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Filipa I. P. Samarra and fips2@st-andrews.ac.ukCMVolker B. Deecke and volker.deecke@st-andrews.ac.ukCMKatja Vinding and katjavp@gmail.comCMMarianne H. Rasmussen and mhr@hi.isCMRené J. Swift, Patrick J. O. Miller, and rjs30@st-andrews.ac.uk, pm29@st-andrews.ac.ukCM

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Killer whales (*Orcinus orca*) produce ultrasonic whistles

Filipa I. P. Samarra^{a)}

Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom
fips2@st-andrews.ac.uk

Volker B. Deecke

Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom and Cetacean Research Laboratory, Vancouver Aquarium, P.O. Box 3232, Vancouver, British Columbia V6B 3X8, Canada
volker.deecke@st-andrews.ac.uk

Katja Vinding

Zoovisions, Cumberlandsgade 5, 3. tv., 2300 København S., Denmark
katjavp@gmail.com

Marianne H. Rasmussen

Húsavík Research Centre, University of Iceland, Hafnarstétt 3, 640 Húsavík, Iceland
mhr@hi.is

René J. Swift and Patrick J. O. Miller

Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom
rjs30@st-andrews.ac.uk, pm29@st-andrews.ac.uk

Abstract: This study reports that killer whales, the largest dolphin, produce whistles with the highest fundamental frequencies ever reported in a delphinid. Using wide-band acoustic sampling from both animal-attached (Dtag) and remotely deployed hydrophone arrays, ultrasonic whistles were detected in three Northeast Atlantic populations but not in two Northeast Pacific populations. These results are inconsistent with analyses suggesting a correlation of maximum frequency of whistles with body size in delphinids, indicate substantial intraspecific variation in whistle production in killer whales, and highlight the importance of appropriate acoustic sampling techniques when conducting comparative analyses of sound repertoires.

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1. Introduction

Evolutionary studies of animal communication seek to identify selective pressures that influence signal design and variation. In delphinids, frequency parameters of tonal signals (“whistles”) have low intraspecific variation when compared to variation across species (e.g., Ding *et al.*, 1995). Body size has been suggested to explain interspecific variation as it is negatively correlated with whistle frequency (e.g., Ding *et al.*, 1995; Podos *et al.*, 2002), although once phylogeny is taken into account this relationship no longer holds for whistle maximum frequency (May-Collado *et al.*, 2007). However, measurements made to describe acoustic sig-

^{a)} Author to whom correspondence should be addressed.

nals are inherently constrained by acoustic sampling decisions. For example, an insufficient sampling frequency may result in whistles or parts of whistles being missed (e.g., [Oswald *et al.*, 2004](#)).

Killer whales are the largest delphinid and therefore particularly relevant to investigate the relationship between body size and whistle frequency. Although the harmonics of killer whale calls and whistles can extend well above 20 kHz (e.g., [Miller, 2002](#)), whistle fundamental frequencies have only been reported up to 16.7 kHz ([Thomsen *et al.*, 2001](#)). However, most studies of killer whale sound production have only investigated the frequency band audible to humans (up to 20 kHz). Here we use recordings with high sampling rates to demonstrate that killer whale whistles extend to ultrasonic frequencies (>20 kHz), but apparently only in certain populations.

2. Methods

Acoustic recordings were made off British Columbia, Alaska, Norway, Iceland and Shetland using a 96 kHz sampling rate. Only Northern Residents (fish-eating, [Ford *et al.*, 1998](#)) were recorded in British Columbia and only West Coast Transients (mammal-eating, [Ford *et al.*, 1998](#)) were recorded in Alaska. No effort was made to control the orientation or range of the whales to the recording devices. Recording systems varied between locations and included towed and vertical hydrophone arrays and sound recording tags attached using suction cups ["Dtags;" [Johnson and Tyack, 2003](#); see [Supplementary material](#) for details on all recording systems]. A smaller sample of higher sampling frequency recordings was collected in Norway and Iceland using Dtags and a single hydrophone (see [Supplementary material](#)).

High frequency whistles were defined as tonal sounds with fundamental frequency contours entirely above 17 kHz, as this was the maximum frequency previously reported for killer whale whistles ([Thomsen *et al.*, 2001](#)). Although terminology used to refer to tonal sounds of short duration may vary between authors, here we have refrained from making such distinctions without further knowledge on the potential functions of whistles of varying durations. Recordings were inspected using Adobe Audition 2.0[®] (Blackmann-Harris window; FFT=2048 or 4096, for 96 kHz and 192 kHz sampling rates, respectively; 100% window width). Whistle contours entirely above 17 kHz and with sufficient signal to noise ratio were traced from visual inspection of the spectrogram using a peaks contour extraction algorithm ([Buck and Tyack, 1993](#); Hann window; frequency resolution=46.875 Hz; time resolution=0.667 ms). From the extracted fundamental frequency contour we measured the following descriptive parameters: beginning, half-way point (mid) and end frequency, minimum and maximum frequency, frequency range (maximum-minimum frequency), duration and whistle complexity as zero, one or more inflection points (after [Ding *et al.*, 1995](#)).

3. Results and discussion

Killer whale whistles were found to extend into the ultrasonic frequency range with observed fundamental frequencies ranging up to 75 kHz (Fig. 1; Table 1), higher than previously described for any delphinid. However, high frequency whistles were only detected off Iceland, Norway and Shetland. High frequency whistles were detected in most encounters (Iceland=96%; Norway=73%; Shetland=100%; [Supplementary material](#)) and occurred during bouts of calling but represented on average only 6% (Norway, based on 14 Dtags), 10% (Iceland, based on 4 Dtags) and 2% (Shetland, based on 1 towed array recording) of communicative signals detected (pulsed calls, low and high frequency whistles). Most high frequency whistles detected had an entirely ultrasonic fundamental frequency contour (Iceland=97%; Norway=99%; Shetland=87.5%). On the smaller sample of Dtags sampling at 192 kHz some of the detected whistles had a fundamental frequency contour entirely above 48 kHz but these were usually less frequent than whistles in the 17–48 kHz band. In one Dtag record from Norway 2008, however, only whistles above 48 kHz were detected.

We can confidently ascribe these sounds to killer whales as no other cetaceans were observed during recordings of killer whales in Iceland, Norway or Shetland. Localization of

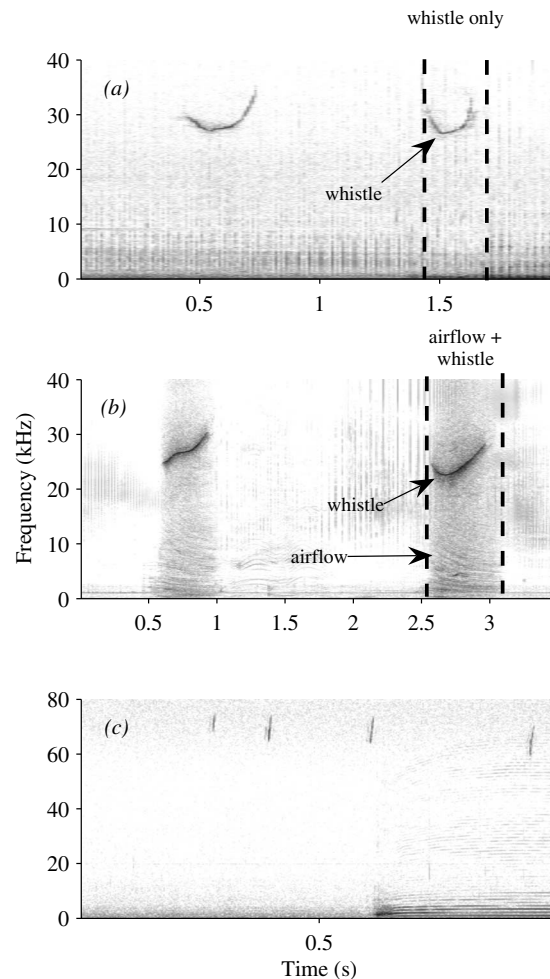


Fig. 1. Example spectrograms of ultrasonic whistles from Icelandic killer whales (*Orcinus orca*): (a) below 48 kHz; (b) below 48 kHz with overlapping airflow sound; (c) above 48 kHz. Note the presence of an airflow sound entirely overlapping the whistles in (b) but not in (a). In real time only the airflow is audible, but once slowed down both the ultrasonic whistles and the airflow sound are audible (see multimedia files [Mm. 1.wav](#) and [Mm. 2.wav](#)). Recordings (a) and (c) were sampled at 192 kHz, and (b) at 96 kHz. Spectrogram parameters: FFT size: (a) 4094, (b) 2048, (c) 1024; overlap: 50%; window function: Hann; frequency resolution: [(a) and (b)] 46.875 Hz, (c) 187.5 Hz; time resolution: [(a) and (b)] 10.67 ms, (c) 2.67 ms.

whistles with the vertical array resulted in short ranges, agreeing with visual observations of killer whale groups. Finally, air movement sounds clearly overlapped some intense whistles recorded by one Dtag deployed close to the blowhole [Fig. 1(b); [Mm. 1](#) and [Mm. 2](#)]. Most of the energy of the airflow sound is in lower frequencies, and its frequency decreases through time, suggesting airflow into the nasal air sacs changes their resonant frequencies during whistle production. This likely artifact of whistle production indicates that those whistles were produced by the tagged animal. Further work should evaluate whether characteristics of the airflow sound itself might be used to study the sound-production mechanism of high frequency whistles.

Mm. 1. Recording made using an animal-attached sound recording tag (Dtag) sampling at 192 kHz and deployed close to the blowhole. This sound clip corresponds to the spectrogram presented in Fig. 1(b). An airflow sound is audible twice in this real time recording but not the coinciding ultrasonic whistles. Faint clicks and a call can also be heard in the background.

Table 1. Descriptive statistics (mean \pm stdv and range given in parentheses) of high frequency whistle fundamental frequency contours recorded from killer whales off Iceland, Norway and Shetland. For Iceland and Norway whistles with fundamental frequencies entirely above 48 kHz are listed in separate rows. Sample sizes and the Nyquist frequency of recordings from which contours were measured are given in parentheses. Note that due to the small sample size from Shetland, descriptive statistics from this sample may not be representative.

	Beginning frequency (kHz)	Frequency at $\frac{1}{2}$ -way point (kHz)	End frequency (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Frequency range (kHz)	Duration (s)	% with ≤ 1 inflection points
Iceland ($n=548$, 48 and 96 kHz)	31.3 ± 6.7 (16.9–47.3)	32.5 ± 5.8 (17.6–45.2)	37.0 ± 6.3 (19.4–50.5)	30.4 ± 5.9 (16.9–44.5)	37.2 ± 6.4 (19.4–50.5)	6.8 ± 3.7 (0.8–21.2)	0.14 ± 0.14 (0.008–0.81)	98
Norway ($n=234$, 48 and 96 kHz)	31.7 ± 6.1 (17.6–45.2)	32.1 ± 5.8 (19.0–42.8)	35.3 ± 6.4 (19.8–46.6)	30.7 ± 5.9 (17.4–42.3)	35.7 ± 6.0 (22.3–46.6)	5.0 ± 2.5 (1.0–19.9)	0.17 ± 0.30 (0.01–4.2)	97
Shetland ($n=8$, 48 kHz)	22.6 ± 2.1 (20.2–26.1)	23.6 ± 2.7 (21.3–29.3)	28.0 ± 3.4 (25.2–35.3)	22.2 ± 2.3 (19.9–25.9)	28.0 ± 3.4 (25.3–35.4)	5.8 ± 2.1 (3.5–9.5)	0.34 ± 0.13 (0.14–0.47)	88
Iceland >48 kHz ($n=22$, 96 kHz)	64.0 ± 2.7 (60.6–71.2)	65.9 ± 2.3 (58.1–68.8)	68.5 ± 3.2 (60.0–74.7)	63.1 ± 2.8 (55.6–68.3)	68.7 ± 3.0 (61.9–74.7)	5.6 ± 2.4 (0.7–10.4)	0.04 ± 0.07 (0.006–0.25)	95
Norway >48 kHz ($n=23$, 96 kHz)	64.3 ± 3.6 (56.6–71.0)	59.2 ± 3.3 (53.3–64.3)	58.1 ± 5.4 (47.1–68.3)	55.9 ± 4.0 (47.1–64.3)	65.1 ± 3.4 (57.9–71.0)	9.1 ± 4.1 (3.6–19.5)	0.04 ± 0.03 (0.02–0.14)	100

Mm. 2. The same recording as in [Mm. 1](#) but slowed down six times. The airflow sounds become clearer and the ultrasonic whistles audible. Note that the airflow sound coincides with the whistles, suggesting it is an artifact of whistle production.

These results suggest that killer whales fall well outside the proposed relationship between body size and maximum whistle frequency (e.g., [Ding *et al.*, 1995](#)) and therefore reinforce the conclusion that maximum whistle frequency does not seem to be constrained by body size in this species group ([May-Collado *et al.*, 2007](#)). Interestingly, whistle maximum frequency appears to vary substantially across killer whale populations, in contrast to what is usually reported for delphinids (e.g., [Ding *et al.*, 1995](#)). Whistles from Northern Residents and West Coast Transients seem restricted to the audible frequency range, while whistles recorded off Iceland, Norway and Shetland are commonly produced in the ultrasonic range. As we had no recordings of Northern Residents or West Coast Transients at sampling rates higher than 96 kHz, we cannot rule-out the possibility that these whales also produce whistles entirely above 48 kHz. Nevertheless, as Icelandic and Norwegian killer whales have been suggested to form a separate ecotype due to their unique behavior ([Simon *et al.*, 2007](#)) they may be under different selective pressures, which may explain these differences in whistle production. Further research is necessary to clarify what factors drive such intraspecific variation in killer whales, nevertheless, it emphasizes the importance of sampling different populations to infer species' whistle frequency parameters used in comparative studies.

Killer whales have the best hearing sensitivity between 18 and 42 kHz with an upper hearing limit of roughly 100 kHz ([Szymanski *et al.*, 1999](#)). They therefore should be able to detect the whistles described here, although signal duration may affect absolute thresholds ([Johnson, 1968](#)). It remains unclear how killer whales detect and use high frequency whistles in their communication, yet the fact that these signals are recorded in most encounters suggests they are a relevant part of their communication system. Harmonics were present in 65 of 78 high frequency whistles recorded at 500 kHz sampling rate. Of these 65 whistles, only 22 had harmonic energy extending above 100 kHz, with 164 kHz being the maximum frequency of any harmonic. Relative levels of harmonics may provide information on the signaler's direction of movement (e.g., [Miller, 2002](#)), which could be important in cooperative contexts. The frequency characteristics of these signals suggest a use in short-range communication. However unlike the long and complex low frequency whistles ([Thomsen *et al.*, 2001](#)), high frequency whistles are short and simple ([Table 1](#)) and therefore may encode different information. As Icelandic and Norwegian killer whales are generally silent when traveling and call most intensively during feeding or socializing ([Simon *et al.*, 2007](#)) high frequency whistles, which are produced primarily during bouts of calling, are likely related to such contexts.

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