Characteristics of whistles from the acoustic repertoire of resident killer whales (Orcinus orca) off Vancouver Island, British Columbia

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The acoustic repertoire of killer whales (Orcinus orca) consists of pulsed calls and tonal sounds, called whistles. Although previous studies gave information on whistle parameters, no study has presented a detailed quantitative characterization of whistles from wild killer whales. Thus an interpretation of possible functions of whistles in killer whale underwater communication has been impossible so far. In this study acoustic parameters of whistles from groups of individually known killer whales were measured. Observations in the field indicate that whistles are close-range signals. The majority of whistles (90%) were tones with several harmonics with the main energy concentrated in the fundamental. The remainder were tones with enhanced second or higher harmonics and tones without harmonics. Whistles had an average bandwidth of 4.5 kHz, an average dominant frequency of 8.3 kHz, and an average duration of 1.8 s. The number of frequency modulations per whistle ranged between 0 and 71. The study indicates that whistles in wild killer whales serve a different function than whistles of other delphinids. Their structure makes whistles of killer whales suitable to function as close-range motivational sounds. © 2001 Acoustical Society of America. [DOI: 10.1121/1.1349537]

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I. INTRODUCTION

Odontocete social sounds are generally of two fundamental physical types: pulsed sounds, often referred to as pulsed calls, and tonal sounds, referred to as whistles (Popper, 1980). Generally one of each type, or both types of sounds, play an important role in the acoustic communication of most odontocete species (Herman and Tavolga, 1980; Evans, 1990; Tyack, 1998). Whistles are important in the underwater communication of most members of the dolphin family (Herman and Tavolga, 1980; Evans, 1990; Richardson et al., 1995; Tyack, 1998).

For killer whales (Orcinus orca), the emphasis of acoustic studies has been on pulsed vocalizations and their relation to social organization, genealogy, and behavior (Ford and Fisher, 1983; Ford, 1989, 1991; Bain, 1986; Hoelzel and Osborne, 1986; Strager, 1996; Deecke et al., 1999). Killer whales off British Columbia have stable, pod-specific repertoires of stereotyped discrete pulsed calls (Ford and Fisher, 1983; Ford, 1989, 1991). Ford (1989) suggests that discrete calls are used to maintain contact between group members and serve as indicators of group affiliation (Ford, 1989, 1991).

The whistles of killer whales have received little study and their function in killer whale underwater communication remains completely unclear. Schevill and Watkins (1966) recorded sounds of a captive subadult male collected from the by Steiner et al. (1979) and Awbrey et al. (1982) from killer whales off Newfoundland and the Antarctic respectively. Dahlheim and Awbrey (1982) reported an average frequency of 5 kHz and an average duration of 2.3 s of whistles from captive individuals collected from different locations. Ford and Fisher (1983) and Hoelzel and Osborne (1986) reported whistles from wild killer whales off the coast of British Columbia. Ford (1989) noted a frequency range between 1.5 kHz and 18 kHz with the most energy between 6 and 12 kHz. Whistle durations ranged from 50 ms to 10-12 s. These reports gave valuable basic information on some parameters of whistles. However, no detailed quantitative characterization of whistles from wild killer whales has been undertaken to date. There is no information on fine-scale physical characteristics of this sound class nor on general structural characteristics; for example, the complexity of these sounds indicated by duration and number of frequency modulations. Therefore, an interpretation of possible functions of whistles in killer whale underwater communication has been impossible.

waters off British Columbia and found no whistle emissions from this animal. Since then, whistles have been described

Here we report our findings from a study of the structure of whistles from wild killer whales off Vancouver Island, British Columbia. Parameters of whistles from groups of individually known killer whales are be presented. Results of a fine-scale waveform analysis are described, as are investigations on dominant carrier frequencies of whistles in this

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population. Based on our results, possible functions of whistles for the communication in wild killer whales will be discussed.

II. METHODS

A. Study population

We studied killer whales from the northern community of resident killer whales off Vancouver Island, British Columbia. Resident killer whales live in stable matrilineal groups of 2 to 14 animals and feed primarily on fish (Bigg et al., 1990; Ford et al., 1998, 2000). The northern resident community ranges from mid-Vancouver Island north to southeastern Alaska (Bigg et al., 1990; Ford et al., 2000). In 1996/1997 the northern resident community comprised approximately 215 individuals in 33 matrilines (Ford et al., 2000; Graeme Ellis, personal communication).

B. Data collection

Acoustic recordings and surface behavioral observations were made in western Johnstone Strait and adjacent waters, British Columbia (50° 30' N, 126° 35' W). The study was conducted between July 1 and October 13, 1996 and July 11 and October 17, 1997. Most of the data were obtained from two 20-m motorvessels on 3-9 (average 4.5) h long commercial whale-watching excursions based from Telegraph Cove (northern Vancouver Island). Additionally some recordings were obtained from small (<2 m) outboard powered inflatables and motorboats. A total of 222 excursions were undertaken in 1996 and 1997 with more than 1000 h spent at sea. Killer whales were observed on 196 excursions with approximately 200 h observation time. Underwater sounds were recorded with a Bruel and Kjaer 8101 hydrophone in 1996, and an Offshore Acoustics hydrophone in 1997 (sensitivity: greater than -180 dB re: 1 V/ μ Pa). Recordings were made on Sony 60-, 90- and 120-min digital audio tapes using Sony TCD-D8 (1996) and Sony TCD-D7 (1997) DAT recorders (system frequency response: 20 Hz-20 kHz ±1 dB). Simultaneous voice recordings of behavioral observations were made on a separate track of the same tape. Killer whale individuals were identified by natural markings on the dorsal fin and back (Ford et al., 1994). A total of 167 recordings with a total length of 40 h were obtained.

C. Behavior categories

Based on surface behavior observations, the activities of killer whales were classified into two long-range and two short-range categories (modified from Ford, 1989; Barrett-Lennard *et al.*, 1996).

Long-range categories were defined as the distance between observed animals of more than one body length. One is foraging. During foraging whales were usually dispersed over a wide area. Nondirectional swimming, irregular diving patterns, and varying swimming speeds with short periods of high speed swimming at the surface indicated foraging activities. Another category is slow traveling, loosely organized groups on a consistent course of 3 to 6 km/h. Shortrange categories were defined by the distance between observed animals of less than one body length. One category is social traveling by a closely knit group on a consistent course at 3 to 6 km/h. During social traveling whales engaged sporadically in interactions such as body contact or in activities such as flipper or fluke slapping. A second category is socializing. Socializing whales group together, often in body contact, and engage in social displays and interactions such as breaching, flipper and fluke slapping, chasing each other, rolling over each other, and sexual interactions. During socializing killer whales made little or no consistent progress.

D. Acoustic analysis

The selection of whistles was done with the bioacoustics software, RTS, version 2.0 (Engineering Design, Inc.). To avoid aliasing, a Frequency Device 901 low-pass filter set at 20-kHz corner frequency was used before the signal was digitized. The signal was then sampled at 50 kHz (16 bit), giving a real-time spectrogram with a range of 0–20 kHz. The dynamic range was set at 42 dB. A continuous colorenhanced 512 point spectrographic display with a 98-Hz frequency resolution and a simultaneous waveform display, both in a 4-s window, were viewed. The recordings were then re-played and killer whale sounds were classified into the categories listed below (modified from Ford, 1989):

Pulsed calls are sounds made up of pulses generated at a high rate. In spectrographic analysis, these pulses are resolved as sidebands equivalent to the pulse repetition rate (Watkins, 1967). Repetition rates range from 2.5 to 4 kHz. The main energy is usually between 1 and 6 kHz. Pulsed calls are further divided into discrete calls, which are calls that are repetitive, remain stable over years, and are pod specific (Ford and Fisher, 1983; Ford, 1989, 1991); variable calls are calls that are nonrepetitive with a variety of forms such as squeaks, squawks, grunts, and growls. Variable calls were usually rich in sidebands and low in frequency (1–4 kHz).

Whistles are sounds based on a tonal format, generally with a continuous waveform which appears in spectrographic analysis as a narrow-band tone with or without harmonics. Ford (1989) reported frequencies between 1.5 and 18 kHz with the most energy between 6 and 12 kHz.

Problems seldom arose in distinguishing discrete calls from whistles. However, problems sometimes occurred in distinguishing higher pitched variable calls from whistles. If doubts were present from spectrographic analysis as to whether to assign a sound to the call or whistle category, the decision was made aurally. Whistles sound soft-high pitched "whistlelike," whereas pulsed calls generally sound harsh, metallic, and screamlike.

A total of 200 whistles were selected for further analysis. We chose 50 whistles randomly from each of the 4 behavior categories. Whistles were then digitized directly with the bioacoustics-software SIGNAL, version 3.0 (Engineering Design, Inc.). High-resolution color spectrograms were calculated using a Hanning Window and a 512 point FFT (over-

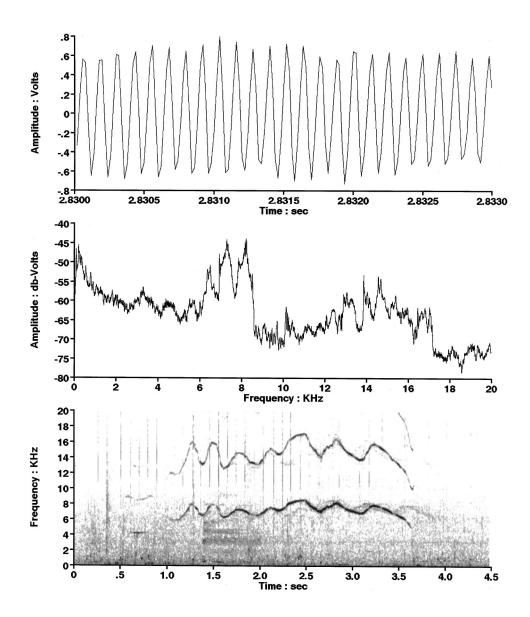


FIG. 1. Spectrogram (below), power-spectrum (mid), and section (3 ms, above) of the time waveform of a whistle with harmonics. The whistle starts at 4 kHz rises up to 8 kHz and ends after 3 s at 5 kHz. This whistle has a dominant frequency between 7 and 8 kHz. Vertical lines in the spectrogram: sonar-clicks. Spectrogram: DF=98 Hz, DT=10.2 ms, FFT=512 points. The oscillogram above shows a continuous waveform of 8 kHz.

lap: 50%). Based on visual inspection of the spectrogram, sections of interest were analyzed in detail. We performed a waveform analysis and selected several 3-ms long sections of the signal to investigate fine-scale temporal patterns. These sections were then printed. Whistles were then categorized in the classes below. The following parameters were measured for each whistle with cursors directly from the spectrographic display: start frequency (sf); end frequency (ef); minimum frequency (min.f); maximum frequency (max.f) of the fundamental or the carrier frequency; frequency range (max.f-min.f); duration (dur.); number of inflection points (frequency modulations, fm). The number of inflection points was defined as a change in slope of the spectrographic contour from negative to positive and vice versa (Steiner, 1981). Additionally the *dominant frequency (df)* was calculated for each whistle using a power spectrum analysis. Power spectra were performed with 32768 FFT points, frequency resolution of 1.2 Hz, and a time resolution of 818 ms. The dominant frequency was indicated by the main peak in the power spectrum display and was measured with cursors directly from the screen.

III. RESULTS

A. Delectability of whistles

All observations in the field indicate that whistles have a relatively short range of delectability. Regardless of the observed behavior of the whales, whistles were recorded only when whales were relatively close to the recording vessel (<500 m). Whistle recordings of the highest quality were obtained from whales swimming directionally toward the hydrophone at a distance not exceeding 300 m. As whales passed the boat, whistles dropped in volume, quickly indicating a directional effect.

B. Characteristics of whistles

The majority of whistles were tones of a fundamental frequency and harmonics which were integer multiples of the fundamental. The main energy of these sounds was concentrated in the fundamental frequency. The fundamental often showed considerable modulations. The waveform of this sound was continuous (Fig. 1). Sporadically some of the whistles showed higher energy not in the fundamental but in

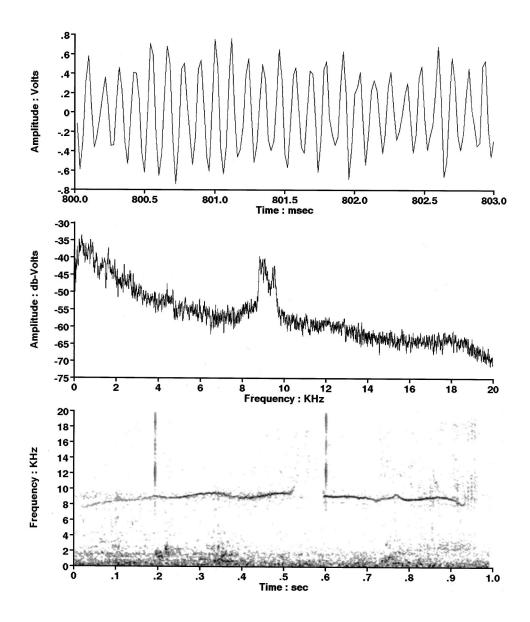


FIG. 2. Spectrogram (below), power-spectrum (mid), and section (3 ms, above) of the time waveform of whistle without harmonics. The whistle starts at 8 kHz and ends at 8 kHz. Duration is 0.9 s. Vertical lines in the spectrogram: sonar clicks. Spectrogram: DF=98 Hz, DT=10.2 ms, FFT=512 points. The oscillogram above shows a continuous waveform of 9 kHz.

one of the higher harmonics. Power spectrum analysis showed a major peak at the level of this enhanced harmonic. The waveform of these sounds showed a high degree of amplitude modulation (Fig. 2). Tones without harmonics were present but rare (Fig. 3).

C. Whistle Parameters

From the 200 selected whistles 180 (90%) were tones with harmonics, 7 (3.5%) were tones with enhanced harmonics, and 13 (6.5%) were tones without harmonics.

The average minimum frequency was $5.4\pm1.9\,\mathrm{kHz}$ ($\pm \mathrm{s.d.}$, range $2.4-12.8\,\mathrm{kHz}$). The average maximum frequency was $9.9\pm2.4\,\mathrm{kHz}$ (range $3.6-16.7\,\mathrm{kHz}$). The frequency range of the whistles averaged $4.5\pm2.2\,\mathrm{kHz}$ (range $0.5-10.2\,\mathrm{kHz}$). The dominant frequency averaged $8.3\pm2.8\,\mathrm{kHz}$ (range $3-18.5\,\mathrm{kHz}$). Whistles had an average duration of $1.8\pm2\,\mathrm{s}$ (range $0.06-18.3\,\mathrm{s}$). The average number of frequency modulations was 5 ± 7.8 . The maximum number of frequency modulations in one whistle was 71. Some of the whistles had no frequency modulations.

IV. DISCUSSION

The results of this study show that whistles of northern resident killer whales are physically more complex than previously described. Earlier descriptions which defined whistles as pure tones with little or no harmonic structure (Ford, 1989) should be revised. Our results indicate that pure tones are absent from the acoustic repertoire of killer whales. Whistles without harmonics are rare and are always frequency modulated and therefore not pure. Most whistles emitted by northern resident killer whales are tonal sounds of a fundamental frequency with the addition of several harmonics. It is very likely that most whistles of other killer whale populations are also tones with several harmonics. Published spectrograms of killer whale whistles which are undoubtedly tones without harmonics can be found only in Ford and Fisher (1983). Other published spectrograms of whistles are either difficult to interpret because the frequency range is too limited and possible additional harmonics are therefore not visible (Steiner, 1979; Dahlheim and Awbrey, 1982) or the spectrograms clearly show harmonics (Awbrey, 1982; Hoelzel and Osborne, 1986; Bowles et al., 1988).

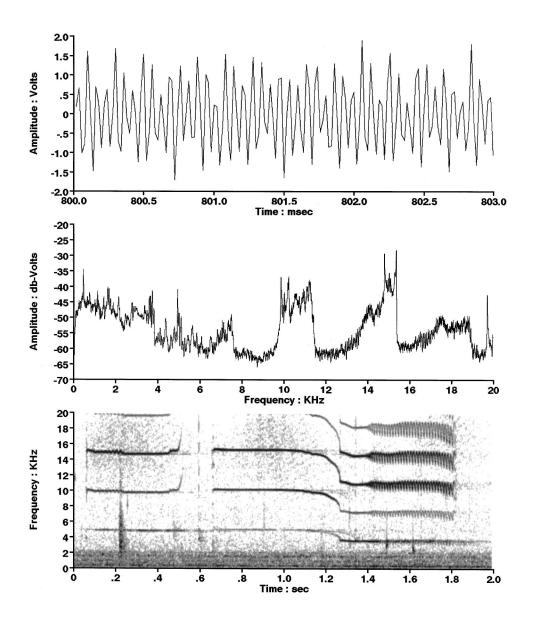


FIG. 3. Spectrogram (below), power-spectrum (mid), and sections (3 ms, above) of the time waveform of a whistle with enhanced higher harmonic. This whistle starts at 5 kHz and falls down to 3 kHz. Duration is 1.8 s. Spectrogram shows a harmonic structure with emphasis on the third harmonic (15 kHz). Vertical lines in the spectrogram: DF=98 Hz, DT=10.2 ms, FFT=512 points. The oscillogram above shows a continuous waveform with amplitude modulation.

Therefore most killer whale whistles appear to be structurally similar to those of other delphinids which in most cases show several harmonics (spectrograms in: Lilly and Miller, 1961; Busnel and Dziedzic, 1966, 1968; Caldwell and Caldwell, 1971; Caldwell *et al.*, 1973, 1990; Sjare and Smith, 1986; dos Santos, 1990; Schultz and Corkeron, 1994).

Some of the whistles in our data set contained more energy in higher harmonics and not in the fundamental. This enhancement of higher harmonics has also been described for bottlenose dolphin whistles (Saprykin et al., 1977) and might be the result of pulsation. Pulsed signals are resolved in spectrographic analysis in discrete harmonic bands. The interval between the harmonic bands indicates the pulse repetition rate. The harmonic band where most of the energy is concentrated represents the carrier frequency of the pulsed signal (Schevill and Watkins, 1966; Watkins, 1967; Gerhardt, 1998). Therefore whistles with the most energy concentrated in higher harmonics might be interpreted as pulsed rather than continuous signals. The results of fine-scale waveform analysis are difficult to interpret in our case. On the one hand, the waveform of these whistles never went to zero for consecutive A/D samples and therefore indicated a continuous sound. On the other hand, recordings obtained from the wild contain noise in the background which might distort the waveform slightly and make it difficult to identify distinctive intervals of zero amplitude. However, if these sounds are pulsed, they are very likely to be perceived as a single tone by the receiver since intervals between harmonic bands exceeded 1 kHz in every case and the temporal resolution of killer whales is limited to pulses with a repetition rate slightly above 1 kHz (Szymanski *et al.*, 1998).

Alternatively enhancement of higher harmonics can be caused by filtering mechanisms in the sound production complex or by sound production in two independent sites, as described for songbirds (Bradbury and Vehrencamp, 1998; Gerhardt, 1998). The site of sound production in delphinids is proposed to be localized pairwise in the upper nasal passages (Au, 1993; Cranford *et al.*, 1996, 1998). It is therefore likely that enhancement of higher harmonics is the result of a biphonation with different energy on different frequencies rather than pulsation.

Whistles of northern resident killer whales have a greater frequency range and a higher dominant frequency than those described by Dahlheim and Awbrey (1982). The

average duration of the whistles is similar. However, whistles exceeding 18 s were not described by Dahlheim and Awbrey (1982) or by Ford (1989). In general, whistles of northern resident killer whales are much more complex than those described for other delphinids. They are comparably longer in duration and contain a greater number of frequency modulations. Whistles from other dolphin species have an average duration from 0.13 s (*Sousa chinensis*) to 1.3 s (*Tursiops truncatus*) (Matthews *et al.*, 1999). The average number of frequency modulations per whistle ranges between 0.04 (*Peponocephala electra*) and 3.43 (*Stenella frontalis*) (Matthews *et al.*, 1999).

It has been hypothesized that in some dolphin species, whistles are acoustic signatures that are used as long-range contact signals among group members when out of sight (Caldwell et al., 1990; Tyack, 1998). To fulfill such a task such signals should be comparably simple in structure and loud, suitable to carry over several hundred meters underwater. In fact source levels of bottlenose dolphin whistles are estimated to be as high as 173 dB re: 1 \(\mu\)Pa @ 1 m giving them a range of at least 1 km (Richardson et al., 1995). Our results indicate that whistles in northern resident killer whales have a different function in underwater communication than those of other delphinids. Our observation that the whistles of northern resident killer whales are short-range sounds are confirmed by recent studies of Miller and Tyack (1999), who measured a consistently "soft" source level of 138 dB re: 1 μPa @ 1 m of whistles from northern resident killer whales. Observations in the field, as well as investigations on the behavioral context, suggest that northern resident killer whales use whistles mostly during close-range interactions (Ford, 1989; Thomsen *et al.*, in preparation). Structurally more variable and complex signals are suitable to carry information on various motivational states of the signaller at close range (Morton, 1977; Owings und Morton, 1998). Thus their structure makes whistles of northern resident killer whales suitable to coordinate interactions at close range.

V. CONCLUSIONS

This study shows that whistles of killer whales are physically diverse signals with the majority being harmonical sounds. Parameter measurements indicate that they are much more complex than whistles described for other delphinids. Finally, observations during this study indicate that whistles in resident killer whales are mostly close-range sounds.

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