estimated 30% of the 13-month dataset. Archived spectrograms covering at least 2500 h (15000 images) were visually inspected.

Vocalization types that occurred exclusively when the ship's channel was open (Jan. – early Apr. 2018) were excluded from analyses. As such, novel sounds from killer whales or other species in the nearby open water would not be attributed to Weddell seals. All broad-spectrum click sounds were excluded as many evidently originated from sea ice movements and, lacking predictable repetition rates or frequency characteristics, none could be attributed to the seals. Broad-spectrum “jaw claps” (to > 200 kHz) produced by Weddell seals (Thomas and Kuechle, 1982) were excluded since they are not vocalizations *per se*.

Ultrasonic vocalizations from the search set were assigned to call types based on whether they consistently occurred alone or, for multi-element calls, in series with one or more other sounds in recurrent stereotyped patterns (Moors and Terhune, 2004). Archived spectrogram images from select days throughout the 13-month dataset were then visually browsed in order to collect multiple examples of each call type at levels substantially above background noise. To attempt to reduce bias towards individual seals, calls were typically chosen for analysis only if separated from their previous occurrences by ≥ 24 h. Call types and their elements were analyzed for frequency, waveform and time characteristics in Raven Pro 1.5 (Center for Conservation Bioacoustics, 2014). Analysis settings varied depending on call type and are presented in **Table I**. For multi-element chirp-based calls, inter-chirp intervals were measured between the beginnings of successive chirps. Durations of individual chirp elements were measured for the time containing 90% of the energy in order to avoid misinterpretation of start and stop times due to echoes or multipath transmission.

For an initial assessment of whether the usage of ultrasonic call types varied throughout the year, their presence or absence were tabulated by calendar month over the 13-month dataset. Beginning at the start of each month, archived spectrograms were visually inspected until at least one instance of each call type was found, or until the end of the month was reached.

The proportional usage of ultrasonic calls was investigated by analyzing a single 24-h period in austral spring (Nov. 20, 2017) and one from near the winter solstice ("midwinter", June 19, 2018). The sampled days were chosen because they maximized differences in solar illumination and breeding status, vocalizations occurred throughout the entire 24-h period, and because vocal activity appeared to be broadly representative of their respective seasons. The spring sample was in the height of the breeding season and characterized by 24-h of continuous sunlight (sun altitudes from 8° to 32°, always above the horizon). Conversely, the midwinter sample was likely prior to the commencement of major breeding-oriented behaviors (Thomas and Terhune, 2009) and was characterized by near absolute darkness (sun altitudes from −11° to −36°, always below the horizon; crescent moon ≤ 1.8° above the horizon for about 5 h).

In each 24-h sample, all archived spectrograms were visually inspected, counting occurrences of ultrasonic call types that were readily distinguishable (see example labeled spectrogram in supplementary material online[1]). Sonic-range vocalizations could not be accurately counted due to their high abundance and frequent overlap in the spring sample. Instead, occurrence of a relatively common and easily identified sonic vocalization was used as a proxy for overall sonic-range vocal activity. This narrowband descending-frequency whistle (from 18 to 12 kHz over about 5 s) has been previously attributed to Weddell seals (Thomas and Kuechle, 1982; see example in supplementary material online[1]), and is referred to herein as the “sonic standard call.” Results from one study suggest that seasonal variation in the proportional usage of sonic descending whistles is relatively low (32 to 38% of total sonic calls, in non-breeding and breeding seasons, respectively; Doiron *et al.*, 2012).

A simultaneous video and audio recording of a Weddell seal producing a repetitive ultrasonic chirp-based call (C102, see Results) in close proximity to the MOO permitted estimation of the source sound pressure levels (SPLs) of its elements. The seal-hydrophone distance was estimated using the apparent size of benthic landmarks on video together with their measured dimensions and distances (by divers with tape measure), the known geometry of the mooring, and the estimated length of an adult seal using a range of plausible values (2.5 to 3.3 m total length; Thomas and Terhune, 2009). Using hydrophone calibration coefficients, “inbound power” was measured in Raven Pro for the fundamental and prominent harmonics (25 to 70, 15 to 65, and 0 to 70 kHz bands for the C102-a, C102-b and C102-c elements, respectively) over the duration of the sounds while excluding obvious echoes. Lower and upper estimate bounds for the source SPLs were computed using the sonar equation to account for transmission loss (source SPL = received level + transmission loss) assuming spherical spreading [$\text{transmission loss} = 20 \times \log_{10}(\text{distance}_{\text{seal–hydrophone}})$] over the range of estimated seal-hydrophone distances (Rogers, 2014). With the seal ≤ 26 m from the hydrophone (see Results), spherical spreading of sound could be assumed and any frequency-dependent absorption was considered negligible (Au, 1993).

III. RESULTS

A. Attribution of vocalizations to Weddell seals

All ultrasonic vocalizations described herein were attributed to Weddell seals with high confidence. For the majority of the dataset, the thick, shore-fast sea ice would generally preclude all other marine mammals and penguins from diving within 10 to 30 km of the recording site (**Fig. 2A**; Kim *et al*., 2018; Thomas *et al*. 1987; Thomas and Kuechle, 1982). This is supported by the results of comprehensive surveys of seals in the greater Erebus Bay area, conducted about six times annually in November through mid-December since 1969 (Rotella, 2018). In each survey during the present study (2017 and 2018) about 1000 hauled-out Weddell seals were documented. By comparison, there were only 3 total sightings of crabeater seals, and no other pinnipeds or whales were observed on or diving beneath the shore-fast sea ice in areas away from the ice edge (J.J. Rotella, personal communication). Errant Adelie and emperor penguins occasionally wander over the ice throughout southeastern McMurdo Sound, but they do not typically dive through the isolated holes or cracks in the shore-fast sea ice (PAC personal observations).

With the exception of killer whale vocalizations, present only intermittently in February 2018 when the ship's channel was open (Jan. – Mar.), the underwater vocalizations of Weddell seals were the only identifiable sounds of non-human biological origin in the recordings. The novel ultrasonic vocalizations described herein were both comparatively common and nearly always interspersed with the sonic trills, chirps, buzzes and chugs that have been previously attributed to Weddell seals (see example spectrogram in supplementary material online[1]; Thomas and Kuechle, 1982; Pahl *et al.*, 1997). Finally, the MOO's underwater camera provided regular visual confirmation of Weddell seals producing multiple sonic call types and, in one instance, an ultrasonic call (see below). However, most vocalizing individuals were beyond the visual range of the camera (≤ 300 m).

B. Call types with ultrasonic fundamental frequencies

Nine recurrent call types were identified that were composed of 17 vocal element types whose fundamental frequencies (F0) were partially or entirely ≥ 20 kHz (**Fig. 3, Table I**; recordings available in supplementary multimedia online[1]). Individual elements of multi-element calls sometimes occurred alone, though the vast majority occurred within the presented stereotyped calls. Call types were named based on their predominant ultrasonic elements, i.e., chirps ("C"), U-shaped whistles ("U"), relatively constant-frequency whistles ("W"), and FM trills ("T"), with numbers starting at 101 to avoid confusion with other naming systems. Distinct element types identified within multiple-element calls were designated with lowercase letters. No clipping or other acoustic artifacts were found that could have skewed the results.

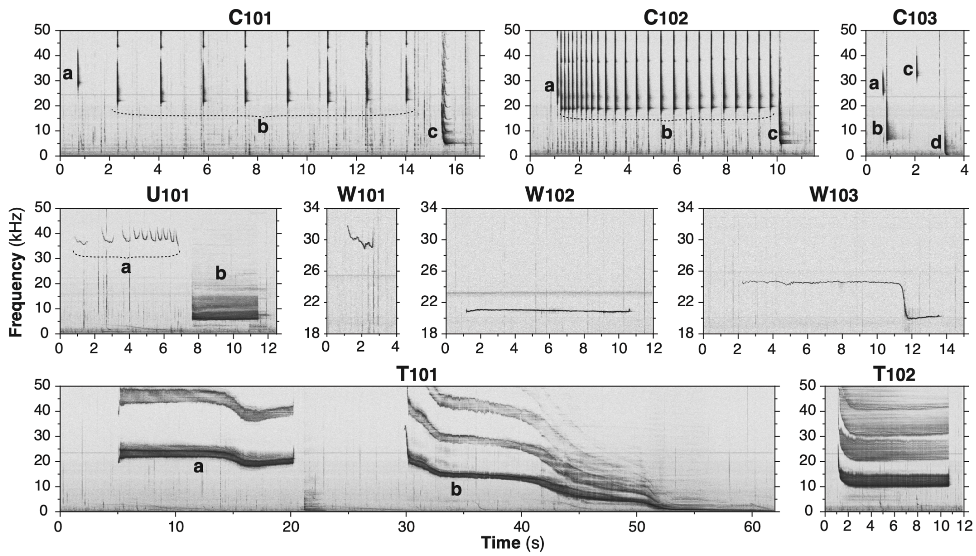

Fig. 3. Spectrograms of Weddell seal ultrasonic underwater vocalizations. These recurrent, stereotyped single and multiple-element call types were based on chirp ("C"), U-shaped ("U"), relatively constant-frequency whistle ("W"), and frequency-modulated trill ("T") elements having ultrasonic fundamental frequencies (≥ 20 kHz). Distinct element types of multi-element calls are named with lowercase letters. Some details are shown in **Fig. 4.** Note different time and frequency scales between panels. Summary statistics are presented in **Fig. 5** and **Table I**. Presented spectrograms were computed from resampled data (128 kSs^{-1}) using an 8192-pt. Hann window, 90% overlap, with 8192-pt DFT sample length. Recordings are available in supplementary multimedia online[1].

The fundamental frequencies of individual vocal elements spanned the ultrasonic spectrum from 20 to 49.8 kHz (**Figs. 4, 5**; **Table I**). The highest-frequency fundamental was found at the start of a C101-a chirp element (49.8 kHz), and the element type with the highest mean maximum frequency was the C103-c chirp (42.7 ± 3.3 kHz, mean ± SD). As shown by their center frequencies (the frequency that divides the selection into two frequency intervals of equal energy) the most energy in all elements was focused in the lower half of their fundamental's frequency spectrum. Nevertheless, 11 element types had mean fundamental center frequencies ≥ 20 kHz, with 2 element types > 30 kHz (C101-c, U101-a). The fundamental frequencies of six elements were entirely > 21 kHz. Element U101-a exhibited the highest mean fundamental center frequency at 36.2 kHz.

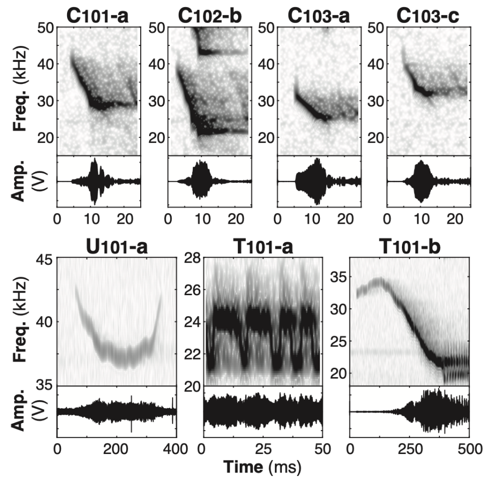

Fig. 4. Some details of the ultrasonic vocalizations presented in **Fig. 3**. The various element types with the highest fundamental frequencies are presented as spectrograms (**top sub-panels**) and waveforms (**bottom**). Only a portion of T101-a and the leading whistle for T101-b are shown. Note different axis scales between panels. Presented spectrograms were computed from 512 kSs^{-1} data using a 256-pt. Hann window, 90% overlap, with 4096-pt. DFT sample length. Amplitude is presented as raw instrument voltage output (at various scales) after bandpass filtering (15 to 50 kHz) for clarity.

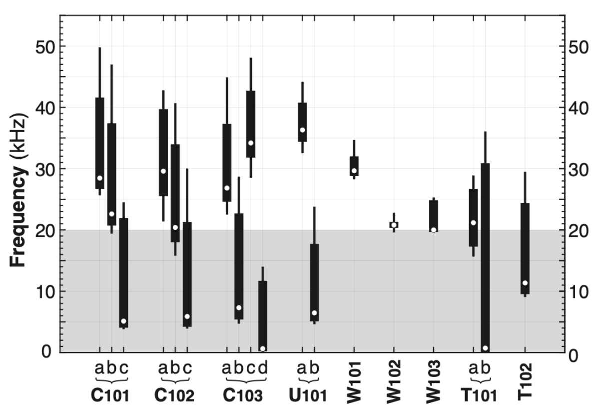

Fig. 5. Characteristics of the fundamental frequencies of Weddell seal ultrasonic underwater call types analyzed in this study. Bars: Mean maximum and minimum frequencies of the fundamental. Lines: Range of fundamental frequencies. White circles: mean center frequencies. The ultrasonic range (≥ 20 kHz) is shown with a white background. n = 4 to 23 for each element type. Values and analysis parameters are presented in **Table I**.

Call type U101 typically presented as a repetitive series of 5 to 37 discrete ultrasonic U-shaped whistles (U101-a) between 32.5 and 44.2 kHz (min. and max.), followed by a rapid, sonic buzz (U101-b). Occasionally, the U-shaped elements appeared to be merged into a continuous, irregular sinusoid.

Call types T101 and T102 were based on trills that began at ≥ 20 kHz, i.e., continuous long-duration FM calls with relatively wide envelopes. T101 included two distinct trill elements that frequently occurred sequentially and only in the presented order, though element type T101-b also occurred alone. Element type T101-a maintained relatively constant frequency contours over its duration, with most energy ≥ 20 kHz and reaching to 28.9 kHz. A lower-frequency variant of this element (≤ 22 kHz) was presented by Russell *et al*. (2016). A low-frequency trill element often occurred between T101-a and T101-b (visible at 21 s in **Fig. 3**), though its usage was sporadic and it was not characterized. A portion of T101-b (≤ 12.8 kHz) appears to have been previously described as call type T6 by Thomas and Kuechle (1982). The recordings herein now show that this element begins as a somewhat variable descending narrowband ultrasonic whistle (≤ 36.1 kHz, **Fig. 4**) before transitioning to a trill whose frequency envelope descends into the sonic range as the amplitude increases. A similar leading whistle also characterized call type T102, whose single element occurred both independently and in a call similar to C103, where it replaced chirp element C103-b.

C. Chirp-based calls and source levels

Multiple-element chirp-based calls C101, C102 and C103 (**Figs. 3, 4**) recurred regularly in the dataset. Ultrasonic chirps initiated with fundamental frequencies ranging from 21.3 to 44.7 kHz (mean maximums; **Fig. 5**, **Table I**) followed by rapid downward linear or exponential FM sweeps. Chirp fundamentals descended at 1.2 to 2.0 kHz/ms (46 to 192 octaves/s, min. and max., excluding the lower-frequency terminal elements) with 90% of the energy contained within 3.6 to 9.2 ms (**Table I**).

Call types C101 and C102 each began with a unique ultrasonic chirp (C101-a, C102-a) at the highest frequencies of the call, followed by a series of 5 to 29 similar fully- or partially-ultrasonic chirps (C101-b, C102-b) at predictable intervals and somewhat lower frequency contours, and terminated with the lowest-frequency chirp (C101-c, C102-c). These two call types segregated based on small but consistent differences in the frequency contours of their elements (**Figs. 3, 4, 5** and **Table I**) and by the relatively stereotyped progression of their inter-chirp time intervals (ICIs; **Fig. 6**). Conversely, the ICIs of call type C103 were rather variable, having a typically short first ICI (< 1 s), and longer ICIs thereafter (1 – 10 s). A fourth chirp-based call type occurred infrequently in the dataset and was not analyzed. It was similar to C101 and C102 but with fewer elements and seemingly consistent but much longer ICIs (8 to 10 s; visible in **Supplementary Fig. 1**[1]). Calls resembling those presented by Schevill and Watkins (1971) were not found. No calls were observed to terminate with rapidly decreasing ICIs akin to the “terminal buzz” commonly referenced in the echolocation literature (e.g., DeRuiter *et al*., 2009).

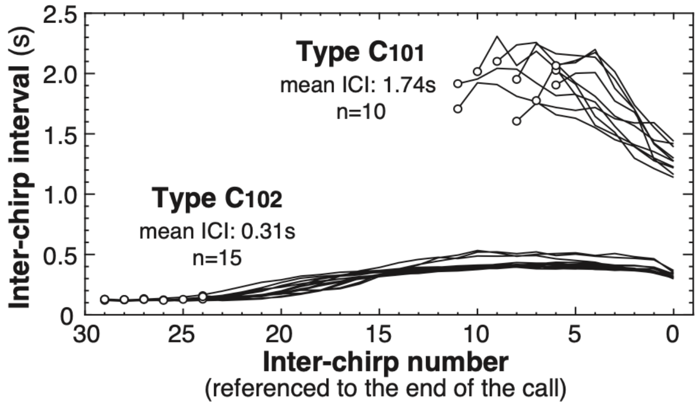

Fig. 6. Repetitive ultrasonic chirp-based call types (C101 and C102) segregated based on the stereotyped progression of their inter-chirp intervals (ICIs). ICI was measured as the time interval between the onset of successive chirp elements within a series of chirps within an individual call. Circles mark the time interval between the first and second chirp (the start of the call), with subsequent chirps in each series shown by connected lines. For clarity, given the characteristics of the calls, ICI number is referenced to the final ICI (0, the end of the call). Some datapoints are hidden by overlap.

An example of call type C102 was recorded simultaneously with underwater video observation of the source individual (likely an 18-y-old male based on contemporaneous surface sightings, yellow tag #9410; Rotella, 2018). The vocalizing seal was estimated to be between 18 and 26 m from the hydrophone and facing about 90° off-axis (see video in supplementary material online[1]). Movements of the seal's head, throat and chest area coincided with the emissions of individual chirps, and no air was observed to escape from the mouth or nostrils. Estimated source SPLs were lower for the ultrasonic chirps (from 135 to 152.0 dB re 1 μPa-m for C102-a and C102-b) than for the terminal sonic chirp (154 to 158 dB re 1 μPa-m, **Table II**). Equivalent continuous sound level (L_{eq}) values for all elements were essentially equal to inbound power measurements, and background noise levels in the bandwidths used to measure the sounds were < 91 dB re 1 μPa.

D. Temporal variation in ultrasonic calling

The ultrasonic calls of Weddell seals were common almost year-round. Based on an assessment of presence/absence only, 8 out of the 9 ultrasonic call types were found at least once in ≥ 11 of the 13 analyzed months (**Fig. 7A**). None were recorded in February. Overall, the prevalence of ultrasonic and sonic vocalizations appeared to be highly correlated. Both were most common during the austral spring breeding season (Oct. – Dec.), comparatively less frequent at other times, and rare or absent for extended periods in austral summer (Jan. – Mar.; data not shown). A similar pattern has been previously reported for sonic-range vocalizations at other locations (Green and Burton, 1988; Thomas *et al*., 1988; van Opzeeland *et al*., 2010). It likely results from seasonal changes in the abundance of seals at the recording site (Goetz, 2015; Smith 1965) and/or their propensity to vocalize. Weddell seals may also reduce their vocal activity in summer to avoid detection by potential predators (e.g., killer whales) in nearby open water (Thomas *et al*., 1987).

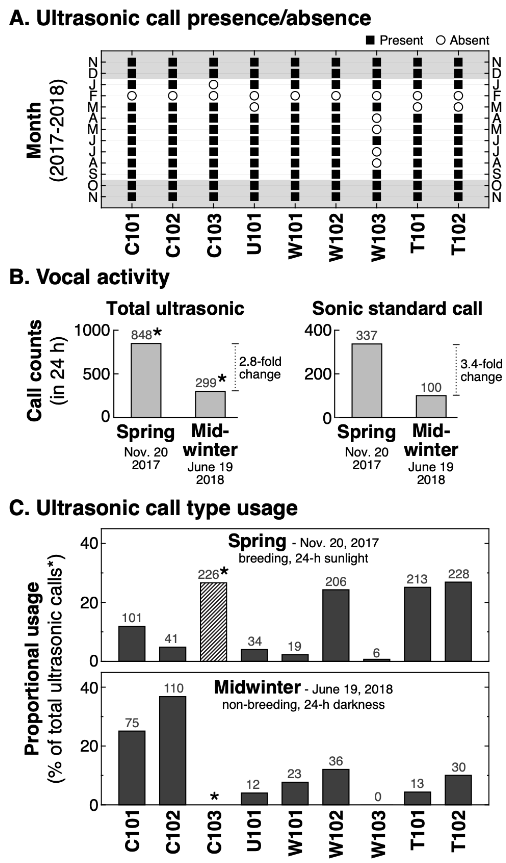

Fig. 7. Monthly occurrence and seasonal variation in ultrasonic calling. **(A)** Presence (black squares, ≥ 1 occurrence) or absence (white circles) of ultrasonic call types in each of 13 calendar months. Gray shading demarcates the breeding seasons. **(B)** Vocal activity over a single 24-h period in austral spring and one in midwinter. The relative prevalence of total ultrasonic calls compared to the sonic standard call was approximately constant in the two samples, though vocal activity for each was about 3-fold lower in midwinter. C103 was excluded from calculations because its detection was unreliable in the midwinter sample (asterisks). The sonic standard call (a descending whistle) was used as a proxy for overall sonic vocal activity. **(C)** Proportional ultrasonic call type usage in the spring and midwinter samples. Bar heights for each call depict their percentage of the total ultrasonic calls in each 24-h period, excluding counts of C103 (hatched bar, asterisks; not counted in midwinter). Four disparate call types occurred at similarly high proportions in spring, whereas the two similar repetitive ultrasonic chirp-based calls dominated in midwinter. The actual call counts are presented above the bars in (B) and (C).

Seasonal variation in ultrasonic call activity and proportional call type usage was assessed by counting calls over a single 24-hour period in austral spring (Nov. 20, 2017; 24-h sunlight, breeding season) and one near the winter solstice (June 19, 2018, “midwinter”; 24-h darkness, non-breeding). Detection of call type C103 was unreliable in the midwinter sample because of its visual similarity to the prevalent cracking sounds from the sea ice. Thus, it was not counted in midwinter and excluded from comparative analyses. The sonic standard call was taken as a proxy for total sonic vocal activity in both samples (see Methods).

Using this methodology, total ultrasonic vocal activity was found to be 2.8-fold lower in midwinter compared to spring (299 and 848 total ultrasonic calls in 24 h, respectively, both excluding counts of C103; **Fig. 7B**). The midwinter decrease in total ultrasonic calling was approximately matched by the decrease in occurrences of the sonic standard call (3.4-fold). This may signify that the seals’ relative use of ultrasonic vs. sonic vocalization remains relatively constant year-round.

The proportional usage of the individual ultrasonic call types varied between the two sampled days (**Fig. 7C**). In the spring sample, four disparate call types (C103, W102, T101 and T102) were most prevalent. Each accounted for between 19 and 27% of total ultrasonic calls (full range of proportional usage, both including and excluding counts of C103; each call averaging 8.5 to 9.5 occurrences per h). Conversely, the two similar repetitive ultrasonic chirp-based calls (C101 and C102) were dominant in the midwinter sample where, together, they accounted for 62% of all ultrasonic calls (averages of 3.1 and 4.6 occurrences per h, respectively).

E. Harmonics

Vocalizations with both sonic and ultrasonic fundamentals exhibited harmonics with energy regularly present above background levels to over 100 kHz and occasionally to over 200 kHz, especially when received with high signal-to-noise ratios (SNR ≥ 40 dB, as measured in the same 1/3 octave band as the fundamental). Some examples are presented in **Fig. 8**. No clipping of high-intensity sounds was observed, i.e., the presented harmonics are not artifacts. No emphasis on higher-order harmonics were noted for any vocalizations, rather the fundamental frequency always contained the most energy. When received at these high SNRs, ultrasonic chirps were accompanied by coincident very low intensity sounds at frequencies below the fundamental (e.g., C101-b, C102-b in **Fig. 3** and at 15 to 25 ms in C103-c in **Fig. 8).**

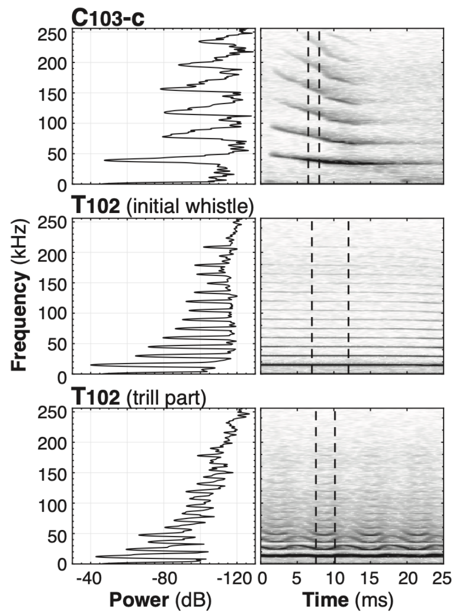

Fig. 8. Harmonics of sonic and ultrasonic chirp, whistle and trill elements extended to > 200 kHz when received with high signal-to-noise ratios. To illustrate this, the entire recorded harmonic series for portions of three diverse element types are presented. Power spectra (**left panels,** 2 kHz resolution), computed for the time segment between the dashed lines in the spectrograms (**right panels**), are referenced to raw instrument voltage. The fundamental always contained the most energy. Subharmonics below the fundamental were not evident. In these examples, signal-to-noise ratios exceeded 60 dB, as measured in the same 1/3 octave band as the fundamental. Presented spectrograms were computed from 512 kSs^{-1} data using a 1024-pt. Hann window, 90% overlap, with 2048-pt. DFT sample length.

IV. DISCUSSION

A. Ultrasonic vocalizations of Weddell seals

Despite years of acoustic studies on Weddell seals throughout the Antarctic, this study is the first documentation of their relatively extensive and diverse ultrasonic repertoire. With fundamental frequencies reaching to nearly 50 kHz, Weddell seals now appear to be rivaled only by killer whales (75 kHz; Samarra *et al.*, 2010) and possibly leopard seals (164 kHz; Awbrey *et al*., 2004; Thomas and Awbrey, 1983; if validated, see Introduction) for the highest frequencies of tonal vocalizations produced by aquatic mammals. In considering the presented ultrasonic call types, the present findings increase the known Weddell seal vocal repertoire by 9 call types. Adding these to the accounting by Terhune (2019) increases the total size of the species' known vocal repertoire to 59 call types, of which 17% have elements with ultrasonic center frequencies (10 of 59, including chirps described by Schevill and Watkins, 1971). From the previously reported lowest-frequency fundamentals (32 Hz; Terhune, 2019) to the highest-frequency fundamental reported herein (49.8 kHz), Weddell seal vocalizations span > 10 octaves.

While the Weddell seals' routine use of higher frequencies was unknown, the time-frequency contour shapes of these ultrasonic call types have been previously described for calls at sonic frequencies (Doiron *et al*., 2012; Pahl *et al*., 1997; Thomas and Kuechle, 1982). Similarly, the stereotyped repetition of similar elements within calls (Moors and Terhune, 2004) and mixed-element calls (Terhune and Dell'Apa, 2006) also occur in the sonic range. The mixing of ultrasonic and sonic elements in stereotyped multi-element calls suggests that some sonic elements previously thought to occur individually may have belonged to more complex calls.

B. How common are ultrasonic vocalizations?

It is likely that similar vocalizations were missed in previous recordings from around Antarctica owing primarily to temporal biases and/or limitations of recording equipment (e.g., **Fig. 1**), however other possibilities exist. Weddell seals have geographically distinct repertoires on various scales (e.g., Thomas and Stirling, 1983), thus ultrasonic call usage could be unique to the McMurdo Sound population. This could explain why most other researchers did not note ultrasonic components despite some ability to record at the necessary frequencies. It is also conceivable that other recording sites were more influenced by environmental or biological sounds (e.g., Klinck *et al.*, 2008) that precluded the detection of ultrasonic vocalizations or their attribution to seals. It is implausible that ultrasonic vocalization constitutes a behavior learned by the local population since the earlier recordings in McMurdo Sound (e.g., Thomas and Kuechle, 1982), given that Schevill and Watkins (1971) previously recorded a sequence of ≤ 30 kHz chirps in the area.

It is relevant to question whether the ultrasonic vocalizations presented herein are the product of a single individual (or a few) with an atypical repertoire, or rather represent a more general feature of the species as a whole. The former case is unlikely given the temporal distribution of calls over the lengthy dataset (**Fig. 7A**), the large local population (Ainley *et al.*, 2015), the diving range of the seals (5 km; Thomas and Terhune, 2009), and that overlapping ultrasonic calls were occasionally recorded (data not shown). The present recordings may be biased towards certain individuals over shorter time periods (hours to weeks), and the trill-type vocalizations may be specific to males (Oetelaar *et al.*, 2003; Thomas and Kuechle, 1982). On the other hand, one of the present authors (JMT) recorded trills that appeared to commence above 22 kHz (the upper FR of the equipment) at Davis Station in 1997 (> 5000 km from McMurdo Sound).

This suggests that ultrasonic vocalizations may be a common feature of the Weddell seal repertoire throughout their distribution.

C. Ultrasonic sound production and reception

Exactly how seals produce their vocalizations has been the subject of some speculation. Sonic Weddell seal underwater vocalizations occur with the mouth and nostrils closed such that no air escapes, and they may be accompanied by pulsing or bobbing of the head, neck, or torso (Oetelaar *et al*., 2003; Schevill and Watkins, 1971). The video evidence (presented online[1]) indicates that the same is likely true for ultrasonic vocalizations. Seals, including Weddells, are thus thought to vocalize by vibrating vocal folds and resonating pressure waves in contained air spaces, as in between the larynx and the trachea (Piérard, 1969). In a response-driven system such as this, the emitted frequency would be at least partially controlled by the properties of the air chambers that the vibrations excite (Bradbury and Vehrencamp, 1998; Moors and Terhune, 2005), and higher frequencies should arise from the compression of air spaces with increasing hydrostatic pressure during dives (Falke *et al*., 1985; Kooyman *et al*., 1970).

However, for harp (*Pagophilus groenlandicus*) and Weddell seal audible vocalizations, Moors and Terhune (2005) found no relationship between vocalization frequency and the depth of emission up to 90 m, suggesting that the characteristics of the air spaces have minimal influence on the frequencies of emitted sounds. Likewise, the ultrasonic elements presented herein likely do not represent sonic calls shifted to higher frequencies because they were produced at great depth, given especially the presented video evidence[1], the local bathymetry of the recording site (**Fig. 2B**), and previous recordings of ultrasonic chirps produced near the surface (Schevill and Watkins, 1971).

Taken together, the fundamental frequencies of the ultrasonic element types spanned the full range from 20 to 50 kHz (**Fig. 5**). Weddell seals do not therefore appear to be limited to the use of a discrete set of ultrasonic frequencies as might occur in response-driven systems with specific resonances due to the geometry of the vocal tract (Au and Suthers, 2014). The coincident emission of low-intensity sounds below the frequencies of highest intensity (**Figs. 3, 8**) could possibly indicate that sonic-range fundamentals (i.e., subharmonics) are selectively filtered in the vocal tract of the seals, allowing predominantly ultrasonic overtones to escape (e.g., Hartley and Suthers, 1988). However, the spectra of the sounds do not support this conclusion (**Fig. 8**). It is more likely that the low-frequency sounds arise from physical movements of the body or displacement of air internally during vocalization. At this point, the most parsimonious explanation for the production of ultrasonic vocalizations in Weddell seals is that, as for those in the sonic range, they are primarily created by vibrations of the vocal folds themselves, i.e., they are source-driven.

It appears that the ultrasonic vocalizations of Weddell seals are produced at lower amplitude than their sonic vocalizations, given the range of estimates for the elements of a single C102 call (135 to 152 dB re 1 μPa-m, for C102-a and C102-b vs. 153 to 193 dB re 1 μPa-m for previously described sonic vocalizations; **Table II**; Thomas and Kuechle, 1982). For calls that contained both ultrasonic and sonic fundamental frequencies, the ultrasonic components were always received at lower amplitude than those in the sonic range. However, the presented estimates of source SPLs remain only a minimum bound, given the vocalizing seal was oriented approximately 90° away from the hydrophone and their greatest sound pressure is likely to emanate in a more-or-less wide cone (possibly to 90° wide) angled somewhat downward from the throat area (Schevill and Watkins, 1971). For harp seal sonic vocalizations, source SPLs apparently vary by up to 12 dB around the animal (Rossong and Terhune, 2009), thus it is possible that on-axis source SPLs for the ultrasonic chirps of Weddell seals could reach to over 164 dB re 1 μPa-m.

It is likely that the seals can perceive at least the fundamental frequencies of all of their ultrasonic vocalizations presented herein. Phocids as a group have an overall best underwater hearing range (+ 20 dB from the lowest threshold) of about 125 Hz to 50 kHz with maximum sensitivity around 12 kHz (Southall *et al*., 2019). While the upper frequency limit of Weddell seal hearing has not been tested, it is unlikely that the seals would be able to produce stereotyped vocalizations to 50 kHz that they could not hear themselves. Although harmonics of both sonic and ultrasonic elements were detected to over 200 kHz **(Fig. 8),** the Weddell seals' auditory sensitivity is likely poor > 60 kHz, given data for other phocids (Cunningham and Reichmuth, 2016; Kastelein *et al*., 2009). Thus, the higher-order harmonics are probably undetectable to them.

D. Functions of ultrasonic vocalizations

Most known Weddell seal vocalizations are expected to be produced for intraspecific communication purposes (e.g., Russell *et al*., 2016; Thomas *et al*., 1983), and the same may be true for those in the ultrasonic range. Schevill and Watkins (1971) noted that the ultrasonic chirps they recorded were used by seals travelling between access holes, perhaps a warning of their impending arrival to conspecifics at the distant site. Similarly, the supplementary video[1] shows a seal producing ultrasonic chirp-based call C102 at < 20 m depth, immediately after leaving a breathing hole and with no other seals in view (visible range to > 200 m). However, in the preliminary analysis herein, the proportional usage of the ultrasonic call types varied substantially between periods of sunlight/breeding and darkness/non-breeding (**Fig. 7C**). This suggests that individual call types may be associated with specific behaviors that change seasonally.

Sound production over a larger frequency range could provide various benefits. Given that higher frequencies attenuate more rapidly with distance compared to lower frequencies (Au, 1993), the use of the ultrasonics could restrict communications to conspecifics at short range, while also avoiding detection by distant predators such as killer whales (Rogers, 2014). At present, these suppositions remain poorly supported since most ultrasonic calls included lower-frequency components and were also generally interspersed with sonic vocalizations.

The Weddell seals' use of ultrasonic frequencies could also serve as an additional communication channel in areas where the lower frequencies are cluttered with the vocalizations of other species or conspecifics. Moreover, because ultrasonic emissions typically have a narrower beam than those at lower frequencies (Sales and Pye, 1974), their use could possibly allow communicative signals to be emitted with better directionality. The relative extent to which higher frequencies and overtones are attenuated in received calls could also provide another metric besides intensity for determining the distance or orientation of vocalizing conspecifics (Wartzok *et al.*, 1992).

E. Relevance to echolocation

Previous authors have asserted that pinnipeds do not echolocate, using a definition of the term associated only with food capture and the high-precision biosonar of toothed whales and bats (Schusterman *et al.*, 2000). Weddell seals may, however, possess the characteristics necessary for at least a rudimentary form of echo-based acoustic spatial perception (for which no standardized gradational terminology seems to exist). As with other seal species, they likely have relatively sensitive hearing over a wide frequency range (Southall *et al.*, 2019), can localize sound sources (Terhune, 1974; Wartzok *et al.*, 1992), and are now known to produce repetitive, short-duration ultrasonic vocalizations (this study; Schevill and Watkins, 1971). Any communicative functions of ultrasonic calls would not exclude the possibility that echo and reverberation patterns also provide some information about the surroundings. However, there remain substantial differences between these seals and animals with an acute echolocating ability: seals do not possess any specialized structures for directional emission or reception of sounds (Schusterman *et al.*, 2000; Vater and Kössl, 2004) and their target detection range would be limited by the lower amplitudes of their vocalizations (> 40 dB lower than the maximum of toothed whale echolocation clicks; Au, 1993). Moreover, the durations of the shortest ultrasonic chirps presented herein are still comparatively long (≥ 3.6 ms), resulting in a ranging error of ≥ 5.4 m given the speed of sound in seawater (≅ 1500 m/s).

Nevertheless, the echoes of the ultrasonic vocalizations emitted by Weddell seals could conceivably provide finer-scale information on obstacles, the sea/ice surface, or the water depth compared to those at lower frequencies. They might therefore facilitate orientation and navigation, especially in dark or limited-visibility conditions under the sea ice where egress points are limited. Notably, the proportional usage of repetitive ultrasonic chirp-based calls (C101 and C102) appeared to be higher in midwinter darkness compared to spring (**Fig. 7C**). Though only a preliminary finding, this might lend support to their use in acoustic spatial perception. Additional studies are needed to determine to what extent Weddell seals use their own sounds to navigate and find prey in nature.

V. CONCLUDING REMARKS

Given that Weddell seals have long been the subjects of acoustic research, the discovery that they routinely use a relatively diverse repertoire of ultrasonic vocalizations reinforces the need for broad-bandwidth, long-term passive acoustic monitoring. At present, it is unclear whether ultrasonic emissions could comprise an important facet of the underwater vocalizations of other seals. As for Weddell seals, many previous studies of other species used recording equipment or analyses with relatively low upper FR. It is also possible that infrequently-used or low-intensity ultrasonic vocalizations were simply missed, or attributed to other species. Given the evolution of recording and analysis technologies, future researchers might consider replicating previous studies to assess whether other seals also produce ultrasonic vocalizations. Indeed, recording at higher frequencies could contribute to a better understanding of the range of ways that marine mammals employ sounds to enable their survival in a complex underwater environment (e.g., Tyack, 1997).

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TEXTUAL FOOTNOTES

[1]See supplementary material and multimedia at [*Staff inserts URL here*] for: (1) Details of previous Weddell seal recordings cited in Fig. 1, (2) an example of the archived spectrogram images used for assessing call prevalence, (3) spectrograms of the “sonic standard call”, (4) audio files of the presented calls in full resolution and (5) modified human-audible versions, and (6) an underwater video of a vocalizing seal from which chirp source SPLs were derived.

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TABLES

Table I. Characteristics of the fundamental frequencies of Weddell seal ultrasonic underwater vocalizations recorded by the MOO in McMurdo Sound, Antarctica. Means ± SD are presented, with other listed values in brackets.[a]

Call type	Element type	Number analyzed	Max. freq. [max.] (kHz)	Min. freq. [min.] (kHz)	Center freq. [range] (kHz)	Peak amplitude freq. [range] (kHz)	Duration [range]
C101[b]	Full call	10	-	-	-	-	16.5 ± 3.5 s[e]
							[11.2 - 21.0]
	a	10	41.6 ± 4.7	26.7 ± 0.7	28.5 ± 0.7	28.0 ± 0.8	6.6 ± 1.7 ms[f]
			[49.8]	[25.7]	[27.5 - 29.8]	[26.8 - 29.0]	[4.8 - 9.2]
	b	10	37.4 ± 2.1	20.7 ± 0.4	22.6 ± 1.1	22.3 ± 1.3	5.8 ± 1.1 ms[f]
			[47.0]	[19.4]	[21.0 - 25.3]	[21.0 - 25.8]	[4.0 - 7.2]
	c	10	21.9 ± 1.8	4.0 ± 0.2	5.1 ± 0.2	4.9 ± 0.1	128.6 ± 21.5 ms[f]
			[24.5]	[3.8]	[5.0 - 5.5]	[4.8 - 5.0]	[107.1 - 179.8]
C102[b]	Full call	15	-	-	-	-	8.7 ± 0.6 s[e]
							[7.8 - 9.5]
	a	15	39.7 ± 2.4	25.5 ± 1.8	29.6 ± 1.3	28.7 ± 1.8	5.9 ± 1.3 ms[f]
			[42.8]	[21.4]	[27.3 - 31.3]	[25.5 - 31.5]	[4.0 - 8.8]
	b	15	34.0 ± 2.3	18.0 ± 0.4	20.4 ± 1.4	19.3 ± 0.9	4.5 ± 0.4 ms[f]
			[40.7]	[15.8]	[17.8 - 24.3]	[17.5 - 24.0]	[3.6 - 4.8]
	c	15	21.3 ± 2.9	4.2 ± 0.2	5.9 ± 0.3	5.6 ± 0.3	39.6 ± 10.1 ms[f]
			[30.0]	[3.9]	[5.5 - 6.5]	[5.0 - 6.0]	[29.6 - 63.7]
C103[b]	Full call	12	-	-	-	-	3.2 ± 3.5 s[e]
							[1.2 - 10.7]
	a	12	37.3 ± 4.1	24.6 ± 1.9	26.8 ± 1.9	26.4 ± 1.8	6.6 ± 1.5 ms[f]
			[44.9]	[22.5]	[24.5 - 30.5]	[24.3 - 30.0]	[4.8 - 8.8]
	b	12	22.7 ± 2.8	5.4 ± 0.4	7.3 ± 0.8	6.8 ± 0.3	5.5 ± 3.2 ms[f]
			[28.7]	[4.7]	[6.3 - 9.0]	[6.3 - 7.3]	[3.6 - 12.0]
	c	12	42.7 ± 3.3	31.8 ± 1.5	34.1 ± 2.2	33.8 ± 2.2	5.5 ± 0.9 ms[f]
			[48.1]	[28.5]	[29.3 - 37.5]	[29.0 - 37.8]	[4.4 - 6.8]
	d	4	11.7 ± 2.2	0.2 ± 0.2	0.6 ± 0.3	0.6 ± 0.4	66.8 ± 49.5 ms[f]
			[14.0]	[0.04]	[0.3 - 1.0]	[0.3 - 1.0]	[22.4 - 110.5]
U101[c]	Full call	20	-	-	-	-	10.5 ± 4.0 s[e]
							[5.2 - 21.4]
	a	20	40.8 ± 1.7	34.4 ± 1.4	36.3 ± 1.5	36.0 ± 1.7	6.3 ± 3.0 s
			[44.2]	[32.5]	[34.8 - 41.0]	[33.9 - 41.5]	[2.7 - 11.9]
	b	20	17.7 ± 3.1	5.1 ± 0.3	6.4 ± 0.5	5.9 ± 0.5	4.5 ± 2.6 s
			[23.8]	[4.6]	[5.8 - 7.4]	[5.3 - 7.4]	[1.9 - 9.9]
W101[d]	-	6	32.0 ± 1.5	28.8 ± 0.3	29.6 ± 0.5	29.4 ± 0.7	1.9 ± 0.3 s
			[34.7]	[28.3]	[29.2 - 30.4]	[28.4 - 30.5]	[1.5 - 2.2]
W102[d]	-	31	21.3 ± 0.4	20.3 ± 0.3	20.8 ± 0.3	20.8 ± 0.3	7.7 ± 1.7 s
			[22.8]	[19.6]	[20.3 - 21.3]	[20.2 - 21.3]	[4.8 - 10.7]
W103[d]	-	5	24.9 ± 0.3	19.7 ± 0.1	20.0 ± 0.1	20.1 ± 0.3	9.7 ± 2.1 s
			[25.3]	[19.5]	[19.9 - 20.1]	[19.8 - 20.6]	[6.2 - 11.3]
T101[d]	Full call	19	-	-	-	-	50.9 ± 13.9 s[e]
							[10.6 - 75.6]
	a	19	26.7 ± 1.2	17.3 ± 0.6	21.2 ± 1.2	21.0 ± 1.9	14.3 ± 1.9 s
			[28.9]	[15.6]	[19.4 - 24.1]	[17.7 - 24.7]	[7.3-15.6]
	b	19	30.9 ± 4.4	0.1 ± 0.1	0.7 ± 0.2	0.7 ± 0.1	28.3 ± 10.7 s
			[36.1]	[0.0]	[0.5 - 1.4]	[0.5 - 0.8]	[2.4 - 52.3]
T102[d]	-	23	24.4 ± 2.2	9.5 ± 0.3	11.3 ± 0.7	10.8 ± 1.0	6.7 ± 2.5 s
			[29.5]	[9.0]	[10.4 - 13.3]	[10.0 - 14.7]	[3.7 - 10.1]

[a] All files were 512 kSs^{-1}, 24 bit WAV; only the fundamental frequencies of vocalizations were included in analysis selection bounds.
[b] Analyzed with 2048-pt Hann window, 90% overlap, 2048-pt DFT sample length = 250 Hz filter bandwidth.
[c] Analyzed with 4096-pt Hann window, 90% overlap, 4096-pt DFT sample length = 125 Hz filter bandwidth.
[d] Analyzed with 8192-pt Hann window, 50% overlap, 8192-pt DFT sample length = 62.5 Hz filter bandwidth.
[e] For multiple-element calls, full call duration was measured from the beginning of the first element to the end of the last element.
[f] For chirp-type elements only, duration is the interval containing 90% of energy for 10 randomly-selected individual elements.

Table II. Estimated source sound pressure levels (SPLs) of chirps from a single type C102 call, derived from a simultaneous underwater video and audio recording by the MOO (estimated seal-observatory distance = 18 to 26 m).[a]

Element type	Center freq. (kHz)	Duration[b] (90%, ms)	Source SPL[c] (dB re 1 μPa-m)
C102-a (initial chirp; n=1)	29.5	6.0	137 (135 to 138)
C102-b (repetitive chirps; n=26)	19.7 ± 0.9[d]	5.7 ± 0.7[d]	144 ± 1[d] (142 to 152)
C102-c (terminal chirp; n=1)	6.3	37.2	156 (154 to 158)

[a] Selection bounds included the fundamental and prominent harmonics excluding obvious echoes (see Methods). Analyzing filter bandwidth 250 Hz (2048 DFT length, 512 kSs^{-1} data).

[b] Time containing 90% of the energy for individual elements.

[c] At median estimated seal-hydrophone distance; range of source SPL values for individual chirps given full range of distance uncertainty in parentheses; calculated as inbound power plus estimated transmission loss; the seal was facing about 90° off-axis.

[d] Means ± SD.