ARTICLE

Exchange of "signature" calls in captive belugas (*Delphinapterus leucas*)

**Tadamichi Morisaka · Yayoi Yoshida ·
Yuichiro Akune · Hideki Mishima ·
Sayo Nishimoto**

Abstract Belugas (*Delphinapterus leucas*) produce echolocation clicks, burst pulses, and whistles. The sounds of 3 captive belugas were recorded using 2 hydrophones at the Port of Nagoya Public Aquarium. There were stable individual differences in the pulse patterning of one type of pulsed sounds (PS1 call), suggesting that belugas use these as "signature" calls. Eighty-eight percent of PS1 calls initiated PS1 calls from other animals within 1 s. PS1 calls repeated by the same individual occurred primarily when other belugas did not respond within 1 s of the first call. Belugas delayed successive PS1 calls when other belugas responded with a PS1 call within 1 s. There was no clear temporal pattern for whistles. It appears that the time limit for responding to calls is 1 s after the initial call. If other individuals do not respond to the PS1 call of a beluga within 1 s, belugas tend to repeat the call and wait for a response. The results of this study suggest that the belugas exchange their individual signatures by using PS1 calls, in a manner similar to that of signature whistles used by bottlenose dolphins.

Keywords Vocal exchange · Beluga · *Delphinapterus leucas* · Contact call · Signature

T. Morisaka (✉) · Y. Yoshida
Wildlife Research Center of Kyoto University,
2-24 Tanaka-sekiden-cho, Sakyo, Kyoto 606-8203, Japan
e-mail: chaka@wrc.kyoto-u.ac.jp

Y. Akune · H. Mishima · S. Nishimoto
The Port of Nagoya Public Aquarium, 1-3 Minato-machi,
Minato-ku, Nagoya, Aichi 455-0033, Japan

Introduction

Vocal exchange, specifically, temporally associated vocal exchange (Schulz et al. 2008), is a communication form in which a receiver responds to a sender's sound signal by producing a sound within a brief interval (Miller et al. 2004; Sugiura 2007; Kondo and Watanabe 2009; Nakahara and Miyazaki 2011). Several group-living mammals, including non-human primates (Snowdon and Cleveland 1984; Biben et al. 1986; Masataka and Biben 1987; Sugiura 1993; Oda 1996; Sugiura 1998; Koda 2004), rodents (Yosida et al. 2007), bats (Carter et al. 2009), and odontocetes (Janik 2000; Miller et al. 2004; Nakahara and Miyazaki 2011), as well as birds (e.g., Kondo et al. 2010) and amphibians (e.g., Gerhardt et al. 2000), exchange vocal signals. Schulz et al. (2008) listed possible functions of vocal exchanges with conspecifics, including mate attraction (e.g., Gerhardt et al. 2000), territorial defense (e.g., Mennill and Ratcliffe 2004), social-bonding (e.g., Schulz et al. 2008), and group cohesion (e.g., Sugiura 1998; Miller et al. 2004).

It has been well documented that bottlenose dolphins (*Tursiops truncatus*) produce individually distinctive "signature whistles" that function as individual recognition cues and help maintain contact with other members of the same group (Caldwell and Caldwell 1965; Tyack 1986; Sayigh et al. 1990; Janik and Slater 1998; Janik et al. 2006). Bottlenose dolphins not only produce signature whistles but also imitate other signature whistles (Tyack 1986; Janik 2000). Nakahara and Miyazaki (2011) reported that a second bottlenose dolphin engaged in a vocal exchange tends to produce whistles within 1 s of the first individual's whistle. They also reported that individuals appeared to repeat the whistles unless response whistles were heard within 1 s.

Belugas (*Delphinapterus leucas*), also known as "sea canaries," have been reported to produce various types of sounds, both in the wild and in captivity (Sjare and Smith 1986a; Karlsen et al. 2002; Van Parijs et al. 2003; Belikov and Bel'kovich 2008; Vergara et al. 2010; Chmelnitsky and Ferguson 2012). These sounds fall into 3 broad categories: whistles, burst pulse sounds, and echolocation clicks (Sjare and Smith 1986a; Vergara et al. 2010). Sjare and Smith (1986b) and Panova et al. (2012) reported that pulsed sounds with lower pulse repetition rate (blare, moan, groan, "eeee") were emitted by wild belugas from both Canada and Russia more often during periods of rest, quiet swimming, and social interaction than those emitted during other behaviors, such as alarm situations, or feeding. Click series, which have a wider range of frequencies, more consistent repetition rates, and longer durations than other pulsed sounds with broadband frequency, are produced more frequently during social interaction than in alarm situations (Sjare and Smith 1986b). Temporarily captured mother–calf pairs and a solitary female also produce such click series (Van Parijs et al. 2003), which implies that click series have a communication function.

One type of burst pulse sound, the Type A call, is reported to function as a contact call between a mother and her offspring (Vergara and Barrett-Lennard 2008). Vocal exchanges between a mother and her calf has also been reported, and responses usually occur within 2 s of the first call (Vergara et al. 2010). Although Vergara et al. (2010) reported several variants of Type A calls, these variants did not correspond to individual signatures.

Here, we report one type of burst pulse sound (PS1 call), with individual identity, that was produced by captive belugas and was used for vocal exchange. We analyzed the pulse repetition rate patterns and acoustic sequence of PS1 calls from 3 captive belugas. The belugas were originally from Russia, and the sounds were recorded at the Port of Nagoya Public Aquarium in Japan. The pulse repetition rate patterns were studied to determine whether there were individual differences in PS1 calls. The temporal patterns of sounds, including PS1 calls and whistles, were studied in order to understand how belugas exchange sounds. Individual differences in PS1 calls, sound exchanges between individuals, and acoustical variation during sound exchanges are discussed in this report.

Materials and methods

Study sites and subjects

Video and acoustic recordings of belugas were made at the Port of Nagoya Public Aquarium in Japan. Two adult female belugas (#5 and #6) and 1 male beluga (#1) were
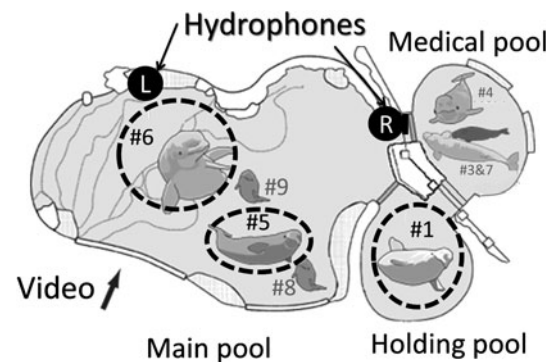
Fig. 1 Schematic view of the pools containing belugas in the Port of Nagoya Public Aquarium, Japan. Locations of video and sound recording equipment are shown. *Numbers* (e.g., #1) refer to individual belugas (*Delphinapterus leucas*): *#1*, *#5*, and *#6* were the belugas used in this study

the subjects of this study. Female beluga #5 was estimated to be 8 years of age and #6 was estimated to be 12 years of age. The male beluga #1 was estimated to be 19–24 years of age. All 3 belugas came from Russia in 2001. Belugas #5 and #6 were housed in the main pool (24 m in length, 16 m in width, and 6 m in depth) with their calves (#8 and #9, respectively). Beluga #1 was housed in a holding pool that was 7 m in diameter and 5 m in depth, while the remaining 3 belugas (females #3 and #4 and 3-year-old male calf #7) were housed in a medical pool. A schematic view of the pools is provided in Fig. 1. A metal lattice or net separated the 3 pools and prevented the belugas from entering the other pools, but permitted acoustic communication.

Video and acoustic recordings

Video and acoustic recordings were made from June 9 to October 29, 2007, as a part of a beluga acoustic development project. Beluga #8 was born on July 22, 2007, and #9 was born on July 25, 2007. On the basis of good signal-to-noise ratio, we selected three 60-min sessions after #8 and #9 were born for this analysis. During all 3 sessions, there was no social interaction, including tactile behavior or aggressive interaction between mothers, and no human disturbance of the belugas. The belugas engaged in circular swimming with their own calves during these sessions. Video recordings were made using a Sony HVR-A1J video camera (Tokyo, Japan) from an underwater viewing location that had a view of the entire pool. Vocalizations were recorded at a 16-bit, 96 kHz sampling rate on 2 channels of a Roland R-4 HDD recorder (Shizuoka, Japan) that was connected to 2 OKI SW1030 amplifiers with OKI ST1030 hydrophones (Tokyo, Japan) that had 1 kHz high-pass filters. On October 29, 2007, high frequency recordings at a 16-bit, 500 kHz sampling rate were created using an NF

EZ7510 data recorder (Kanagawa, Japan) that was connected to the same amplifiers and hydrophones used for previous recordings. This second recording included the entire spectra of the calls. The 2 hydrophones were placed in the main pool at a depth of 1 m and were separated by 17.8 m.

Data analysis

All sounds were analyzed using Avisoft SASLab Pro version 4.50 software (Avisoft Bioacoustics, Berlin, Germany, 2008). Sound spectrograms of all sounds with a good signal-to-noise ratio were generated using the fast Fourier transform (FFT) algorithm, with FFT length of 512, 100 % frame size, a Hamming window, and 50 % overlap. This resulted in a frequency resolution of 977 Hz and a temporal resolution of 0.512 ms. An inter-pulse interval was defined as the interval between the envelope peak of one pulse and that of the next pulse. Inter-pulse intervals were measured using the pulse train analysis function in Avisoft SASLab Pro. All statistical analyses were performed using JMP v.7 software (SAS Institute, Cary, NC, USA).

Identification of the sound-producing individuals was performed by associating the position of all individuals in the video frame with the direction of the sound source. The direction of the sound source was determined by measuring the difference in the timing of sound arrival at the 2 hydrophones. Sound speed was calculated to be 1,504 m/s on the basis of salinity (31.5 ppt) and temperature (15.5 °C) measurements that were used in the Medwin equation (Medwin 1975). Since the 2 hydrophones were located on the left and right side of the main pool and were 17.8 m apart (Fig. 1), the sound source could be identified as follows: (1) if the sound was recorded by the left hydrophone before the right, the sound was deemed to have come from the left side of the main pool; (2) if the time difference (all calculated as left time − right time) between sounds recorded was between 0 and 10.06 ms, the sound was deemed to have come from the right side of the main pool; (3) if the time difference was between 10.06 and 11.83 ms, the sound came either from the right side of the main pool or from the holding pool; (4) if the time difference was approximately 11.83 ms, the sound was produced by beluga #1 in the holding pool; and (5) if the time difference was >11.83 ms, the sound was deemed to have come from the medical pool.

Sound category

Preliminary recordings were made on May 20–22, 2007, before the birth of the 2 neonates (#8 and #9). One of the authors (T.M.) classified the sounds by using both
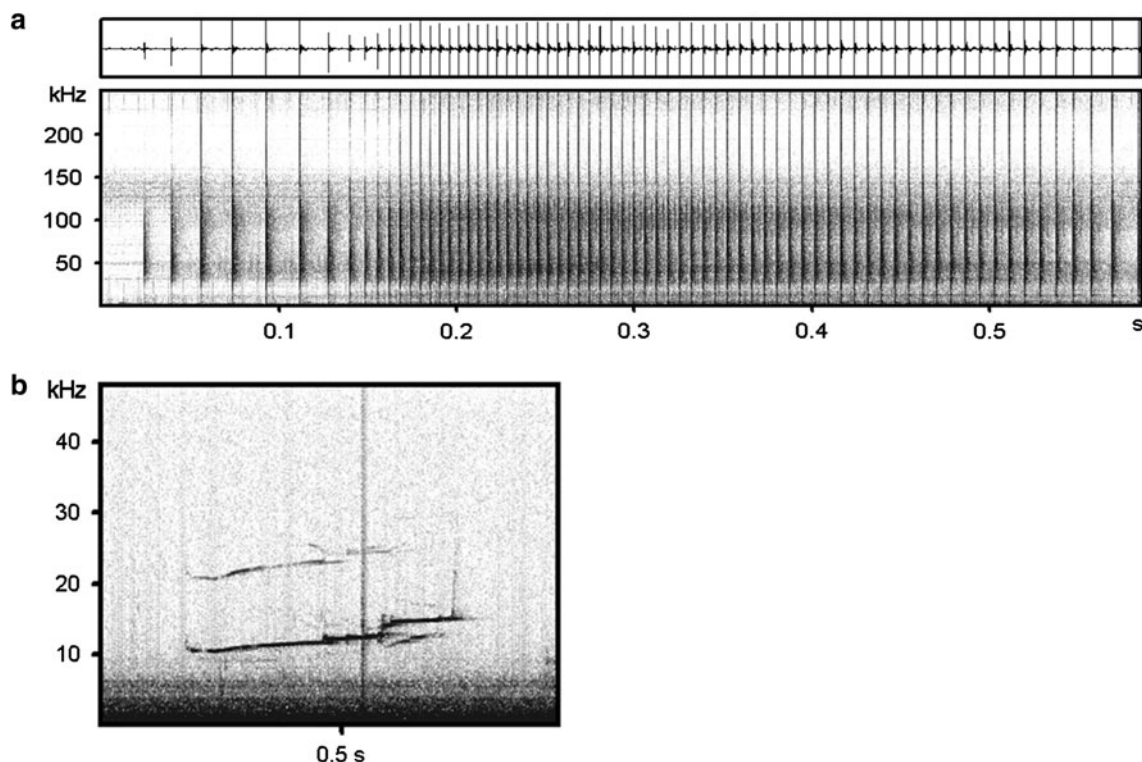

Fig. 2 Examples of spectrograms for sounds produced by captive belugas in the Port of Nagoya Public Aquarium. Sounds are: **a** PS1 call and **b** whistle

spectrograms and the recorded sounds. One type of pulsed sound (PS1 call; Fig. 2a) was predominant among the sounds produced by the belugas at the Port of Nagoya Public Aquarium (49 % of all sounds) on the day of the recording. The PS1 call is a fixed pulse train that sounds like a ratchet or a door creaking to human ears, and it is easy for humans to discriminate PS1 calls from other sounds made by belugas. PS1 calls have a typical pulse-repetition pattern structure: the inter-pulse intervals (IPIs) decrease at first, become constant, and then rapidly increase at the end of the call. Because belugas have various sound repertoires, especially burst-pulse sound repertoires, we categorized sounds into 4 categories: clicks, whistles, PS1 calls, and other sounds. Clicks are pulsed sounds and have a high dominant frequency that result in a "click" sound to the human ear. Clicks also have longer IPIs than PS1 calls. In our preliminary recordings, 95 % of click IPIs were 0.02–0.12 s. Whistles are "tonal" or narrowband signals without pulses and usually have harmonics similar to those of delphinid whistles (Fig. 2b). If the "tonal" or narrowband signals without pulses have sideband or "polyphonic" harmonics, we categorized them as other sounds. A variety of sounds were categorized as other sounds, including many kinds of pulsed sounds and mixed sounds (pulsed sounds and whistles). Variations within whistles, clicks, and other sounds were not considered in this study.

Sound character and sound exchange pattern analysis

IPIs and the number of pulses within PS1 calls with good signal-to-noise ratios were measured and analyzed for individual differences. Duration of the PS1 calls (time difference between the peak of the first pulse and the peak of the end pulse) were also measured. Inter-sound intervals, defined as the latency period from the end of a sound to the beginning of the next sound, were measured and used to examine sound exchanges between individuals. Inter-sound intervals were limited to 10 s. Inter-call intervals were
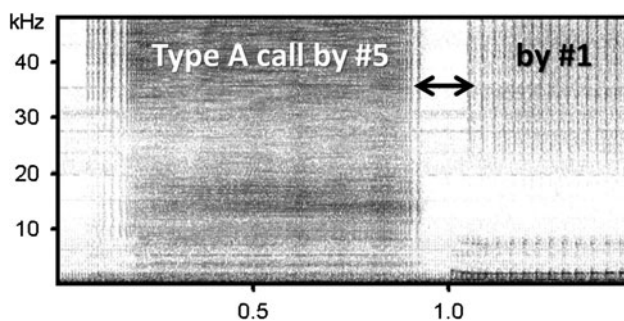
Fig. 3 An example of a PS1 call exchange between belugas. Beluga #1 responded with a PS1 call to #5's PS1 call (DC sequence). The *arrow* indicates the inter-call interval

defined as the latency period from the end of a PS1 call to the beginning of the next PS1 call (Fig. 3). Inter-whistle intervals were defined as the latency period from the end of a whistle to the beginning of the next whistle. A sequence of 2 consecutive sounds were classified according to Sugiura (1993) and Nakahara and Miyazaki (2011) as follows: (1) 2 consecutive sounds emitted by 2 different callers (DC sequence; Fig. 3) or (2) 2 consecutive sounds emitted by the same caller (SC sequence). Only sound exchanges between the 3 focal individuals (#1, #5, and #6) were analyzed.

Results

A total of 550 sounds, including 323 PS1 calls, 184 whistles, and 43 other sounds were recorded and the callers identified. These sounds included 75 PS1 calls from beluga #1, 140 from #5, 63 from #6, and 45 from non-focal individuals. Figure 2a provides an example recording of a PS1 call, and Fig. 2b shows an example of a whistle.

Individual differences in PS1 calls

Sixteen PS1 calls from beluga #1, 25 from #5, and 16 from #6, all with good signal-to-noise ratio, were selected and used for this analysis. Individual PS1 calls differed significantly in average inter-pulse interval of each call (one-way ANOVA, $F(2,54) = 2,194$; $p < 0.0001$) and number of pulses within one call (one-way ANOVA, $F(2,54) = 42$; $p < 0.0001$). All pairwise comparisons using Tukey–Kramer HSD tests ($\alpha = 0.05$) showed significant differences between the average inter-pulse interval of individual calls and between the number of pulses within individual calls. Multivariate discriminant function analysis correctly classified 100 % of the PS1 calls made by 3 individuals using the average inter-pulse interval of each call and the number of pulses within a single call ($n = 57$, Wilks $\lambda = 0.008$, $F = 266.4$, $p < 0.0001$). The male beluga (#1) had longer inter-pulse intervals (29.3 ms on average) and fewer pulses within calls (32.1 pulses) than the female belugas (#5, 6). Female beluga #5 and #6 averaged 8.01 and 11.7 ms per inter-pulse interval, and 110 and 66 pulses per call, respectively (Table 1). The pulse repetition patterns shown in Fig. 4 provide a snapshot of the individual differences in PS1 calls. All calls used for this analysis (57 calls) are shown in Fig. 4. The duration of PS1 calls was also significantly different among individuals (Wilcoxon/Kruskal–Wallis test, $\chi^2 = 35.4$, $p < 0.0001$). Tukey–Kramer HSD tests ($\alpha = 0.05$) indicated significant differences in the duration of PS1 calls between #1 and #5 and between #1 and #6, but not between #5 and #6 (Table 1).

Table 1 Sound characteristics of the PS1 calls made by belugas (*Delphinapterus leucas*), including the average IPI within each PS1 call, number of pulses within each PS1 call, and duration of PS1 calls

ID	Averaged IPI within each PS1 call (ms)					Number of pulses within each PS1 call					Duration of PS1 calls				
	n	Average	SD	Min	Max	n	Average	SD	Min	Max	n	Average	SD	Min	Max
#1	16	29.3	1.2	27.1	32.0	16	32.1	5.7	24	43	70	0.95	0.19	0.56	1.40
#5	25	8.0	1.1	6.3	9.7	25	109.6	39.6	67	217	130	0.82	0.19	0.41	1.48
#6	16	11.7	0.7	10.7	12.8	16	66.0	8.9	52	80	60	0.77	0.14	0.40	1.15
All	57	15.0	9.2	6.3	32.0	57	75.6	42.3	24	217	260	0.85	0.19	0.40	1.48

Data from 3 focal individuals and all summed data are shown

n number of analyzed sounds, *SD* standard deviation, *min* minimum value, *max* maximum value
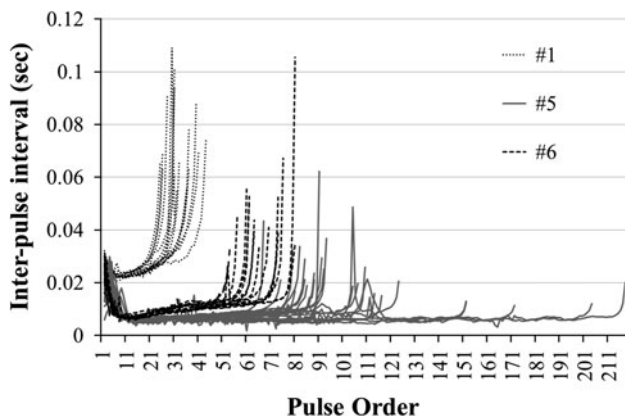
Fig. 4 Pulse repetition patterns of PS1 calls from 3 belugas. "#1" refers to a PS1 call from beluga #1, "#5" from beluga #5, and "#6" from beluga #6

Sound exchanges between individuals

Table 2 shows the total sequence numbers and average number of sound exchanges. A total of 175 DC and 24 SC sequences of PS1 calls and 41 DC and 32 SC sequences of whistles were identified. We identified 82 DC sequences of PS1 call–whistle exchanges and 90 DC sequences of whistle–PS1 call exchanges (Table 2). The distribution of the inter-sound intervals of DC and SC sequences in PS1–PS1 and whistle–whistle exchanges are shown in Fig. 5a and b, respectively. The distributions of the inter-sound intervals of DC sequences in PS1–whistle and whistle–PS1 exchanges are shown in Fig. 5c. There was a significant difference between inter-call intervals of DC and SC sequences for PS1 calls (Wilcoxon/Kruskal–Wallis test, $Z = 5.87$, $p < 0.0001$). No difference was observed between the inter-whistle intervals of DC and SC sequences for whistles (Wilcoxon/Kruskal–Wallis test, $Z = -1.32$, $p = 0.19$). Eighty-eight percent of PS1-call DC sequences occurred within 1 s, while 67 % of PS1-call SC sequences occurred after 1 s (Fig. 5a). There were

Table 2 The total number of sound exchanges and the average and standard deviation of sound exchange intervals in captive belugas. PS1 refers to a PS1 call

Exchange type	Sequence	n	Average (s)	SD
PS1-PS1	DC	175	0.13	1.01
	SC	24	1.46	1.40
Whistle-whistle	DC	41	1.53	2.03
	SC	32	0.57	0.65
Whistle-PS1	DC	90	0.69	1.12
PS1-whistle	DC	82	1.05	1.36

significant differences among the inter-sound intervals of DC sequences for the 4 sound exchange types (Kruskal–Wallis test, $\lambda^2 = 80.2$, $p < 0.0001$). DC sequences of PS1–PS1 exchanges had significantly shorter inter-call intervals (0.13 s on average) than the other 3 types of sound exchanges. The other 3 types of sound exchanges did not differ in inter-sound interval, except for the intervals between whistle–whistle and whistle–PS1 exchanges (Tukey–Kramer's HSD test, $q = 2.58$, $\alpha = 0.05$).

Acoustical change during sound exchange: preliminary analysis

To measure how response calls affected the caller's next acoustic behavior, we analyzed successive PS1 calls produced by the same individuals (#1, #5, #6) that occurred with and without response calls within 1 s of the initial call. Inter-call intervals between successive PS1 calls produced by the same individual without any other sound (inter-call interval in the PS1-call SC sequence) were significantly shorter than those with other's PS1 response calls (Wilcoxon/Kruskal–Wallis test, $Z = -2.11$, $p = 0.04$). We did not observe a DC sequence of PS1–whistle that was followed by a second PS1 call from the animal that produced the initial PS1 call. Therefore, we could not compare the effect of whistles on subsequent PS1 calls produced by the same animal.
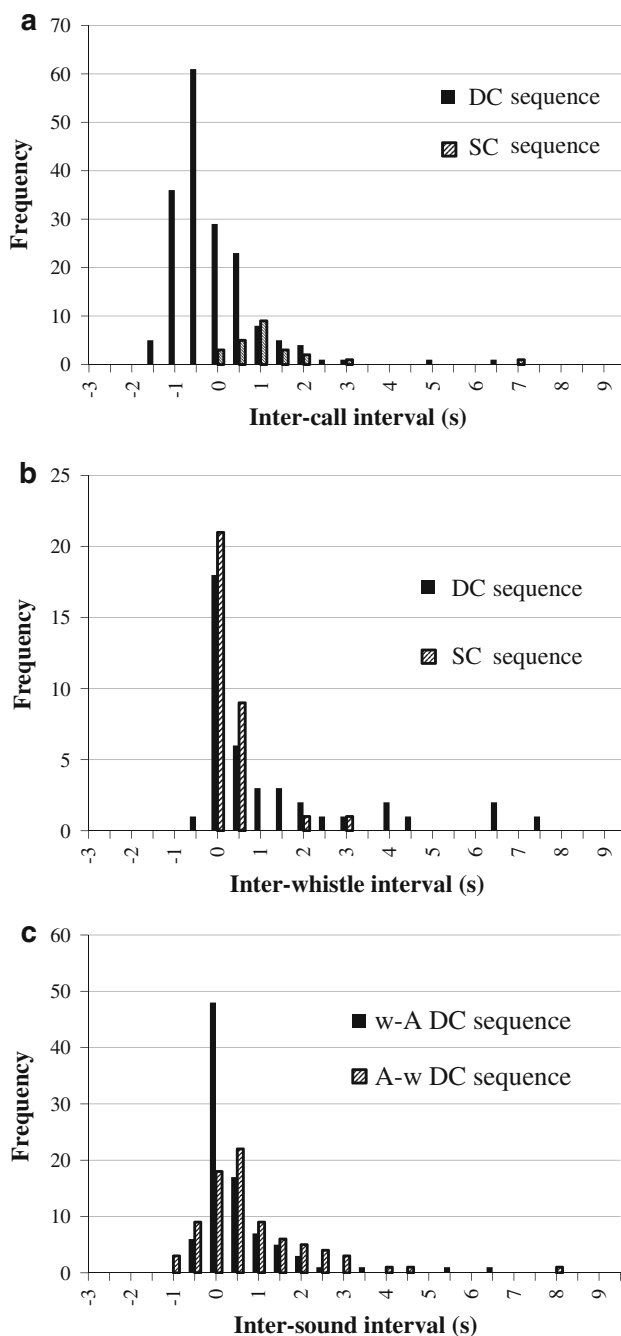
Fig. 5 The distribution of the inter-sound intervals of DC and SC sequences for 4 types of sound exchange: **a** PS1 call–PS1 call, **b** whistle–whistle exchange, **c** DC sequences of whistle–PS1 call exchanges (w-A DC sequence), and **d** DC sequence of PS1 call–whistle exchanges (A-w DC sequence)

Discussion

The results of this study showed clear individual differences and sound exchange patterns of PS1 calls. This suggests belugas use PS1 calls as a "signature" and for sound exchanges. This pattern is similar to the "signature whistle" of bottlenose dolphins (Nakahara and Miyazaki 2011). The exact function of sound exchanges involving PS1 calls in belugas is unknown, but mate attraction and territorial defense are not likely because 2 females exchanged PS1 calls, as did a male with females. In addition, there are no reports of "territory" in belugas. Social bonding or group cohesion are candidates for the function of PS1 calls.

Individual differences in PS1 calls

Clear individual differences in PS1 calls among adult captive belugas were observed in this study. There are no previous reports of stable individual differences in specific calls of belugas. Shapiro (2006) reported that there were clear individual differences in the pulse repetition rate patterns of the tonal/pulsed signals produced by narwhals (*Monodon monoceros*) that were similar to the individual differences among the PS1 calls of belugas in this study. As narwhals and belugas belong to the same family, Monodontidae, it is not surprising that they have similar communication patterns. Group-specific pulsed sounds ("codas") in sperm whales (*Physeter macrocephalus*) also show individual differences (Antunes et al. 2011).

"Signature" call exchange

Nakahara and Miyazaki (2011) showed that the intervals of DC sequences were significantly shorter than those of SC sequences in the whistles of captive bottlenose dolphins. In addition, approximately 70 % of second whistles in DC sequences occurred <1.0 s after the first whistle, whereas approximately 90 % of second whistles in SC sequences occurred more than 1.0 s after the first whistle (Nakahara and Miyazaki 2011). These sound exchange patterns of whistles in bottlenose dolphins resemble those of PS1 calls in belugas, but not those of whistles in belugas. Our preliminary analysis showed that belugas tend not to repeat PS1 calls if other individuals respond with a PS1 call within 1 s. Thus, it appears belugas wait 1 s for the response from other belugas, and will repeat a PS1 call unless they hear a response within 1 s. Similar call-back patterns are found in group-living mammals such as Japanese macaques (*Macaca fuscata*) (Sugiura 1993, 2007), killer whales (*Orcinus orca*) (Miller et al. 2004), sperm whales (Schulz et al. 2008), and bottlenose dolphins (Janik 2000; Nakahara and Miyazaki 2011), where individuals need to stay close to other group members. Belugas are also a gregarious species and appear to have a relatively fluid social structure. Several stable female "assemblages" in summer reproductive gatherings have been observed in Russia (Chernetsky et al. 2011; Krasnova et al. 2012), whereas Michaud (1999) reported a fission–fusion-like

society of St. Lawrence belugas that was revealed during a long-term photo identification study. Odontocetes with stable societies include sperm whales and killer whales, both of which have group-specific calls that are used for sound exchange (Miller et al. 2004; Schulz et al. 2008, 2011). In contrast, odontocetes with fission–fusion societies, including bottlenose dolphins, have individual-specific signature whistles that are used for sound exchange (Nakahara and Miyazaki 2011). The functions of these call-back patterns have not been fully revealed, but Japanese macaques, killer whales, and bottlenose dolphins might use these patterns to locate each other when visually isolated. Sperm whales might use these patterns for reinforcing group-level social bonds (Schulz et al. 2008). Further research is needed to investigate whether PS1 calls in belugas are group-specific, and to investigate the function of the PS1 call. This would clarify the relationship between social structure (fission–fusion or stable society), sound individuality (group-specific and/or individual distinct), and sound exchange patterns (call-back or not) in odontocetes.

Different whistle functions in belugas

Belugas produced whistles in SC sequences (44 %) as often as in DC sequences (56 %), whereas PS1 calls were produced much more frequently in DC sequences (88 %) than in SC sequences (12 %). This suggests that belugas tend to repeat whistles and to respond to other PS1 calls. These results, combined with the lack of difference between the DC and SC whistle sequence intervals, implies that whistles have a different function in belugas than in bottlenose dolphins. Van Parijs et al. (2003) also discussed the difference between whistle usage in belugas and in many delphinid mother-calf contact behaviors. The results of the present study suggest that future observation of individual differences in beluga whistle structure should not be regarded as "signature whistles" that have a similar function to those of bottlenose dolphins.

Comparison with other published papers

Several researchers have attempted to categorize the sounds from both captive and wild belugas (Sjare and Smith 1986a; Karlsen et al. 2002; Van Parijs et al. 2003; Belikov and Bel'kovich 2008; Vergara et al. 2010; Chmelnitsky and Ferguson 2012). The PS1 calls reported here had fixed pulse-repetition patterns (down-constant-up IPIs) with 15 ± 9 ms IPIs (average ± standard deviation), an average of 67 pulses/s, 76 ± 42 pulses within each call, and 0.85 ± 0.2 s call duration (Table 1). The pulsed tone type H categorized in group 3 calls (lower repetition rate moans and "eeee" sounds) of wild belugas in the Northwest Territories, Canada, with 80–290 pulses/s and click

series type J or K with 85 and 130 pulses/s reported by Sjare and Smith (1986a, b) were similar to PS1 calls in terms of pulse repetition rate and spectrogram. Type H tones, in particular, seem to have the same pulse repetition pattern as PS1 calls: inter-pulse intervals (IPIs) decrease at first, become constant, and rapidly increase at the end (fig. 3 in Sjare and Smith 1986a). The calls categorized in group 3 calls had little variation in pulse repetition rate, varied in duration at the end of the call (Sjare and Smith 1986a), which is similar to the PS1 call pattern. A greater number of pulsed calls categorized in group 3 calls were emitted during periods of rest and social interaction than during alarm situations, and so were an indication of compact and stationary groups of belugas near the water surface (Sjare and Smith 1986b). Click series were also emitted more frequently during social interaction than during other situations, such as resting, directive swimming, and alarm situations (Sjare and Smith 1986b). This implies that click series may have a communicative function.

The lPT3 and lPT4 pulsed tones with low pulse repetition rate produced by wild belugas in Russia and reported by Belikov and Bel'kovich (2008) and Panova et al. (2012) have spectrograms that resemble PS1 calls and appear to have the same pulse-repetition pattern: down-constant-up IPIs. The lPT3 tone has 13–630 pulses/s and a duration of 0.87 ± 0.43 s, while lPT4 has 418–500 pulses/s (these numbers may have been misprinted because the same numbers appeared for the initial, terminal, minimal, and maximal pulse repetition rate in table 2 of Belikov and Bel'kovich 2008) and a duration of 1.52 ± 0.36 s (Belikov and Bel'kovich 2008). The lPT3 and lPT4 tones have faster pulse repetition rates than the PS1 call, but are of similar duration. Pulsed tones with low pulse repetition rates, including lPT3 and lPT4 (moans and groans), were emitted significantly more often during quiet swimming and during social interactions than during other behavior types such as feeding and exploration (Panova et al. 2012). This pattern is similar to that of the group 3 pulsed calls reported by Sjare and Smith (1986b). Click series were emitted during social interaction and resting, but were less frequent than during exploration of the hydrophone. Similar to Sjare and Smith (1986b), click series were emitted significantly less frequently during directive swimming and feeding situations than during other behaviors (Panova et al. 2012). Since these behaviors (directive swimming and feeding) need echolocation behavior more frequently than the other behaviors (such as resting and social interaction), click series have a function that is different from, or in addition to, echolocation.

The pulsed type II calls (click series with low pulse repetition rates) reported by Karlsen et al. (2002) for wild belugas in Norway have similar spectrograms to PS1 calls, with down-constant-up IPI patterns. Type II calls also have a similar pulse repetition rate to PS1 calls, with 104 ± 64

(23–240) pulses/s of start pulse repetition rate, and a slightly shorter duration than PS1 calls, at 0.55 ± 0.54 (0.07–3.12) s in duration. A mother beluga that was temporarily captured in the same area (Svalbard) produced distinct audible "crooning" click trains while her head was toward her calf (Van Parijs et al. 2003). These repetitive click trains had an average of 27 pulses/s (0.012–0.46 s IPIs) and were 1.9 ± 1.3 s in duration. Her calf produced click trains that were an average of 18 pulses/s (0.09–0.5 s of IPIs) and 0.6 ± 0.5 s in duration. A different sub-adult female produced click trains that were an average of 22 pulses/s (0.03–0.41 s IPIs) and 0.3 ± 0.08 s in duration (Van Parijs et al. 2003). These calls had shorter IPIs than PS1 calls, but were similar in duration.

The pulsed call type P5 (clink) and P2 (thick creak) of wild belugas in the Churchill River, Canada, that were reported by Chmelnitsky and Ferguson (2012) have similar spectrograms to PS1 calls. P5 calls are similar in IPI and duration to PS1 calls, with 48 ± 8 pulses/s and 1.09 ± 0.64 s in duration. P2 calls have shorter IPIs than PS1 calls, with 207 ± 57 pulses/s, but have a slightly longer duration than PS1 calls, at 1.16 ± 0.36 s. Belugas captured at this river and kept in captivity produce a "contact call" using a "Type A call" (Vergara et al. 2010). Type A calls are similar to the C5 calls reported by Chmelnitsky and Ferguson (2012), who discussed the similarity between Type A calls and C5 calls. C5 calls consist of a mixture of a P2 call and a higher whistle.

PS1 calls are thus similar to the pulsed sounds with low pulse repetition rates or fixed "click series" reported in various papers, as discussed above. Such calls are produced more frequently during social interaction, quiet swimming, resting, between mother and calf pairs, from male, or from solitary subadult females, and less frequently during feeding, directive swimming, and alarm situations. These calls may therefore function as "peaceful" contact or isolation calls, as do whistles in bottlenose dolphins, rather than as echolocation sounds, or "aggressive" alarm calls. The PS1 calls reported here were also produced during "peaceful" swimming by mothers with calves and a physically (but not acoustically) isolated male. No social contact between mothers and other individuals and no human disturbance occurred during the recording periods. PS1 calls are therefore the same as, or a variant of, the pulsed sounds with low repetition rate or fixed "click series" reported by other researchers and function as contact or isolation calls. This idea may be supported by the fact that mothers (#5 and #6) repeatedly emitted PS1 calls when their calves (#8 and #9) were captured (Morisaka, personal observation).

Future studies

This study showed individual differences among PS1 calls, sound exchange patterns between individuals, and acoustical changes during sound exchange in belugas. However, this study did not investigate whether PS1 calls convey individual identity via their pulse repetition pattern in a similar manner as signature whistles in bottlenose dolphins. Playback experiments are needed to further evaluate our hypothesis that PS1 calls function as "signature" calls in belugas and to investigate whether PS1 calls convey individual identities via pulse repetition patterns. Further studies examining the function of whistles in belugas should also be conducted.

It is difficult to find the "same" call type as PS1 calls in other papers because belugas produce an enormous number of pulsed sounds that researchers categorize using their own methodology (mainly through visual inspection). Future studies should focus on PS1 calls, pulse sounds with low repetition rate or fixed click series that are used in vocal exchanges, and examine variations between individuals and populations, especially variations in pulse repetition patterns.

References

Antunes R, Schulz T, Gero S, Whitehead H, Gordon J, Rendell L (2011) Individually distinctive acoustic features in sperm whale codas. Anim Behav 81:723–730

Belikov RA, Bel'kovich VM (2008) Communicative pulsed signals of beluga whales in the reproductive gathering off Solovetskii Island in the White Sea. Acoust Phys 54:115–123

Biben M, Symmes D, Masataka N (1986) Temporal and structural analysis of affiliative vocal exchanges in squirrel monkeys (*Saimiri Sciureus*). Behaviour 98:259–273

Caldwell MC, Caldwell DK (1965) Individualized whistle contours in bottlenose dolphins (*Tursiops truncatus*). Nature 207:434–435

Carter GG, Fenton MB, Faure PA (2009) White-winged vampire bats (*Diaemus youngi*) exchange contact calls. Can J Zool 87:604–608

Chernetsky AD, Krasnova VV, Bel'kovich VM (2011) Studies of the structure of the Solovetsky reproductive gathering of beluga whales (*Delphinapterus leucas*) in the White Sea using the photo identification method. Oceanology 51:275–280

Chmelnitsky EG, Ferguson SH (2012) Beluga whale, *Delphinapterus leucas*, vocalizations from the Churchill River, Manitoba, Canada. J Acoust Soc Am 131:4821–4835

Gerhardt HC, Roberts JD, Bee MA, Schwartz JJ (2000) Call matching in the quacking frog (*Crinia georgiana*). Behav Ecol Sociobiol 48:243–251

Janik VM (2000) Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289:1355–1357

Janik VM, Slater PJ (1998) Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Anim Behav 56:829–838

Janik VM, Sayigh LS, Wells RS (2006) Signature whistle shape conveys identity information to bottlenose dolphins. Proc Natl Acad Sci USA 103:8293–8297

Karlsen JD, Bisther A, Lydersen C, Haug T, Kovacs KM (2002) Summer vocalisations of adult male white whales (*Delphinapterus leucas*) in Svalbard, Norway. Polar Biol 25:808–817

Koda H (2004) Flexibility and context-sensitivity during the vocal exchange of coo calls in wild Japanese macaques (*Macaca fuscata yakui*). Behaviour 141:1279–1296

Kondo N, Watanabe S (2009) Contact calls: information and social function. J Psych Res 51:197–208

Kondo N, Watanabe S, Izawa K (2010) A temporal rule in vocal exchange among Large-billed crows (*Corvus macrorhynchos*) in Japan. Ornithol Sci 9:83–91

Krasnova VV, Chernetsky AD, Kirillova OI, Bel'kovich VM (2012) The dynamics of the abundance, age, and sex structure of the Solovetsky reproductive gathering of the beluga whale *Delphinapterus leucas* (Onega Bay, White Sea). Russ J Mar Biol 38:218–225

Masataka N, Biben M (1987) Temporal rules regulating affiliative vocal exchanges of squirrel monkeys. Behaviour 101:311–319

Medwin H (1975) Speed of sound in water—simple equation for realistic parameters. J Acoust Soc Am 58:1318–1319

Mennill DJ, Ratcliffe LM (2004) Overlapping and matching in the song contests of black-capped chickadees. Anim Behav 67:441–450

Michaud R (1999) Social organization of the St. Lawrence beluga whale. In: 13th biennial conference on the biology of marine mammals. The Society for Marine Mammalogy, Hawaii, pp 124

Miller PJO, Shapiro AD, Tyack PL, Solow AR (2004) Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. Anim Behav 67:1099–1107

Nakahara F, Miyazaki N (2011) Vocal exchanges of signature whistles in bottlenose dolphins (*Tursiops truncatus*). J Ethol 29:309–320

Oda R (1996) Effects of contextual and social variables on contact call production in free-ranging ringtailed lemurs (*Lemur catta*). Int J Primatol 17:191–205

Panova EM, Belikov RA, Agafonov AV, Bel'kovich VM (2012) The relationship between the behavioral activity and the underwater vocalization of the beluga whale (*Delphinapterus leucas*). Oceanology 52:79–87

Sayigh LS, Tyack PL, Wells RS, Scott MD (1990) Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*—stability and mother-offspring comparisons. Behav Ecol Sociobiol 26:247–260

Schulz TM, Whitehead H, Gero S, Rendell L (2008) Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. Anim Behav 76:1977–1988

Schulz TM, Whitehead H, Gero S, Rendell L (2011) Individual vocal production in a sperm whale (*Physeter macrocephalus*) social unit. Mar Mamm Sci 27:149–166

Shapiro AD (2006) Preliminary evidence for signature vocalizations among free-ranging narwhals (*Monodon monoceros*). J Acoust Soc Am 120:1695–1705

Sjare BL, Smith TG (1986a) The vocal repertoire of white whales, *Delphinapterus leucas* summering in Cunningham Inlet, Northwest Territories. Can J Zool 64:407–415

Sjare BL, Smith TG (1986b) The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. Can J Zool 64:2824–2831

Snowdon CT, Cleveland J (1984) "Conversations" among Pygmy Marmosets. Am J Primatol 7:15–20

Sugiura H (1993) Temporal and acoustic correlates in vocal exchange of coo calls in Japanese macaques. Behaviour 124:207–225

Sugiura H (1998) Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. Anim Behav 55:673–687

Sugiura H (2007) Adjustment of temporal call usage during vocal exchange of coo calls in Japanese macaques. Ethology 113:528–533

Tyack P (1986) Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? Behav Ecol Sociobiol 18:251–257

Van Parijs SM, Lydersen C, Kovacs KM (2003) Sounds produced by individual white whales, *Delphinapterus leucas*, from Svalbard during capture. J Acoust Soc Am 113:57–60

Vergara V, Barrett-Lennard LG (2008) Vocal development in a beluga calf (*Delphinapterus leucas*). Aquat Mamm 34:123–143

Vergara V, Michaud R, Barrett-Lennard L (2010) What can captive whales tell us about their wild counterparts? Identification, usage, and ontogeny of contact calls in belugas (*Delphinapterus leucas*). Int J Comp Psychol 23:278–309

Yosida S, Kobayasi KI, Ikebuchi M, Ozaki R, Okanoya K (2007) Antiphonal vocalization of a subterranean rodent, the naked mole-rat (*Heterocephalus glaber*). Ethology 113:703–710