Echolocation clicks from killer whales (*Orcinus orca*) feeding on herring (*Clupea harengus*) (L)

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Echolocation clicks from Norwegian killer whales feeding on herring schools were recorded using a four-hydrophone array. The clicks had broadband bimodal frequency spectra with low and high frequency peaks at 24 and 108 kHz, respectively. The −10 dB bandwidth was 35 kHz. The average source level varied from 173 to 202 dB re 1 μPa (peak-to-peak) @ 1 m. This is considerably lower than source levels described for Canadian killer whales foraging on salmon. It is suggested that biosonar clicks of Norwegian killer whales are adapted for localization of prey with high target strength and acute hearing abilities. © *2007 Acoustical Society of America.*
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I. INTRODUCTION

Toothed whales (Order: Odontoceti) listen for echoes from their intense, brief echolocation clicks to find prey. There have been many studies on the biosonar of captive odontocetes, but our understanding of how these animals use echolocation in the field is limited (Au, 2002). Killer whales (*Orcinus orca*) specialize in a large variety of prey species in different parts of the world. The acoustic properties of their biosonar signals have been described for the NE Pacific resident killer whales that feed mainly on salmon (Barrett-Lennard *et al.*, 1996; Au *et al.*, 2004). Comparing these data with those from other killer whale populations that feed on other prey species may reveal how the biosonar in this odontocete is adapted to different foraging situations and prey.

Here we present the first acoustic analysis of full-bandwidth hydrophone array recordings of echolocation clicks from wild killer whales foraging on Atlantic herring (*Clupea harengus*).

II. MATERIALS AND METHODS

Recordings of killer whales foraging on herring were made from October to December 2001 in Vestfjord and adjacent fjords, Norway. The rocky seabed of the recording site had a depth between 50 and 500 m. Foraging activity was defined as killer whales surfacing in different directions, arching their body before diving, seabirds taking fish at the site of diving and the presence of fish or fish parts at the surface (Similä and Ugarte, 1993). The boat was placed approximately 100 m upwind from the foraging whales and the engine switched off before recording in order to minimize disturbance of the whales and herring.

The recording system consisted of an array of four omnidirectional Reson (Copenhagen, Denmark) TC4034 hydrophones with a flat (±3 dB) frequency response from 0.1 to 300 kHz (sensitivity −218 dB±3 dB re 1 V/μPa). Three hydrophones were placed at the tips of an equilateral triangle, separated by 0.5 m from a fourth hydrophone in the center. The array was mounted on a pole and held from the side of the boat so that the center hydrophone was 1.5 m below the water surface (see Simon *et al.*, 2005). Each hydrophone was connected via a 26 dB amplifier and 1 Hz high-pass filter (Etec, Copenhagen, Denmark) to a Racal Store 4DS high-speed tape recorder (tape speed 30 in./s on $\frac{1}{4}$-in. magnetic Ampex tapes). A calibration signal from a B&K pistonphone calibrator [250 Hz, 171 dB re 1 μPa (pp)] was recorded on the tape and used for measuring the received level (see below). The analog recordings were played back eight times slower and digitized on a computer at a sampling rate of 48 kHz (20 kHz antialiasing filter), giving an effective sample rate of 384 kHz (recording software CoolEdit Pro, Syntrillium Software, Phoenix, AZ). The distance from the phonating whales to the array was calculated from the time-of-arrival differences of a click recorded at the four hydrophones (Au and Herzing, 2003; Schotten *et al.*, 2004). These differences were calculated by measuring the interval between highest-amplitude peaks of the envelope of cross-correlation curves between the center channel and each of the three outer channels (using a custom designed MATLAB program, The MathWorks, Inc., Cambridge, MA).

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The apparent source level (ASL) is defined as the sound pressure level 1 m away in any direction of the sound source (Møhl *et al.*, 2000). The ASL of the clicks, on all four hydrophones, was calculated as

$$ASL = RL + TL \quad [\text{Eq.}(1)\text{modified from Urick}(1983)],$$

where Received level, $RL = 20 \log(Vpp/Vppcal)\text{-dBcal}$, Transmission loss, $TL = \text{Spherical spreading} + \text{absorption loss} = 20 \log(R) + \alpha \cdot R$, and $Vpp = \text{recorded peak-to-peak}$ voltage of killer whale signal; $Vppcal = \text{recorded peak-to-peak}$ voltage of calibration signal; $dBcal = \text{peak-to-peak}$ sound level of the calibration signal, 171 dB re 1 μPa (pp); $R = $calculated range in meters; and $\alpha = $absorption coefficient$= 0.008$ dB/m (Urick, 1983).

Measurements of the localization accuracy of the recording system revealed that source levels were underestimated by up to 5 dB at distances of less than 15 m from the array, mainly due to slight variations of tape speed in the analog tape recorder (Simon, 2004). Only clicks located at distances of less than 15 m in front of the array were chosen for further analysis. On-axis clicks were defined by having a higher or equally high ASL on the center hydrophone relative to the surrounding hydrophones.

The click duration ($\tau E97$) is defined as the time period containing 97% of the click energy (Simon *et al.*, 2005) and was measured according to Madsen *et al.* (2004). The frequency bandwidth and the center frequency f_0 were measured as in Au (1993). The signal analysis was performed using CoolEdit Pro (Syntrillium Software, Phoenix, AZ), BatSound Pro (Petterson Elektronik, Upsala, Sweden), MAT-LAB and SIGPRO (Pedersen, Centre for Sound Communication, Denmark).

III. RESULTS

From 19 different recording sessions a total of 748 clicks were recorded on all four channels, 516 of which were found to be within 15 m from the array. Eighty-four of the clicks (recorded during seven sessions) were considered on-axis. Examples of clicks and their spectra are given in Fig. 1. The signal parameters of on-axis clicks were compared to similar measurements made by Au *et al.* (2004) of killer whales foraging on salmon (Table I). Although measured ranges of click parameters overlapped, echolocation clicks from herring-eating killer whales had mostly lower ASLs, center frequencies and frequency bandwidth than the echolocation clicks from salmon-eating killer whales. The click durations for herring-eating killer whales covered a broader range than those of salmon-eating killer whales, but this probably due to methodological differences (Table I).

IV. DISCUSSION

The method used in this study classified on-axis clicks as those with the highest or equally high source level on the center hydrophone compared to the surrounding hydrophones. Our method is similar, though more restrictive than that used by Au *et al.* (2004) and Au and Herzing (2003). Our method could include off-axis clicks if they are recorded from a direction where the apparent source level is not
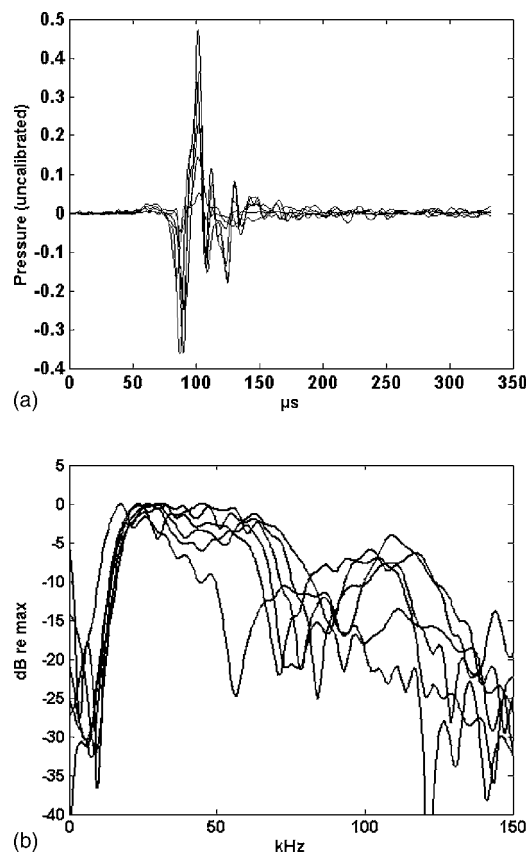
FIG. 1. (a) Wave form of six typical on-axis echolocation clicks recorded from feeding Norwegian killer whales (recording bandwidth: 150 kHz). (b) Normalized frequency spectra of the clicks in Fig. 1(a). (Rectangular window, fast Fourier transform window size: 128, frequency resolution: 2.3 kHz, spectra interpolated ten times).

changing substantially with the off-axis angle. However, our results can be compared to those reported by Au *et al.* (2004) from NE Pacific resident killer whale.

Even though the frequency characteristics and duration of Norwegian killer whale clicks are similar to those of the NE Pacific killer whales, the source levels are lower for the former (Table I). This may be explained by the fact that Norwegian and NE Pacific resident killer whales feed on prey with very different schooling behavior. NE Pacific resident killer whales feed on Chinook salmon (*Oncorhynchus tshawytscha*), which generally do not form schools (Ford *et al.*, 1998). Norwegian killer whales feed on Atlantic herring, which have a pronounced schooling behavior (Christensen,

TABLE I. Acoustic properties of on-axis clicks recorded from herring-eating (this study) and salmon-eating killer whales (from Au *et al.* 2004). [The mean and standard deviation are given in parenthesis as ($X \pm SD$).]

Killer whale ecotype	N	ASL, dB re 1 μPa (pp)	−10 dB bandwidth (kHz)	Center frequency f_0 (kHz)	Duration (μs)
Scandinavian herring-eaters	84	173–202 (189±7.1)	8–58 (35±15.9)	22–49 (38±6.7)	31–203 (89±51.0)
NE Pacific salmon-eaters	1185	195–224	35–50	45–80	80–120

In the Scandinavian study the duration was measured as τ_{E97}; for the Salmon-eating study the method used is unknown.
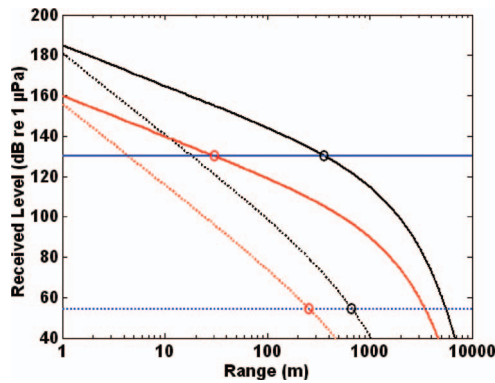
FIG. 2. Acoustic interactions between killer whales and herring. The black and red solid lines illustrate high and low level killer whale clicks (low-pass filtered at 5 kHz). The dashed black and red lines illustrate the broadband echo from high level and low level killer whale clicks, respectively. The rings shows the maximum distance at which the received level is sufficient for the herring to detect the click (solid blue line) and for the killer whale to detect the echo of the herring (dashed blue line). Norwegian killer whales using low level clicks can detect the echo from a herring at greater distances than the herring can detect the whale's click giving the killer whale an advantage over the herring.

1982; Similä *et al.*, 1996; Nøttestad and Axelsen, 1999). A school of herring has much larger target strength than a single salmon (Simmonds and MacLennan, 2005). Pacific resident killer whales might therefore need a higher source level when locating their prey than do Norwegian killer whales. In addition, the Pacific killer whales recorded by Au *et al.* (2004) were searching for individual fish that presumably try to escape predation by swimming away. While swimming away, their target strength would be lowered by the skewed angle to the killer whale (Au *et al.*, 2004). Under such circumstances powerful, long-range sonar might be advantageous. In contrast, the Norwegian killer whales recorded in this study encircled relatively stationary schools of fish and powerful, long-range sonar was not necessary to detect the schools. Norwegian killer whales may actually benefit by producing low energy clicks when feeding on prey of high target strength and with good hearing. The hearing abilities of Atlantic herring (measured by Mann *et al.*, 2005) should be much better than those of Pacific salmon. Although the hearing abilities of Pacific salmon are unknown they are probably similar to those of Atlantic salmon (*Salmo salar*) that are insensitive to frequencies above 200–300 Hz (Hawkins and Johnstone, 1978).

The advantage of using different levels of echolocation clicks can be illustrated by modeling the echolocation performance of a killer whale while searching for prey. In Fig. 2 received levels are shown as a function of range of a 5 kHz low-pass-filtered click with a source level similar to that of a salmon-eating (black line, from Au *et al.*, 2004) and a herring-eating (red line, data from this paper) killer whale, respectively. The 5 kHz low-pass filter results in a 40 dB drop in the click source level and crudely imitates the frequency response of the herring auditory system (data from Mann *et al.*, 2005). The intersections between the solid lines and the herring hearing threshold (blue solid line, taken from Mann *et al.*, 2005 at 4 kHz) indicate the ranges at which the herring can hear the two different types of killer whale

clicks. Even though the hearing abilities of herring improve considerably below 1 kHz there is very little energy in the killer whale clicks at such low frequencies, which is the rationale of choosing the hearing threshold at 4 kHz for the calculations in Fig. 2.

The dashed red and black curves in Fig. 2 illustrate the intensity of echoes received by the killer whale from a herring at various ranges when using different click source levels, that of herring and that of salmon eating killer whales. These curves are calculated from the full-bandwidth click source levels, as the echoes are detected by a whale with a very large receiving bandwidth (Szymanski *et al.*, 1999). The target strength of the herring was chosen as −44 dB, corresponding to a 25 cm long herring (Foote, 1987). The killer whale hearing threshold is assumed to be limited by background noise integrated over the bandwidth of the click rather than by the hearing threshold measured in quiet conditions. Assuming a noise spectral density of 30 dB re $1\ \mu\mathrm{Pa/Hz}^{1/2}$ (which is approximately the ambient noise level at sea state 2 at 50 kHz; see Wenz, 1962), integrating the bandwidth of the click (35 kHz) and subtracting an assumed directionality index of 20 dB (estimated by Au *et al.*, 2004) we obtain a total received ambient noise level of $30+10\log(35\,000)-20=55$ dB re 1 $\mu\mathrm{Pa}$. Here, this is used as an approximate detection threshold for the killer whale, indicated in Fig. 2 with a blue dotted line. The intersections of the echoes with the killer whale hearing threshold (marked with a red and a black circle) are the maximum ranges at which a killer whale could detect a herring using echolocation.

The model shows that if the herring-eating Norwegian killer whales used clicks with the same high source levels as those used by salmon-eating NE Pacific killer whales, the herring would detect the clicks over much larger distances, giving little advantage to the killer whale (the two black circles in Fig. 2). However, by using lower source levels the killer whale can detect an echo from a herring at much greater distances than the herring can detect the predator (the two red circles in Fig. 2).

When exposed to click trains resembling those of foraging killer whales, Pacific herring (*Clupea pallasii*) react by increasing schooling density, swimming speed and depth (Wilson and Dill, 2002). Even though killer whales can dive to depths of more than 300 m (Similä *et al.*, 2002), they seem to be unsuccessful in herding herring schools to the surface if the herring are deeper than 180 m (Nøttestad *et al.*, 2002). Therefore, diving may be an effective antipredator strategy. Thus it may be crucial for the killer whales to detect the herring before the herring hear their echolocation clicks and increase their depth.

The patterns in Fig. 2 may change dramatically when considering variations in target strength, hearing thresholds, and other parameters. Nevertheless, Fig. 2 illustrates that it might be an advantage for an echolocating predator to reduce the source level when foraging on prey with sensitive hearing abilities. On the other hand, it is advantageous to use high source level echolocation clicks when foraging on prey with low hearing sensitivity (salmon), as a high source level will increase the search range. The hearing abilities of

salmon are restricted to low frequencies and killer whale clicks are probably not detectable by the salmon even at very high received levels. Similar arguments have been used to explain variations in source levels found in bats hunting for tympanate insects (Surlykke, 1988). More accurate data are needed on the acoustic interaction between killer whales and their prey to confirm that the mechanisms outlined in Fig. 2 are actually used by the whales in real life.

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