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Whistles and clicks from white-beaked dolphins, *Lagenorhynchus albirostris*, recorded in Faxaflói Bay, Iceland

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Abstract

Vocalizations from free-ranging white-beaked dolphins, *Lagenorhynchus albirostris* (Gray, 1846), were recorded in Icelandic waters. They use a variety of whistles with frequencies up to 35 kHz when socializing. Whistles could be classified into 21 different categories based on duration and frequency contours. Their click sounds resemble those reported from bottlenose dolphins, *Tursiops truncatus*, recorded in open waters. Clicks have a peak frequency at about 115 kHz and some clicks had another lower amplitude peak at about 250 kHz. Click intervals varied between 2.8 ms to 56.2 ms in 23 click sequences analysed. Duration of a click was between 10 to 29 µs. Clicks from three sequences were analysed in detail for acoustical properties: click interval, duration, peak frequency, centre frequency (about 90 kHz), 3-dB bandwidth (about 50 kHz), rms bandwidth (about 30 kHz), and 90% energy bandwidth (about 70 kHz).

Key words: white-beaked dolphins, *Lagenorhynchus albirostris*, sounds, whistles, echolocation, and clicks.

Introduction

Most dolphins produce a variety of sounds described as clicks, whistles, buzzes, squawks, screams and barks (Herzing, 1996). Whistles consist of narrow-band tones of constant frequency (CF) or tones that vary in frequency. Harmonic components are normally present (Popper, 1988). Whistles are probably used for communication and have only been described from cetaceans in the superfamily Delphinoidea. Dolphin whistles have been categorized using two different approaches (see Tyack, 1997). One approach assumes that dolphins share a species-specific repertoire of whistles, where each whistle is used in a particular behavioural context (e.g., Lilly, 1963; Dreher & Evans, 1964). The other approach assumes that each dolphin tends to produce its own individually distinctive whistle, which was called a signature whistle by Caldwell *et al.* (1990). One approach may not exclude the other, but may be due to differences in the recording situations like isolated captive or trained dolphins as opposed to free-ranging dolphins. Caldwell *et al.* (1990) recorded signature whistles mainly from isolated captive dolphins. Of all whistles analysed, 94% were signature whistles the rest they called variant whistles. Tyack (1986) reported 23% variant whistles when two captive dolphins were interacting socially. Janik *et al.* (1994) found that 20% of a dolphin's whistles were variants when it was isolated, but nearly 50% of the whistles were variants when it was being trained or was together with other dolphins.

The echolocation sounds of most delphinid species studied are short, broadband pulses (Evans, 1973). They are emitted in low repetition rate trains or in high repetition rate bursts. Bursts of pulses can be used during prey capture (Verfuss *et al.*, 1996) and during aggressive or agonistic interactions (Blomqvist & Amundin, 1998). Echolocation of bottlenose dolphins has been intensively studied. The bottlenose dolphin uses echolocation clicks with a peak frequency (frequency with maximum amplitude in the spectrum) between 115 and 121 kHz when recorded in open waters (Au, 1993). Other characteristics of their sonar clicks are: centre frequency (which divides the energy of the spectrum into two equal halves; see Au, 1993) is between 93 and 125 kHz, 3-dB bandwidth (-3 dB to each side of the peak frequency) is between 39 and 45 kHz, rms bandwidth (which is a weighted distance of the frequencies in the spectrum from 0 Hz; Menne & Hackbarth, 1986) is between 21 and 28 kHz, and typical duration is between 40 and 70 µs (Au & Nachtigall, 1997). The sonar beam is very directional, becoming narrower as the frequencies increase. Average 3-dB beam bandwidth is about 10° in both the vertical and horizontal planes. The beam is projected about 5° above the animal's head in the vertical plane (Au, 1993).

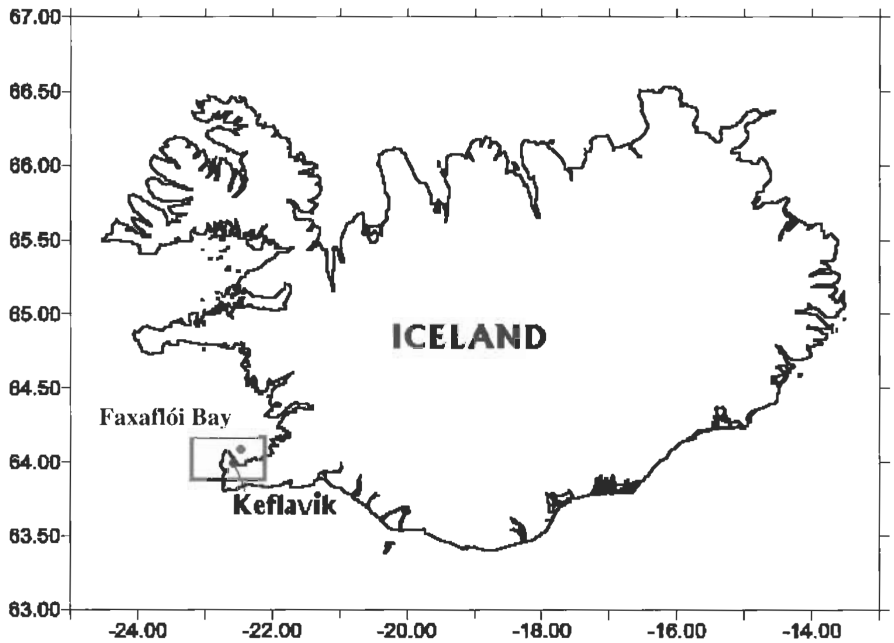

Figure 1. Study site and map of Iceland showing Faxaflói Bay.

Mitson (1990) recorded acoustic emissions from white-beaked dolphins by using a passive sonar with a bandwidth of 40 kHz centred at 305 kHz. Due to equipment used for recordings, they suggested white-beaked dolphin signals to have significant energy at frequencies about 305 kHz. The dolphins were as far away as 70 m during this recording (Mitson, 1990). Watkins (1980) described clicks from delphinids (including white-beaked dolphins) as short, broadband with maximum frequencies at 30 to 150 kHz. The purpose of this study was to describe the acoustical characteristics of whistles and clicks recorded using broadband equipment from free-ranging white-beaked dolphins in Faxaflói Bay, Iceland.

Material and Methods

Field recordings of whistles and clicks from white-beaked dolphins were made in Faxaflói Bay, not far from Keflavik harbor, 64°00.49′N, 22°33.37′W (Fig. 1), during the summers of 1997 and 1998. The water in Faxaflói Bay is mainly 35 to 37 m deep and the bottom consists of sand or basalt. Dolphins were commonly found between one and three nautical miles off shore.

Whistles and clicks were recorded from a 10 m fibreglass motorboat with hydrophones over the side of the boat at a depth of about 4 m Brüel & Kjær (B&K, Copenhagen, Denmark) 8103 hydrophones were connected to Etec (Copenhagen, Denmark) amplifiers, and to a Racal Store 4DS high-speed tape recorder using Ampex tapes. Tape speed of the Racal recorder was set at 30 inches-per-second (ips) or 60 ips when recording dolphin signals. The recording system was calibrated up to 300 kHz using 8103 calibration data kindly provided by B&K. Comments, like group size, behaviour of the dolphins and the presence of fish as indicated from the sonar of the boat, were recorded on one channel on the tape recorder. Behaviour of the dolphins was divided into four categories: traveling, resting, socializing, and feeding. Feeding behaviour was identified as described by Evans (1987). The dolphins could be observed under water from the boat and an estimated distance from the dolphin to the hydrophone was also noted. Distances to dolphins were between 1–10 m with the dolphins swimming towards the hydrophones when recording click sequences for analysing. A majority of whistles were recorded with a monitoring hydrophone or a B&K 8103 on a Sony digital cassette recorder (DAT) (DTC-D7, flat frequency response up to 20 kHz). Some whistles (345) were recorded on the Racal recorder with tape speed set at 30 ips.

Recordings were analysed using custom and commercial software on a PC. Whistles were sampled at an effective rate of 88.2 kHz and analysed using spectrograms in BatSound (Petterson Elektronik, Uppsala, Sweden) with a 512-point FFT using a Hann weighing function and 85% overlap. On-screen cursors were used to measure whistle

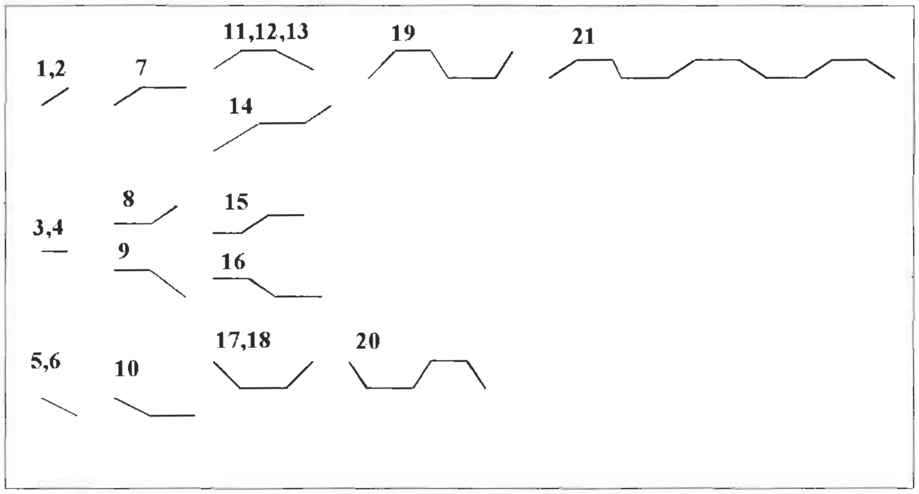

Figure 2. Scheme used to classify whistle contours. The first vertical column of whistles consists of a rise, constant, and falling contours (1–6). The second vertical column shows whistles having a combination of two contours (7–10), the third column whistles having three contours (11–18), and the fourth whistles having five contours (19–20). No whistles having four contours were recorded. Whistle 21 is composed of multiple contours. Double numbers indicate differences in duration e.g. 1, 2 correspond to whistle durations <0.1 s or >0.1 s (see Table 1). Triple numbers (11, 12, 13) indicate three different whistle durations (<0.1 s, >0.1 s or >0.3 s).

duration, start frequency, and end frequency. A drawing of each frequency contour was also made. Whistles were visually categorized based on duration and frequency contour similar to the method used by Moore and Ridgway (1995). Contours could be categorized as rising, falling, or constant frequency or as combinations of these contours (Fig. 2). Five untrained observers categorized a sample of 50 different whistle contours. Their classification agreed with ours by 92%.

All Ampex tapes were played back slowly and it was possible to determine aurally if a click sequence was recorded from one, two, or more dolphins. Only click sequences from one dolphin were used for analyses. The clicks from slowed tape recordings were sampled at an effective rate of 705.6 kHz. Click duration and click intervals were automatically measured using special software (EventRec, S.B. Pedersen, Copenhagen, Denmark). Digitizing occurred between preset triggers, each containing a click with about 320 µs pre-history time and 115 µs post-history time. These signals were saved in a data file along with an accompanying catalog file containing trigger times, click intervals, and click durations. Click duration was defined as the time period containing 87.5% of the energy of the signal. A click sequence was defined as a continuous series of clicks. Power spectra of clicks were made using a 256-point FFT with a rectangular weighing function using BatSound. On-screen cursors were used to measure peak frequency and 3-dB bandwidth. In addition, the same clicks without pre- or post-history times were selected with Spectra Plus (Pioneer Hill Software, Poulsbo, WA) and converted to ASCII files using a custom-made program (Sconvert, S.B. Pedersen, Copenhagen, Denmark) and imported into Mathcad (ver. 7.0, MathSoft, Cambridge, MA). Mathcad was used to calculate centre frequency (Au, 1993) and rms bandwidth (Menne & Hackbarth, 1986) using the definitions mentioned in the introduction. Mathcad was also used to calculate the 90% energy bandwidth, which is the bandwidth containing 90% of the energy of the click.

Results

A total of 1536 whistles were analysed, all of which were recorded in 1997. We only heard whistles when dolphins were socially active, showing different aerial displays, or when they swam around a humpback whale or a diver. Many dolphins whistled at the same time. No whistles were heard when dolphins were feeding or travelling. The frequencies of whistles ranged from 3 kHz up to 35 kHz with only a few whistles having harmonics. The duration of a single whistle was from 0.03 to 1.62 s. Whistles could be classified into 21 different categories (Fig. 2 and Table 1). Figure 3 shows spectrograms of some whistles from category 2, 'long, rising-frequency' and category 18, 'long, falling-constant-rising frequency'. Figure 4 shows

Table 1. Whistle repertoire of the white-beaked dolphin recorded in 1997. Most recordings were made using a DAT, but high-speed recordings are also included (345 whistles of a total 1536 whistles). Whistles from categories 13, 14, 15, 18, and 20 were not found in the high-speed recordings. The start and end frequencies are mean values.

Categories	Signals	Number	Duration (s)	Duration (s) (mean)	Frequency range (kHz)	Frequency start (kHz)	Frequency end (kHz)
1	´	86	<0.1	0.06	4.8–18.9	9.5	12.5
2	/	268	>0.1	0.26	3.0–29.1	9.9	13.0
3	-	42	<0.1	0.07	5.2–26.6	9.7	9.8
4	–	21	>0.1	0.33	3.4–18.5	9.9	10.0
5	`	45	<0.1	0.07	3.5–18.8	10.7	8.9
6	\	72	>0.1	0.20	3.7–23.3	10.4	8.4
7	⌐	12	>0.1	0.32	6.7–35.0	9.6	12.1
8	⌡	10	>0.1	0.26	6.9–18.9	8.5	11.0
9	¬	11	>0.1	1.05	5.6–20.1	11.1	8.7
10	⌣	7	>0.1	0.34	6.0–17.7	10.9	9.1
11	⌒	145	<0.1	0.07	3.6–29.8	10.2	10.4
12	⌒	139	>0.1	0.27	5.4–20.4	9.9	10.3
13	⌒	17	>0.3	0.68	5.2–16.3	7.6	7.3
14	~	13	>0.1	0.22	6.6–20.1	11.8	15.5
15	∫	309	>0.1	0.32	5.1–16.9	10.3	16.1
16	⌄	28	>0.1	0.16	6.2–17.5	10.6	8.9
17	˅	62	<0.1	0.07	4.0–23.3	10.8	11.7
18	∪	124	>0.1	0.17	4.3–33.6	12.0	13.9
19	~	34	>0.1	0.32	5.1–18.4	10.2	12.0
20	∽	12	>0.1	0.24	4.2–16.4	11.1	10.4
21	∿∿	15	>0.1	0.73	4.8–14.5	10.0	10.5
22	others	64					

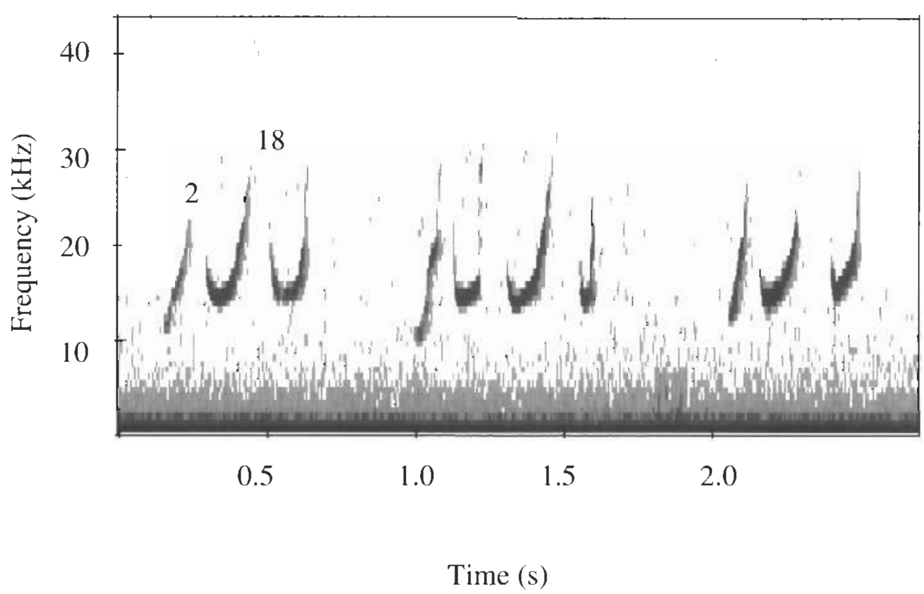

Figure 3. Spectrogram of whistles from a white-beaked dolphin, *Lagenorhynchus albirostris*. The spectrogram was generated using a sample rate of 88.2 kHz and consecutive 512-point FFT's with Hann windows (85% overlap). Note that some whistles contain frequencies higher than 30 kHz. The whistles here are of types 2 and 18.

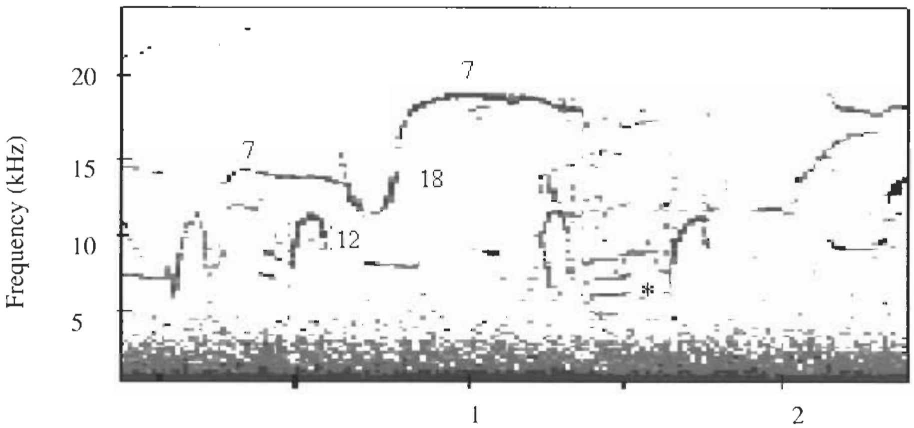

Figure 4. Example of some whistles from two dolphins swimming around a diver. The spectrogram was generated like that in Figure 3. The numbers refer to whistle types shown in Figure 2. Star (*) shows possible weak pulse bursts.

spectrograms of some whistles from categories 7, 12 and 18. Two dolphins were constantly whistling while swimming around a diver for 45 min in this recording. No other dolphins were seen during this time.

A total of 3946 clicks with associated intervals were quantified, 2671 clicks from 11 click sequences in 1997 and 1275 clicks from 12 click sequences in 1998. These 23 click sequences were presumably produced by individual dolphins. Click intervals varied from 40.0 ms to 2.8 ms (mean click interval was 4.6, SD=5.5 ms) in 1997 and click intervals varied from 56.2 to 3.0 ms (mean click interval was 15.7, SD=8.9 ms) in 1998. Click bursts were rare and only heard together with whistles. The star (*) in Fig. 4 may indicate weak click bursts.

The clicks in three sequences were analysed in detail, one sequence from 1997 (Fig. 5) and two from 1998 (Figs. 6 and 7). Clicks with high amplitudes had an average peak frequency of 115 ± 3 kHz (n=100), with a secondary amplitude peak at about 250 kHz (Fig. 5C). The highest click repetition rate (357 click/s) was measured in this sequence (Fig. 5A), which contained 490 clicks. Click intervals varied from 6.8 ms to 2.8 ms, and durations of single clicks in this sequence (Fig. 5B) were between 10 μs and 24 μs (mean duration 15 ± 3 μs). Other properties of the clicks are given in Table 2.

Another click sequence is shown in Figure 6 and consisted of 22 clicks from a single individual. Spectra of the clicks had an average peak frequency of 106 ± 5 kHz (maximum 117 kHz). A second high frequency peak occurred at about 190 kHz. Click intervals varied between 20 ms and 18 ms and durations of clicks (Fig. 6B) were between 9 μs and 22 μs (mean duration 17 μs $\pm$ 3 μs). Other properties of the clicks are given in Table 2.

A third click sequence consisted of 20 clicks again from a single individual (Fig. 7). Spectra of the clicks had an average peak frequency of 109 ± 13 kHz (maximum 122 kHz) with a second high frequency peak about 200 kHz. Click intervals varied from 105 ms to 35 ms and durations (Fig. 7B) were between 14 μs and 30 μs (mean duration 22 ± 3 μs). Other properties of the clicks are given in Table 2. All parameters of click characteristics (Table 2) of these three examples were significantly different (one-way ANOVA, $P<0.01$).

Discussion

We only heard and recorded whistles when white-beaked dolphins were socially active near the water surface, which supports that white-beaked dolphin use whistles for communication and that whistles are not important when traveling or resting. The same is true for free-ranging bottlenose dolphins where whistles were especially prevalent in localized feeding and social interactions at the surface (dos Santos, 1990).

Whistles from white-beaked dolphins contained higher frequencies than reported from other dolphin species. Although we used a DAT to record most of the whistles, some were recorded on a Racal tape recorder with a tape speed at 30 ips giving a frequency range up to 150 kHz. Some high frequency whistles ranged between 8 kHz and

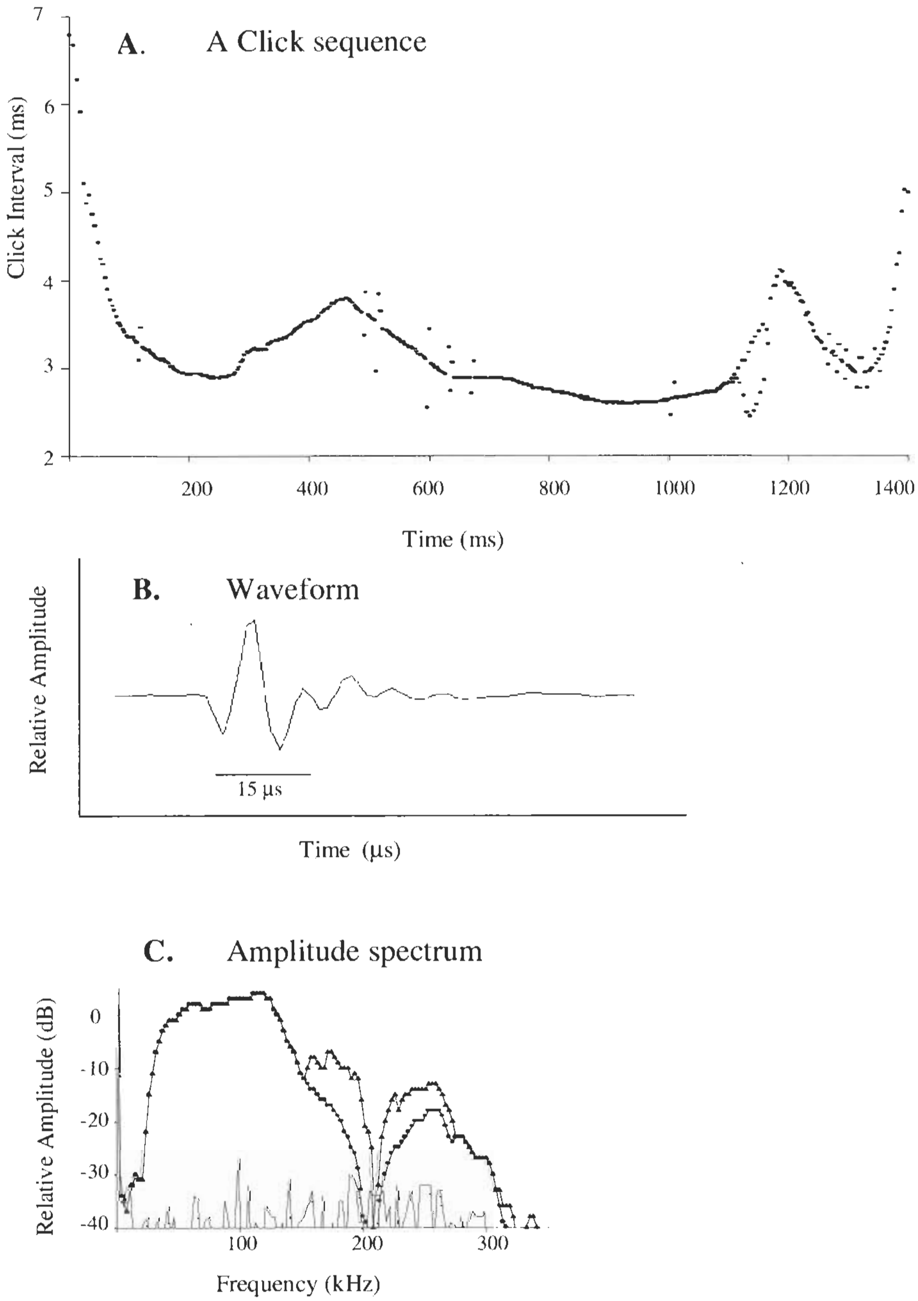

Figure 5. Example of a click sequence (A) with 490 clicks recorded from a white-beaked dolphin, *Lagenorhynchus albirostris* recorded in 1997. The sample rate was 705.6 kHz. The single click (B) was chosen 290 ms from the start of the sequence (A). The horizontal time bar in (B) represents 15 µs, which is the duration containing 87.5% of the energy in the click. The amplitude spectrum of the single click (C) was constructed using a 256-point FFT (rectangular window). Typical calibration data for the B&K 8103 was used to correct the amplitude spectrum at frequencies above 120 kHz. The solid-line in each amplitude spectrum is the background noise. The dotted-line is the amplitude spectrum of a click and the line with triangles is the amplitude spectrum of a click corrected using the B&K calibration chart.

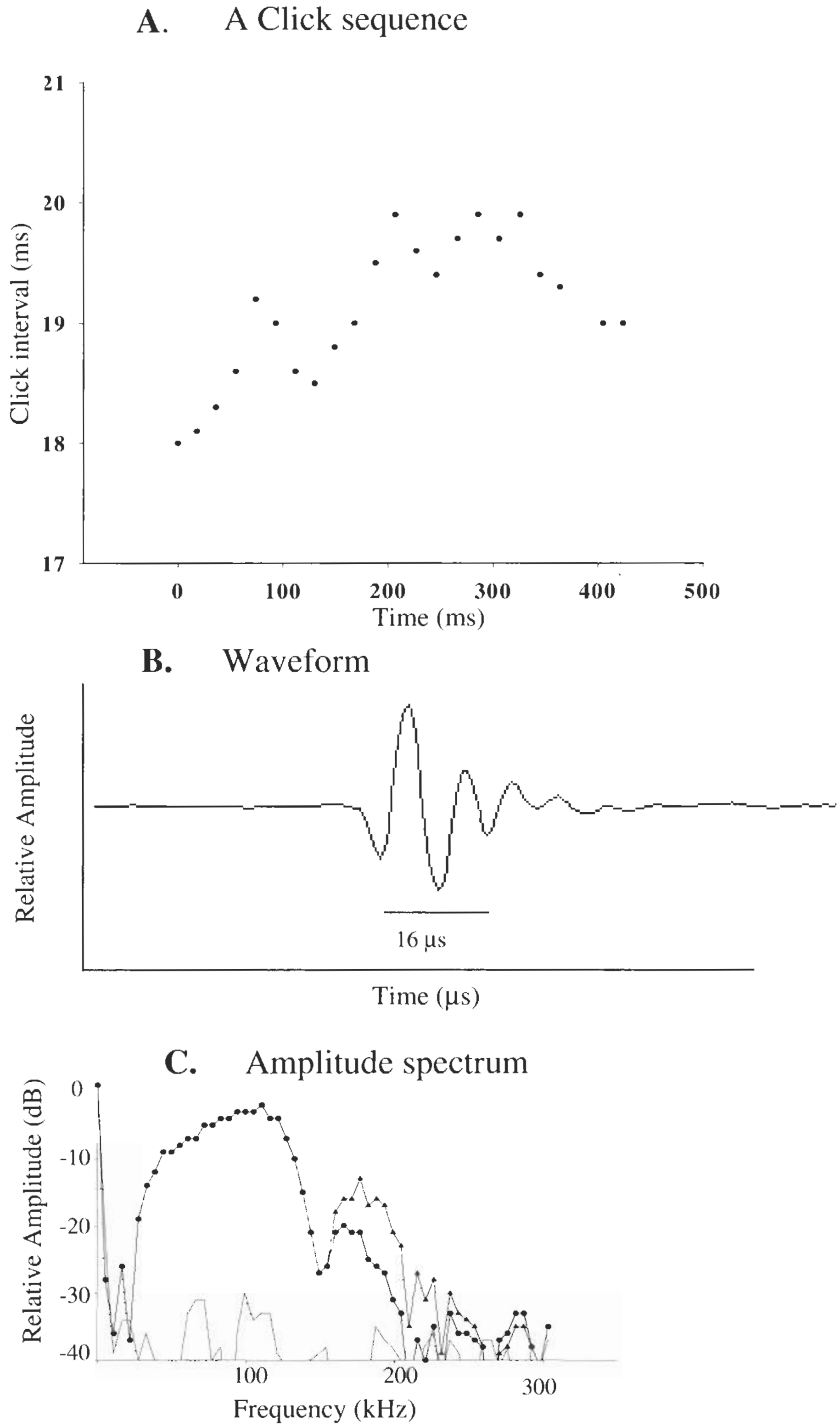

Figure 6. Example of a click sequence (A) with 22 clicks recorded in 1998. The single click (B) was chosen 220 ms from the start. The horizontal time bar represents 16 µs. For other details see the legend for Figure 5.

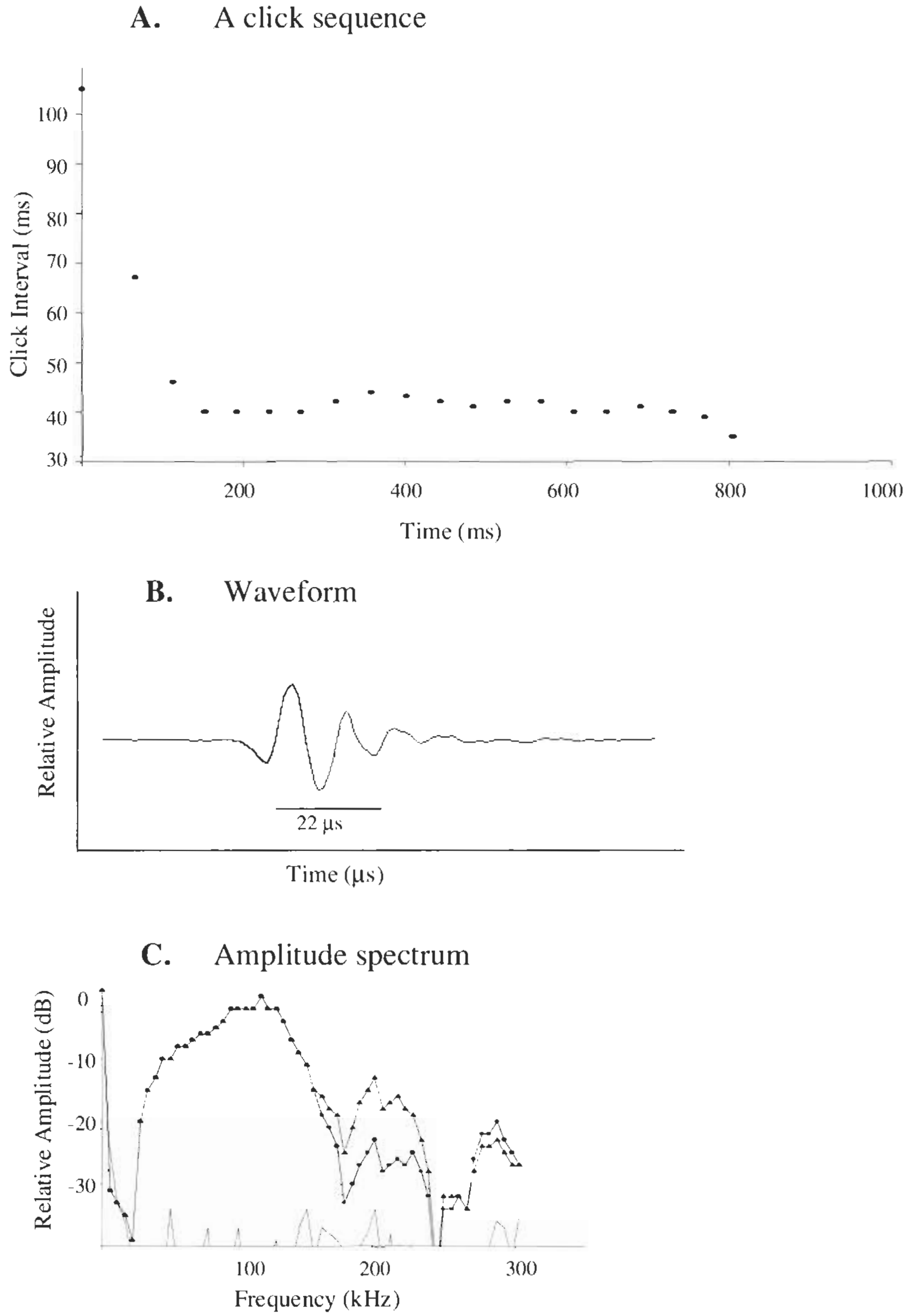

Figure 7. Example of a click sequence (A) with 20 clicks recorded in 1998. The single click (B) was chosen 380 ms from the start. The horizontal time bar represents 22 µs. For other details see the legend for Figure 5.

35 kHz. Maximum frequency range reported for dolphin whistles for other dolphin species is about 20 kHz, but most recordings have been limited by audio equipment. For example, Steiner (1981) described whistles with frequencies up to 20 kHz from five different species (bottlenose dolphins, Atlantic

Table 2. Summary of the acoustical click characteristics of white-beaked dolphin clicks as compared to those of trained bottlenose dolphins in open water. All values in table are either mean values with standard deviations from white-beaked dolphin clicks or ranges from bottlenose dolphin clicks. Sequences where recorded on a Racal with tape speed at 60 ips and using a B&K 8103 hydrophone. F-values in the table all have *P*-values of <0.01.

	Click sequence 1 (n=100) Figure 5	Click sequence 2 (n=22) Figure 6	Click sequence 3 (n=20) Figure 7	F-values (df=2)	Click sequences from bottlenose dolphins (Au, 1993, Au & Nachtigall, 1997)
Click interval (ms)	3 ± 0.6	19 ± 1	46 ± 15		10–180
Duration (µs)	15 ± 3[1]	17 ± 3[1]	22 ± 3[1]	124.3	40–70[2]
Peak frequency (kHz)	115 ± 3	106 ± 5	109 ± 13	23.1	115–121
Center frequency (kHz)	85 ± 4	94 ± 4	98 ± 7	84.0	93–125
3-dB bandwidth (kHz)	70 ± 12	43 ± 11	42 ± 12	76.4	39–45
Rms-bandwidth (kHz)	32 ± 2	24 ± 3	31 ± 5	81.1	21–28
90%-energy bandwidth	75 ± 3	59 ± 11	74 ± 13	168.2	Not calculated

[1]Durations containing 87.5% of the click energy. [2]Durations measured for the signal above noise (arbitrary).

white-sided dolphins (*Lagenorhynchus acutus*), long-finned pilot whales (*Globicephala melaena*), Atlantic spotted dolphins (*Stenella plagiodon*), and spinner dolphins (*Stenella longirostris*)). Recently, however, Au *et al.* (1999) reported ultrasonic harmonic components above 70 kHz in the whistles of spinner dolphins recorded with broadband equipment. Ding *et al.* (1995) also compared whistles from seven odontocete species: Amazon river dolphins (*I. geoffrensis*), bottlenose dolphins, dusky dolphins (*Lagenorhynchus obscurus*), spinner dolphins, Atlantic spotted dolphins, Pantropical spotted dolphins (*Stenella attenuata*), and tucuxi (*Sotalia fluviatilis*). Dusky dolphins had a higher maximum frequency in their whistles than all other dolphin species in this comparison. Ding *et al.* (1995) concluded that whistles from the three *Stenella* species were most similar. From our study and that of Ding *et al.* (1995) it currently appears that *L. albirostris* and *L. obscurus* use a higher maximum frequency of their whistles than what is reported from other species. Taxonomically related species could have similar ancestral whistle patterns and sound production anatomy contributing to similar whistle characteristics.

Whistle contours were similar to those of other dolphin species, for example bottlenose dolphins in captivity (McCowan, 1995; McCowan & Reiss, 1995) or for free-ranging dolphins (Steiner, 1981). Moore & Ridgway (1995) divided whistles from captive and free-ranging common dolphins (*Delphinus delphis*) into eight different categories based on duration and frequency contours. Whistles from white-beaked dolphins fell into similar categories (categories 1, 2, 4, 5, 10, 20, 21 in Table 1), but we could classify additional categories. The more varied whistle repertoire from white-beaked dolphins could reflect the large sample size (1536 whistles in our study compared to 186 whistles from free-ranging common dolphins (Moore & Ridgway, 1995).

Interestingly, we saw 20 of the 21 categories (only category 21, the multiple loop was missing) when recording from only two dolphins in 1998 (these whistles were not included in our analyses). They whistled constantly for 45 min while swimming around a diver. We recorded about 1000 whistles in this situation. According to the signature whistle hypothesis, we might have expected a greater number of whistles in two (or at least a few) categories, having only two dolphins. However, we found a varied whistle repertoire and no obvious sign of signature whistles in this situation. An explanation could be that most signature whistles reported in the literature are from isolated dolphins, captive dolphins, or mother and calf when they are reunited during capture/release programs (Tyack & Sayigh, 1997). None of these studies were with free-ranging dolphins under natural circumstances. The signature whistle hypothesis proposes that dolphins use such whistles to broadcast their identity and location to conspecifics (Tyack & Sayigh, 1997). In other situations, the dolphins may not need or use their signature whistles, as in our case with two dolphins swimming around a diver. McCowan & Reiss (1995) wrote: 'It is possible that in the studies where dolphins were recorded in isolation or under restraint, the vocal repertoire may have been limited by the effects of contained space, limited social interaction, and stress'. It is a clear advantage for a mother and a calf to use signature whistles to establish and maintain contact. Smolker *et al.* (1993) observed wild bottlenose dolphin calves using signature whistles before reunion with their mothers. Janik *et al.* (1994) showed how a bottlenose dolphin could vary parameters of whistle types depending on context, which was either isolation or a two choice experiment. For the experiment, the dolphin was trained to choose one of two objects presented in the air. The animal emitted 1743 whistles in 221 choice trials and 18 isolations. It used signature whistles 80% of time when isolated and around 53% of the time during the choice experiment. Janik & Slater (1998) also showed how a group of four bottlenose dolphins in captivity used signature whistles when isolated, but used other whistles when swimming together. Perhaps wild dolphins use fewer signature whistles than isolated dolphins in captivity.

Spectral and temporal properties of clicks from white-beaked dolphins resembled the echolocation clicks produced by bottlenose dolphins (Au & Nachtigall, 1997; Au, 1993). Therefore, we assume that white-beaked dolphins use their clicks for echolocation. Table 2 shows the similarity between the acoustic properties of wild white-beaked dolphin clicks and those reported from trained bottlenose dolphins (Au, 1993). Free-ranging, white-beaked dolphins use broadband clicks. However, the bandwidth and the peak frequency depend on the recording situation. Evans (1973) and Fahner *et al.* (in press) reported peak frequencies of 60–80 kHz for the Pacific white-sided dolphin (*L. obliquidens*), but these clicks were recorded in a tank. Bottlenose dolphins have a peak frequency of 30 kHz–60 kHz when recorded in a tank as compared to a peak frequency of 115 kHz–121 kHz when recorded in open waters (Au, 1993). Peak frequency varies considerably in white-beaked dolphin clicks (40 kHz–120 kHz), but the centre frequency varies less (80 kHz–100 kHz) because of its more robust definition. Therefore, the centre frequency is a more descriptive measure of clicks. We compared the rms bandwidth to what is known from other dolphin species. The average rms bandwidth was between 24 kHz–32 kHz for white-beaked dolphin clicks and 21–28 kHz for bottlenose dolphin clicks. Rms bandwidth is satisfying mathematically, but it does not give much information about the nature of the signal. We suggest the 90% energy bandwidth is more descriptive since this gives information about energy in the actual click. Average 90% energy bandwidths are between 59 kHz to 75 kHz for white-beaked dolphin clicks. In comparison, a narrow-band harbour porpoise click has a 90% energy bandwidth of about 22 kHz. The click properties of the three sequences analysed were all significantly different, suggesting either slight head movement away from the axis between the hydrophone and the animal gave the difference or that the three sequences originated from different animals. The latter possibility has credence since Au (1980, 1993) could attribute individual click properties to each of four different bottlenose dolphins doing the same sonar task.

A white-beaked dolphin click often had a second high-frequency region between 200 kHz and 250 kHz, which confirms earlier studies reporting very high frequencies in signals recorded from this species (Mitson, 1990). We observed waxing and waning in the amplitude of the power spectrum above 150 kHz for signals in a long sequence (Fig. 5). This is probably due to the narrower beamwidth for high signal frequencies and to the dolphin turning its head or body. Only clicks projected directly at a hydrophone will contain high frequencies (Au, 1993). We do not know if white-beaked dolphins can hear these very high frequencies since their auditory abilities are unknown. Au (1993) showed audiograms from seven species of odontocetes that all had best hearing sensitivity between 15 kHz–110 kHz. Tremel *et al.* (1998) measured hearing sensitivity of a Pacific white-sided dolphin, and it also had best hearing sensitivity between 2 kHz–128 kHz. Audiograms are obtained using pure tones at frequencies up to 150 kHz, but no researchers have measured audiograms of odontocetes at higher frequencies.

Assuming white-beaked dolphins can hear the full frequency range of their clicks, why should they have a second high frequency peak in their sonar signals? One explanation could be that they are mainly feeding on sandeels (*Ammodytes sp.*) during the summer months around Iceland. Sandeels have very small otoliths with lengths between 0.5 and 4.0 mm, which correlate to a fish length between 41.6–201.7 mm (Härkönen, 1986). Also the sandeel has no swimbladder (Reay, 1986). Swimbladders are often the most important reflective structures within a fish (Foote, 1980). Using high frequency sonar up to 300 kHz gives a wavelength of 5 mm (c. ≈1500 m/s), which improves the chance of detecting a sandeel.

Another explanation for high frequency clicks in white-beaked dolphins might be found in the mechanism of sound production. According to Cranford *et al.* (1996) sound is produced in the dorsal bursae complex. CT-scans of heads of Pacific white-sided dolphins were not very different from those of white-beaked dolphins, but quite different from bottlenose dolphins. The most striking difference is two enlarged fatty basins located between the melon and the dorsal bursae complex seen in the Pacific white-sided dolphin. Height, width, and length of the dorsal bursae are also slightly larger for the Pacific white-sided dolphin than for other dolphin species. Besides, less skull asymmetry is found in Pacific white-sided dolphins than in bottlenose dolphins. We do not know if these morphological differences have an effect on the production of sonar signals.

Click intervals decrease with decreasing distance to target (Au, 1993). Click intervals in different sequences usually decreased as the white-beaked dolphin closed in on a target (the hydrophone). Sometimes click intervals showed a slightly cyclic pattern (see for example the last part of Fig. 5A). This behaviour actually could reduce ambiguity as shown for bottlenose dolphins (Kardane & Penner, 1983). Au (1993) has shown that the dolphins receive the target echo before sending out the next click after a specific lag-time. Lag-time is defined as the time difference between the click interval minus the two-way transit time (that is time the signal travels from a dolphin to target and back). Lag-times have values between 19 ms and 45 ms for bottlenose dolphins (Au, 1993). Mean click intervals for the three sequences analysed from white-beaked dolphins were 46 ms, 19 ms and 3 ms (Table 2). These values were measured from click sequences where dolphins were seen about 10 m from the boat. Average click intervals from trained bottlenose dolphins recorded in open waters varied from 22 ms to 38 ms at a range of 6 m to target and varied from about 12 ms to 30 ms at a range of 1 m to target (Au, 1980). Thus, the larger click intervals used by white-beaked dolphins in these situations are comparable to click intervals from bottlenose dolphins considering the difference in distances to targets. Assuming white-beaked dolphins have the same lag-time as bottlenose dolphins (19 ms to 45 ms) they cannot emit click, and send out the next click with an interval shorter than 19 ms. However, we recorded click intervals from white-beaked dolphins down to 2.8 ms, thus the white-beaked dolphins must either be processing several echoes simultaneously, or selecting specific echoes for processing.

In conclusion, sounds of free-ranging white-beaked dolphins resemble those of other dolphin species. However, white-beaked dolphins use higher maximum frequencies in both their whistles and clicks than reported from most other dolphin species. Since most studies are performed on dolphins in captivity, continued studies of free-ranging dolphins with broad-band recording equipment will help explain how wild dolphins use sound for communication, navigation, and prey capture.

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