Source levels and harmonic content of whistles in white-beaked dolphins (*Lagenorhynchus albirostris*)

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Recordings of white-beaked dolphin whistles were made in Faxaflói Bay (Iceland) using a three-hydrophone towed linear array. Signals from the hydrophones were routed through an amplifier to a lunch box computer on board the boat and digitized using a sample rate of 125 kHz per channel. Using this method more than 5000 whistles were recorded. All recordings were made in sea states 0–1 (Beaufort scale). Dolphins were located in a 2D horizontal plane by using the difference of arrival time to the three hydrophones, and source levels were estimated from these positions using two different methods (I and II). Forty-three whistles gave a reliable location for the vocalizing dolphin when using method II and of these 12 when using method I. Source level estimates on the center hydrophone were higher using method I [average source level 148 (rms) ± 12 dB, $n=36$] than for method II [average source level 139 (rms) ± 12 dB, $n=36$]. Using these rms values the maximum possible communication range for whistling dolphins given the local ambient noise conditions was then estimated. The maximum range was 10.5 km for a dolphin whistle with the highest source level (167 dB) and about 140 m for a whistle with the lowest source level (118 dB). Only two of the 43 whistles contained an unequal number of harmonics recorded at the three hydrophones judging from the spectrograms. Such signals could be used to calculate the directionality of whistles, but more recordings are necessary to describe the directionality of white-beaked dolphin whistles. © *2006 Acoustical Society of America.* [DOI: 10.1121/1.2202865]

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I. INTRODUCTION

Dolphins are known to produce whistles for communication (e.g., Dreher and Evans, 1964; Lilly, 1963). In order to investigate the possible range over which dolphins can communicate using whistles, an on-axis source level must be calculated. This has been done for bottlenose dolphin (*Tursiops truncatus*) whistles (Janik, 2000) and Hawaiian spinner dolphin (*Stenella longirostris*) whistles (Lammers and Au, 2003). To determine source levels of whistles we need to know the position, distance, and orientation to an animal. The former can be estimated from the time of arrival differences (TOADs) of the signal at each receiver in an array using cross correlation and hyperbolic calculations (e.g., Spiesberger and Fristrup, 1990). The sound level at 1 m from the source is called source level (SL) and a minimum of three receivers are needed to calculate the distance to the source in 2D (two dimensions) (e.g., Wahlberg *et al.*, 2001). Calculated source levels of dolphin whistles vary between 109 and 180 dB *re*. 1 μPa (Table 7.2 in Richardson *et al.*, 1995). Source levels of whistles from the Hawaiian spinner dolphin varied from 149.7 (rms) ± 3.2 dB *re*. 1 μPa to 156.0 (rms) ± 4 dB *re*. 1 μPa (Lammers and Au, 2003). The mean source level was 158 ± 0.6 dB *re*. 1 μPa for bottlenose dolphin *(Tursiops truncatus)* whistles and the maximum source level was 169 dB (rms) *re*. 1 μPa (Janik, 2000).

Previously, it was reported that dolphin whistles were limited to an upper frequency of 20 kHz (e.g., Popper, 1980) but recently, using broad band equipment, it has been shown that spectrograms of dolphin whistles can extend beyond 20 kHz (e.g., Rasmussen and Miller, 2002; 2004; Lammers *et al.* 2003). The lowest frequency is called the fundamental frequency, and each higher-integer multiple of the fundamental frequency is a harmonic (Yost, 2000). Rasmussen and Miller (2002, 2004) reported white-beaked dolphin whistles with fundamental frequencies up to 35 kHz. Lammers *et al.* (2003) described whistles of Hawaiian spinner dolphins and Atlantic spotted dolphins (*Stenella frontalis*) and reported a mean frequency of the fourth harmonic at 69.0 kHz for spinner dolphins and 54.5 kHz for spotted dolphins. Some of the whistles had the maximum frequency of the fundamental above 20 kHz (Lammers *et al.*, 2003).

The whistles of spinner dolphin's are directional. Lammers and Au (2003) suggest that the high frequency part of the dolphin whistles and the different number of harmonic components can be used by the dolphins as cues for directionality. Miller (2002) also found killer whales' communication calls to be directional. The directionality has been suggested to be a cue used by the animals to position themselves in the group and useful for keeping group cohesion (Lammers and Au, 2003; Miller, 2002).

White-beaked dolphins are found within a few nautical miles from shore from June to August in Faxaflói Bay, Iceland. These dolphins probably live in a fission-fusion community like that described for bottlenose dolphins (e.g., Smolker *et al.*, 1993; Tyack 1997) and for Hawaiian spinner dolphins (Norris *et al.*, 1994). Brownlee and Norris (1994) suggested the whistles of the Hawaiian spinner dolphins are used as an indicator of activity state, for example the occurrence of many whistles indicates a high activity state. This is most likely the same for white-beaked dolphins. Usually white-beaked dolphins travel in small groups of three to six dolphins (Rasmussen, 1999) that are often widely separated in the bay. However, they can quickly gather into larger groups. How do the dolphins coordinate these gatherings? A good explanation would be that they use their whistles for this purpose.

Directional properties of whistles (and of the receiver) along with *a priori* knowledge of typical source levels are important cues for animals to determine the positions of neighbors. Directional properties of whistles are more difficult to determine than source levels. The aims of this study were to calculate source levels, communication range, and directionality of white-beaked dolphin whistles in coastal Icelandic waters.

II. METHODS

The recordings were made in August 2002 in Faxaflói Bay (Iceland) about 6 miles NNW of Keflavik (64°00.49′N,22°33.37′W). The water depths were between 30 and 50 m in the area of recordings. The ambient noise level was measured from a small boat with the engine turned off and in sea-states 0–1 (Beaufort Scale) using a Reson 4032 hydrophone connected via an amplifier to a lunchbox computer sampling at 800 kHz; except for the hydrophone this setup was the same as that described in Rasmussen *et al.* (2004). Recordings of whistles were made using the same towed linear hydrophone array as that described by Lammers and Au (2003) and consisted of three custom-built hydrophones (A, B, C) spaced 11.5 m apart and separated from the boat by 25 m (see Fig. 1 and Lammers and Au, 2003). The array was towed behind the boat at speeds of 6–7 knots and a custom made "tow-fish" was used to sink the array to a depth of approximately 2 m while a "tattletale" assured the array was stable under water. Hydrophones A and C had a sensitivity of −200 dB *re*. 1 V root mean square (rms) per μPa, and hydrophone B had a sensitivity of −197 dB *re*. 1 V rms per μPa.

The hydrophones had flat frequency responses (±3 dB) up to 150 kHz. The calibration of the hydrophone array was described in Lammers and Au (2003). The hydrophones were connected to a custom built amplifier using a 300-Hz high-pass filter and to a lunchbox computer on board the boat. The sample rate was 125 kHz per channel giving a Nyquist frequency of 62.5 kHz. We did not use antialiasing filters. Had aliasing occurred the result would have appeared as mirror-imaged frequency sweeps of the fundamental in the spectrogram. We saw none of this. For aliased frequency components in echolocation clicks to influence the amplitude of the cross-correlation function (see below), the clicks must be emitted simultaneously with the whistle. We did not test for this.

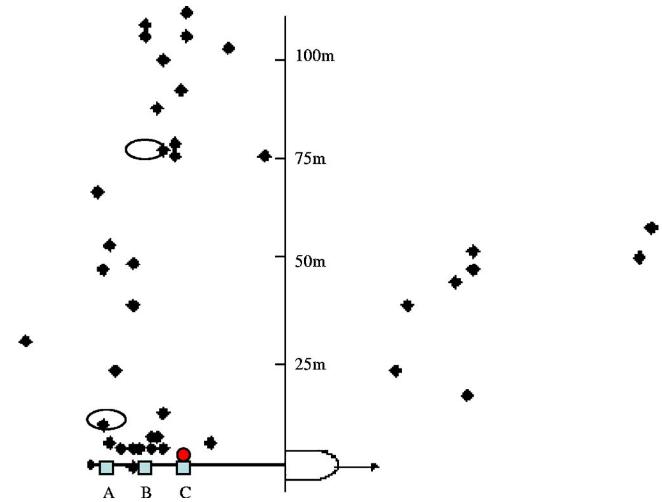

FIG. 1. (Color online) Placement of the 43 whistles (diamonds) relative to the boat and the hydrophone array (squares: A, B, C) when using method II. Note that it is only possible to calculate the position of the dolphins in two dimensions when using three hydrophones. The abscissa has the same dimensions as the ordinate and all positions on the starboard side of the boat are mirrored on the port side. The small circle close to hydrophone C indicates an orange buoy 25 m behind the boat. The circles around two diamonds (two dolphins) corresponds to two whistles with unequal number of harmonics recorded on the three hydrophones [see Fig. 2(a)].

An orange buoy towed 25 m behind the boat marked the location of hydrophone C and was used as a reference point by observers for estimating the distance and bearing of surfacing dolphins relative to the hydrophones. We tried to get the dolphins parallel to the boat during the recordings because this afforded the greatest opportunity for determining both source levels and directionality. Group size estimates were also noted during recordings.

Sound files were opened in Cool Edit Pro (version 2, Syntrillium Software) and band-pass filtered to dampen unwanted tones at 17.33, 37.59, 48.7 kHz on all three channels. Recordings were then scanned to identify times without overlapping whistle contours from different individuals and also for harmonic content. Nonoverlapping whistle contours were preferably used as these represented the best opportunity for localizing an individual and determining the source levels.

We used two different methods for localizing the underwater positions of vocalizing dolphins. Method II was introduced because a low signal-to-noise ratio, particularly on channel A, made cross correlation difficult using method I. Two of the recording channels had a low-power electrical interference signal that was highly correlated. This had the effect that signals were almost always—presumably falsely—localized on a line normal to and equidistant between the two hydrophones. In a correlation analysis of long signals, correlated noise is problematic without making individual judgments from call to call. To avoid this we chose to

TABLE I. Average source level estimates recorded on the three hydrophones (A, B, C), minimum and maximum source level, and minimum and maximum distance of recordings. The estimates are shown both for method I and method II.

Method	Hydrophones	Average SL (rms) ±SD	Min. SL (rms)– Max. SL (rms)	Min. distance– Max distance
	A	148 dB *re*. 1 μPa±12	124–160 dB *re*. 1 μPa	6–182 m
Method I	B	144 dB *re*. 1 μPa±12	124–159 dB *re*. 1 μPa	6–180 m
(N=12)	C	152 dB *re*. 1 μPa±10	136–166 dB *re*. 1 μPa	13–180 m
	A	139 dB *re*. 1 μPa±11	120–153 dB *re*. 1 μPa	7–176 m
Method II	B	139 dB *re*. 1 μPa±10	121–152 dB *re*. 1 μPa	7–175 m
(N=12)	C	140 dB *re*. 1 μPa±10	125–156 dB *re*. 1 μPa	13–174 m
	A	144 dB *re*. 1 μPa±8	126–163 dB *re*. 1 μPa	5–176 m
Method II	B	142 dB *re*. 1 μPa±8	118–163 dB *re*. 1 μPa	7–175 m
(N=43)	C	146 dB *re*. 1 μPa±8	129–167 dB *re*. 1 μPa	13–174 m

analyze only those signals with enough power to be correctly localized. This criterion excludes signals that would have been correctly localized on the equidistant line between the two affected hydrophones.

Method I: This method is described in Lammers and Au (2003) and uses cross-correlation functions to calculate the differences in arrival times of a signal at each of the three hydrophones in the array. Localization was implemented in Matlab (version 6.0, The MathWorks, Inc.) using a custom written script. To determine the sound level, the program steps through the selected whistle in 100-ms steps (12 500 samples). Within each step the voltage values are squared, summed, and divided by the step size (12 500 samples) to get the mean. The square root is then taken of the mean to get the rms value for that step (volts rms). The process is repeated through the selected whistle. Next, the sound pressure level (SPL) is calculated using the following equation: SPL (*re*. 1 μPa)= hydrophone output (dB at 1 V rms)−gain (dB)+20 log (signal (volts rms)/(1 V rms)). Finally, the SL is calculated by taking the transmission and absorption losses (alpha) into account, which are a function of the distance using $\mathrm{SL} = \mathrm{SPL} + 20\log(\mathrm{distance}) + (\mathrm{alpha}(\alpha) \times \mathrm{distance}/1000)$. The absorption coefficient (α) can be expressed as $\alpha=0.036 f^{1.5}$ (dB/km) (after Richardson *et al.*, 1995).

Method II: Cross-correlation functions were used to calculate the difference in arrival time of a signal at each of the three hydrophones in the array (as described in method I). The difference of arrival time between channel A and B and the difference between B and C were shown as cross-correlation functions in Matlab. We added another cross-correlation function, the time difference between A and C as a control (Δt_{AC}). This time difference had to equal the sum of the time difference between A and B (Δt_{AB}), and B and C (Δt_{BC}), i.e.,

$$\Delta t_{AC} = \sum \Delta t_{AB} + \Delta t_{BC}.$$

If this was not the case, the whistle was not used since the calculated position would not be reliable. Often we had to choose the second highest peak in the cross-correlation function to get a reliable position of the dolphin and not the highest peak because noise gave the highest peak. (The noise contribution often resulted in a high peak at 0 in the cross-correlation function.)

Method II is similar to the method described by Spiesberger (1998) using the amplitudes of the peaks in the cross-correlation functions to estimate source levels. Spiesberger (1998) solved the equations in general for n transducers, however we used the method with three hydrophones ($n=3$). The principle is described for three transducers in the Appendix. This is a method to minimize the contribution of the noise when calculating source levels.

Finally the locations calculated using methods I and II were compared with the locations of dolphin groups noted during visual observations in the field. If the locations were comparable, whistles were used, if not they were discarded.

III. RESULTS

Whistles from white-beaked dolphins were recorded during the evenings of 19 and 21 August 2002. More than 5000 whistles were recorded in about 6 h (from 17:12 to 20:41 on 19 August and from 18:13 to 20:39 on 21 August). In both cases whistles were not detected during the first half hour of recording, then occasional whistles were heard, and finally continuous whistling was recorded. In each case when recordings were linked to visual observations, group size varied over time (min. 3 and max. 15 animals), with a tendency for group size to increase during the recording and decrease at the end of recordings.

A. Source levels of whistles

The selection criteria outlined in Sec. II allowed for 43 whistles to be reliably found using method II and of these 12 whistles were found using method I (Fig. 1). These calculated positions matched visual observations. This gave a total of 129 source levels estimations from the recordings when using method II and 36 source level estimates when using method I. Source levels ranged from 118 to 167 dB (rms) *re*. 1 μPa (Table I). Source levels were higher when using method I than when using method II and the difference was significant [$N=12$, one way ANOVA, $F=12.3$, $p<0.05$, (Zar, 1996) see Table I]. This can be explained by the fact

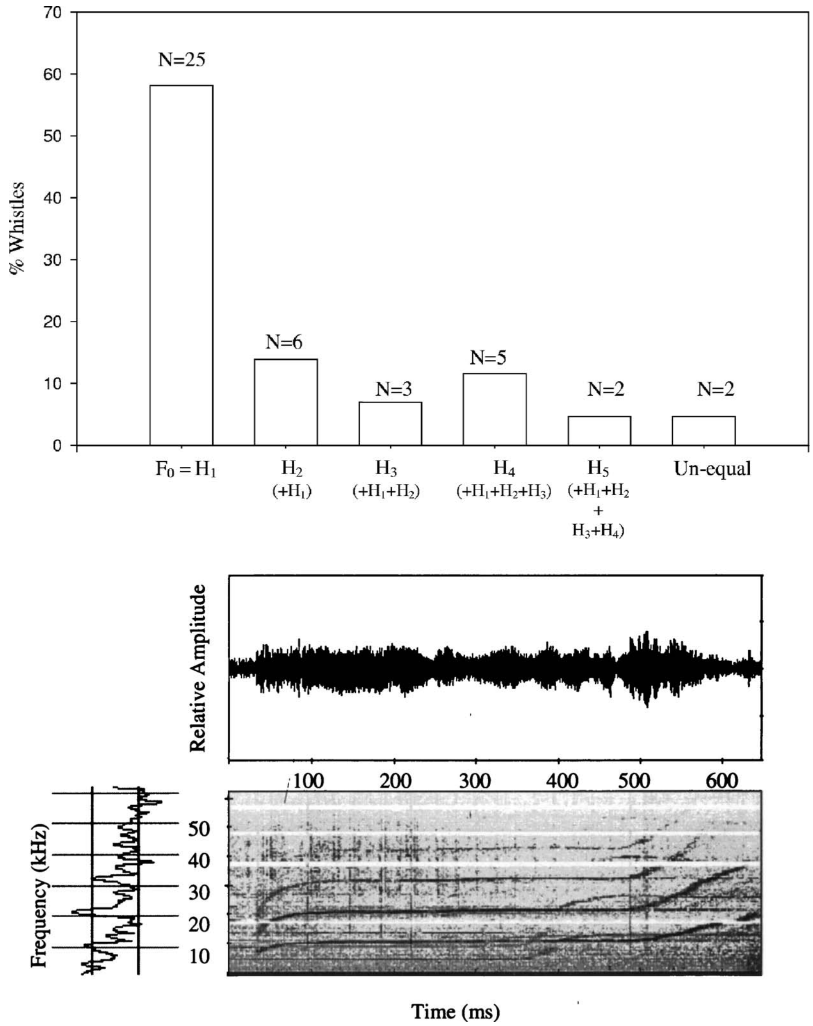

FIG. 2. (a) The percentages of whistles containing the fundamental and higher harmonic components judged from visual inspection in spectrograms recorded on the three hydrophones ($F_0=H_1$ whistles containing only the fundamental or the first harmonic, H_1+H_2=whistles containing the first and second harmonic, $H_1+H_2+H_3$ =whistles containing the first, second, and third harmonic, $H_1+H_2+H_3+H_4$=whistles containing the first, second, third, and fourth harmonic, $H_1+H_2+H_3+H_4+H_5$=whistles containing the first, second, third, fourth, and fifth harmonic). Note that only two whistles (5%) contained unequal harmonic components recorded on the three hydrophones. One of the two whistles had three harmonics on hydrophones A and B, but only two harmonics on hydrophone C. The other had five harmonics on hydrophone B and four harmonics on hydrophones A and C (see Figs. 1 and 4). (b) Example of a whistle containing four harmonics ($H_1+H_2+H_3+H_4$ =whistle containing the first, second, third, and fourth harmonics). The whistle is shown as the time signal (above), the spectrogram (below), and the power spectrum (to the left). The spectrum is an average power spectrum using the whole time signal. Note the frequency content extends to frequencies above 50 kHz.

that source levels estimated using method I include ambient noise, whereas when using method II we were using the amplitude of the peak in the cross correlation and the noise is reduced in the source level estimates (see the Appendix). A significant difference was found both between the methods [mixed model, $F=101.62$, $p<0.05$, (Hand, 1997)] and the hydrophones [mixed model, $F=10.2$, $p<0.05$ (Hand, 1997)] and also an interaction between the methods and hydrophones [mixed model, $F=4.5$, $p<0.05$ (Hand, 1997)]. This indicates that the differences in source levels recorded on the three hydrophones are not the same when using the two different methods. The noise levels are reduced when using method II resulting in less variation of source levels at the three hydrophones when compared to method I.

B. Harmonic content

The percentages and numbers of the 43 whistles with and without harmonics, judged from visual inspection of spectrograms in Cool Edit, are shown in Fig. 2(a). Fifty-eight percent of the whistles contained only the first harmonic or the fundamental frequency and the rest (42%) had higher harmonic components. Only 5% (or two whistles) had unequal numbers of harmonics recorded on the three hydrophones. Figure 2(b) shows an example of a whistle with four harmonics containing frequencies to at least 50 kHz.

The number of harmonics plotted against average source level (±SD) and the maximum source levels on the three channels (A, B, C) along with distances are shown in Figs. 3(a)–3(c) of whistles when using method II. No relationship was found between source level and the number of harmonics, suggesting that energy in the fundamental dominates. The number of harmonics recorded decreased with increasing distance (linear regression, $r^2=0.84$, one way ANOVA, $p<0.005$; for hydrophone A; $r^2=0.94$, one way ANOVA, $p<0.005$, for hydrophone B; $r^2=0.95$, one way ANOVA, $p<0.05$ for hydrophone C). Whistles with five harmonics were only recorded when the dolphins were close to the array. The maximum distance to an animal was 31 m when five harmonics were recorded and 176 m when the fundamental (first harmonic) was recorded on all three hydrophones (Fig. 3).

The fundamental frequency of all the whistles with harmonic components varied between 7 and 13 kHz (average =10.7 kHz, SD=1.5 kHz). Most whistles were upsweeps and had a fundamental frequency of about 10 kHz (61%), giving the second harmonics at 20 kHz, the third at 30 kHz, the fourth at 40 kHz, and the fifth at 50 kHz. We therefore used a simulated third octave filter (made in Cool Edit) using a center frequency close to these frequencies and bandwidth as described in the Brüel and Kjær handbook (1985) in hopes

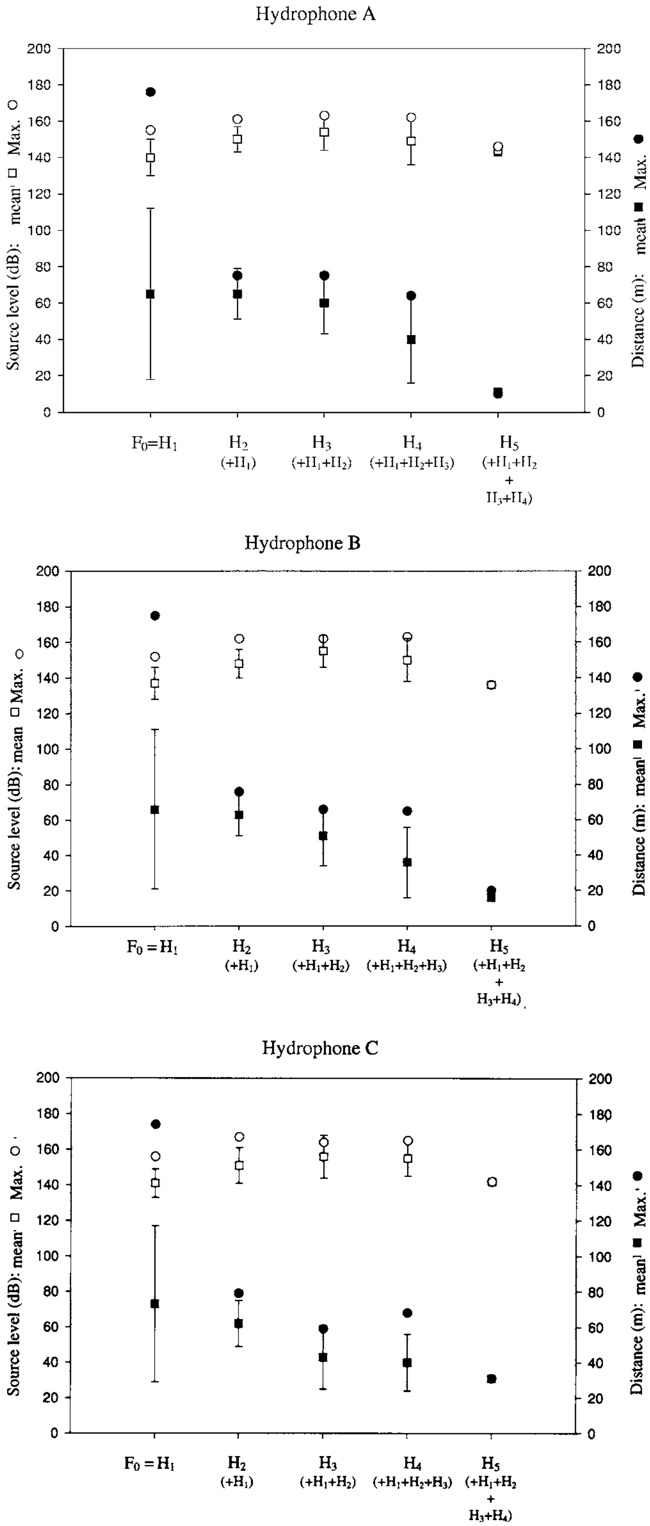

FIG. 3. Distribution of the whistles containing a different number of harmonics plotted with the average source level (±SD) (white squares) and the maximum source level (white circles) using method II. In addition the average distance (±SD) (black squares) and the maximum distance (black circles) are included in (a) hydrophone A, (b) hydrophone B, and (c) hydrophone C. See Fig. 2 for the number of signals in each category. Note the lack of a trend between source level and distance, and that the number of harmonics is inversely proportional with distance.

of detecting directionality effects, especially at higher frequencies. No trend was found. The signal-to-noise ratio (S/N) varied within a whistle when looking at the different third octave bands (Table II), but a large variation was also found between the different channels. However, in general the signal-to-noise ratio decreased with the increasing number of harmonics, with good S/N for whistles containing only the fundamental frequency and poor S/N for the fourth harmonic in whistles with multiple harmonics.

IV. DISCUSSION

Signal intensity and directionality are important acoustic communication parameters. Despite recording about 5000 whistles, only a few (43) satisfied our criteria for determining source levels. The source levels of white-beaked dolphin whistles [118–167 dB *re*. 1 μPa (rms)] are similar to those found for other dolphin species (e.g., Janik, 2000; Lammers and Au, 2003), independent of the methods we used for the calculations. The most difficult aspect in estimating the source levels of dolphin whistles is obtaining reliable positions of individuals. Freitag and Tyack (1993) discuss this problem with respect to multiple reflections both from the surface and from the bottom as well as the problem of poor signal-to-noise ratio. Dolphins must deal with the same problems, but it may not be as important for them to know the exact position of another whistling dolphin or of a vocally active distant group, reducing the need for high signal-to-noise ratios. However, whistles may be used to identify individuals, so-called "signature whistles" (Caldwell *et al.*, 1990). "Signature whistles" have been suggested to be cohesion calls as to keep contact between dispersed group members (Janik and Slater, 1998) and they may be important for maintaining contact between a mother and a calf (Smolker *et al.*, 1993). In this case it must be important for the mother and/or the calf to locate the other precisely from the whistles, especially in murky waters and at night. The dolphins use multi-harmonic whistles and since directionality of the emitted signal and of the auditory receiver increases with increasing frequency, higher harmonics could be used by a dolphin for positioning a caller (Au, 1993; Lammers and Au, 2003). Determining directionality from harmonics of the 43 signals was not possible with our recording methods. But it should be trivial for a dolphin to determine the direction and distance to a whistling conspecific. They are continuously moving and whistling when acoustically active and they can presumably identify the signals of other group members and perhaps those of individuals in other groups. With this and their directional hearing, as well as directionality of the signal, an animal should have sufficient information for localization. Our monitoring methods do not offer these advantages.

The extensive recordings of whistles from white-beaked dolphins using broad band recording equipment presented here reveal whistles rich in harmonics that were not reported earlier (Rasmussen and Miller, 2002, 2004). As mentioned above, harmonics could be used to determine direction to a source, at least at closer rangers. Figure 4 shows the position of a dolphin estimated from two whistles. These two whistles were recorded with an interval of about 10s and could be produced by the same animal. One whistle had five harmonics on all three hydrophones and the other had five harmonics on hydrophone B, the middle hydrophone, and four har-

TABLE II. Third octave analyses of three whistles including the fundamental, second, third, and fourth harmonics. The distance from each hydrophone to the dolphin is included in the table. The whistles were filtered using a third octave filter constructed in Cool Edit centered at 10, 20, 31.5, and 40 kHz. The rms value in dB of the filtered portion of the signal at each hydrophone relative to the unfiltered whistle and the noise in each third octave band relative to the full band width noise were measured in Cool Edit. In addition the signal-to-noise ratio (S/N) is noted in each third octave band. Note poor S/N at higher frequencies; this cannot be explained by loss due to absorption at higher frequencies, but rather by less energy in higher frequencies, more noise, and maybe some directionality. Note the poorer S/N for the higher harmonics, a factor that makes it difficult to determine whistle directionality.

Whistle no. (and duration)	Hydro-phones	Distance (m)	10 kHz Signal (rms) (dB)	10 kHz Noise (rms) (dB)	10 kHz S/N (dB)	20 kHz Signal (rms) (dB)	20 kHz Noise (rms) (dB)	20 kHz S/N (dB)	31.5 kHz Signal (rms) (db)	31.5 kHz Noise (rms) (dB)	31.5 kHz S/N (dB)	40 kHz Signal (rms) (dB)	40 kHz Noise (rms) (dB)	40 kHz S/N (dB)
1 (600 ms)	A	22	−35	−50	15	−45	−50	5	−44	−51	7	−44	−51	7
1	B	32	−37	−56	19	−52	−60	8	−50	−60	10	−50	−60	10
1	C	43	−34	−56	22	−43	−49	6	−39	−49	10	−41	−51	10
2 (1 s)	A	11	−28	−49	21	−27	−42	15	−32	−35	3	−34	−35	1
2	B	20	−33	−54	21	−32	−52	20	−38	−48	10	−42	−45	3
2	C	31	−36	−48	12	−39	−50	11	−44	−51	7	−46	−49	3
3 (500 ms)	A	54	−26	−52	26	−32	−53	21	−46	−55	9	−51	−52	1
3	B	46	−28	−56	28	−34	−59	25	−49	−63	14	−58	−61	3
3	C	40	−28	−53	25	−31	−57	26	−47	−59	12	−53	−57	4

monics on hydrophones A and C. Unfortunately it was not possible to estimate the beam pattern of the whistle owing to few usable signals recorded with this type of array. Increasing the number of hydrophones in the array would decrease range error (e.g., Spiesberger and Fristrup, 1990; Wahlberg *et al.*, 2001) and provide more data for determining the beam pattern of white-beaked dolphin whistles.

Sound production in odontocetes has been evaluated with a piston model (e.g., Au, 1993). Lammers and Au (2003) described a theoretical beam pattern of bottlenose dolphin whistles using a 4-cm piston radius. The beam pattern of white-beaked dolphin clicks is narrower than that of bottlenose dolphin clicks (Rasmussen *et al.*, 2004). A piston radius of 6 cm gave the best fit for white-beaked dolphin clicks so we used 6 cm to model the beam pattern for whistles. At 30 kHz the 10-dB beam is 40°, at 40 kHz it is 30°, and at 50 kHz we get 20°. These frequencies correspond closely to those in the third, fourth, and fifth harmonics of

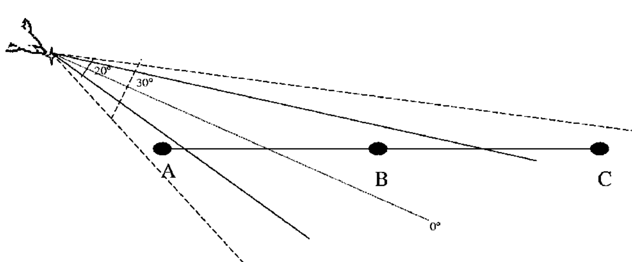

FIG. 4. Two whistles recorded at 10-s intervals giving the same position; one whistle contained unequal harmonics and the other equal harmonics. The former had five harmonics on hydrophone B and four on hydrophones A and C. The latter had five harmonics on all three hydrophones. The calculated distances to the dolphin were 11, 20, and 31 m from hydrophones A, B, and C, respectively (see Fig. 1). The two whistles could have come from the same dolphin or two different dolphins. We used a radius of 6 cm in the piston model to calculate the directionality of white-beaked dolphin whistles. The calculated beam width for the fifth harmonic is 20° and for the fourth harmonic is 30°. See text for further explanation.

white-beaked dolphin whistles. Figure 4 illustrates the beam pattern of two consecutive whistles separated by a 10-s interval. Assuming the whistles came from the same animal, it is possible for a dolphin at a distance of 11 m from hydrophone A to ensonify all hydrophones with five harmonics (dashed lines, 30°), but with another whistle, and by changing the beam width, to only ensonify hydrophone B with five harmonics (solid lines, 20°) and hydrophones A and C with four harmonics of its beam. The bottlenose dolphin shows considerable control over its echolocation beam width (Dankiewicz *et al.*, 2005).

Contact ranges are also important factors in communication. These can be calculated by using signals with highest (167 dB) and lowest (118 dB) source levels and some assumptions. If we assume white-beaked dolphins have similar hearing sensitivity as bottlenose dolphins (Au, 1993), then at 10 kHz the detection threshold (DT) should be 65 dB *re*. 1 μPa. The ambient noise level (NL) in Faxaflói Bay (sea state 0–1) measured using a $\frac{1}{3}$-oct filter centered at 10 kHz (Spectra Plus, Sound Technology Inc.) was about 75 dB *re*.1 μPa (Fig. 5). In this case the hearing of the dolphins is limited by the ambient noise level. When using a source level of 167 dB (SL), the maximum transmission loss before the sound becomes inaudible will be 167 dB(SL) −75 dB (NL)=92 dB. At 10 kHz the loss due to absorption is 1.1 dB/km and the transmission loss of 92 dB corresponds approximately to a range of 10.5 km. When using a minimum source level of 118 dB, the transmission loss equals 43 dB, giving a communication range of up to about 140 m.

Assuming that our distance determinations using acoustic and visual methods are reasonable, how can we account for the large variation in source level? We found the source level of white-beaked dolphin whistles to vary between 118 and 167 dB (n=129) using method II and between 124 and 166 dB (n=36) using method I (see Table I), resulting in

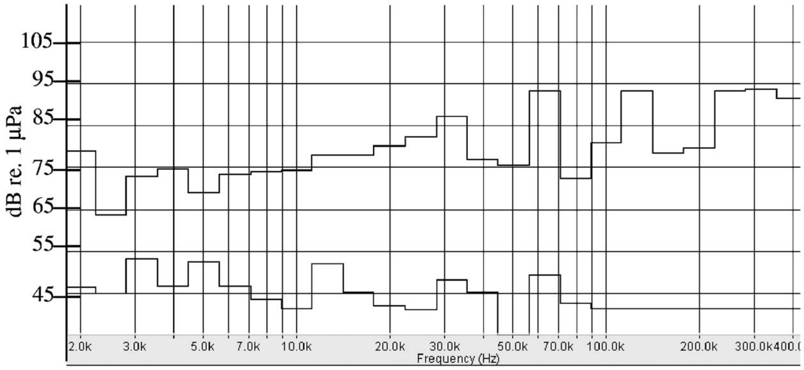

FIG. 5. System noise level (light gray line) with frequency plotted using $\frac{1}{3}$ octave filter and ambient sea noise level (black line) in Faxafloí Bay, Iceland, recorded at Beaufort 0-1.

source level variations of 42 to 49 dB. This variation cannot be explained by the orientation of the animals. The first harmonic of the white-beaked dolphin whistles contains the main part of the energy (Table II), which is about 10 kHz. Dolphin whistles are almost omni-directional at 10 kHz with a 3-dB beam width of 180° (Lammers and Au, 2003).

The variation in source levels may be explained by dolphins communicating at different ranges. On the first recording day we initially recorded quiet whistles with a single group of dolphins around our boat. The whistles became louder shortly before new dolphins joined the group and finally became more quiet at the end of the recording session with only a single group of dolphins in view. This scenario suggests that louder whistles were attracting distant individuals. Consequently, individuals communicating within the group may use quieter whistles while those communicating between distant groups may use louder whistles.

In conclusion this study shows that white-beaked dolphin whistles could be used both for short-range (up to about 140 m) and for long-range communication (up to about 10.5 km). In addition, our study indicates that white-beaked dolphin whistles are directional, an important factor for acoustic communication.

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APPENDIX: SOURCE LEVEL ESTIMATES FOR THREE TRANSDUCERS

First, we observe that the peaks of the cross-correlation functions (CCFs) between the signals at the three channels (a,b,c) are readily obtainable. We use the delay estimates derived from these CCFs to align the signals.

The three aligned signals,

$$x_j(t) = s_j(t) + n_j(t), \quad j \in \{a,b,c\}, \tag{A1}$$

then represent the observed signals, delayed so that the correlation between them is maximal. The noise terms, n_j, are assumed to be independent in the three channels. The "signal" terms, s_j, represent attenuated copies of the unknown signal ultimately to be estimated. The alignments mean that, for instance, for signals x_a and x_b,

$$\int x_a(t)x_b(t)\,dt = \max[\mathrm{CCF}(x_a,x_b)] \equiv P_{ab} \tag{A2}$$

with similar definitions for P_{ac} and P_{bc}. The sought after energies, E_j, of the signals, s_j, are given by

$$E_j = \int S_j^2(t)\,dt. \tag{A3}$$

The signals s_j can be factorized so that

$$s_j(t) = \sqrt{E_j}s_j(t), \quad \text{with} \int s_j^2(t)\,dt = 1. \tag{A4}$$

Since the variation between the signals s_j is dominated by a scaling factor, we can write (A1) as

$$x_j(t) = \sqrt{E_j}s(t) + n_j(t), \tag{A5}$$

that is, as three amplitude factors times the common unit energy signal plus an uncorrelated noise term for each signal. Inserting (A5) in (A2) gives

$$\begin{aligned} P_{ab} &= \int \left(\sqrt{E_a}s(t) + n_a(t)\right)\left(\sqrt{E_b}s(t) + n_b(t)\right)dt \\ &= \int \sqrt{E_a}s(t)\sqrt{E_b}s(t) + n_a(t)n_b(t) + \sqrt{E_a}s(t)n_b(t) \\ &\quad + \sqrt{E_b}s(t)n_a(t)\,dt. \end{aligned} \tag{A6}$$

In (A6), the noise terms at the three receivers are uncorrelated with each other and the signals are uncorrelated with noise, so—using (A4)—only

$$\approx \int \sqrt{E_a}s(t)\sqrt{E_b}s(t)\, dt = \sqrt{E_a}\sqrt{E_b} \tag{A7}$$

remains. The amplitude of each peak of the CCFs is the product of the square roots of the signal energies. With the three cross-correlation peaks we can therefore find the energies of s_j as

$$E_a = \frac{P_{ab}P_{ac}}{P_{bc}}, \quad E_b = \frac{P_{ab}P_{bc}}{P_{ac}}, \quad E_c = \frac{P_{ac}P_{bc}}{P_{ab}}. \tag{A8}$$

Au, W. W. L. (**1993**). *The Sonar of Dolphins* (Springer-Verlag, New York).

Brownlee, S. M., and Norris, K. S. (**1994**). "The Acoustic Domain," in *The Hawaiian Spinner Dolphin*, edited by K. S. Norris, B. Würsig, R. S. Wells, and M. Würsig (Univ. of California, Berkeley, CA).

Brüel and Kjær (**1985**). "Noise and vibration," *Pocket Handbook*, Lyngby, Denmark.

Caldwell, M. C., Caldwell, D. K., and Tyack, P. L. (**1990**). "A review of the signature whistle hypothesis for the Atlantic bottlenose dolphin, *Tursiops truncatus*" in *The Bottlenose Dolphin*, edited by S. Leatherwood and R. Reeves (Academic, London).

Dankiewicz, L. A., Houser, D. S., and Moore, P. W. B. (2005). "Sonar beam control, beam steering, and off-axis target detection by a bottlenose dolphin," in *16th Biennial Conference on the Biology of Marine Mammals*, p. 68.

Dreher, J., and Evans, W. E. (**1964**). "Cetacean communication," in *Marine Bioacoustics*, edited by W. N. Tavolga (Pergamon, Oxford), Vol. 1.

Freitag, L. E. and Tyack, P. L. (**1993**). "Passive acoustic localization of the Atlantic bottlenose dolphin using whistles and echolocation clicks," J. Acoust. Soc. Am. **93**, 2197–2205.

Hand, D. J. (**1997**). *Multivariate Analysis of Variance and Repeated Measures: A Practical Approach for Behavioural Scientists* (Chapman and Hall, London).

Janik, V. M. (**2000**). "Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland," J. Comp. Physiol., A **186**, 673–680.

Janik, V. M., and Slater, P. J. B. (**1998**). "Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls," Anim. Behav. **56**, 829–838.

Lammers, M. O., and Au, W. W. L. (**2003**). "Directionality in the whistles of Hawaiian Spinner dolphins (*Stenella Longirostris*): A signal feature to cue direction of movement," Marine Mammal Sci. **2**, 249–264.

Lammers, M. O., Au, W. W. L., and Herzing, D. L. (**2003**). "The broadband social acoustic signalling behaviour of spinner and spotted dolphins," J. Acoust. Soc. Am. **114**, 1630–1639.

Lilly, J. C. (**1963**). "Distress call of the bottlenose dolphin: Stimuli and evoked behavioral responses," Science **139**, 116–118.

Miller, P. J. O. (**2002**). "Mixed-directionality of killer whale stereotyped calls: A direction of movement cue?", Behav. Ecol. Sociobiol. **52**, 262–270.

Norris, K. S., Würsig, B., Wells, R. S., and Würsig, M. (**1994**). *The Hawaiian Spinner Dolphin* (Univ. of California, Berkeley, CA).

Popper, A. N. (**1980**). "Sound emission and detection by Delphinids," in *Cetacean Behaviour: Mechanisms and Function*, edited by L. M. Herman (Wiley-Interscience, New York), pp. 1–52.

Rasmussen, M. H. (1999). "Hvidnæsens lydproduktion, adfærd samt udbredelse," Masters thesis. Institute of Biology, University of Southern Denmark, Odense (in Danish).

Rasmussen, M. H., and Miller, L. A. (**2002**). "Whistles and clicks from white-beaked dolphins, *Lagenorhynchus albirostris* recorded in Faxaflói Bay," Aquat. Mamm. **28**, 78–89.

Rasmussen, M. H., and Miller, L. A. (**2004**). "Echolocation and social signals from white-beaked dolphins, *Lagenorhynchus albirostris*, recorded in Icelandic water," in *Echolocation in Bats and Dolphins*, edited by J. Thomas, C. Moss, and M. Vater (Univ. of Chicago, Chicago), pp. 50–53.

Rasmussen, M. H., Wahlberg, M., and Miller, L. A. (**2004**). "Estimated transmission beam pattern of clicks recorded from free-ranging white-beaked dolphins (*Lagenorhynchus albirostris*)," J. Acoust. Soc. Am. **116**, 1826–1831.

Richardson, W. J., Greene, C. R., Malme, C. I., and Thomson, D. H. (**1995**). *Marine Mammals and Noise* (Academic, San Diego).

Smolker, R., Mann, J., and Smuts, B. (**1993**). "Use of signature whistles during separations and reunions by wild bottle nosed dolphin mothers and infants," Behav. Ecol. Sociobiol. **33**, 393–402.

Spiesberger, J. L. (**1998**). "Linking auto and cross-correlation functions with correlation equations: Application to estimating the relative travel times and amplitudes of multipath," J. Acoust. Soc. Am. **104**, 300–312.

Spiesberger, J. L., and Fristrup, K. M. (**1990**). "Passive localization of calling animals and sensing of their acoustic environment using acoustic tomography," Am. Nat. **135**, 107–153.

Tyack, P. (**1997**). "Development and social functions of signature whistles in bottlenose dolphins, *Tursiops truncatus*," Bioacoustics 8, 21–46.

Wahlberg, M., Møhl, B., and Madsen, P. T. (**2001**). "Estimating source position of a large-aperature hydrophone array for bioacoustics," J. Acoust. Soc. Am. **109**, 397–406.

Yost, W. A. (**2000**). *Fundamentals of Hearing* (Academic, New York).

Zar, J. H. (**1996**). *Biostatistical Analysis* (Prentice-Hall, Englewood Cliffs, NJ).