Variability of Echolocation Clicks in Beluga Whales (*Delphinapterus leucas*) Within Shallow Waters

Zhongchang Song,[1,2] T. Aran Mooney,[2] Lori Quakenbush,[3] Roderick Hobbs,[4]
Eric Gaglione,[5] Caroline Goertz,[6] and Manuel Castellote[7]

[1]*State Key Laboratory of Marine Environmental Science, College of Ocean and Earth Sciences,*
Xiamen University, 361005 Xiamen, Fujian, China
[2]*Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543-1050, USA*
E-mail: amooney@whoi.edu
[3]*Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA*
[4]*Retired from Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service,*
NOAA, 6130 NE 204th Street, Kenmore, WA 98028, USA
[5]*Georgia Aquarium, 225 Baker Street NW, Atlanta, GA 30313, USA*
[6]*Alaska SeaLife Center, Seward, AK 99664, USA*
[7]*Cooperative Institute for Climate, Ocean, and Ecosystem Studies (CICOES),*
University of Washington and Marine Mammal Laboratory, Alaska Fisheries Science Center,
National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, USA

Abstract

While echolocation is vital to the sensory ecology of odontocetes, we have few data characterizing the signals of most species, limiting our understanding of key attributes of these animals, especially for those with a diverse range of habitats. Beluga whales (*Delphinapterus leucas*) have successfully overcome the pressures of living in both shallow and deep open water habitats. We characterized the echolocation clicks of 13 wild beluga whales during temporary capture-and-release events in Bristol Bay, Alaska (USA). We extracted and examined 556 high-quality clicks from approximately 22 hours of recordings. As a group, the duration (41.1 ± 17.3 µs; mean $\pm$ SD), peak frequency (97.9 ± 34.4 kHz), centroid frequency (101.9 ± 23.9 kHz), -3 dB bandwidth (29.1 ± 14.4 kHz), -10 dB bandwidth (67.7 ± 31.8 kHz), and root mean square (RMS) bandwidth (27.8 ± 8.1 kHz) were assessed. These are the first on-axis data from wild belugas in their natural shallow water habitat within 1 m. Beluga whales emit clicks with high frequency and high source level in extremely shallow waters regardless of the potential strong reverberations and clutter. These results provide a foundation for future studies on how this species manipulates its sonar to successfully operate in acoustically challenging shallow waters.

Key Words: odontocete, noise, soundscape, echolocation click, signal, cue

Introduction

Beluga whales (*Delphinapterus leucas*) are a coastal species widely distributed across often shallow Arctic and subarctic waters (O'Corry-Crowe, 2009). They produce a wide range of sounds and are generally considered a vocally active species (Belkovich & Shchekotov, 1992, 1993). Sounds produced include more than a dozen types of frequency-modulated calls and whistles. Belugas can also modify the acoustic properties of calls during social activities or when vessel noise is present. These have been fairly well examined (Caldwell et al., 1990; Angiel, 1996; Lesage et al., 1999; Belikov & Belkovich, 2007; Chmelnitsky & Ferguson, 2012; Garland et al., 2015). Given the general increase in human-produced ocean noise in the Arctic and beyond (Belkovich & Shchekotov, 1992; O'Corry-Crowe, 2009; Hobbs et al., 2019), characterizing acoustic behavior is vital as we seek to estimate, mitigate, and manage noise impacts. Certainly, understanding their acoustic signals would aid and support passive acoustic monitoring and evaluating impacts by noise. Such data may be particularly important for endangered populations such as the Cook Inlet beluga whale (Hobbs et al., 2019; Muto et al., 2019), and for those facing development and encroachment into their coastal habitats.

Much of our understanding of beluga echolocation clicks comes from studies of belugas in aquaria. Overall, their echolocation clicks generally have short durations and peak frequency ranges from 40 to 160 kHz (Au et al., 1985, 1987; Zahn et al., 2021). Under behaviorally controlled conditions, belugas

have shown that they are able to vary their clicks in a variety of ways (Au et al., 1985; Turl & Penner, 1989). For example, they can vary their peak frequency of emitted clicks from 40 to 120 kHz (Au et al., 1985). Belugas can also adjust source levels (SLs) and spectral distribution of clicks with more energy, extending to high frequency and increasing output in higher noise environments (Au et al., 1985).

This basic understanding of echolocation behavior of aquaria belugas has been extended with a few assessments of the echolocation behavior of wild individuals (Roy et al., 2010; Zahn et al., 2021). Yet, despite being a relatively well-studied odontocete, only two papers addressed the click parameters of wild belugas foraging in open waters (Roy et al., 2010; Zahn et al., 2021). Neither of these papers considered clicks emitted in shallow waters where beluga whales often forage (Martin & Smith, 1992; Ezer et al., 2008; Goetz et al., 2012). Information on click behavior in shallow waters over natural substrates will help define the natural parameters of wild beluga clicks and provide key information on how belugas use their capabilities in the acoustic environment to which they reside, as well as support the evaluation of potential noise impacts on the echolocation function of this species.

Beluga populations often reside in embayments or fjords. In these habitats, belugas take advantage of tidal cycles to swim to shallow waters, such as tidal flats, which are inundated by the rising tide, to follow runs of salmon and other anadromous fish spawning in rivers (Ezer et al., 2008; Citta et al., 2016). In Cook Inlet, for example, over 80% of the year is spent in shallow estuary waters and tidal areas (Goetz et al., 2012). In these shallow habitats, turbidity is often high, and sediment dynamics continuously change the configuration of channels such that echolocation is critical for navigation. Despite this unique scenario, the clicks produced by belugas during prey detection in shallow and turbid waters have not been quantified, and it is

unknown how such signals may compare to those of open-water and trained animals.

The goal of this study was to quantitatively analyze the patterns of clicks emitted by restrained wild beluga whales in their natural shallow water habitat (~1 m) and characterize their signals. Sounds were recorded at 1 m (a standard distance for SL measurements) directly in front of the animal during a temporary capture-and-release health assessment. These data provide examples of the variability of echolocation signals by belugas clicking in shallow waters within their habitat in Bristol Bay, Alaska, and may reflect strategies that belugas use under such shallow water scenarios.

Methods

Data Collection
We recorded vocalizations of belugas during two study periods—August-September 2014 and May 2016—for a total of 14 d in their natural shallow water habitat (Figure 1). We collected the recordings as part of a program aimed to assess the biology of individual belugas and the overall population health in Bristol Bay, Alaska. Work was co-coordinated by the Marine Mammal Laboratory (MML) at the Alaska Fisheries Science Center and the Alaska SeaLife Center. The research was conducted under National Marine Fisheries Service (NMFS) Marine Mammal Research Permit #14245 and approved by the Woods Hole Oceanographic Institute (WHOI), MML, and the Alaska Department of Fish and Game's Institutional Animal Care and Use Committees (Protocol IDs BI166330, AFSC-NWFSC2012-1, ADFG2014-03, and ADFG2016-23). More details of the capture-and-release procedures on the beluga whales can be found in previous papers (Castellote et al., 2014; Mooney et al., 2018). Briefly, belugas were captured using nets and temporarily restrained (2-h maximum) for health assessment sampling and attachment of biologging tags.

Figure 1. (a) Beluga (*Delphinapterus leucas*) groups in shallow waters, upriver in the Nushagak Bay, Alaska; (b) beluga groups in Black Slough, near the Nushagak River mouth; and (c) beluga pods near Clark's Point and Clark's Sough. Note the nearshore, shallow depth at which the belugas reside; their backs (dorsal surface) are often visible above the water. (Photos taken under NMFS Marine Mammal Research Permit #14245)

Acoustic signals were recorded during the health assessment process using a DMON broadband acoustic recorder (Kaplan et al., 2015). The DMON is a custom-built underwater audio recording system containing three configurable channels, all with a low-noise preamplifier (20 dB gain), 13.2-dB user programmable gain, a 6-pole Sallen-Key anti-alias filter, a 16-bit analog-to-digital converter, and 32 GB of flash memory. Data from the high-frequency channel were used as belugas can produce clicks over 100 kHz (Au et al., 1985, 1987). The sampling rate was 480 kHz with a bandpass filter of 1 to 160 kHz for the high-frequency channel. The preamplifier and ADC converter were embedded inside its main body, and the tool functioned as one unit, suspended 1 m directly in front of the beluga at a depth of 15 cm.

Care was taken to ensure on-axis recordings (Au et al., 1987). The instrument was handheld to maintain an on-axis alignment with the head during the recording period. The person responsible for the acoustic recording had the specific task of maintaining the recorder at 1 m from the tip of the rostrum by using a 1 m piece of rope attached to the recorder as reference and constantly following the belugas' head movements as closely as possible during recordings to maintain the hydrophone on the echolocation main beam axis. Veterinary evaluations and procedures often occurred concurrently with recordings; however, these were typically caudal of the blowhole, and no person or object was between the animal and the DMON recorder. The goal was to obtain clicks within the main beam axis of the echolocation emissions at 1 m distance from the beluga's rostrum, a distance outside the acoustic near field and relevant for SL and spectral measurements (Au et al., 1987).

During the tests, the respective belugas were maintained in ~1 m or less of water using a belly-band under their thorax, both anterior and posterior to their pectoral flippers. The dorsal surface was exposed to air, but the head and melon were underwater except when they exposed their blowhole to breathe. The belugas' underside usually rested on the sandy or muddy bottom. The belly-band had handholds for moving and controlling the belugas to help keep them in a constant position, although belugas could move their heads from side to side, hence the need to hold the recorder by hand to adjust position. The substrate was typically soft mud or fine-grain sand, and the water was turbid, precluding any visual subsurface observations. Capture-and-release events as well as the signal recordings were carried out throughout the Nushagak estuary, part of the Bristol Bay estuary system; the substrate and the level of turbidity varied by location. Within the sonar field of the belugas were the DMON recorder at 1 m, the lower body of the DMON handler at 1.5 to 2 m, and the soft substrate, thus the clicks that the belugas made were likely to image these objects and to monitor the waters directly ahead.

Data Analysis
Data recordings from 16 beluga whales were audited manually to identify click trains, while 13 belugas produced qualified clicks for subsequent analysis. These belugas are numbered as DL1, DL2, DL3, DL4, DL5, DL6, DL7, DL8, DL9, DL10, DL11, DL12, and DL13, corresponding to the whale IDs DLBBB16_01, DLBBB16_02, DLBBB16_03, DLBBB16_04, DLBBB16_05, DLBBB16_07, DLBBB16_09, DLBBB14_01, DLBBB14_02, DLBBB14_03, DLBBB14_06, DLBBB14_07, and DLBBB14_09, respectively, in a previous study (Mooney et al., 2018). Signals were then filtered using a Butterworth high-pass filter with a cutoff frequency of 5 kHz to dispel the low-frequency noise such as seawater fluctuation. Customized MATLAB scripts were then developed to extract individual clicks from the trains. Briefly, click trains were transformed into a time-frequency domain (Figure 2a). For signals sampled at 480 kHz, spectrogram $P(f, m)$ was calculated using the following formula:

$$P(f, m) = 10 \log_{10}(\text{abs}(F(f, m))) \qquad (1)$$

where $F(f, m)$ represents the short-time Fourier transform of the click and is calculated using a 1,024-point fast Fourier transform (FFT) with a 43.5% overlap and a Hann window (Yang et al., 2017), providing a time resolution of 1.2 ms and frequency resolution of 468.8 Hz. A median filter was then used to eliminate noise. In the spectrogram representation of the clicks, the higher pixel values $P(f, m)$ of the clicks could be distinguished from the lower values of surrounding noise.

Click Processing—To avoid off-axis and clipped clicks, and to extract quality ones, several steps of treatments were presented. To begin, a pixel threshold was determined in spectrogram (Figure 2a), and pixel values lower than the threshold were set to zero to isolate the clicks from the surrounding background noise (Figure 2b). The clicks were presented as separate vertical bands in a time-frequency domain. Thus, the time location of each click can be roughly determined, which was then used to extract clicks.

Then, in most extracted clicks, reflections followed the main (highest amplitude and 1st arrival) portion of the click (Figure 2c). To separate the principal part from each click, we used the time of the signal peak as a reference point and then selected a certain number of neighboring data points, which varied and depended on the specific click. A click clearly presents a broadband property
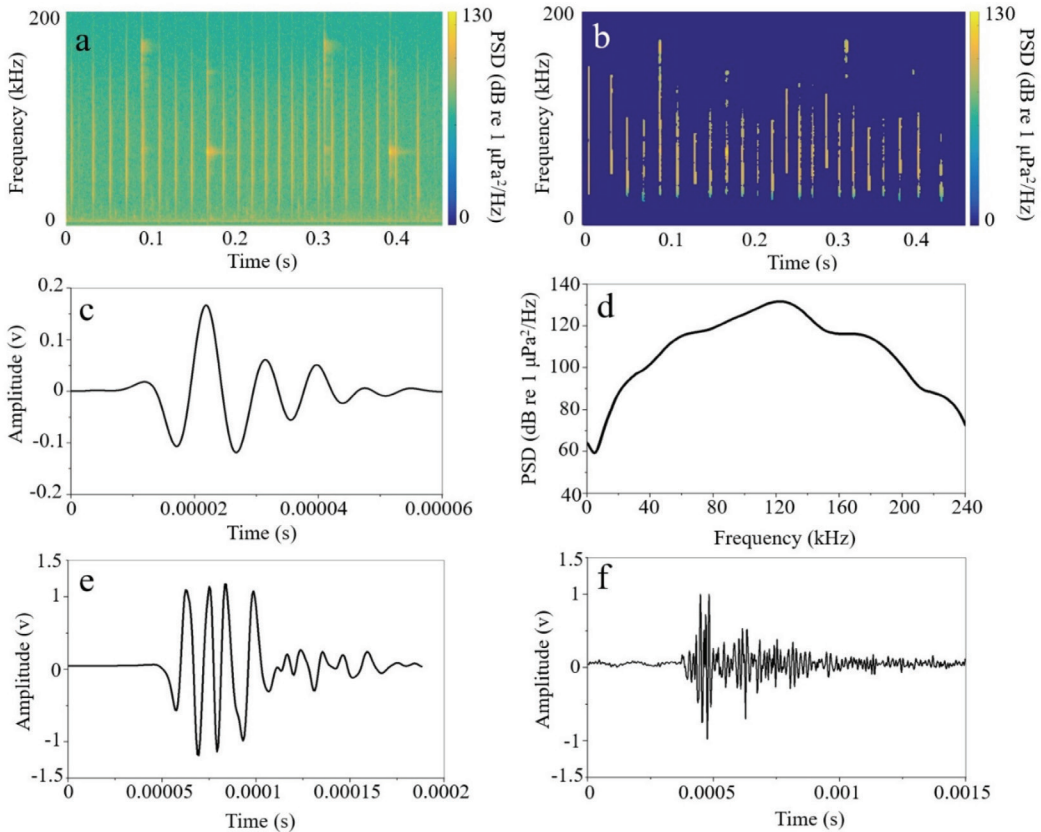
Figure 2. (a) A typical click train in time-frequency domain, (b) a typical click train presented after thresholding, (c) time series of a typical click extracted from the train, (d) fast Fourier transform (FFT) spectrum distribution of the click, (e) an example of a clipped click, and (f) an example of clicks with strong reverberations and reflections for which the principal part of the click is hard to extract.

(Figure 2d). For each click, the starting point was determined when the click oscillations rose from the background noise, while the ending point was set when the oscillations descended back into the background noise prior to the beginning of the reflection. The ultimate goal was to obtain a clean click without reflections. After extraction, clicks were examined manually to determine if they met the quality criterion for subsequent analysis.

The sensitivity of the hydrophone embedded in DMON had a mean value of -180.2 ± 6.2 dB re 1 μPa, ranging from -189.4 dB at 160 kHz to -174.2 dB at 5 kHz. Due to this variation, sensitivity at each frequency was used instead of applying the mean value to all frequencies. We used three criteria to select quality clicks from trains for further analysis. First, clicks with a signal/noise ratio (SNR) below 20 dB were removed from further analysis. Peak-to-peak noise levels were computed from 100-point (0.2 ms) time segments of

the raw signal without clicks and averaged over the duration of the recording for each beluga. The peak-to-peak level of click was compared to this noise level, and clicks with $SNR_{pp} \geq 20$ dB were used in subsequent analysis.

Second, clipped clicks were excluded from subsequent analysis. In subsequent review, these clipped waveforms had characteristic flattened peaks and a squared waveform (Figure 2e).

Third, clicks with strong reverberations were also rejected for subsequent analysis. In some cases, strong reverberations were noted (Figure 2f) that overlapped the principal part of the clicks. For these cases, it is often not possible to extract the principal part of the clicks. We did not use a click if the principal part of the click could not be extracted. Following these steps, off-axis and clipped clicks were omitted in the analysis, and we selected high-quality clicks (556 of 3,952) produced by the belugas from approximately 22 h of recordings.

Song et al.

Click Parameters—We measured the following parameters for each click: peak-to-peak source level (SL$_{pp}$; dB re 1μPa), source level root mean square (SL$_{RMS}$; dB re 1μPa), source energy flux density (SL$_{efd}$; dB re 1μPa^{2}s), duration (τ), peak frequency (f$_p$), centroid frequency (f$_{cen}$), -3 dB bandwidth (BW$_{-3dB}$), -10 dB bandwidth (BW$_{-10dB}$), and root mean square bandwidth (BW$_{RMS}$) (following Madsen & Wahlberg, 2007; Au et al., 2016). Here, SL$_{RMS}$ and SL$_{efd}$ were both calculated over the -10 dB duration of the signal, consistent with previous studies (Madsen & Wahlberg, 2007; Fang et al., 2015; Au et al., 2016). Duration was determined by the difference of two times between which the integrated energy included 95% of the total signal energy. The spectrum level, inter-click-interval (ICI), and the parameters described above for each animal were given to show a cross-individual comparison. The clicks from all individuals are analyzed together to estimate parameters for the Bristol Bay population and beluga species.

Results

Following strict procedures to guarantee that the clicks we selected were on-axis, we extracted 556 high-quality clicks out of a total of 3,952 clicks produced by 13 of the 16 restrained and sampled belugas, and determined these samples as suitable for analyses (i.e., high SNR$_{pp}$, non-clipped, with low reverberation); this included seven animals from 2016 and six from 2014 (Mooney et al., 2018). Clicks from the 13 belugas were fully characterized, providing 56 click trains and 556 clicks. These pulsed signals were generally similar in waveform to those of other odontocetes (Figure 2c). The spectrum distribution of the example click clearly shows a broadband property (Figure 2d). The spectra show variability among individuals with respect to peak frequency and bandwidth (Figure 3). Some animals produced clicks peaking at frequencies lower than 60 kHz.

Compiled, the median ICI for all the belugas was 25.2 ms. Beluga clicks had a mean duration of 41.1 μs; a centroid frequency of 101.9 kHz; a peak frequency of 97.9 kHz; and a bandwidth$_{-3dB}$, bandwidth$_{-10dB}$, and bandwidth$_{RMS}$ of 29.1, 67.7, and 27.8 kHz, respectively (Figure 4). Peak frequency varied substantially among belugas, and two belugas (DL2 and DL10) produced clicks peaking at 51.5 ± 14.9 kHz and 52.9 ± 17.9 kHz, respectively, much lower than others (Figure 4c). The remaining ten belugas produced only occasional clicks with such low peak frequencies. In general, peak frequency ranged from 27 to 168 kHz. The inter-individual variability was notable in click bandwidths, duration, and centroid frequency.
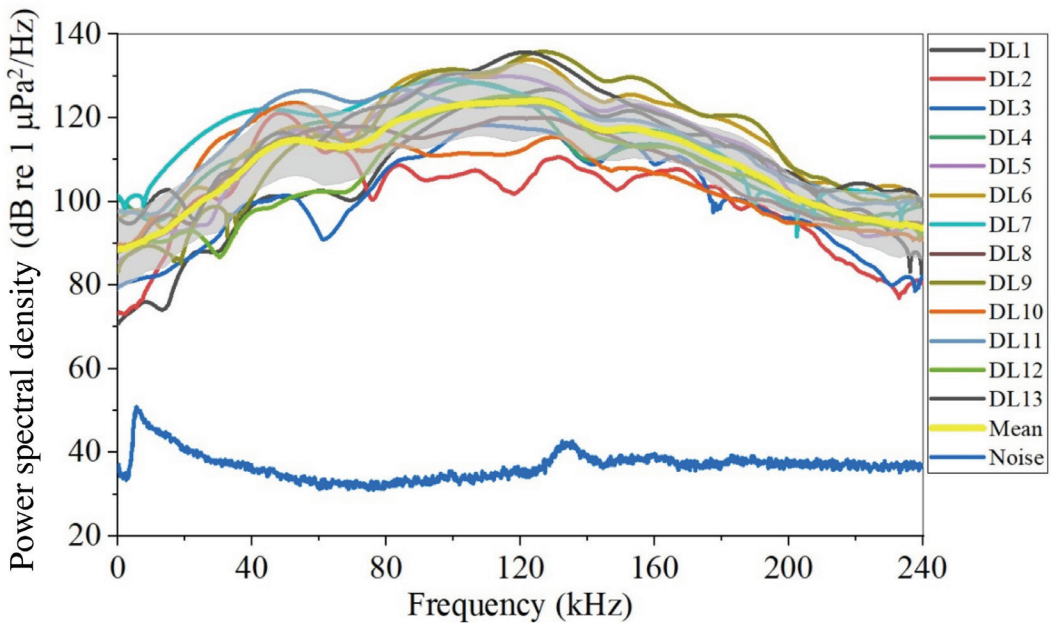

Figure 3. Power spectral density of the clicks for each beluga, background noise, and the mean spectrum of the clicks assembled from all belugas for which the shadow gives standard deviation

Histograms of the parameters were shown in Figure 5. Interestingly, peak frequency showed a bimodal distribution (Figure 5c). Thirty-four percent of the click peak frequencies were found between 20 and 60 kHz, and a second, slightly larger distribution (66%) was found between 80 and 140 kHz. Centroid frequency had a high proportion from 100 to 130 kHz (Figure 5b). Almost 90% of click durations were less than 60 μs, and less than 5% of the durations were over 90 μs (Figure 5a). Most clicks had a -3 dB bandwidth lower than 30 kHz and a -10 dB bandwidth between 20 and 100 kHz. The RMS bandwidth approached a normal distribution, with approximately 90% of the clicks between 15 and 40 kHz.

The relationships between SL_{pp} and other parameters were estimated using linear regression analysis (Figure 6). The slopes for duration and
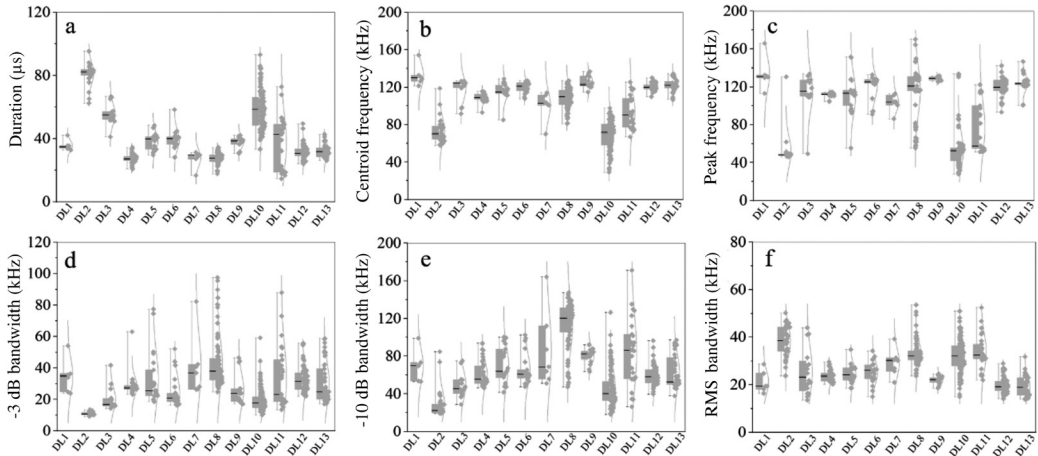

Figure 4. Bar distributions of (a) duration, (b) centroid frequency, (c) peak frequency, (d) -3 dB bandwidth, (e) -10 dB bandwidth, and (f) root mean square (RMS) bandwidth of echolocation signals for 13 restrained beluga whales from Bristol Bay, Alaska. Box bottom and top denote 25 and 75% percentile of the distribution, while median and mean values are represented by the line and square inside the box. Extension lines at the bottom and top provide the lower and upper edge values.
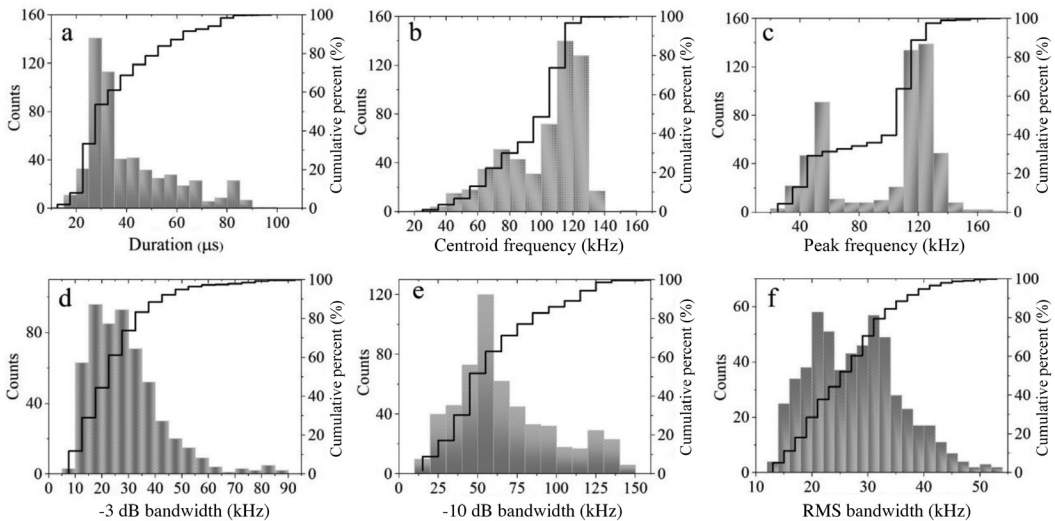

Figure 5. Histograms of (a) duration, (b) centroid frequency, (c) peak frequency, (d) -3 dB bandwidth, (e) -10 dB bandwidth, and (f) RMS bandwidth of all 556 analyzed clicks. The black line represents cumulative percentage. Peak frequency apparently presents a bimodal distribution.
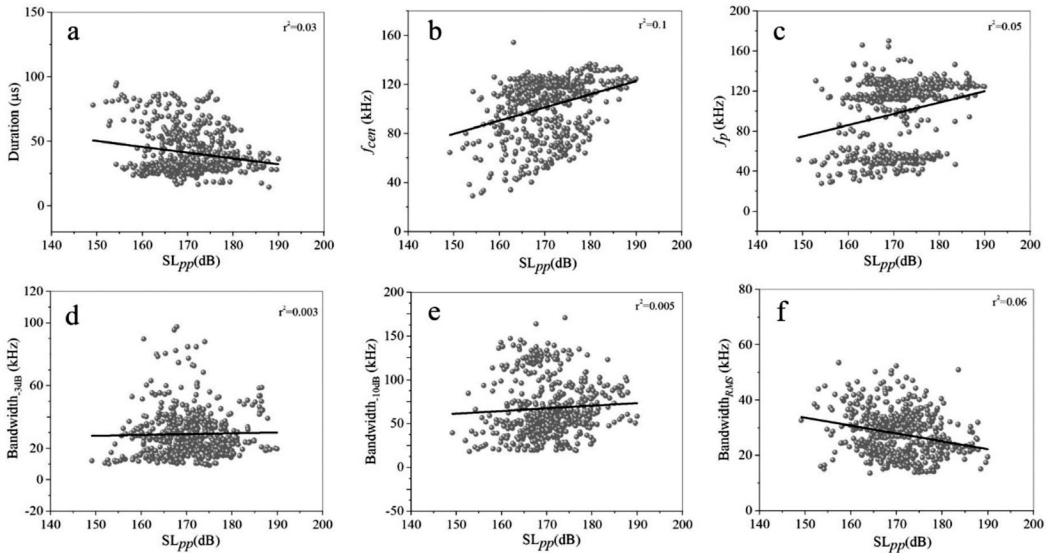
Figure 6. Scatter plots of the peak-to-peak source level (SL_{pp}) vs all parameters: (a) duration, (b) centroid frequency, (c) peak frequency, (d) -3 dB bandwidth, (e) -10 dB bandwidth, and (f) RMS bandwidth for the echolocation signals (clicks) of 13 beluga whales.

bandwidth$_{RMS}$ were negative ($p < 0.001$), while slopes for the remaining parameters were positive ($p < 0.001$), which means clicks with higher SL_{pp} have a lower duration and bandwidth$_{RMS}$. The rates of changes of centroid frequency and peak frequency with SL were close and not very high. The mean SL_{pp} for clicks produced by these belugas were 172.7, 166.8, 166.0, 165.6, 175.4, 179.7, 169.7, 167.5, 181.3, 169.9, 173.0, 169.5, and 177.3 dB. The maximum SL we noted was 189.9 dB from beluga DL6; beyond that, signals were clipped. The lowest SL_{pp} noted was 149.1 dB (DL2).

Over the bandwidth from 1 to 160 kHz, we evaluated the mean background noise level (dB re 1μPa) for each beluga as 120.7, 119.1, 121.8, 117.7, 122.6, 117.8, 127.6, 120.0, 121.5, 120.9, 120.0, 121.5, and 117.5 dB when clicks were recorded during the capture-and-release events. The background noise was relatively consistent across animals.

Discussion

Some populations of belugas are coastal using habitats that are typically shallow and exposed to tidal waters. For example, Goetz et al. (2012) quantified the foraging behaviors of belugas in Cook Inlet, Alaska, across 3 y and found that they tended to prefer shallow inshore waters throughout the year. Belugas were also found to take advantage of large tides (8 to 10 m range) to swim toward river mouths in shallow regions that are inaccessible during low tide (Ezer et al., 2008).

These shallow waters with constantly changing depths present an acoustically complex environment for belugas to navigate and forage. Yet, their broadband echolocation clicks are poorly understood, especially in shallow waters. In this article, the data provide the first analyses of on-axis echolocation clicks for wild beluga whales echolocating in extremely turbid shallow waters. This turbid water is the natural habitat for these animals where they carry out vital behaviors, including foraging and avoiding predators. The on-axis data provide a key reference when comparing and analyzing echolocation clicks of belugas from other populations (Roy et al., 2010; Zahn et al., 2021). These individuals showed the ability to produce clicks that differed substantially in SL, peak frequency, centroid frequency, duration, and bandwidth. These variabilities were found in clicks within and across individuals. Similar phenomena have been observed in trained (Au et al., 1985, 1987; Turl & Penner, 1989) and wild (Au & Benoit-Bird, 2003; Atem et al., 2009; Jensen et al., 2009) odontocetes, often as a result of changing range, target type, or background noise conditions. We sought to record clicks 1 m from the beluga as is standard for SL measurements (Au, 1993; Madsen & Wahlberg, 2007; Au & Hastings, 2009). This would also reduce the effect of reflections that would be more prevalent at greater distances, which later proved to be challenging given

that at 1 m, some signals were clipped, and in some cases, it was impossible to reduce all reverberation. However, we were able to discern and remove those problematic signals from further analyses to ensure reliability. Despite the need to exclude many clicks, the sample size of 556 clicks from 13 beluga whales allowed a complete analysis and characterization of the echolocation clicks emitted by belugas in their shallow habitat.

The analysis provided insights into the acoustic nature of beluga echolocation clicks. Beluga whales from this study produced clicks that peaked simultaneously at two different frequency ranges: (1) a relatively low peak value between 20 and 60 kHz and (2) a higher frequency range between 80 and 140 kHz. This bimodal structure of peak frequency has also been noted in captive belugas (Castellote et al., 2013), in wild tucuxi (*Sotalia fluviatilis*; Yamamoto et al., 2015), as well as in a single false killer whale (*Pseudorca crassidens*; Au et al., 1995). These studies are based on recordings from animals swimming around the hydrophone system, and this bimodal structure reflects the overall distribution from a population aspect. Our findings herein show these bimodal clicks can also be generated by a single animal. For many other odontocetes, the peak frequency distribution of clicks nearly follow a normal distribution (Au et al., 1999; Li et al., 2005; Fang et al., 2015). Au et al. (1985) found that a beluga can shift its click to higher frequencies when exposed to higher background noise levels, demonstrating the adaptability of its biosonar system. The background noise remained similar when the acoustic recordings were conducted on each of the 13 belugas, but many belugas produced clicks with bimodal peak frequency. Addressing the reason for this bimodal distribution may be best resolved using acoustic observations of free-swimming animals and addressing their broader sensory ecology.

There were some notable differences between the click parameters quantified here and those measured in other wild populations or in captive belugas (Au et al., 1985, 1987; Roy et al., 2010; Zahn et al., 2021). The clicks of belugas from Pointe-Noire, Québec, Canada, had a mean duration of 163 μs (Roy et al., 2010), longer than the 41.1 μs (n = 556) reported here. Roy et al. (2010) recorded signals from remotely deployed passive hydrophones in the water column, which might result in off-axis recordings that could lead to reflections following the main part of the click, causing longer durations. The peak frequency reported by Roy et al. was substantially lower (30 to 50 kHz) than that of the 96.9 kHz reported for wild belugas in West Greenland (Zahn et al., 2021), which was similar to our mean peak frequency of 97.9 kHz from individual belugas. Our findings show variability among individuals with some belugas capable of clicks peaking consistently over 100 kHz.

The SL_{pp} of a trained beluga reported by Au et al. (1985, 1987) was more than 195 dB, much higher than 170.5 dB as reported in this study. This is probably due to a downward bias of our data by removing certain clipped signals of the highest amplitude and perhaps also because of Au et al.'s (1985) noisy test environment with abundant broadband snapping shrimp pulses, which could have led to belugas increasing their SLs to achieve target detection within elevated background noise. Further, Au et al. (1985, 1987) likely tested the beluga in more challenging echolocation tasks that may have required higher amplitude clicks, thus their data may have been less similar to a "natural" situation. Also, only one beluga was tested in their study (compared to the 13 individuals examined here), thus individual differences might have contributed to the SL_{pp} difference. In our experimental scenario, recordings were made when the DMON, along with the person holding it, were likely the only two objects within the beluga's acoustic window in highly turbid waters. Much of what was recorded may be the beluga's efforts to image these two objects 1 to 2 m away, which might represent a limited click demonstration for the population and lead to a lower SL_{pp} than their full potential range.

Yet, SLs still approached up to 189.9 dB despite the fact that the clipped clicks with a higher SL were removed from our current dataset. The results reflected that the clicks examined in our shallow water habitat were comparable to those emitted by belugas foraging in deep waters with regard to SL, peak frequency, centroid frequency, and bandwidths (Zahn et al., 2021). Jensen et al. (2013) hypothesize those clicking in shallow waters might tend to produce clicks with low SLs and broad beam to avoid high acoustic clutter and reverberation. They examined the clicks from Irrawaddy dolphins (*Orcaella brevirostris*) and Ganges river dolphins (*Platanista gangetica gangetica*) in waters at 6.5 m and above, much deeper than our recording waters. The acoustic parameters of the clicks emitted by belugas during our study do not seem to follow the consistent low amplitude strategy in shallow waters as stated above. However, the belugas in our study did click at a higher rate, with a median ICI of 25.2 ms, comparable to those of Irrawaddy dolphins (30.1 ms) and Ganges river dolphins (27.8 ms) (Jensen et al., 2013), and much higher than that of the belugas (97.4 ms) in open waters (Zahn et al., 2021). A high repetition of clicks can ensure timely information updates, which are beneficial to life in shallow waters and may indicate a biosonar adaptation to shallow waters for belugas.

Of course, there may be variability across species. Ganges river dolphins may have a broader beam width, while the high-frequency and strong clicks in our dataset may correspond to a narrow beam for belugas (Au et al., 1985, 1987; Zahn et al., 2021), leading to a potentially narrow acoustic gaze, which seemed to have been a disadvantage for the livelihood in shallow waters. This may reflect belugas' specific biosonar adaptations to their diverse habitats in the Arctic and subarctic areas and result in a greater sonar variability in this species. Or, the beluga whales might have evolved other means to manipulate beam formation to compromise the adverse effect of emitting clicks of high frequency and high SL in shallow waters. This demonstrates the complexity of mechanism on echolocation process across the odontocetes.

A constraint of the work was considering whether the signals were on- or off-axis. Movements of the head could not always be precisely followed by the DMON positioning at the time of recording, and the capacity to visually estimate the on-axis location of the DMON was obviously limited, which might have led to occasional off-axis recordings. The beam width of a beluga was measured as 6.5° both in horizontal and vertical planes (Au et al., 1987). The DMON was positioned 1 m from the rostrum tip. Adding this value to an approximate head length of 0.4 m (horizontal distance between tip and blowhole), the distance between the DMON and the sound source was ~1.4 m. To ensure recorded clicks are within the main transmission beam width, as head movements occurred in horizontal and vertical planes, the DMON should be maintained within 15 cm of the beam axis at 1 m from the rostrum, which could be roughly estimated using

$$(\tan 6.5°/2) \times 1.4 \text{ (m)} \qquad (2)$$

While the belugas' heads were usually directed toward the DMON, we cannot rule out that belugas might occasionally orient their heads off this medial-axis, beyond the estimated 15 cm, thus distorting some recorded clicks. Despite it being a "natural" water depth environment for the belugas, recording at this low depth turned out to be challenging as can be seen in the rejection of a large number of recorded clicks (only 556 clicks qualified out of 3,952). Reflections from the seafloor, surface, or nearby objects did seem to influence the recordings at times. However, we were able to successfully exclude distorted clicks from further analysis by applying the set of selection criteria described in the "Methods" section. Because only clicks with a clean waveform were used in this study (Au et al., 1985, 1987; Li et al., 2007; Madsen & Wahlberg, 2007), our final sample size was limited to 556 clicks. This sample size was not unreasonable for

odontocete call analyses when selection criteria is needed and data are collected from focal animals (Kaplan et al., 2014; Silva et al., 2016, 2019).

A hydrophone array was often used in other field studies for which head orientation could not always be observed with respect to the hydrophone (Au et al., 1995, 2003; Fang et al., 2015). Here, we could not fulfill a recording array using a single DMON, yet it was surely helpful to directly observe the belugas during the recordings to ensure the head was underwater, directed toward the hydrophone, while allowing for corrections in the position of the DMON following the head's movements.

This study provides a basic echolocation signal database for wild belugas in shallow waters in Bristol Bay, Alaska. These data also provide a foundation from which we may compare echolocation in other shallow or estuary habitats such as Cook Inlet, St. Lawrence River, or Somerset, Manitoba, Canada. Further, one key step, perhaps valuable for noise-stressed belugas of other habitats, would be to evaluate how click parameters of Bristol Bay belugas change in the presence of anthropogenic noise and what frequencies might be more sensible to masking or echolocation interference by noise.

The data showed that beluga whales can produce clicks containing high frequencies and of high SLs at a high repetition rate (short ICI), and probably a narrow beam in extremely shallow waters, despite the potential severe reverberations and clutter. This suggests that beluga whales may have developed ways to inhabit their diverse habitats. These belugas showed variability in click spectrum and amplitude parameters. This degree of variability suggests that, at least in belugas, there may not be a stereotypical echolocation click that can be used to describe this species' echolocation signal. Certainly, more recordings and analyses of on-axis echolocation clicks from multiple (separately recorded) individuals at consistent distances and orientations are needed to better evaluate variation within a population or species. As man-made noise sources are increasing within the habitats of belugas and other odontocetes, it is important to work toward a comprehensive understanding of the acoustic repertoire and niche to better estimate the potential effects of anthropogenic noise on the daily lives of beluga whales and other odontocetes that depend on sound to survive.

Acknowledgments

Literature Cited

Angiel, N. M., DeMaster, D. P., & VanBlaricom, G. R. (1996). A comparison of the vocal repertoires of beluga whale populations in Bristol Bay and the Beaufort Sea, Alaska. *The Journal of the Acoustical Society of America*, *100*(4), 2609-2610. https://doi.org/10.1121/1.417643

Atem, A. C. G., Rasmussen, M. H., Wahlberg, M., Petersen, H. C., & Miller, L. A. (2009). Changes in click source levels with distance to targets: Studies of free-ranging white-beaked dolphins *Lagenorhynchus albirostris* and captive harbor porpoise *Phocoena phocoena*. *Bioacoustics*, *19*, 49-65. https://doi.org/10.1080/09524 622.2009.9753614

Au, W. W. L. (1993). *The sonar of dolphins*. Springer-Verlag.

Au, W. W. L., & Benoit-Bird, K. J. (2003). Automatic gain control in the echolocation system of dolphins. *Nature*, *423*, 861-862. https://doi.org/10.1038/nature01727

Au, W. W. L., & Hastings, M. C. (2008). *Principles of marine bioacoustics*. Springer.

Au, W. W. L., Penner, R. H., & Turl, C. W. (1987). Propagation of beluga echolocation signals. *The Journal of the Acoustical Society of America*, *82*(3), 807-813. https://doi.org/10.1121/1.395278

Au, W. W. L., Carder, D. A., Penner, R. H., & Scronce, B. L. (1985). Demonstration of adaptation in beluga whale echolocation signals. *The Journal of the Acoustical Society of America*, *77*(2), 726-730. https://doi.org/10.1121/1.392341

Au, W. W. L., Ford, J. K. B., Horne, J. K., & Newman Allman, K. A. (2003). Echolocation signals of free-ranging killer whales (*Orcinus orca*) and modeling of foraging for chinook salmon (*Oncorhynchus tshawytscha*). *The Journal of the Acoustical Society of America*, *115*(2), 901-909. https://doi.org/10.1121/1.1642628

Au, W. W. L., Kastelein, R. A., Rippe, T., & Schooneman, N. M. (1999). Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). *The Journal of the Acoustical Society of America*, *106*(6), 3699-3705. https://doi.org/10.1121/1.426038

Au, W. W. L., Martin, S. W., Moore, P. W., Branstetter, B., & Copeland, A. M. (2016). Dynamics of biosonar signals in free-swimming and stationary dolphins: The role of source levels on the characteristics of the signals. *The Journal of the Acoustical Society of America*, *139*(3), 1381-1389. https://doi.org/10.1121/1.4944636

Au, W. W. L., Pawloski, J. L., Nachtigall, P. E., Blonz, M., & Gisner, R. C. (1995). Echolocation signals and transmission beam pattern of a false killer whale (*Pseudorca crassidens*). *The Journal of the Acoustical Society of America*, *98*(1), 51-59. https://doi.org/10.1121/1.413643

Belikov, R. A., & Belkovich, V. M. (2007). Whistles of beluga whales in the reproductive gathering off Solovetskii Island in the White Sea. *Acoustical Physics*, *53*, 528-534. https://doi.org/10.1134/S1063771007040148

Belkovich, V. M., & Shchekotov, M. N. (1992). Individual signals of belugas associated with hunting behavior in the White Sea. In J. A. Thomas, R. A. Kastelein, & A. Ya. Supin (Eds.), *Marine mammal sensory systems* (pp. 439-447). Springer. https://doi.org/10.1007/978-1-4615-3406-8_30

Belkovich, V. M., & Shchekotov, M. N. (1993). *The belukha whale: Natural behavior and bioacoustics*. Woods Hole Oceanographic Institution. https://doi.org/10.1575/1912/75

Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990). Review of the signature whistles hypothesis for the Atlantic bottlenose dolphin. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 199-234). Academic Press.

Castellote, M., Mooney, T. A., Quakenbush, L., Hobbs, R., Goertz, C., & Gaglione, E. (2014). Baseline hearing abilities and variability in wild beluga whales (*Delphinapterus leucas*). *Journal of Experimental Biology*, *217*, 1682-1691. https://doi.org/10.1242/jeb.093252

Castellote, M., Leeney, R. H., O'Corry-Crowe, G., Lauhakangas, R., Kovacs, K. M., Lucey, W., Krasnova, V., Lydersen, C., Stafford, K. M., & Belikov, R. (2013). Monitoring white whales (*Delphinapterus leucas*) with echolocation loggers. *Polar Biology*, *36*, 493-509. https://doi.org/10.1007/s00300-012-1276-2

Chmelnitsky, E. G., & Ferguson, S. H. (2012). Beluga whale, *Delphinapterus leucas*, vocalizations from the Churchill River, Manitoba, Canada. *The Journal of the Acoustical Society of America*, *131*(6), 4821-4835. https://doi.org/10.1121/1.4707501

Citta, J. J., Quakenbush, L. T., Frost, K. J., Lowry, L., Hobbs, R. C., & Aderman, H. (2016). Movements of beluga whales (*Delphinapterus leucas*) in Bristol Bay, Alaska. *Marine Mammal Science*, *32*, 1272-1298. https://doi.org/10.1111/mms.12337

Ezer, T., Hobbs, R., & Oey, L-Y. (2008). On the movement of beluga whales in Cook Inlet, Alaska: Simulations of tidal and environmental impacts using a hydrodynamic inundation model. *Oceanography*, *21*, 186-195. https://doi.org/10.5670/oceanog.2008.17

Fang, L., Li, S., Wang, K., Wang, Z. T., Shi, W. J., & Wang, D. (2015). Echolocation signals of free-ranging Indo-Pacific humpback dolphins (*Sousa chinensis*) in Sanniang Bay, China. *The Journal of the Acoustical Society of America*, *138*(3), 1346-1352. https://doi.org/10.1121/1.4929492

Garland, E. C., Castellote, M., & Berchok, C. L. (2015). Beluga whale (*Delphinapterus leucas*) vocalizations and

call classification from the eastern Beaufort Sea population. *The Journal of the Acoustical Society of America*, *136*(7), 3054-3067. https://doi.org/10.1121/1.4919338

Goetz, K. T., Robinson, P. W., Hobbs, R. C., Laidre, K. L., Huckstadt, L. A., & Shelden, K. (2012). *Movement and dive behavior of beluga whales in Cook Inlet, Alaska* (AFSC Processed Report 2012-03). Alaska Fisheries Science Center.

Hobbs, R. C., Reeves, R. R., Prewitt, J. S., Desportes, G., Breton-Honeyman, K., Christensen, T., Citta, J. J., Ferguson, S. H., Frost, K. J., Garde, E., Gavrilo, M., Ghazal, M., Glazov, D. M., Gosselin, J-F., Hammill, M., Hansen, R. G., Harwood, L., Heide-Jørgensen, M. P., Inglangasuk, G., Kovacs, K. M., . . . Watt, C. A. (2019). Global review of the conservation status of monodontid stocks. *Marine Fisheries Review*, *81*(3-4), 1-53.

Jensen, F. H., Bejder, L., Wahlberg, M., & Madsen, P. T. (2009). Biosonar adjustments to target range of echolocating bottlenose dolphins (*Tursiops* sp.) in the wild. *Journal of Experimental Biology*, *212*, 1078-1086. https://doi.org/10.1242/jeb.025619

Jensen, F. H., Rocco, A., Mansur, R. M., Smith, B. D., Janik, V. M., & Madsen, P. T. (2013). Clicking in shallow rivers: Short range echolocation of Irrawaddy and Ganges river dolphins in a shallow, acoustically complex habitat. *PLOS ONE*, *8*(4), e59284. https://doi.org/10.1371/journal.pone.0059284

Kaplan, M. B., Mooney, T. A., Partan, J., & Solow, A. R. (2015). Coral reef species assemblages are associated with ambient soundscapes. *Marine Ecology Progress Series*, *533*, 93-107. https://doi.org/10.3354/meps11382

Kaplan, M. B., Mooney, T. A., Sayigh, L. S., & Baird, R. W. (2014). Repeated call types in Hawaiian melon-headed whales (*Peponocephala electra*). *The Journal of the Acoustical Society of America*, *136*(3), 1394-1401. https://doi.org/10.1121/1.4892759

Lesage, V., Barrette, C., Kingsley, M. C. S., & Sjare, B. (1999). The effect of vessel noise on the sound production behavior of belugas in the St. Lawrence estuary, Canada. *Marine Mammal Science*, *15*, 64-84. https://doi.org/10.1111/j.1748-7692.1999.tb00782.x

Li, S., Wang, K., Wang, D., & Akamatsu, T. (2005). Echolocation signals of the free-ranging Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*). *The Journal of the Acoustical Society of America*, *117*(5), 3288-3296. https://doi.org/10.1121/1.1882945

Li, S. H., Wang, D., Wang, K. X., Xiao, J. Q., & Akamatsu, T. (2007). The ontogeny of echolocation in the Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*). *The Journal of the Acoustical Society of America*, *122*(2), 715-718. https://doi.org/10.1121/1.2747203

Madsen, P. T., & Wahlberg, M. (2007). Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales. *Deep-Sea Research Part I: Oceanographic Research Papers*, *54*(8), 1421-1444. https://doi.org/10.1016/j.dsr.2007.04.020

Martin, A. R., & Smith, T. G. (1992). Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas*. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(3), 462-466. https://doi.org/10.1139/f92-055

Mooney, T. A., Castellote, M., Quakenbush, L., Hobbs, R., Gaglione, E., & Goertz, C. (2018). Variation in hearing within a wild population of beluga whales (*Delphinapterus leucas*). *Journal of Experimental Biology*, *221*, jeb171959. https://doi.org/10.1242/jeb.171959

Muto, M. M., Helker, V. T., Delean, B. J., Angliss, R. P., Boveng, P. L., Breiwick, J. M., Brost, B. M., Cameron, M. F., Clapham, P. J., Dahle, S. P., Dahlheim, M. E., Fadely, B. S., Ferguson, M. C., Fritz, L. W., Hobbs, R. C., Ivashchenko, Y. V., Kennedy, A. S., London, J. M., Mizroch, S. A., Ream, R. R., . . . Zerbini, A. N. (2020). *Alaska marine mammal stock assessments, 2019* (NOAA Technical Memorandum NMFS-AFSC-404). National Oceanic and Atmospheric Administration, U.S. Department of Commerce. 395 pp.

O'Corry-Crowe, G. M. (2009). Beluga whale: *Delphinapterus leucas*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 108-112). Academic Press. https://doi.org/10.1016/B978-0-12-373553-9.00030-4

Roy, N., Simard, Y., & Gervaise, C. (2010). 3D tracking of foraging belugas from their clicks: Experiment from a coastal hydrophone array. *Applied Acoustics*, *71*, 1050-1056. https://doi.org/10.1016/j.apacoust.2010.05.008

Silva, T. L., Mooney, T. A., Sayigh, L. S., & Baumgartner, M. F. (2019). Temporal and spatial distributions of delphinid species in Massachusetts Bay (USA) using passive acoustics from ocean gliders. *Marine Ecology Progress Series*, *631*, 1-17. https://doi.org/10.3354/meps13180

Silva, T. L., Mooney, T. A., Sayigh, L. S., Tyack, P. L., Baird, R. W., & Oswald, J. N. (2016). Whistle characteristics and daytime dive behavior in pantropical spotted dolphins (*Stenella attenuata*) in Hawai'i measured using digital acoustic recording tags (DTAGs). *The Journal of the Acoustical Society of America*, *140*(1), 421-429. https://doi.org/10.1121/1.4955081

Turl, C. W., & Penner, R. H. (1989). Differences in echolocation click patterns of the beluga (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, *86*(2), 497-502. https://doi.org/10.1121/1.398229

Yamamoto, Y., Akamatsu, T., da Silva, V. M. F., Yoshida, Y., & Kohshima, S. (2015). Acoustic characteristics of biosonar sounds of free-ranging botos (*Inia geoffrensis*) and tucuxis (*Sotalia fluviatilis*) in the Negro River, Amazon, Brazil. *The Journal of the Acoustical Society of America*, *138*(2), 687-693. https://doi.org/10.1121/1.4926440

Yang, W. Y., Luo, W. Y., & Zhang, Y. (2017). Automatic detection method for monitoring odontocete echolocation clicks. *Electronics Letters*, *53*(6), 367-368. https://doi.org/10.1049/el.2016.4590

Zahn, M. J., Laidre, K. L., Stilz, P., Rasmussen, M. H., & Koblitz, J. C. (2021). Vertical sonar beam width and scanning behavior of wild belugas (*Delphinapterus leucas*) in West Greenland. *PLOS ONE*, *16*(9), e0257054. https://doi.org/10.1371/journal.pone.0257054