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Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*)

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Summary

Norwegian killer whales debilitate prey by slapping their tails into herring schools. These underwater tail slaps produce a thud-like sound. It is unclear whether this sound is caused by cavitation and/or physical contact between herring and whale tail. Also the forces causing debilitation of the fish are not understood. Here we present an acoustic analysis of underwater tail slaps using a multi-channel wide (150 kHz) band recording system. Underwater tail slaps produced by Norwegian killer whales generated sounds consisting of multiple pulses with source levels of 186±5.4 dB (pp) re.1 µPa at 1 m (±1 S.D., *N*=4). The –3 dB and 97% energy bandwidths were 36.8±22.5 kHz and 130.5±17.5 kHz (±1 S.D., *N*=13), respectively, with a centre frequency of 46.1±22.3 kHz. The similarities between the acoustic properties of underwater tail slaps recorded from killer whales in Norway, and thud-like sounds recorded from killer whales in Iceland suggest that Norwegian and Icelandic killer whales use similar hunting techniques. The acoustic characteristics of sounds produced by underwater tail slaps were similar to the ones from other cavitation sound sources described in the literature, both in term of temporal and frequency features as well as in source level. We suggest that multiple factors generated by the tail slaps like particle fluctuations, turbulence, pressure changes and physical impact cause debilitation of herring.

Supplementary material available online at
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Key words: killer whale, *Orcinus orca*, foraging, prey debilitation, tail slap, cavitation, acoustics

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Introduction

The foraging behaviour of killer whales can vary considerably between populations, both in terms of prey choice and hunting strategy (Boran and Heimlich, 1999). Atlantic herring, *Clupea harengus,* is an important prey for killer whales in Norwegian and Icelandic waters (Christensen, 1982; Sigurjónsson and Leatherwood, 1988; Similä et al., 1996). Norwegian killer whales debilitate herring by slapping at the school with the underside of their tail flukes (Similä and Ugarte, 1993; Domenici et al., 2000a). This behaviour was first described by Similä and Ugarte (1993) who called it ‘tail slapping’. Tail slapping has been observed in a number of large marine vertebrates, for example by thresher sharks, *Alopias vulpinus* (Muus et al., 1988), billfish (Van der Elst and Roxburgh, 1981; McGowan, 1988) and bottlenose dolphins, *Tursiops truncatus* (Smolker and Richards, 1988). It has been suggested that tail slapping is an alternative strategy to whole-body attacks (like grasping the prey with the mouth) for large marine predators hunting small agile prey with good abilities for rapid acceleration and manoeuvrability (Domenici, 2001; Domenici et al., 2000a).

Prey debilitation prior to capture has also been noted in invertebrate predators, such as snapping shrimp, *Alpheidae spp.* (MacGinitie and MacGinitie, 1949), which debilitate their prey by producing abrupt pressure changes when rapidly closing the snapper claw (Versluis et al., 2000). This action generates cavitation: the ambient pressure falls to such low levels that dissolved gas in the water is released. When the pressure returns to ambient, the gas bubbles collapse and a distinct, very loud, sound pulse is produced. Cavitation is a well-known phenomenon associated with rotating propellers and other vibrating man-made structures (Medwin and Clay, 1998). However, it is also produced by biological systems as in snapping shrimp (mentioned above), and during photosynthesis and xylemic action inside plants (Nardini et al., 2001).

Many toothed whales; Odontoceti, produce loud sounds with source levels as high as 236 dB RMS re. 1 µPa at 1 m measured from sperm whales (Møhl et al., 2003). Prey debilitation using intense sounds has been discussed as a possible hunting strategy among toothed whales (Bel’kovich and Yablokov, 1963; Norris and Møhl, 1983). Playing loud, short duration sound signals to cephalopod and fish species to test the acoustic prey debilitation hypothesis showed no debilitation effects (Zagaeski, 1987; Mackay and Pegg, 1988). However, long duration sounds had a debilitating and, in some cases, lethal effect on guppies, *Lebistes reticulatus* (Zagaeski, 1987). Underwater tail slaps produce several transient sounds of a long total duration, which potentially could have a debilitating effect on the fish. It has been suggested that the sound produced by underwater tail slaps of bottlenose dolphins and killer whales is caused by cavitation around the tail moving through the water (Smolker and Richards, 1988; Similä and Ugarte, 1993). Intense sound pressure associated with cavitation could potentially be the cause of prey debilitation. The fish may also be debilitated by the physical impact of the tail, or by turbulence, large movements of water particles and pressure changes that could affect the lateral line system of fish (Smolker and Richards, 1988; Similä and Ugarte, 1993; Domenici et al., 2000a; Coombs and Braun, 2003). While the damaging effects of physical impact on herring are obvious, the effects of pressure changes, turbulence and water particle movements have, to our knowledge, not been described in detail. Likewise, the intensity of the sounds produced by the underwater tail slaps of killer whales has not previously been estimated. To understand the sound production mechanism and the possible effect of the sounds on the herring, it is important to know the sound intensity and frequency content of signals from the tail slaps.

The aim of the present study was to record underwater tail slaps of Norwegian killer whales using broadband recording equipment and a hydrophone array and to analyse the acoustic characteristics of these sounds. To investigate whether cavitation is caused by underwater tail slaps, we compare these analyses with cavitation sounds from documented sources. In addition, we present evidence that killer whales in Icelandic waters also use underwater tail slaps when foraging on herring.

Materials and methods

Analysis of underwater video recordings

To describe the conditions under which underwater tail slaps are produced, new analyses were performed on underwater video sequences synchronized with 1-hydrophone sound recordings of foraging killer whales (*Orcinus orca* L.) recorded in Norwegian waters in 1992, previously analysed by Similä and Ugarte (1993) and Domenici et al. (2000a,b). The recording methods are described in detail by Similä and Ugarte (1993) and Domenici et al. (2000a). We estimated the approximate depth of tail slaps directly from these video recordings by measuring the distance from the surface to the tail slap using the nominal length of a herring (35 cm; Anonymous, 1993) and of adult female or subadult male killer whales (4.7 m; Domenici et al., 2000a). Calves were identified as individuals measuring 50–75% of the length of an adult. A herring was considered to be debilitated if it lost its swimming ability and became separated from the school. Herring debilitated by tail slaps were observed for up to 1 min to determine the short-term effect of debilitation.

Sound recordings of Norwegian killer whales

Recordings of Norwegian killer whales were made from a 30 ft cabin cruiser during October–December 2001 in Vestfjord and adjacent fjords in northern Norway. Here killer whales gather in late fall and winter to feed on the overwintering schools of Norwegian spring-spawning herring (Simlä et al., 1996). The depth at the recording sites varied from 50 to 500 m. Birds taking fish among whales that dived repeatedly in one area, and fish or fish parts on the surface, identified foraging activity. When a group of foraging killer whales had been located, the boat was placed approximately 30 m upwind and the engine turned off so that the boat could drift across the feeding spot. This procedure gave minimal disturbance of the herring and whales.

The recording system consisted of an array of four omnidirectional Reson TC 4034 hydrophones (frequency response within 3 dB from 0.1 kHz to 300 kHz, Reson, Slangerup, Denmark). Three peripheral hydrophones were placed symmetrically at a distance of 0.5 m from a central hydrophone (Fig. 1). The hydrophones were fitted on PVC tubes minimising reflections from the array. The array was mounted on a pole and positioned so that the depth of the centre hydrophone was 1.5 m below the water surface.

Each hydrophone was connected to an amplifier (26 dB, 1 Hz high pass filter, Etec, Copenhagen, Denmark) and from there to one of the four channels of a Racal Store 4DS high-speed tape recorder. The recordings were made on Ampex magnetic tapes with a tape speed of 30 or 60 ips (inch per second). Before and after the digitalising of the recordings, a

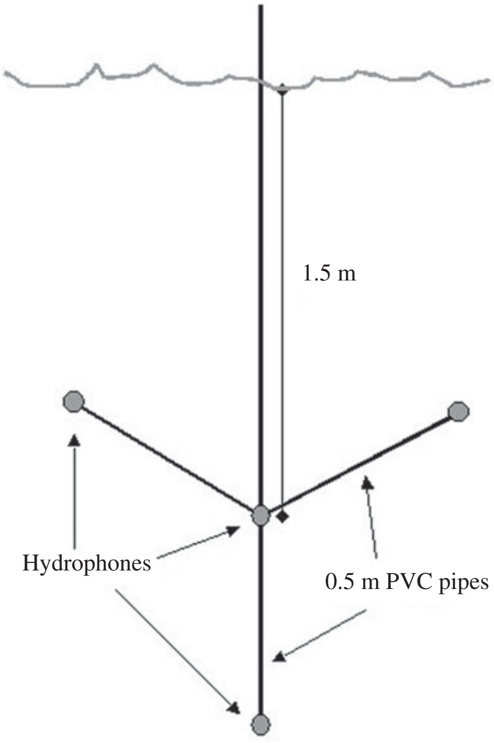

Fig. 1. The four-element hydrophone array used to record underwater sounds of Norwegian killer whales.

calibration signal of 164 dB re. 1 µPa RMS from a BK 4223 calibrator (with a custom-built adapter to fit the shape of the Reson hydrophones) was recorded on the tape. The recording system had a frequency range of 100–150 kHz or 200–300 kHz at tape speeds of 30 ips and 60 ips respectively. Calibration of the array revealed that the source levels might have been underestimated by a maximum of 5 dB at distances up to 15 m from the centre hydrophone (Simon, 2004).

The analogue recordings were played 8 or 16 times slower when digitalised on a computer with a sampling rate of 48 kHz (effective sampling rate: 384 kHz or 768 kHz), using CoolEdit Pro (Syntrillium Software, Phoenix, AZ, USA) and a sound card with built-in antialiasing filter.

Cross correlation programs were written in MatLab (The MathWorks, Inc. Cambridge, MA, USA) and were used to calculate the difference in arrival times of sounds at the four hydrophones. The time-of-arrival differences were used to calculate the distance to the sound source and the apparent source level (ASL, defined as the sound level 1 m from a sound source oriented in an unknown direction; Møhl et al., 2000) of the tail slap (Au and Herzing, 2003). Underwater tail slaps that were recorded on all four channels and located at a distance of <15 m from the array were chosen for further analysis.

Sound recordings of Icelandic killer whales

Underwater sound recordings of foraging Icelandic killer whales were made from a 36 ft gaff-rigged sloop from June to August 2002 around Vestmannaeyjar, Iceland. Just as in Norway, foraging activity was identified from birds taking fish among whales, which dove repeatedly in one area, and fish or fish parts on the surface. Recording sessions of 10 min duration were obtained using a custom-built hydrophone (Woods Hole Oceanographic Institute, with a ±4 dB response up to 20 kHz) connected to a DAT recorder (Sony, TCD-D8, sampling frequency: 48 kHz).

Sound analysis

The total duration of the multi-pulsed sounds (τ_{total}) was measured as indicated between the two vertical lines in Fig. 2. We express frequency bandwidths as the –3 dB bandwidth (Au, 1993) and the 97% energy bandwidth ($E_{97\text{BW}}$), defined as the frequency bandwidth within which 97% of the total energy occurred. We determined centre frequencies (f_0), which divide the frequency spectrum into two halves with an equal amount of energy in each (Au, 1993). We measured the received level of tail slaps as the peak to peak (pp) value of the signal, compared this with the pp value of the calibration signal, and then added 9 dB to the results to convert from peak equivalent (pe) RMS to pp measurements. This rendered received levels in units of dB (pp) re. 1 µPa, which are directly comparable to the sound levels of cavitation sounds produced by snapping shrimp (Au and Banks, 1998). The sound pressure level was back calculated to a distance of 1 m from the tail, rendering the apparent source level (ASL) applying compensation for spherical spreading loss and frequency-dependent sound absorption at the centre frequency of the pulses (–9 dB km^{-1}; Urick, 1983).

We measured the energy content of the same pulses used to measure the ASL by applying a 100 µs time window. By assuming spherical spreading and compensating for the frequency-dependent sound absorption, the energy content was back-calculated to 1 m distance from the tail, rendering the energy content in dB re. 1 µPa^{2}s at 1 m.

ASL estimates and other signal analyses were made using CoolEdit Pro (Syntrillium Software, Phoenix, AZ, USA), BatSound Pro (Petterson Elektronik, Uppsala, Sweden), MatLab (The MathWorks, Inc. Cambridge, MA, USA) and

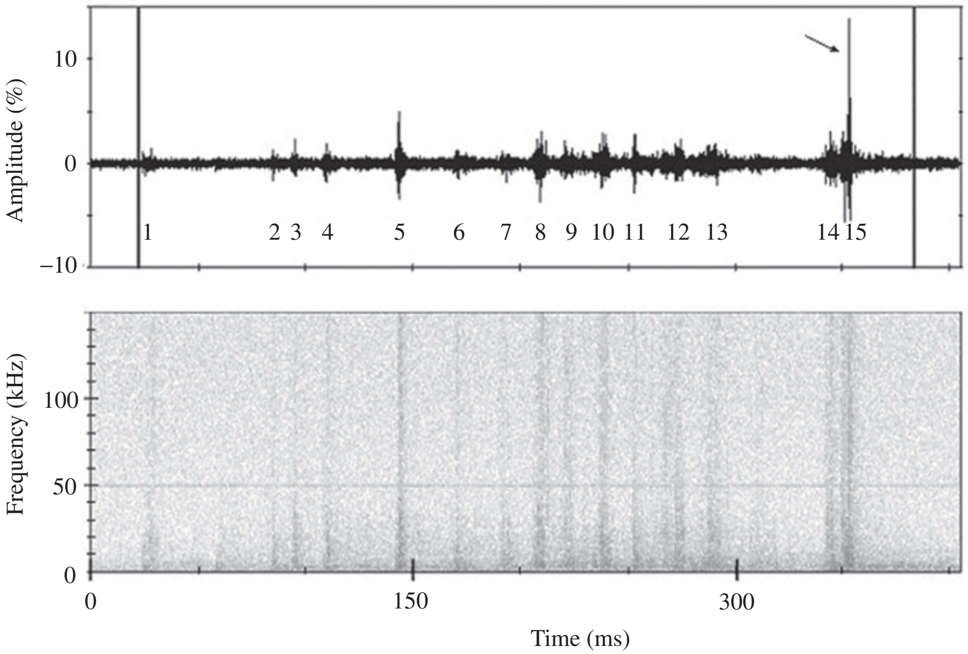

Fig. 2. Waveform (above) and spectrogram (below) of an underwater tail slap recorded from killer whales in Norwegian waters (recording bandwidth: 150 kHz). The waveform shows the multi-pulsed structure of the sounds produced during underwater tail slaps. This tail slap consisted of 15 single bursts of pulses (numbered in the figure). The vertical lines in the waveform mark the total duration (τ_{total}) of the tail slap. The arrow points at the pulse shown in Fig. 4. (Spectrogram settings: FFT size 512 pts. Hann window, overlap 75%, sampling frequency 384 kHz.)

SigPro (S. B. Pedersen, Centre for Sound Communication, Denmark).

Comparing sounds of Icelandic and Norwegian killer whales

The limitation in the recording bandwidth of the Icelandic recordings prevented direct comparison of the source levels and bandwidth with the Norwegian recordings. Therefore, the signals recorded in Norway (bandwidth: 150 kHz) were low-pass filtered at 20 kHz to obtain the same bandwidth as the sounds recorded in Iceland. The differences between two parameters (E_{97BW} and f_0), measured in pulses from multi-pulsed sounds (potential tail slaps) from Icelandic and Norwegian killer whales, were tested with non-parametric, two-way ANOVA (Barnard et al., 2001).

Results

Analysis of video recordings from Norwegian killer whales

Five hours of underwater video recordings covering 16 feeding events were scrutinized. The best quality sequences (*N*=131 min) were selected for further analysis. The size of the killer whales groups varied from 12 to 25 individuals and all group members participated in herding the fish.

Feeding was divided into two phases; first a herding phase, then a feeding phase (Similä and Ugarte, 1993). During the herding phase, the killer whales were observed swimming alone or in groups of up to nine individuals close together under and around the herring school, with their white ventral side along the edge of the school. Calves often swam in synchrony with an adult (*N*=36). Sometimes a whale swam directly through the school without splitting it into smaller groups. In the beginning of the herding phase, the water was very clear (visibility >20 m). The visibility deteriorated as the whales emitted air bubbles (see video 1 in supplementary material), air was dragged down from the surface by the whales' bodies and flukes, and ascending air bubbles were released by the herring schools (see video 2 in supplementary material).

During the feeding phase the killer whales continued the behaviours described for the herding phase, but in addition the whales emitted large volumes of air bubbles from their blowholes close to the herring school (*N*=39) (video 1 in supplementary material), used underwater tail slaps and consumed debilitated fish. Underwater tail slaps started by killer whales swimming directly towards the school. When reaching the school, they followed the edge with the ventral side of their body nearly touching the fish. At this point a whale could forcefully arch its body and slash the school with the underside of its tail fluke performing an underwater tail slap (Fig. 3). The contractions during the tail slap often caused the whale to pitch (see video 3 in supplementary material). The underwater tail slaps produced a loud thud-like sound (Fig. 3). Calves sometimes made underwater tail slaps in synchrony with another whale (video 2 in supplementary material). The whales did not immediately consume all the fish debilitated by their underwater tail slaps, but slowly circled back to eat them one by one. Whales often ate fish debilitated by other members of the group. Killer whales were never observed feeding on herring that had not first been debilitated. A few tail slaps seemed to cause extensive damage to the fish, but sometimes the fish recovered. It was not possible to follow the fate of all debilitated uneaten fish, but we did observe eight debilitated herring recover buoyancy and swim towards the school. Recovery time ranged from 3 to 52 s. The water visibility quickly decreased after continued underwater tail slapping. In addition to large amounts of air bubbles there were substantial amounts of fish body parts and scales in the water.

Ninety-two underwater tail slaps were recorded close enough to the camera to assess whether or not fish had been debilitated. In our observations, adult killer whales had greater success at debilitating herring with underwater tail slaps (76.5% tail slaps debilitated one or more herring, *N*=51) than did calves (36.6% tail slaps debilitated one or more herring, *N*=41). Due to limited resolution of the video recordings, it was difficult to obtain an exact count of the number of fish

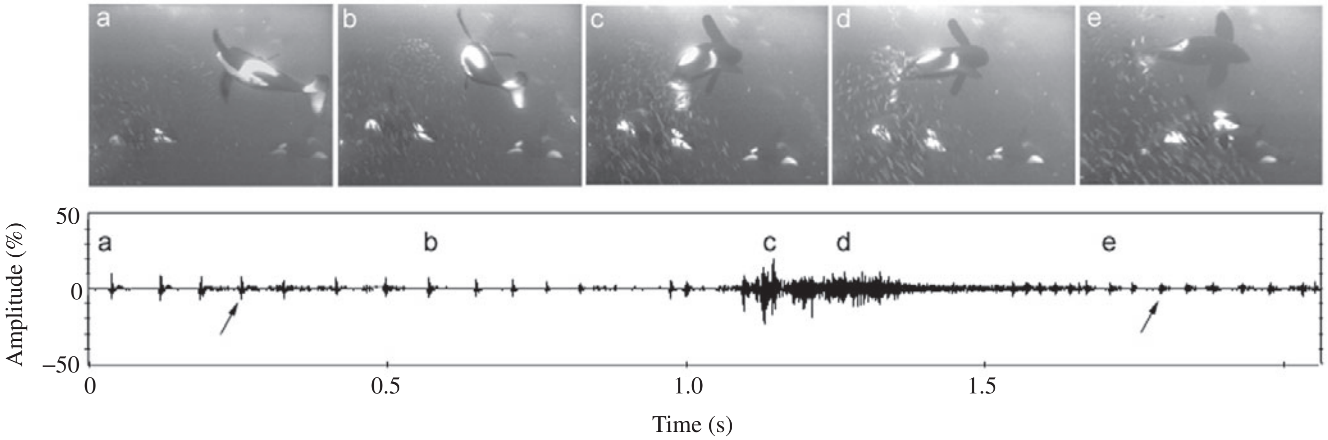

Fig. 3. Killer whale underwater tail slap extracted from video recordings (top) and the corresponding sound track (bottom). The letters of the video frames correspond to the times illustrated in the sound track. The clicks before and after the underwater tail slap are killer whale echolocation clicks (arrows).

debilitated by each underwater tail slap, but this number varied from zero to more than seven. Only herring in the immediate vicinity of the whale tail were debilitated. The approximate depth of 126 underwater tail slaps was determined. Of these, 51% were made at depths of 0–5 m, and 24% occurred at depths of 5–10 m. The remaining 25% were made at depths >10 m, but we could not determine the exact depth because the surface was not visible. However, we estimate that the whales did not use tail slaps below depths of about 20 m.

Most of the video recordings started after the killer whales had surrounded the herring or ended before the feeding ceased due to the boat drifting away from the whales or to changes in weather and light conditions. Only one event was filmed from the beginning to the end. This event involved approximately 15 killer whales and a herring school of 12–18 m in diameter. It took 3.5 min for the killer whales to drive the fish from 20–30 m depth to the surface. The herding phase lasted for 7 min and 45 s. During the following 1 min and 15 s there were three tail slaps marking the beginning of the feeding phase. The whales did not begin to consume fish until after 1 min. Then there was a 30 min period of active feeding with a series of tail slaps at gaps of 15 s to 1.0 min. The whales then swam close to the school and consumed the debilitated fish. During the 30 min feeding phase the whales made 146 underwater tail slaps. The last tail slap was made 37 min and 45 s after the beginning of the feeding session. Shortly after, the whales left the herring school, which remained close to the surface for another 2 min. There was no noticeable change in the size of the fish school suggesting that the killer whales ate a relatively small number of the fish.

Sounds of Norwegian killer whales

A total of six underwater tail slaps were recorded from the Norwegian killer whales with the hydrophone array. Four of the tail slaps were recorded by all four hydrophones and were within 15 m of the array, and these were used for further analysis. Three of the analysed tail slaps were recorded at a tape speed of 30 ips (recording bandwidth: 150 kHz), with the fourth tail slap was recorded at a tape speed of 60 ips (recording bandwidth: 300 kHz). This tail slap was filtered through a 150 kHz low pass filter to make it comparable to the tail slaps recorded at 30 ips before further analysis in SigPro (S. B. Pedersen, Centre for Sound Communication, Denmark). The sound signals produced by underwater tail slaps consisted of multiple bursts of pulses and had a total average duration of 318 ms (S.D.=99, *N*=4) (Fig. 2). The number of bursts of pulses within each tail slap varied with a mean of 16 (S.D.=5.3; Table 1). Each burst of pulses could contain up to 10 single pulses.

The frequency bandwidth and the centre frequency were measured for the single pulses of highest peak amplitude (Fig. 2, arrow, and Fig. 4A) selected from all four tail slaps (*N*=13). The 97% energy bandwidth (E_{97BW}) and the –3 dB bandwidths were 130.5 kHz (S.D.=17.5) and 36.8 kHz (S.D.=22.5), respectively. The centre frequency (f_0) was 46.1 kHz (S.D.=22.3). Fig. 4B shows the frequency spectrum of one such pulse. These intense pulses are extremely broadband and contain frequency components up to the limit of the recording system, 150 kHz or 300 kHz depending on the tape speed of the recordings.

Pulses containing the highest received sound pressure level in each tail slap (Fig. 2, arrow) were chosen for calculating apparent source levels. The underwater tail slaps containing these pulses occurred 11–15 m from the centre hydrophone of the array and gave a mean apparent source level of 186 dB (pp) re. 1 μPa at 1 m (S.D.=5.4 dB, *N*=4; Table 1). The mean energy content of the tail slap pulses was 169 dB re. 1 $\mu Pa^2 s$ at 1 m (S.D.=3.3 dB, *N*=4; Table 1).

Sounds of Icelandic killer whales

Sound recordings of foraging Icelandic killer whales revealed signals consisting of multiple bursts of pulses with an average total duration of 226 ms (S.D.=54, *N*=10), and an average of eight bursts of pulses (S.D.=3.6, *N*=10) per tail slap (Fig. 5 and Table 1). Each burst of pulses could contain up to seven single pulses. The pulses were broadband with a 97% energy frequency bandwidth (E_{97BW}) of 17.6 kHz (S.D.=2.4, bandwidth of the recording system was 20 kHz) and a centre frequency (f_0) of 7.8 kHz (S.D.=4.4) (Table 1). These sounds

Table 1. *Acoustic parameters of underwater tail slaps recorded from Norwegian killer whales*

	Tail slap		Analysed pulses					
	N	τ_{total} (ms)	*N*	–3 dB BW (kHz)	E_{97BW} (kHz)	f_0 (kHz)	ASL (dB)	Energy (dB)
Norway, full BW	4	318±99	13	36.8±22.5	130.5±17.5	46.1±22.3	186±5.4	169±3.3
Norway, filtered	4	318±99	13	–	18.9±1.0	8.7±3.3	–	–
Iceland	10	226±54	19	–	17.6±2.4	7.9±4.4	–	–

Values are means ±S.D.

Acoustic parameters of underwater tail slaps recorded from Norwegian killer whales [bandwidth (BW): 150 kHz] (Norway, full BW), the same sounds filtered with a 20 kHz low pass filter (Norway, filtered) and multi-pulsed sounds recorded from Icelandic killer whales (Iceland, BW: 20 kHz). τ_{total} is the duration of the whole tail slap. E_{97BW} is the 97% energy bandwidth, defined as the frequency bandwidth giving 97% of the total energy. The centre frequency (f_0) divides the E_{97BW} in two halves with equal energy in each. The –3 dB BW was measured for single pulses of tail slaps recorded from Norwegian killer whales (BW: 150 kHz). ASL, apparent source level in dB (pp) re. 1 μPa at 1 m. Energy content in dB re. 1 $\mu Pa^2 s$ at 1 m. For further explanations see text.

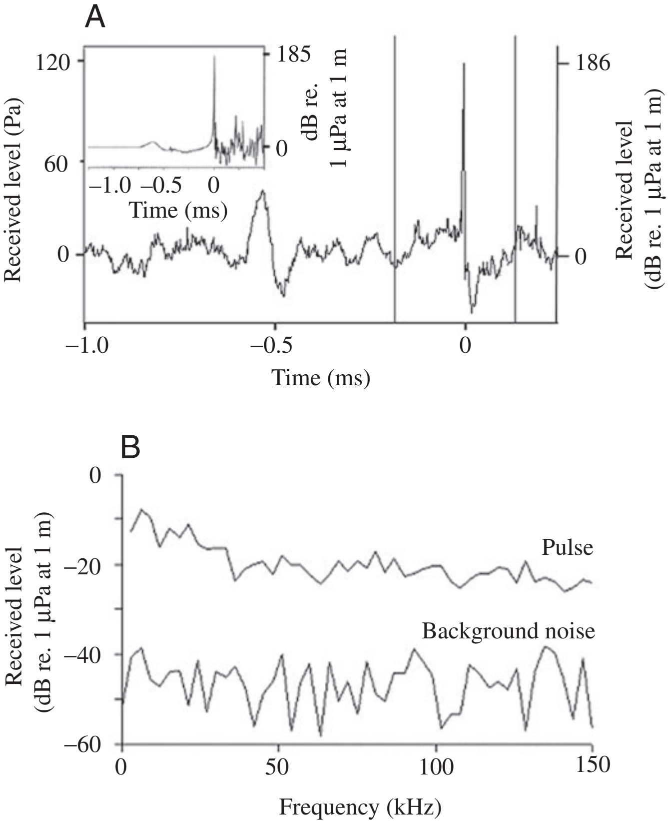

Fig. 4. (A) Single pulse from a burst of pulses made during an underwater tail slap recorded from killer whales in Norway. The main-pulse is from the tail slap shown in Fig. 2 (arrow). The vertical lines limit the area over which the frequency spectrum in Fig. 4B is calculated. The *y*-axes denote the received level in Pascal and dB re. 1 µPa at 1 m. The small figure in the top left corner is the waveform of a pulse produced by snapping shrimp, the *y*-axis denotes dB re. 1 µPa at 1 m (modified after Versluis et al., 2000). (B) Frequency spectrum of the pulse shown in Fig. 4A. The lower line is the background noise sampled before the beginning of the tail slap. Both spectra were calculated with a rectangular window, FFT 128 pts). Noise and signal were measured with exactly the same amplification and filtering, and without any range-dependent compensation.

were produced in 100% of the recording sessions (N=22 10 min recordings of foraging killer whales). Herring was the only observed prey species. During the recordings we picked up nine debilitated fish from the surface by hand. These fish wriggled when touched and swam off when released.

Comparison between sounds of Icelandic and Norwegian killer whales

Table 1 shows the parameters measured from multiple bursts of pulses recorded in Iceland and filtered sounds of underwater tail slaps recorded in Norway for comparison. There was no significant difference between either the 97% energy bandwidths ($E_{97\mathrm{BW}}$) or the centre frequencies (f_0) of signals recorded from Icelandic and Norwegian killer whales (non-parametric two-way ANOVA, $E_{97\mathrm{BW}}$: H=2.60, d.f.=1, P=0.11. f_0: H=1.24, d.f.=1, P=0.27; Barnard et al., 2001).

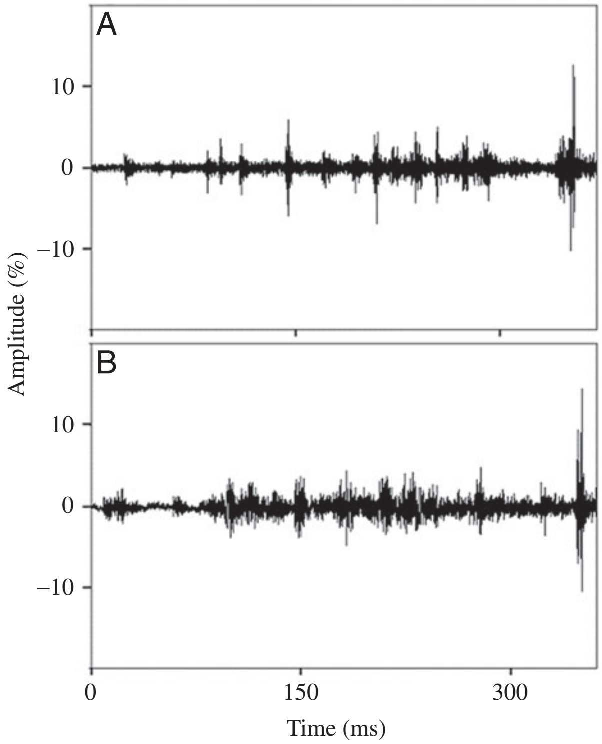

Fig. 5. Example of multi-pulsed sounds recorded from killer whales in Norwegian (A) and Icelandic (B) waters illustrating the similarity between the two sounds. The sounds recorded from Norwegian killer whales (recorded with a bandwidth of 150 kHz) were filtered with a low-pass filter at 20 kHz to make them comparable to the recordings from Icelandic killer whales (which were recorded with a bandwidth of 20 kHz).

Discussion

Do killer whale tail slaps generate cavitation?

Some of the single pulses found in the sounds of killer whale underwater tail slaps had waveforms and spectral characteristics very similar to those obtained from the sound pulses of snapping shrimp, which are produced by cavitations (Fig. 4A, inset from Versluis et al., 2000). Snapping shrimp produce broadband sounds containing frequencies beyond 200 kHz and with a peak frequency in the range of 2–5 kHz (Au and Banks, 1998). The high-speed recordings of killer whale tail slaps revealed that parts of the sound contained frequencies beyond 150 kHz, with peak frequencies below 10 kHz (Fig. 4B). Average source level measurements of cavitation made by snapping shrimps were between 183–191 dB (pp) re. 1 µPa at 1 m (Au and Banks, 1998). The fact that the average source levels measured from single pulses in underwater tail slaps presented here [186 dB (pp) re. 1 µPa at 1 m] were within this range further suggests a similarity between the sound production mechanism of killer whale tail slaps, snapping shrimp and a cavitating propeller.

An acoustic signal generated by cavitation consists of two pulses. There is a low frequency pulse, the precursor, created as air bubbles are formed due to the drastic reduction in pressure from ambient. The precursor is followed by a very broadband transient, the main-pulse, caused by the collapse of the air bubble when the pressure returns to ambient (Young, 1989). We did not observe any clear precursors in our recordings. However, precursors have low intensity (Versluis et al., 2000) and they may have been masked by background noise in the pulse burst. The similarities between the acoustic characteristics of cavitation sounds and the sounds produced by underwater tail slaps strongly suggest that underwater tail slaps cause cavitation.

The incipient cavitation number (relationship between temperature, density, velocity, vapour pressure and pressure) defines the onset of cavitation. Under controlled laboratory conditions, the incipient cavitation number is reached when the pressure decreases under the saturated vapour pressure (Brennen, 1995). High concentrations of bubbles and particles, as well as turbulence in the water, increase the incipient cavitation number, which means that cavitation occurs before the pressure reduces to the saturated vapour pressure (Brennen, 1995). Furthermore, cavitation is more likely to occur at a shallow depth with lower ambient pressure because the pressure gradient needed to produce cavitation is lower (Medwin and Clay, 1998; Ross, 1976). The video recordings revealed that the water in which the killer whales were feeding on herring had high concentrations of air bubbles and particles, as well as turbulence created by the movement of the fish and the whales. Such an environment facilitates cavitation. In addition, the video analyses showed that a substantial number of tail slaps were recorded within the upper 5 m of the water column where cavitation is more likely to occur (Medwin and Clay, 1998). If the incipient cavitation number (Brennen, 1995) could be determined for the waters where killer whales were performing tail slaps, calculations might confirm that cavitation is a plausible sound producing mechanism for tail accelerations measured during underwater tail slaps (maximum 48 ms^{-2} as measured by Domenici et al., 2000a). Our study shows that several characteristics of some of the tail slap sound components resemble cavitation-generated signals.

While cavitation could explain some of the pulses observed in the sound produced during tail slaps, it may not explain all of them. Some pulses are likely to be sound resulting from physical contact between the whale tail and the herring, as discerned from the video sequences showing physically damaged fish and as previously suggested by Similä and Ugarte (1993) and Domenici et al. (2000a). It seems unlikely that contact sounds could produce the very high frequencies in pulses observed in the tail slaps. Recordings of physical impact sounds on herring by an artificial killer whale tail fluke might confirm this.

Debilitation of herring

A photograph published by Sigurjónsson et al. (1988) shows a school of herring that was herded to the water surface by a group of Icelandic killer whales. This photograph suggests that killer whales in Icelandic waters use hunting techniques similar to those used by killer whales in Norwegian waters (Similä and Ugarte, 1993). The acoustic similarities between the signals produced by Icelandic killer whales and those of underwater tail slaps recorded from Norwegian killer whales (Fig. 5 and Table 1) indicate that Icelandic killer whales use underwater tail slaps. In addition, the observations of debilitated herring on the surface above foraging Icelandic killer whales resemble the debilitated herring observed in the video recordings of Norwegian killer whales. We conclude that Icelandic killer whales most likely use underwater tail slaps to debilitate prey, as do Norwegian killer whales.

Herring have a sensitive hearing system with a direct connection between the ear, the lateral line system (acoustico-lateralis) and the swim bladder (Coombs and Braun, 2003). This is probably the reason for their high sensitivity to sound, both in terms of sound pressure and particle displacement (Enger, 1967). Only a few herring are debilitated after each tail slap, and only in the immediate vicinity of the killer whale tail fluke. The sound pressure levels measured in this study were probably not intense enough to cause debilitation of fish. The fact that only fish in the immediate vicinity of the tail were debilitated further suggests that the sound pressure alone is not intense enough to debilitate the herring. Apart from sound pressure, the herring in the immediate vicinity of the tail would be exposed to a number of other factors, which may seriously affect its sensory system and cause debilitation. These factors include: steep pressure gradients, high levels of water acceleration and particle movements and physical contact with the tail or other fish.

To our knowledge, most underwater tail slaps have been reported from predators feeding on schooling herring, exemplified by sharks feeding on clupeids, Norwegian and Icelandic killer whales feeding on Atlantic herring, and Pacific bottlenose dolphins feeding on Perth herring, *Nematolosa vlaminghi* (Muus et al., 1988; Smolker and Richards, 1988; Similä and Ugarte, 1993; present study). In addition to direct contact between the fluke and the fish, the acoustic pressure changes and particle movements in close vicinity of underwater tail slaps could contribute to the effectiveness of this hunting strategy for schooling prey with good hearing and sensitivity to hydrodynamic flow, such as clupeid fish. Sensory overloading and loss of buoyancy control may explain the occurrence of herring floating on their sides on the surface and quiescent in the water following underwater tail slaps, and why some of these debilitated fish regained their swimming abilities.

The analysis of the acoustic signals from killer whale underwater tail slaps revealed insights both into the sound production mechanism and the function of the tail slaps in prey capture. More studies on the acoustic biology of killer whales and herring are needed to reveal further insights into the intricate predator–prey interactions between these species. Such studies should include play back trials on tail slap sounds and hydrodynamic action upon herring schools, as well as more detailed acoustic and video recordings of tail slapping killer whales.

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