


Communication in Cook Inlet beluga whales: Describing the vocal repertoire and masking of calls by commercial ship noise

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ABSTRACT:

Many species rely on acoustic communication to coordinate activities and communicate to conspecifics. Cataloging vocal behavior is a first step towards understanding how individuals communicate information and how communication may be degraded by anthropogenic noise. The Cook Inlet beluga population is endangered with an estimated 331 individuals. Anthropogenic noise is considered a threat for this population and can negatively impact communication. To characterize this population's vocal behavior, vocalizations were measured and classified into three categories: whistles ($n = 1264$, 77%), pulsed calls ($n = 354$, 22%), and combined calls ($n = 15$, 1%), resulting in 41 call types. Two quantitative analyses were conducted to compare with the manual classification. A classification and regression tree and Random Forest had a 95% and 85% agreement with the manual classification, respectively. The most common call types per category were then used to investigate masking by commercial ship noise. Results indicate that these call types were partially masked by distant ship noise and completely masked by close ship noise in the frequency range of 0–12 kHz. Understanding vocal behavior and the effects of masking in Cook Inlet belugas provides important information supporting the management of this endangered population.

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I. INTRODUCTION

Many species rely on vocal communication as a mechanism for mate selection, to share resource information, avoid predators, and organize collective movement (Bradbury and Vehrencamp, 2011; Kershenbaum *et al.*, 2016). Vocal repertoire analysis can provide a baseline for studies on conspecific communication and vocal learning in young animals, and a mechanism to assess population structure. The vocal repertoire of a wide variety of species has been documented, including birds (Saunders, 1983; Trejos-Araya and Barrantes, 2014), primates (Hammerschmidt and Fischer, 2019; Macedonia, 1993), mustelids (Lemasson *et al.*, 2014; Leuchtenberger *et al.*, 2014; McShane *et al.*, 1995), and marine mammals (Brady *et al.*, 2020; Ford, 1989; Martin *et al.*, 2021; Phillips and Stirling, 2001; Sayigh *et al.*, 2013; Weilgart and Whitehead, 1997). Among marine mammals, studies have shown that vocal repertoire may be integral to the maintenance of population structure (Sharpe *et al.*, 2019; Van Cise *et al.*, 2017; Whitehead *et al.*, 1998; Yurk *et al.*, 2002) and is an important tool for mate attraction (Tyack, 1981). Communication via acoustic signaling is especially important in the marine environment, in which visibility is often limited and animals must rely primarily on sound to

navigate their surroundings and communicate with conspecifics (Dudzinski *et al.*, 2009).

Beluga whales (*Delphinapterus leucas*) are toothed whales in the family Monodontidae and have a circumpolar distribution. There are 21 recognized populations (Kovacs *et al.*, 2021), including five distinct populations in Alaska (Hill and DeMaster, 1998). The smallest of these five is the Cook Inlet beluga (CIB) population, which is non-migratory (Hobbs *et al.*, 2005; Laidre *et al.*, 2000) and is geographically and genetically isolated (O'Corry-Crowe *et al.*, 1997). The CIB population had an estimated abundance of 1300 individuals in the late 1970s (Shelden *et al.*, 2015), but declined rapidly in the late 20th century. Despite the restriction of subsistence hunting in 1999, the CIB population has continued to decline (Shelden and Wade, 2019). In 2000, this population was designated as depleted under the Marine Mammal Protection Act (U.S. Federal Register, 2000) and then listed as endangered under the U.S. Endangered Species Act in 2008 (U.S. Federal Register, 2008). This listing led to the designation of critical habitat in 2011 (Fig. 1), which is comprised of 7800 km² of marine habitat (U.S. Federal Register, 2011). The most recent analysis of abundance estimates 331 individuals in the population (95% confidence interval: 290–386) (Goetz *et al.*, 2023). This population remains endangered, despite federal protection, designation of critical habitat, and the implementation of a recovery plan, which lists threats ranked from low to high level of concern. Three threats ranked as high level of

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concern include catastrophic events (e.g., oil spills, mass strandings), cumulative effects of multiple stressors (e.g., co-exposure to chemical pollutants and noise), and anthropogenic noise (National Marine Fisheries Service, 2016).

One of the fundamental knowledge gaps that remain for the CIB population is information surrounding their sociality and communication. Beluga whales are a highly gregarious and vocal species, producing a wide array of vocalizations, including whistles, pulsed calls, combined calls, and echolocation clicks (Au *et al.*, 1985; Fish and Mowbray, 1962). Whistles are narrowband, tonal signals that can be flat (i.e., little or no frequency modulation) or frequency modulated and can contain harmonics that are lower in amplitude. Pulsed calls are bursts of broadband pulses in which the harmonic interval corresponds to the pulse repetition rate (PRR) (Watkins, 1966). Combined calls, also known as biphonic or mixed calls, occur when two concurrent signals are produced by the same individual, often consisting of a tonal and pulsed component (Karlsen *et al.*, 2002). Belugas are also known to exhibit a graded vocalization structure, in which vocalizations can transition into others on a continuum (Sjare and Smith, 1986). Vocal repertoire has been documented for several beluga populations, including Cunningham Inlet, Canada (Sjare and Smith, 1986); St. Lawrence, Canada (Faucher, 1988); Bristol Bay, USA (Angiel, 1997); Svalbard, Norway (Karlsen *et al.*, 2002); White Sea, Russia (Belikov and Bel'kovich, 2006, 2007, 2008); Churchill River, Canada (Chmel'nitsky and Ferguson, 2012); and the eastern Beaufort Sea, USA (Garland *et al.*, 2015). A previous study investigated spatial and temporal calling behavior in the CIB population using broad call categories but did not describe vocal repertoire due to limitations in duty cycle and sampling period (Blevins-Manhard *et al.*, 2017).

Northern Cook Inlet has the highest concentration of belugas during ice-free months and also has the largest potential for negative impacts from anthropogenic noise (Small *et al.*, 2017). This area is in close proximity to the Port of Alaska (Anchorage) as well as the Joint Base Elmendorf-Richardson military base, resulting in persistent levels of anthropogenic noise. In this region, commercial shipping noise is the most prominent source of anthropogenic noise, in both percent of overall time and mean duration (Castellote *et al.*, 2018). The masking of vocalizations by commercial shipping noise, and consequently the disruption of communication, could be one of the main underlying mechanisms of anthropogenic impact. Anthropogenic noise can negatively affect marine mammals in a multitude of ways, including temporary or permanent hearing threshold shifts, changes in behavior, and auditory masking (Branstetter and Sills, 2022; DeRuiter *et al.*, 2013; Finneran, 2015; Holt *et al.*, 2011; Martin *et al.*, 2023; Parsons, 2017; Tyack and Janik, 2013). Auditory masking is often considered the most prevalent and occurs when one sound interferes with an individual's ability to detect and discriminate another sound (Branstetter and Sills, 2022; Erbe *et al.*, 2016).

Due to the extreme turbidity of Cook Inlet waters and the highly vocal nature of these animals, passive acoustic

monitoring (PAM) has proved to be a valuable tool for understanding the spatio-temporal distribution of this population without affecting their behavior. Several long-term PAM studies have been conducted in Cook Inlet to examine the year-round seasonal distribution and foraging occurrence of belugas (Castellote *et al.*, 2016; Castellote *et al.*, 2018; Castellote *et al.*, 2020; Lammers *et al.*, 2013). While these studies provide important insights into the spatio-temporal movement of these whales, little effort has been focused on investigating the vocal repertoire and how vocalizations may be masked by anthropogenic noise.

We produce the first description of CIB vocal repertoire in two critical habitat locations across multiple seasons, which can be used in future studies of acoustic communication and group coordination within the CIB population. We also investigate the degree of masking that commercial ship noise may have on common CIB vocalizations in the frequency range of 0–12 kHz, which provides strong indication that ship noise may have a profound impact on vocal communication in this population.

II. METHODS

A. Study area and acoustic recordings

Cook Inlet is an estuary in south-central Alaska that stretches roughly 370 km from Knik Arm to the Gulf of Alaska. Two arms, Knik and Turnagain, extend from the northern reaches of Cook Inlet, surrounding Anchorage, the most populous city in the state. Cook Inlet is known for its dramatic tidal cycles, strong currents, and extreme turbidity. These factors, combined with ice coverage in the winter, make Cook Inlet an extremely challenging place to conduct field studies year-round. The Cook Inlet Beluga Acoustics Program, located at the National Oceanic and Atmospheric Administration's Marine Mammal Laboratory, in partnership with the Alaska Department of Fish and Game, has been deploying passive acoustic recorders and monitoring the occurrence of cetaceans and anthropogenic noise since 2008 (Castellote *et al.*, 2016; Castellote *et al.*, 2018; Castellote *et al.*, 2020; Lammers *et al.*, 2013; Small *et al.*, 2017). For this study, we selected two locations within the CIB critical habitat where large concentrations of belugas have been documented, both visually and acoustically, during various seasons (Fig. 1). The waters off the Susitna River Delta (hereafter Susitna), which is the core of the CIB documented range (Rugh *et al.*, 2010), draws high concentrations of belugas during summer months while Trading Bay is frequented by belugas in winter and spring (Castellote *et al.*, 2020; Shelden *et al.*, 2015).

The raw data used for this study are from a previous project investigating beluga presence and seasonality (Polasek, 2021). We recorded beluga vocalizations and anthropogenic noise using bottom-mounted DSG-ST acoustic recorders (Loggerhead Instruments, Sarasota, FL) with an HTI-96-min hydrophone (flat frequency response from 2 Hz to 34 kHz and sensitivity of -201 dB re 1 V/ μ Pa). The acoustic recorders sampled at 24 kHz with a $+33$ dB gain.

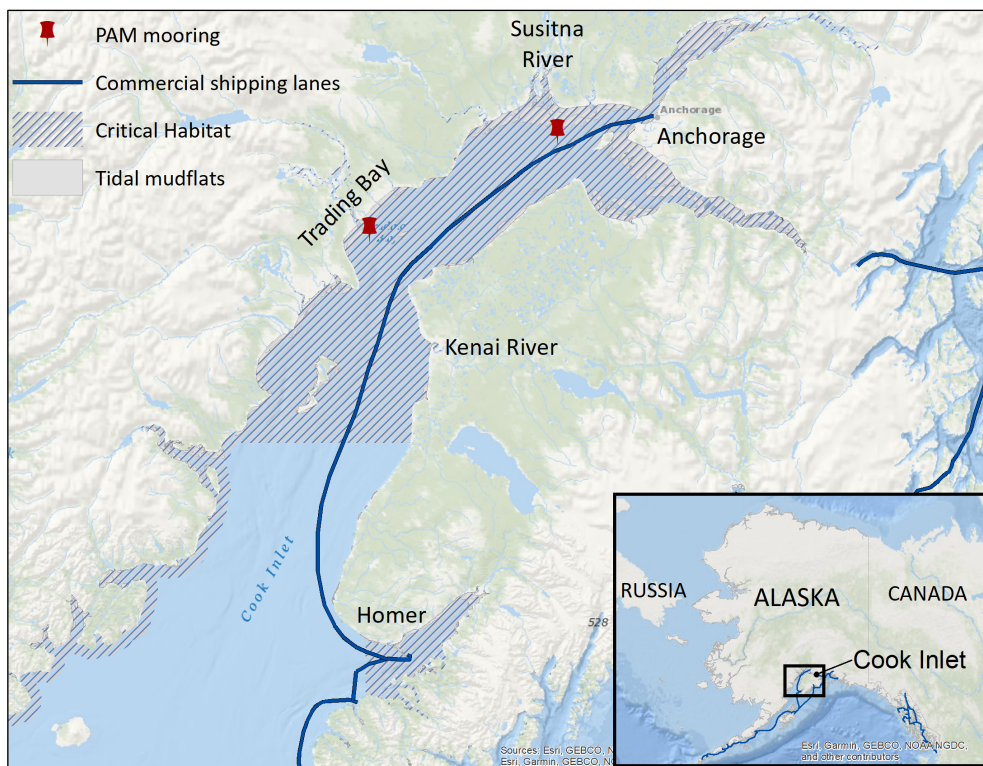


FIG. 1. (Color online) Map of Cook Inlet, Alaska, indicating locations of two acoustic moorings used in this study, CIB critical habitat, and designated Port of Alaska commercial shipping lanes.

Table I provides details regarding location, depth, recording period, and duty cycle of the acoustic recorders. Recordings were on a duty cycle to preserve battery life and extend the duration of the recording period to cover a broader temporal range. Given the 24 kHz sampling rate, we are only able to describe vocal repertoire and anthropogenic masking in the frequency range up to 12 kHz. Belugas are considered mid-frequency odontocetes (National Marine Fisheries Service, 2018), with hearing capabilities above 100 kHz (Castellote *et al.*, 2014; Klishin *et al.*, 2000; Mooney *et al.*, 2020). While some beluga vocalizations contain acoustic energy above 12 kHz, previous studies have found that the fundamental frequencies of whistles, as well as the key acoustic properties used for classification in pulsed and combined calls, occur within the sampled frequency range (Belikov and Bel’kovich, 2006, 2008; Chmelnitsky and Ferguson, 2012; Panova *et al.*, 2019).

B. Acoustic analysis

Previously, we documented beluga acoustic encounters that were used for this study (Polasek, 2021). We define an

acoustic encounter as a grouping of vocalizations during a given time and designate a new encounter when 60 min or more elapses with no vocalizations (Lammers *et al.*, 2013). To capture the vocal repertoire, we analyzed multiple months across the sampling period and documented call types for each location. We qualitatively analyzed 84 encounters across 60 days in Susitna and 90 encounters across 54 days in Trading Bay. From those data, we only included vocalizations that met the following criteria: (1) the beginning and end point were clearly distinguishable, (2) the signal contour could be clearly defined, and (3) the signal-to-noise ratio (SNR) was greater than 10 dB, which was measured using Raven Pro 1.6 (Ithaca, NY) (K. Lisa Yang Center for Conservation Bioacoustics, 2023). We included vocalizations that met these criteria in further quantitative analysis and annotated using Raven Pro 1.6 as 10 s–long smoothed spectrograms over the full frequency range of 0–12 kHz, with a 1024 point fast Fourier transform (FFT), Hanning window, and 75% overlap. We did not include echolocation clicks in this analysis due to the frequency sampling limitations of the acoustic recorders.

TABLE I. Acoustic data used for vocal repertoire analysis.

Location	Latitude (°N)	Longitude (°W)	Depth (m)	Recording period	Duty cycle
Susitna	61 10.482	150 30.012	18.3	5/13/2018–9/9/2018	5 min every 15 min
Trading Bay	60 53.134	151 38.610	21.9	9/15/2018–4/26/2019	5 min every 10 min

C. Manual classification of call types

We classified vocalizations, hereafter referred to as calls, based on aural and visual examination of spectrograms following the protocol and classification scheme originally developed by [Sjare and Smith \(1986\)](#) for beluga and updated by [Garland *et al.* \(2015\)](#). Following these classification schemes, we divided calls into three categories: whistles, pulsed calls, and combined calls, which were further broken down into call types and sub-types. Call types reflect the contour shape of the fundamental frequency (e.g., ascending, descending, flat, modulated), while sub-types reflect the structure of the call (e.g., segmented, sequenced).

We implemented a call classification protocol based on previous beluga vocal repertoire studies ([Chmelnitsky and Ferguson, 2012](#); [Garland *et al.*, 2015](#); [Sjare and Smith, 1986](#)). Calls documented a minimum of three times are considered to be stereotyped call types or sub-types, following precedent from previous analyses of vocal repertoire in belugas and other species ([Chmelnitsky and Ferguson, 2012](#); [Garland *et al.*, 2015](#); [Selbmann *et al.*, 2023](#); [Sharpe *et al.*, 2019](#); [Van Cise *et al.*, 2017](#)). We assigned call contour shape by the contour of the fundamental frequency seen in at least 50% of the call and labeled call types following the nomenclature in [Garland *et al.* \(2015\)](#), with abbreviations based on the category and contour shape. We considered separate calls to be those that were separated by > 0.2 s, following [Chmelnitsky and Ferguson \(2012\)](#). If a call was within ≤ 0.1 s of another call of the same type, we assigned these as segments following [Garland *et al.* \(2015\)](#), and the call was labeled as segmented. For example, if a flat whistle (flatws) had multiple tonal segments of < 0.1 s in time, we designated this as a flat segmented whistle (flatws.seg) and we grouped all the segments within the same annotation box. If two different calls were within the 0.2 s, we annotated them as independent calls. For this study, we added two new rules to the previously published protocol based on call types documented in Cook Inlet. First, we defined a call sequence as multiple units of the same call type repeated in a series separated by ≤ 0.2 s. For example, a descending whistle (dws) repeated in series with time gaps ≤ 0.2 s between units is designated as a descending whistle sequence (dws.seq) and all units in this sequence are grouped within the same annotation box. We followed the same protocol for pulsed calls and whistles, adding one adjustment to the classification of pulsed calls to account for instantaneous steps in PRR, which is the second additional rule to the protocol. Pulsed calls that are continuous in time and contain one or more instantaneous steps in PRR are designated “.bc” for “band change.” For example, a descending pulsed call (pulse.d) with one or more instantaneous steps in PRR, is classified as a descending pulsed call with a band change (pulse.d.bc). For combined calls, we assigned a new number as new contour shapes were discovered with a “CI” identifier for Cook Inlet (CI.c.1, CI.c.2, etc.).

We assessed vocal repertoire richness with a rarefaction curve implemented in the *vegan* package in R ([Oksanen](#)

[et al.](#), 2022) for each location separately and combined. When the curve begins to asymptote, few to no new call types are being added to the repertoire as new samples are added, and it can be assumed that the acquired repertoire of calls is nearly complete. To test for differences in call type and call category compositions among locations, we implemented a Pearson’s χ^2 statistic in R ([R Core Team, 2022](#)). We also conducted a qualitative comparison of call types following methods from previous beluga repertoire studies ([Belikov and Bel’kovich, 2007, 2008](#); [Chmelnitsky and Ferguson, 2012](#); [Garland *et al.*, 2015](#); [Karlsen *et al.*, 2002](#)) to identify which CIB call types are shared and unique. We conducted a visual comparison of call types from our study with published spectrograms in Cunningham Inlet, Canada ([Sjare and Smith, 1986](#)); St. Lawrence, Canada ([Faucher, 1988](#)); Bristol Bay, USA ([Angiel, 1997](#)); Svalbard, Norway ([Karlsen *et al.*, 2002](#)); White Sea, Russia ([Belikov and Bel’kovich, 2006, 2007, 2008](#)); Churchill River, Canada ([Chmelnitsky and Ferguson, 2012](#)); and the eastern Beaufort Sea, USA ([Garland *et al.*, 2015](#)).

D. Quantitative classification of call types

We isolated each beluga call via an annotation box in Raven Pro 1.6. For whistles, following the previously established methodology by [Garland *et al.* \(2015\)](#), we only included the fundamental frequency in the annotation box and therefore, frequency measurements were made only on the fundamental component of the whistle. Because higher frequencies attenuate faster than lower frequencies, the presence of whistle harmonics as well as the high frequency components of pulsed and combined calls will vary with source sound level and distance from the recorder. For pulsed and combined calls, we included the entire broadband signal in the annotation box following [Garland *et al.* \(2015\)](#), with the caveat that the upper frequency limit is highly dependent on signal attenuation as well as the upper limit of our sampling rate. Therefore, our analysis is limited to the harmonic components and broadband signals of pulsed and combined calls below 12 kHz. For each annotated call, Raven Pro generated the following acoustic measurements: duration, minimum frequency, maximum frequency, bandwidth, center frequency, and peak frequency (Table II). We manually measured start frequency, end frequency, frequency trend, number of inflections, number of segments, number of steps, number of units, and PRR in Raven Pro for a subset of 10% of each call type (Table II). We chose high quality calls (i.e., high SNR, non-overlapping) at random throughout all encounters from both locations to capture a representative sample. When 10% was below $n = 10$, we measured ten calls and if there were fewer than ten occurrences, we measured all calls within that call type. For all call types, we calculated the mean and standard deviation of each measurement.

Following the methodology of [Garland *et al.* \(2015\)](#), we conducted both a classification and regression tree (CART) analysis and a Random Forest analysis on our randomly

TABLE II. Description of measurements used in the quantitative classification of call types.

Measurement	Abbreviation	Description
Duration (s)	Dur.	Length of call
Minimum frequency (Hz)	Min.	Minimum frequency
Maximum frequency (Hz)	Max.	Maximum frequency
Bandwidth (Hz)	BW	Maximum–Minimum frequency
Start frequency (Hz)	Start	Start frequency of fundamental
End frequency (Hz)	End	End frequency of fundamental
Frequency trend (ratio)	Trend	Ratio of start/end frequency
Center frequency (Hz)	Center	Frequency that divides call into two intervals of equal energy
Peak frequency (Hz)	Peak	Frequency at the spectral peak
Inflections (#)	Inflect.	Number of slope reversals
Segments (#)	Seg.	Number of segments (temporal gap between segments)
Steps (#)	Steps	Number of frequency steps (no temporal gap between steps)
Units (#)	Units	Number of units within a sequence
Pulse repetition rate (/s)	PRR	Number of pulses per second (for pulsed and combined calls)

selected 10% subset of calls to compare with our manual call classification. A CART analysis is robust to outliers, non-normal and correlated data, and not only gives a classification, but also an estimate of the misclassification probability (Breiman *et al.*, 1984). A Random Forest analysis creates multiple trees, or a forest, which is used to evaluate the error rate (out-of-bag error) and the importance of each predictor (Breiman, 2001). All measurements described in Table II were used for both analyses. For the CART analysis, we used the R package *rpart* (Therneau *et al.*, 2022). We performed a tenfold cross-validation and set terminal nodes to a minimum sample size of three. Nodes were split using the Gini Index, which is a measure of node impurity (Breiman *et al.*, 1984). We then performed upward pruning until the best predictive tree was obtained. For the Random Forest analysis, we used the R package *randomForest* (Liaw and Wiener, 2002). Since Random Forest models estimate error internally, we did not need to implement additional cross-validation (Breiman, 2001). Following Garland *et al.* (2015), we set the number of trees to 1000.

E. Anthropogenic noise analysis

Because commercial ship noise has been identified as the top priority focus for noise mitigation management actions, we focused our call masking analysis on commercial ship noise. Previous studies have described the acoustic signature and occurrence of commercial ship noise in Cook Inlet, which was verified by Port of Alaska ship logs (Castellote *et al.*, 2018; Polasek, 2021). To obtain a representative example of commercial ship noise in this area, we extracted commercial ship noise from the same acoustic data used for repertoire analysis in Susitna, as this location is the core of the designated critical habitat and sees persistent levels of anthropogenic noise due to its proximity to the

Port of Alaska commercial shipping lanes (Fig. 1). We extracted two 5 min–long sound clips representing the center (i.e., highest amplitude) and the edge (i.e., marginal amplitude above background levels) of the acoustic footprint of a commercial ship passing through the commercial shipping lanes to capture the range of received ship noise levels at this location, which is 2000 m away from the commercial shipping lanes. We defined the center of the commercial ship footprint as the 5 min portion with the Doppler effect pattern seen in the spectrogram and the edge as the last 5 min portion of the ship encounter. To compare the center and edge frequency spectral content of the ship noise with the spectral content of beluga calls received at the same location, we selected a minimum of three clips representing the spectral variability of each common call type per category. We selected clips of high quality calls based on the mean center frequency values of each call type. High quality calls were those that had no overlapping calls and had a SNR greater than 10 dB, which was measured using Raven Pro 1.6. We calculated the received sound pressure level (SPL) in one-third octave bands for the representative calls for each common call type and the commercial ship center and edge footprint using the MATLAB Acoustic Ecology Toolbox package (Bioacoustics Research Program, Ithaca, NY) (Dugan *et al.*, 2011). We then plotted the spectrum levels from each common call type against the center and edge ship noise spectra to determine the level of overlap. We included the composite beluga audiogram from Erbe *et al.* (2016), which is comprised of the lowest hearing thresholds from multiple individuals across different populations, to show which portions of the call and ship spectra are within beluga hearing thresholds. It has previously been shown that narrower octave bands (e.g., 1/12) may be a better estimate for the noise-masking potential in belugas (Erbe, 2008); however, we use the 1/3 octave band to facilitate direct comparison between our results and the beluga composite audiogram, which was computed in one-third octave bands per the American National Standards Institute’s standards for measuring odontocete audiograms (ANSI, 2018; Erbe *et al.*, 2016).

III. RESULTS

A. Manual classification of call types

We extracted and classified a total of 1633 calls based on the classification system implemented in previous beluga repertoire studies (Chmelnsky and Ferguson, 2012; Garland *et al.*, 2015; Sjare and Smith, 1986). In Susitna, we classified 944 calls across five encounters spanning May through September 2018. In Trading Bay, we classified 689 calls across ten encounters spanning January through April 2019. Of the 1633 total calls classified, 1626 were repeated three or more times and therefore considered to be stereotyped call types, resulting in 41 call types. The rarefaction curve reflects a near complete repertoire as very few new call types are added with additional data sampled (Fig. 2).

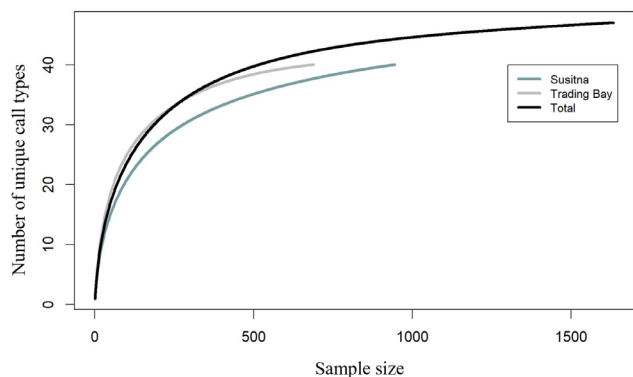


FIG. 2. (Color online) Rarefaction curve depicting CIB vocal repertoire richness at each location sampled and in total. These curves are created by creating an ensemble of curves by randomly re-ordering the calls and then plotting the average of the ensemble.

Of the 41 stereotyped call types we identified in Cook Inlet, 25 were whistles ($n = 1264$, 77.7%) and 15 were pulsed calls ($n = 354$, 21.8%). For combined calls, we only identified one call type that met the repetition requirement of the protocol (Cl.c.5, $n = 8$, 0.5%), with an additional six combined calls that were documented fewer than three times each. Both call type and call category composition differed significantly among the two locations (Pearson's χ^2 p value = 0.0005 for both). Since data from Susitna captured calling behavior in summer and Trading Bay captured calling behavior in winter and spring, we cannot conclude whether the compositional differences were due to location or season. Figure 3 shows call types in order of prevalence and by

category for Cook Inlet total (Susitna and Trading Bay combined) and call category composition broken down by location. Whistles were the predominate call category in Cook Inlet, followed by pulsed calls, then combined calls.

In this study, we expanded on the call type comparison table from Garland *et al.* (2015) to include call types documented in Cook Inlet and their relation to other beluga populations to provide a visualization of similarities and differences in repertoire content (Table III). Of the 41 call types we documented in the CIB population, 18 were not documented in any other population, 7 call types were documented across all populations, and 16 call types were documented in some, but not all, populations based on published spectrograms of calls.

1. Whistles

Whistles are the most common call category in the CIB vocal repertoire, consisting of 77.7% of calls. We identified eight whistle contour categories (ascending, descending, flat, modulated, n-shape, r-shape, u-shape, trill), which we further broke down into 25 unique call types based on contour and structure (segmented, sequenced, terminal tail) (Fig. 4). The three most common whistle types were descending whistle (dws, $n = 359$, 22.1%), flat whistle (flatws, $n = 326$, 20%), and modulated whistle (modws, $n = 157$, 9.7%). We documented several whistle types with terminal tails, which we denoted with ".t," and resulted in the addition of new call types dws.seq.t, modws.t, and modws.seq.t to the repertoire. We also documented sideways S-shaped modulated whistles, which we denoted with

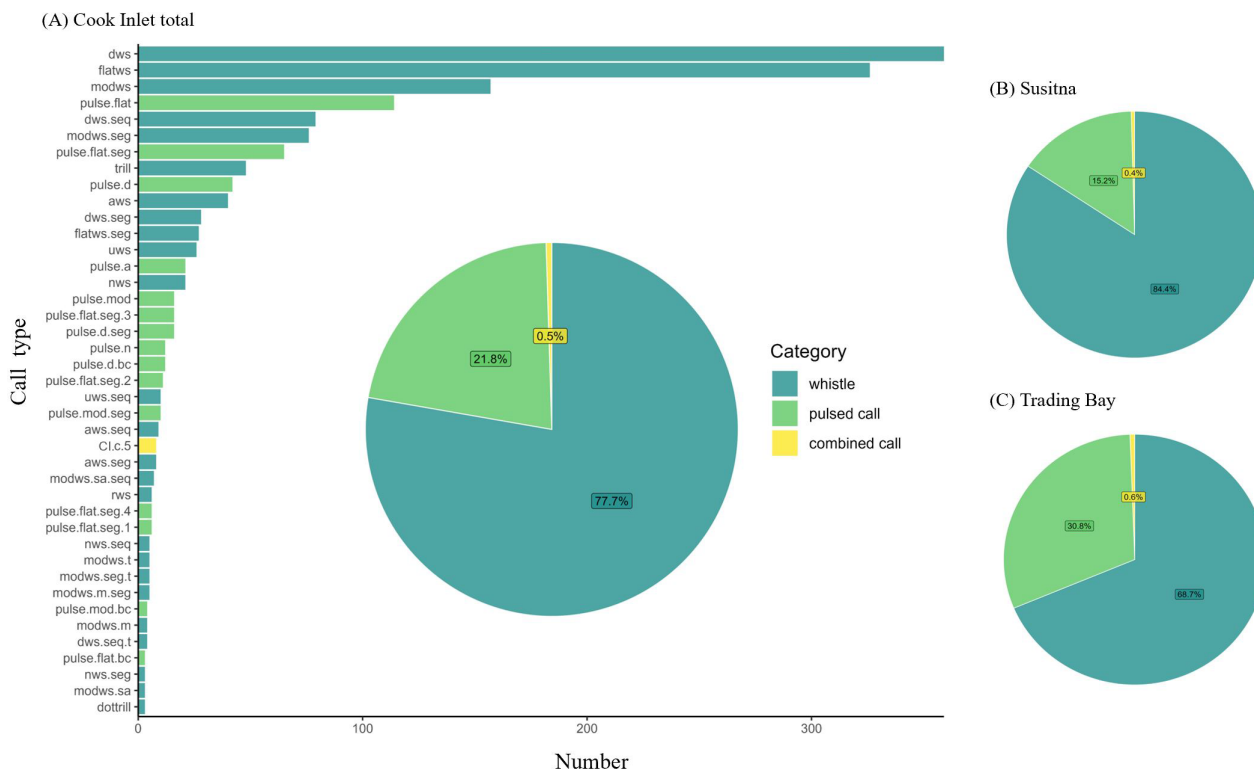


FIG. 3. (Color online) (A) CIB call types shown in order of prevalence by call category, (B) Susitna location call category composition, (C) Trading Bay call category composition.

TABLE III. A visualization of CIB call types that have been documented in other beluga populations, based on published spectrograms (Angiel, 1997; Belikov and Bel’kovich, 2006, 2007, 2008; Chmelnitsky and Ferguson, 2012; Faucher, 1988; Garland *et al.*, 2015; Karlsen *et al.*, 2002; Sjare and Smith, 1986) (See the supplementary material for the full table that includes call type nomenclature from each study.¹)

Cook Inlet, US Current study	Eastern Beaufort Sea, US Garland <i>et al.</i> (2015)	Churchill River, Canada Chmelnitsky and Ferguson (2012)	White Sea, Russia Belikov and Bel’kovich (2006, 2007, 2008)	Svalbard, Norway Karlsen <i>et al.</i> (2002)	Bristol Bay, US Angiel (1997)	St. Lawrence, Canada Faucher (1988)	Cunningham Inlet, Canada Sjare and Smith (1986)
aws	✓	✓	✓	✓	✓	✓	✓
aws.seg	✓	—	—	—	—	✓	✓
aws.seq	—	—	—	—	—	—	—
dws	✓	✓	✓	✓	✓	✓	✓
dws.seg	✓	—	—	—	—	✓	✓
dws.seq	—	—	✓	—	—	—	—
dws.seq.t	—	—	—	—	—	—	—
flatws	✓	✓	✓	✓	✓	✓	✓
flatws.seg	✓	✓	✓	—	—	✓	✓
modws	✓	✓	✓	✓	✓	✓	✓
modws.seg	✓	—	—	✓	✓	✓	✓
modws.m	—	—	—	—	—	—	—
modws.m.seg	—	—	—	—	—	—	—
modws.sa	—	—	—	—	—	—	—
modws.sa.seq	—	—	—	—	—	—	—
modws.t	—	—	—	—	—	—	—
modws.seq.t	—	—	—	✓	—	—	—
nws	✓	✓	✓	✓	✓	✓	✓
nws.seg	✓	—	—	—	—	✓	✓
nws.seq	—	✓	—	—	✓	—	—
rws	✓	✓	—	—	✓	—	—
uws	✓	✓	✓	✓	✓	✓	✓
uws.seq	—	—	✓	—	—	—	—
trill	✓	—	—	✓	—	✓	✓
dottrill	—	—	—	—	—	—	—
pulse.a	✓	✓	✓	—	✓	—	✓
pulse.d	✓	—	✓	—	✓	—	✓
pulse.d.seg	—	—	—	—	—	—	—
pulse.d.bc	—	—	—	—	—	—	—
pulse.flat	✓	✓	✓	✓	✓	✓	✓
pulse.flat.seg	—	—	✓	—	—	—	✓
pulse.flat.seg. 1	—	—	—	—	—	—	—
pulse.flat.seg.2	—	—	—	—	—	—	—
pulse.flat.seg.3	—	—	—	—	—	—	—
pulse.flat.seg.4	—	—	—	—	—	—	—
pulse.flat.bc	—	—	—	—	—	—	—
pulse.mod	—	✓	✓	—	✓	—	—
pulse.mod.seg	—	—	—	—	—	—	—
pulse.mod.bc	—	—	—	—	—	—	—
pulse.n	—	✓	—	✓	—	—	—
CI.c.5	—	—	—	—	—	—	—

a “.sa” label and resulted in the addition of new call types modws.sa and modws.sa.seq. For whistles, we only included the fundamental frequency when measuring acoustic properties because not all of the whistles in our study displayed harmonics. Acoustic measurement results for whistles are presented in Table IV.

2. Pulsed calls

Pulsed calls comprise 21.8% of the CIB vocal repertoire. We identified five pulsed call contour categories

(ascending, descending, flat, modulated, n-shape). We further broke down contours into 15 unique call types based on contour and structure (segmented, change in PRR) (Fig. 5). The three most common pulsed call types were flat pulsed call (pulse.flat, *n* = 114, 7%), flat segmented pulsed call (pulse.flat.seg, *n* = 65, 4%), and descending pulsed call (pulse.d, *n* = 42, 2.6%). We included the entire broadband signal, which for some high SNR cases was truncated by our upper frequency limit of 12 kHz. Acoustic measurement results for pulsed call types are presented in Table V.

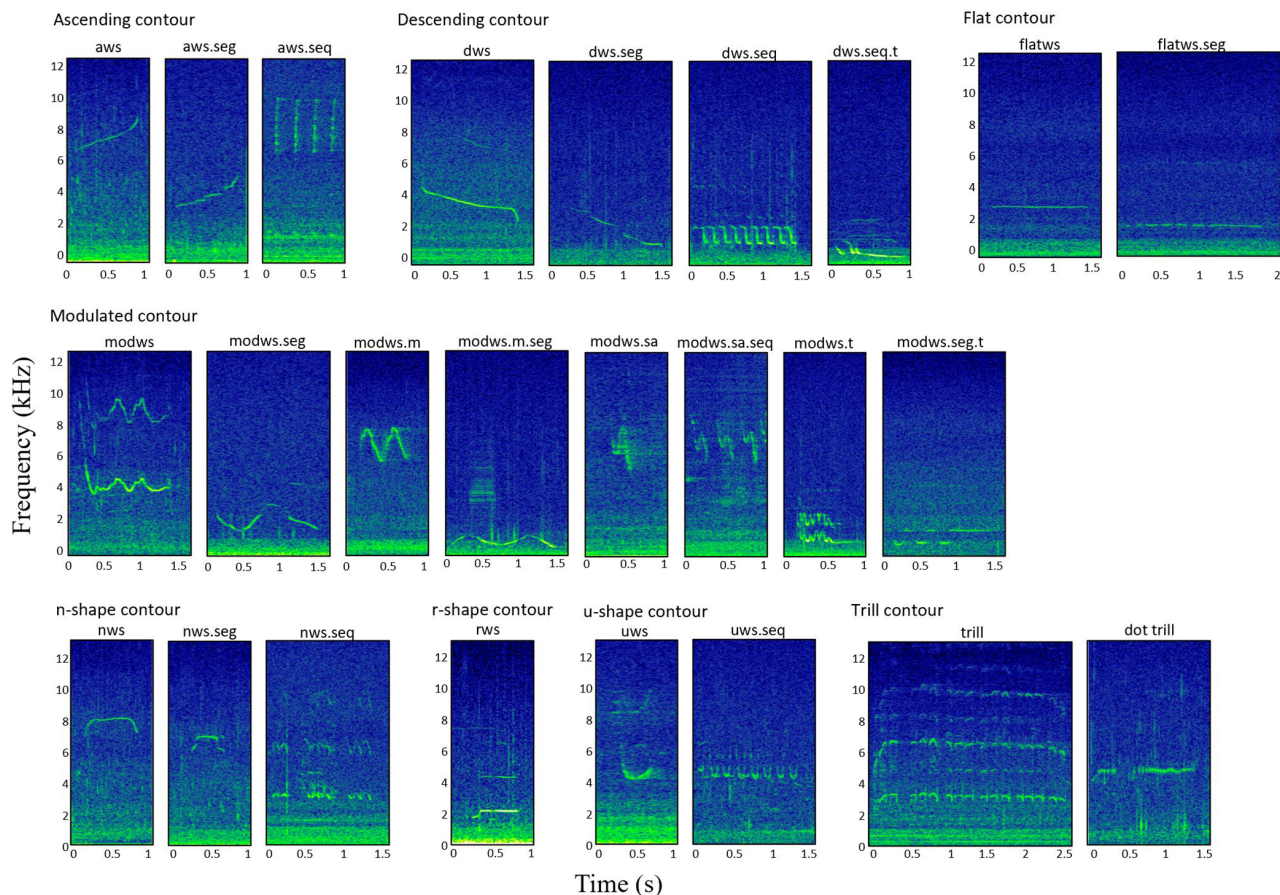


FIG. 4. (Color online) CIB whistle types organized by contour. Spectrograms are 1024 point FFT, Hanning window, and 75% overlap, generated in Raven Pro 1.6.

3. Combined calls

Combined calls were the least common call category documented in Cook Inlet, comprising 0.5% of the repertoire. We identified one stereotypic combined call type, CI.c.5 ($n = 8$, 0.5%), and documented an additional six combined calls that were encountered fewer than three times each (Fig. 6). The six combined calls documented that did not meet our protocol requirements were CI.c.1 ($n = 1$), CI.c.2 ($n = 1$), CI.c.3 ($n = 1$), CI.c.4 ($n = 1$), CI.c.6 ($n = 1$), and CI.c.7 ($n = 2$). Since we documented CI.c.5 eight times, we can be confident that the call was not two independent, overlapping calls. The remainder of the combined calls we documented did not meet the repetition requirement of the protocol but are included here for descriptive purposes and had high SNR clearly showing the characteristics of a combined call, but we cannot assure the stereotypic nature of these calls in this study. For combined calls, we included the entire broadband signal, which for some was truncated by our upper frequency limit of 12 kHz. Acoustic measurement results for CI.c.5 are presented in Table VI.

B. Quantitative classification of call types

Following the methodology from Garland *et al.* (2015), we conducted both a CART and Random Forest analysis to compare with our manual classification. For both analyses,

we used a subset of calls per call type, which resulted in 369 total calls. We did not include the single stereotyped combined call type, CI.c.5, in our analyses, as this was the only call type in this category. The remaining 40 call types (25 whistle types, 15 pulsed call types) were included in both analyses using all measurements described in Table II.

The most informative acoustic variables to CART construction were maximum frequency and bandwidth. These were followed by, in descending order: center frequency, minimum frequency, start frequency, number of segments, end frequency, frequency trend, maximum PRR, duration, peak frequency, minimum PRR, number of units, number of inflections, and number of steps. These variables provided the analysis with 90% classification of call types (root node error) with a misclassification rate of 4.9%. Forty-three terminal nodes were created, which is three more than the 40 call types defined using the manual call classification system (see supplementary material for CART figure).¹ Those three additional nodes were sub-divisions within three of the manually classified call types (aws, dws.seq, pulse.flat). These were based on minimum frequency for aws (1600 Hz cutoff), center frequency for dws.seq (891 Hz cutoff), and frequency trend for pulse.flat (1.3 cutoff). The tree was heavily influenced by contour shape, with different branches representing contour categories (ascending, descending, flat, modulated). The first branching separated flat whistles

TABLE IV. Descriptive statistics of CIB whistle types [mean \pm standard deviation (SD)].

Call type	N	% total	Dur. (s)	Min. (Hz)	Max. (Hz)	BW (Hz)	Start (Hz)	End (Hz)	Center (Hz)	Peak (Hz)	Inflect.	Seg.	Units
aws	40	2.5	0.4 \pm 0.2	3010.4 \pm 2378.7	4639.8 \pm 3588.1	1629.4 \pm 1702.4	2828.9 \pm 2197.3	4210.7 \pm 3332.1	3637.5 \pm 2743.2	3642.2 \pm 2791.8	0 \pm 0	1 \pm 0	1 \pm 0
aws.seg	8	0.5	0.7 \pm 0.3	4649 \pm 1532.8	7058 \pm 1634.8	2409 \pm 1191.4	4649 \pm 1532.8	7038.3 \pm 1623.3	5768.6 \pm 1717	6023.4 \pm 1982.2	0 \pm 0	2.6 \pm 1.1	1 \pm 0
aws.seq	9	0.6	1 \pm 0.4	5356.7 \pm 1464.3	9409.9 \pm 2535.9	4053.2 \pm 1307.1	5901 \pm 1898.1	9155.1 \pm 2494.3	6830.7 \pm 1787.8	6489.6 \pm 1684.1	0 \pm 0	1 \pm 0	4.2 \pm 1.6
dws	359	22.1	0.5 \pm 0.3	1091.6 \pm 1008.5	1948.5 \pm 1327.9	857 \pm 672.9	2186 \pm 1214.3	991.8 \pm 999	1439.5 \pm 1083.8	1426 \pm 1080.4	0 \pm 0	1 \pm 0	1 \pm 0
dws.seg	28	1.7	0.9 \pm 0.3	1684 \pm 1710.7	3274.3 \pm 1992.4	1590.3 \pm 1015.8	3348.1 \pm 1375.2	1446.2 \pm 1376.3	2162.9 \pm 1961.9	2164.6 \pm 1955.1	0 \pm 0	3 \pm 0.9	1 \pm 0
dws.seq	79	4.9	0.9 \pm 0.6	2356 \pm 2606.6	3376.4 \pm 2731.3	1020.5 \pm 441.4	1556 \pm 388.3	742.8 \pm 290.4	2799.4 \pm 2806.9	2790 \pm 2868.7	0 \pm 0	1 \pm 0	8.9 \pm 3.3
dws.seq.t	4	0.2	1.2 \pm 0.5	600.3 \pm 139.3	1749.9 \pm 475.7	1149.6 \pm 359.7	1638.3 \pm 565.7	642.4 \pm 200	779.3 \pm 105.5	808.6 \pm 102.2	0 \pm 0	1 \pm 0	6.2 \pm 4.3
flatws	326	20.0	0.6 \pm 0.3	1461.3 \pm 1415	1672.5 \pm 1416.6	211.2 \pm 65	2092.2 \pm 2165.3	2007.6 \pm 2187.4	1576.1 \pm 1415.1	1576.9 \pm 1416.5	0 \pm 0	1 \pm 0	1 \pm 0
flatws.seg	27	1.7	1.1 \pm 0.5	1875.6 \pm 1670.3	2132.5 \pm 1766.8	256.9 \pm 125.7	1247.3 \pm 409.9	1228.9 \pm 418.1	2013.9 \pm 1736.5	2012.2 \pm 1732.5	0 \pm 0	5 \pm 2	1 \pm 0
modws	157	9.7	1 \pm 0.5	2088.1 \pm 1803.9	3292.3 \pm 2179.5	1204.2 \pm 861.7	2403.5 \pm 1427.1	2090.5 \pm 1549.6	2589 \pm 1955.7	2569.2 \pm 2003.3	8.1 \pm 3.8	1 \pm 0	1 \pm 0
modws.seg	76	4.7	1.2 \pm 0.5	2319.7 \pm 1733.5	4110.3 \pm 2679.9	1790.5 \pm 1192.6	2041.1 \pm 2844.4	1519.5 \pm 1745.2	2950.3 \pm 2119	2879.1 \pm 2067.7	7.3 \pm 3.9	6 \pm 3.8	1 \pm 0
modws.m	4	0.2	0.9 \pm 0.3	3386.6 \pm 1627.2	5066 \pm 2167.6	1679.4 \pm 668.3	3604.7 \pm 1932.1	3606.8 \pm 1708.3	4218.8 \pm 2102.3	3908.2 \pm 1687.5	3 \pm 0	1 \pm 0	1 \pm 0
modws.m.seg	5	0.3	1.1 \pm 0.1	646.1 \pm 67.3	1413.6 \pm 79.3	767.4 \pm 75.4	824 \pm 104.9	646.1 \pm 67.3	928.1 \pm 73.4	909.4 \pm 137.1	3 \pm 0	3 \pm 0	1 \pm 0
modws.sa	3	0.2	0.2 \pm 0	4891.7 \pm 390	8294.2 \pm 234.3	3402.4 \pm 160.7	8294.2 \pm 234.3	4891.7 \pm 390	6210.9 \pm 93.8	5914.1 \pm 500.7	2 \pm 0	1 \pm 0	1 \pm 0
modws.sa.seq	7	0.4	1.5 \pm 0.6	5424.8 \pm 303.1	8249.5 \pm 413.4	2824.7 \pm 665.9	7874.4 \pm 602.4	5745.2 \pm 327.5	6699.8 \pm 167.1	6468.8 \pm 325.3	8.6 \pm 3	1 \pm 0	4.3 \pm 1.7
modws.t	5	0.3	0.9 \pm 0.2	766.5 \pm 635.2	2734.5 \pm 852.1	1968 \pm 1075.7	2497.5 \pm 886.1	818.9 \pm 632	1246.9 \pm 891	1190.6 \pm 913.4	9.4 \pm 4.4	1 \pm 0	1 \pm 0
modws.seg.t	5	0.3	1.1 \pm 0.2	597.6 \pm 188.3	1772.5 \pm 116	1175 \pm 199.4	905.1 \pm 187.1	1146.3 \pm 595.6	1021.9 \pm 309.9	993.7 \pm 325	6.8 \pm 4.4	5.8 \pm 2	1 \pm 0
nws	21	1.3	0.4 \pm 0.2	1488.5 \pm 2010	2378.2 \pm 2004.6	889.7 \pm 310.5	756.4 \pm 291	728.4 \pm 341.9	2021.2 \pm 2064.8	2021.2 \pm 2108.2	1 \pm 0	1 \pm 0	1 \pm 0
nws.seg	3	0.2	0.5 \pm 0.1	2084.3 \pm 2952.6	3356.1 \pm 2789.6	1271.8 \pm 226.3	2306.5 \pm 2760.4	2084.3 \pm 2952.6	2820.3 \pm 3127	3000 \pm 2996.7	1 \pm 0	3 \pm 0	1 \pm 0
nws.seq	5	0.3	0.8 \pm 0.6	2967.4 \pm 1904.8	3462.3 \pm 1832.9	494.9 \pm 209	3078.6 \pm 1825.6	3032.7 \pm 1816.3	3150 \pm 1968.1	3173.4 \pm 2015.5	5.2 \pm 6.1	1 \pm 0	5.6 \pm 5.9
rws	6	0.4	0.3 \pm 0.1	1513.7 \pm 74.7	2019.2 \pm 76.6	505.5 \pm 94.8	1513.8 \pm 74.7	1941.8 \pm 56.9	1906.3 \pm 70.6	1878.9 \pm 127	0 \pm 0	1 \pm 0	1 \pm 0
uws	26	1.6	0.4 \pm 0.3	2787.8 \pm 2102.1	4179.8 \pm 3146.1	1392.1 \pm 1325.4	3537 \pm 2886	3531.8 \pm 2889.8	3229.9 \pm 2404.1	3168.6 \pm 2362.1	1 \pm 0	1 \pm 0	1 \pm 0
uws.seq	10	0.6	1.3 \pm 0.5	3382.6 \pm 935.1	5092.3 \pm 1505.1	1709.7 \pm 906.7	4942.3 \pm 1538.6	4600.2 \pm 1361.8	3808.6 \pm 1054.7	3728.9 \pm 1041	7.5 \pm 3.9	1 \pm 0	7.5 \pm 3.9
trill	48	3.0	1.2 \pm 0.8	3629.4 \pm 774.6	4129.9 \pm 724	500.4 \pm 200.2	3276.3 \pm 815.7	3321 \pm 763.9	3928.2 \pm 762.7	3917.5 \pm 766.2	11.8 \pm 5.1	1 \pm 0	13.1 \pm 5.7
dottrill	3	0.2	0.9 \pm 0.4	4473.4 \pm 1348.7	5034.1 \pm 1294.5	560.7 \pm 179.2	4625.1 \pm 1504.8	4787 \pm 1062.9	4765.6 \pm 1232.7	4726.6 \pm 1115.5	0 \pm 0	1 \pm 0	21 \pm 9.6

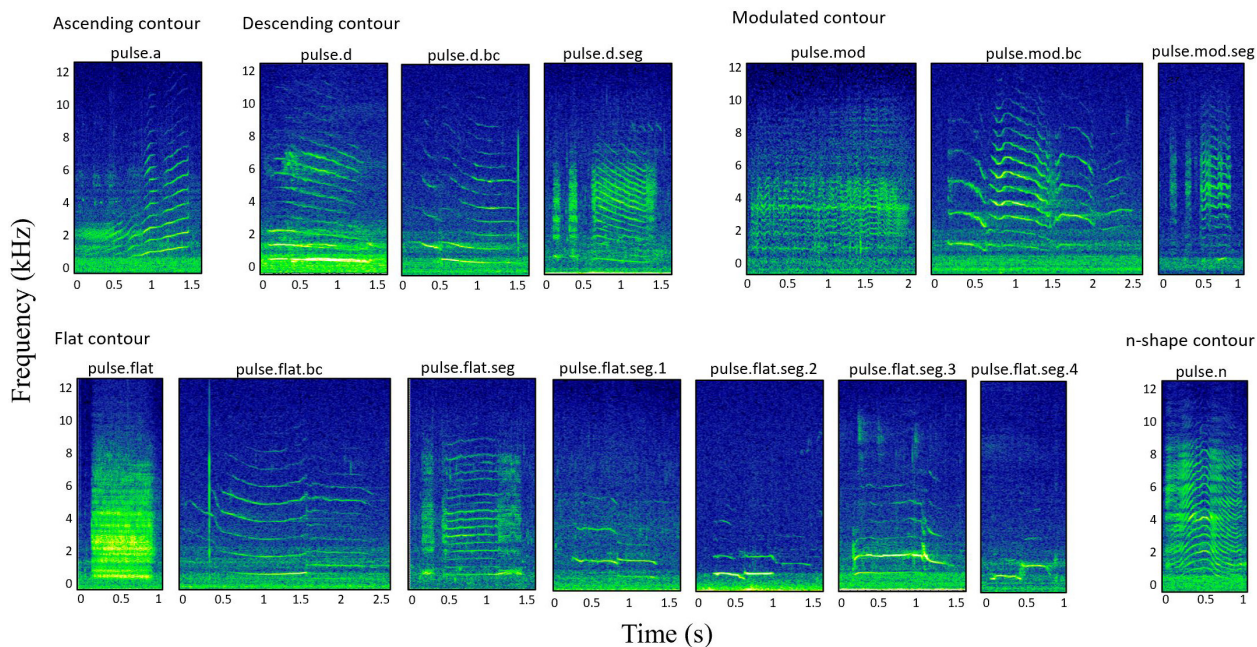


FIG. 5. (Color online) CIB pulsed call types organized by contour. Spectrograms are 1024 point FFT, Hanning window, and 75% overlap, generated in Raven Pro 1.6.

(flatws, flatws.seg) from other calls using bandwidth, then number of inflections was used to separate the remaining calls with no inflections (e.g., dws, aws, pulse.a, pulse.d, pulse.flat) from those with inflections (e.g., modws, nws, uws, pulse.mod, pulse.n). Within these branches, whistles and pulsed calls were separated using the minimum and maximum PRR measurements.

The Random Forest model also yielded similar results to the manual classification, resulting in an 85% agreement (out-of-bag error rate = 15.18%). The most important acoustic variables for the model in terms of accuracy were number of inflections, number of segments, bandwidth, and frequency trend (Fig. 7). In general, call types with small sample sizes (dws.seq.t, modws.m, modws.seq.t, modws.t, nws.seq, pulse.flat.bc, pulse.flat.seg.4, pulse.mod.bc) had higher misclassification rates (0.4–1.0) than those with larger sample sizes, such as dws, flatws, modws, and pulse.flat, which varied from 0.0 to 0.3 (see supplementary material for the Random Forest confusion matrix and call type error rates).¹

C. Anthropogenic noise analysis

We assessed the effect of close and distant commercial ship noise on the three most common call types in the whistle and pulsed call categories and the single stereotyped combined call type. Figure 8 shows a long-term spectral average (LTSA) (10 s and 5 Hz averaging) of 24 h (8 h of duty-cycled data), and a zoomed in spectrogram of 3 h (1 h of duty-cycled data) of the acoustic footprint of the commercial ship encounter we used for masking analysis at the Susitna location.

We plotted the spectra of the three most common whistle types (dws, flatws, modws), pulsed call types (pulse.d, pulse.flat, pulse.flat.seg), and the single most common

stereotyped combined call type (CI.c.5) with close and distant ship noise and in relation to the composite beluga audiogram (Fig. 9). The call type spectra (shown in blue) are completely masked in all seven call types under close ship noise conditions (shown in red). Under distant ship noise conditions (shown in yellow), all call types are partially masked. In the distant ship noise condition, partial masking in whistles occurred from roughly 500–5000 Hz in descending whistles (dws), 500–6000 Hz in flat whistles (flatws) with a break from masking around the spectral peaks at 800 and 1600 Hz, and 500–800 Hz in modulated whistles (modws). For pulsed calls, partial masking occurred from roughly 500–2500 Hz with a break from masking around the spectral peaks at 800 and 2000 Hz in descending pulsed calls (pulse.d), 500–800 Hz in flat pulsed calls (pulse.flat), and 500–2800 Hz with a slight break in masking at the spectral peak of 1000 Hz in flat segmented pulsed calls (pulse.flat.seg). For the combined call, CI.c.5, partial masking occurred from roughly 500–2800 Hz with a slight break in masking around 1500 and 2000 Hz. An important caveat to note is that we were not able to describe masking above 12 kHz due to the frequency sampling limitations of the acoustic recorders used in this study.

IV. DISCUSSION

Our study provides the first description of the vocal repertoire of the endangered CIB population. We further endeavor to provide a broader context for geographic variability in beluga vocal repertoire by conducting a qualitative comparison to other published descriptions of beluga vocal repertoires worldwide. Finally, we describe the levels of masking of the most commonly used call types from

TABLE V. Descriptive statistics of CIB pulsed call types (mean \pm SD).

Call type	N	% total	Dur.(s)	Min. (Hz)	Max. (Hz)	BW (Hz)	Start (Hz)	End (Hz)	Center (Hz)	Peak (Hz)	Inflect.	Seg.	Steps	Min. PRR	Max. PRR
pulse.a	21	1.3	0.9 \pm 0.4	1068.6 \pm 743.6	10279.1 \pm 2749.3	9210.5 \pm 2583.1	1006.1 \pm 1009.5	1567.2 \pm 1338	2405.1 \pm 1643.4	1857.1 \pm 1401.7	0 \pm 0	1 \pm 0	0 \pm 0	470.9 \pm 243.9	631.9 \pm 261.3
pulse.d	42	2.6	0.8 \pm 0.3	917.2 \pm 417.8	8608.6 \pm 2906.2	7691.3 \pm 2807.2	1889.6 \pm 1230	954.5 \pm 564.2	1774.6 \pm 1084.8	1607.1 \pm 1086.4	0 \pm 0	1 \pm 0	0 \pm 0	931.1 \pm 364.6	1235.5 \pm 382.2
pulse.d.bc	12	0.7	1.4 \pm 0.6	803.7 \pm 302.6	9241.3 \pm 1899.5	8437.6 \pm 1996.8	2258.2 \pm 1055.9	1017 \pm 397.8	1533.2 \pm 368.7	1525.4 \pm 385.6	0 \pm 0	1 \pm 0	1.3 \pm 0.5	723.1 \pm 116.8	1672.2 \pm 296.9
pulse.d.seg	16	1.0	1.4 \pm 0.4	740.4 \pm 629.3	9307.7 \pm 2143.7	8567.3 \pm 1967.9	1138.3 \pm 697.8	667.2 \pm 470.4	2572.3 \pm 1558.5	1699.2 \pm 1408	0 \pm 0	3.3 \pm 0.8	0 \pm 0	295.8 \pm 169.4	486.6 \pm 181.2
pulse.flat	114	7.0	0.9 \pm 0.4	1387.9 \pm 1052.6	7747.5 \pm 3271.1	6359.6 \pm 3106.7	1286.7 \pm 922.5	1216.3 \pm 963.9	2571.1 \pm 1586.9	2380.1 \pm 1607.3	0 \pm 0	1 \pm 0	0 \pm 0	848.1 \pm 437.4	897.5 \pm 439.8
pulse.flat. bc	3	0.2	2 \pm 1	1143.2 \pm 341.9	9829.5 \pm 829.6	8686.3 \pm 700.2	2366.7 \pm 993.1	1734.4 \pm 338.3	1421.9 \pm 352.6	1406.2 \pm 353.9	0 \pm 0	1 \pm 0	1.7 \pm 0.6	800.7 \pm 66.1	1329.1 \pm 321.1
pulse.flat. seg	65	4.0	1.8 \pm 1.4	1285.1 \pm 953.2	10403.1 \pm 1943.3	9118 \pm 2127.1	1835.8 \pm 1474.5	1870.4 \pm 1497.1	3298.6 \pm 1413.8	3160.1 \pm 1864.9	0 \pm 0	2.9 \pm 1.9	0 \pm 0	237.5 \pm 143.4	403.9 \pm 81.1
pulse.flat. seg.1	6	0.4	0.9 \pm 0.2	793.7 \pm 368.3	4831.1 \pm 1708.5	4037.4 \pm 1504.2	1852 \pm 115.4	1630 \pm 62.6	1574.2 \pm 428.2	1566.4 \pm 447	0 \pm 0	2 \pm 0	0 \pm 0	884 \pm 46.7	1803.5 \pm 32.0
pulse.flat. seg.2	11	0.7	1 \pm 0.2	663.3 \pm 73.9	3511.5 \pm 1284.8	2848.2 \pm 1347.8	922.3 \pm 100.6	1582.2 \pm 69.4	1031.2 \pm 198.3	1007.8 \pm 228.4	0 \pm 0	3 \pm 0	0 \pm 0	982.9 \pm 59.5	1516.6 \pm 168.3
pulse.flat. seg.3	16	1.0	1 \pm 0.3	722.6 \pm 66.8	6181.7 \pm 2493.5	5459.1 \pm 2465.6	1519.8 \pm 294.7	2767.1 \pm 4182.8	1706.5 \pm 350.3	1646.5 \pm 350.3	0 \pm 0	2 \pm 0	0 \pm 0	921.4 \pm 91.4	1620.1 \pm 88.7
pulse.flat. seg.4	6	0.4	1 \pm 0.3	842.6 \pm 240.6	5109.1 \pm 1724.1	4266.5 \pm 1698	964.8 \pm 231.8	1547 \pm 154.8	1406.2 \pm 332.8	1390.6 \pm 426.7	0 \pm 0	2 \pm 0	0 \pm 0	957.8 \pm 66.8	1578.6 \pm 55.9
pulse.mod	16	1.0	1.2 \pm 0.6	1482.7 \pm 901.8	9330.3 \pm 2020.8	7847.5 \pm 1582.5	2606.7 \pm 1197.3	2469.9 \pm 1129.5	3153.8 \pm 1571.7	2893.1 \pm 1648.5	6.4 \pm 4.9	1 \pm 0	0 \pm 0	459.6 \pm 240.5	614.5 \pm 344.3
pulse.mod. bc	4	0.3	2.4 \pm 0.4	985.9 \pm 197.1	9522.7 \pm 2058.5	8536.8 \pm 2047.7	2244.8 \pm 1297	1719 \pm 663.8	2343.7 \pm 1135.2	2419.9 \pm 1138.8	6.2 \pm 3.1	1 \pm 0	1.2 \pm 0.5	578.9 \pm 245.0	1310.2 \pm 402.1
pulse.mod. seg	10	0.6	1 \pm 0.2	1335 \pm 300.8	9833 \pm 1337.2	8498 \pm 1394	3253.6 \pm 1556.6	3273.2 \pm 1605.4	4591.4 \pm 1128.2	4410.9 \pm 1744.5	7.2 \pm 4	3 \pm 0.9	0 \pm 0	366.7 \pm 245.3	737.8 \pm 236.7
pulse.n	12	0.7	0.5 \pm 0.2	1807.8 \pm 1401.6	8960.4 \pm 2940.1	7152.6 \pm 2764.3	1489.5 \pm 1201.3	1432.2 \pm 1177.2	2933.6 \pm 2067.7	2996.1 \pm 2112.3	1 \pm 0	1 \pm 0	0 \pm 0	838.4 \pm 382.2	1141.0 \pm 409.2

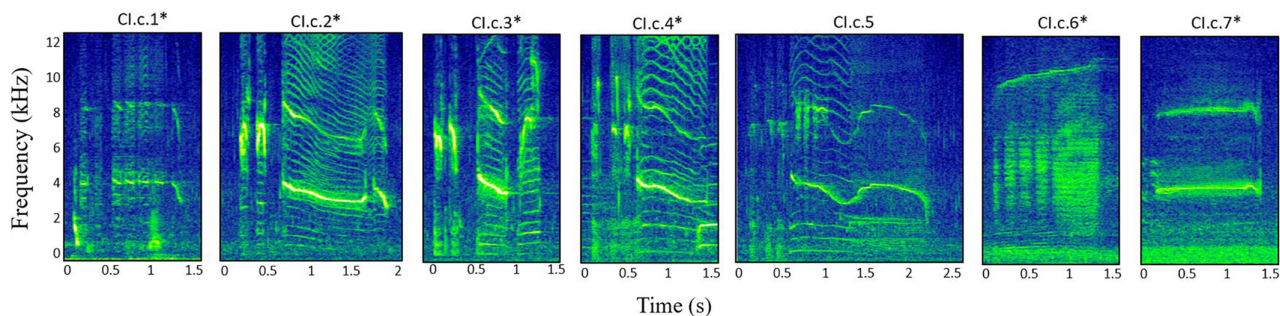


FIG. 6. (Color online) CIB combined calls (both stereotyped and non-stereotyped). Asterisks denote calls that did not meet the protocol repetition requirement but are shown for reference for future studies. Spectrograms were 1024 point FFT, Hanning window, and 75% overlap, generated in Raven Pro 1.6. Note Cl.c.2 to Cl.c.5 show aliasing artifacts in the upper frequencies due to acoustic energy above the Nyquist frequency of 12 kHz.

commercial ship noise at the Susitna location, which is in the core of the CIB critical habitat.

We documented CIB calls during multiple seasons across two core locations of the critical habitat, Susitna and Trading Bay, and manually classified calls into 41 call types. We compared our manual call classification system with two quantitative methods that have proved to be successful when classifying beluga vocal repertoire (Garland *et al.*, 2015). Our CART and Random Forest analyses had a 95% and 85% agreement with the manual call classification, respectively. In the CART analysis, 43 terminal nodes were created, which was 3 more than our manual call classification (see supplementary material for CART figure).¹ Those additional nodes were sub-divisions within three of the manually classified call types (aws, dws.seq, pulse.flat). Aws and dws.seq were split by two frequency measurements, minimum frequency, and center frequency, respectively. These differences in minimum and center frequency indicated that the manual classification of these two call types could have been split into additional subtypes based on frequency; however, in our manual classification, we chose to keep them classified into a single aws and dws.seq call type since the contour remained the same. Pulse.flat was sub-divided based on differences in frequency trend. For the CART analysis, 30% of the pulse.flat call contours showed a slight decrease in frequency at the terminal portion; the remaining 70% were flat throughout the contour. The call contour was used as the main criterion for our manual classification, and call classification was driven by the contour seen in at least 50% of the call. Since a slight decrease in frequency occurred at the very end of the call contour and more than 50% of the call was flat, we designated these call types as pulse.flat.

Our results indicate significant differences in both call type and call category composition between Susitna and Trading Bay. We could not test the effect of season due to the sampling dates of the acoustic recorders used; however, a previous study investigated spatial and temporal calling behavior of the CIB population and also found a significant difference in call category composition both spatially and temporally (Blevins-Manhard *et al.*, 2017). Spatio-temporal differences in call use may be linked to preferred seasonal

habitats and behavior (e.g., feeding, molting, calving). Previous studies have examined which environmental variables may contribute to CIB summer habitat preference and found that there is a greater probability of belugas being present closer to rivers with medium flow accumulation, Chinook salmon runs, tidal mudflats, and areas with sandy coastlines (Goetz *et al.*, 2007; Goetz *et al.*, 2012). A long-term photo identification study documented habitat use and distribution of the CIB population and found that encounters had predictable seasonal patterns and distinct hot spots that were stable across years (McGuire *et al.*, 2020). Spatio-temporal habitat preference, as well as behavior, may be driving the call type and call category compositional differences found in our study.

A. Beluga communication

Belugas are known to be one of the most vocal cetacean species, producing a wide array of calls. Possibly the most unique of those are combined calls, where two signals are produced simultaneously by the same individual. Along with belugas, this phenomenon has also been described in other odontocetes, such as killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*), short-finned pilot whales (*Globicephala macrohynchus*), and bottlenose dolphins (*Tursiops truncatus*) (Caldwell and Caldwell, 1967; Filatova *et al.*, 2009; Ford, 1989; Karlsen *et al.*, 2002; Lilly and Miller, 1961; Murray *et al.*, 1998; Papale *et al.*, 2015; Ridgway *et al.*, 2015; Sayigh *et al.*, 2013; Van Cise *et al.*, 2017; Vergara and Barrett-Lennard, 2008). Belugas also exhibit a graded call structure, in which call types can transition into others on a continuum (Karlsen *et al.*, 2002; Sjare and Smith, 1986). Graded call systems have also been documented in killer whales, false killer whales, and pilot whales, which all exhibit complex social structures (Ford, 1989; Murray *et al.*, 1998; Sayigh *et al.*, 2013). Belugas are known to be very gregarious and have highly complex systems of social organization and interaction (O’Corry-Crowe *et al.*, 2020). Our study has found that the CIB population, like other beluga populations, exhibit a rich and complex vocal repertoire. These findings align with the social complexity hypothesis for communicative complexity, described in Freeberg *et al.* (2012), which posits that species that

TABLE VI. Descriptive statistics (mean \pm SD) of CIB combined call type Cl.c.5 ($n = 8$, 0.5%).

Dur. (s)	Whole call								Whistle								Pulse								
	Min. (Hz)	Max. (Hz)	BW (Hz)	Center (Hz)	Peak (Hz)	Min. (Hz)	Max. (Hz)	BW (Hz)	Start (Hz)	End (Hz)	Trend	Infect.	Min. PRR	Max. PRR	Center	Steps	Max	Start	End	Units	Trend	Infect.	Min. PRR	Max. PRR	
1.9 \pm 0.4	1315.5 \pm 985.3	11989.7 \pm 19.1	10674.2 \pm 995.1	3257.8 \pm 968.5	3293 \pm 1128.8	2711.9 \pm 130.4	4632.6 \pm 247.9	1920.7 \pm 316.5	4542.9 \pm 283.2	2830.8 \pm 289.8	1.6 \pm 0.2	2.1 \pm 0.4	128.4 \pm 14.5	709.5 \pm 27.5											

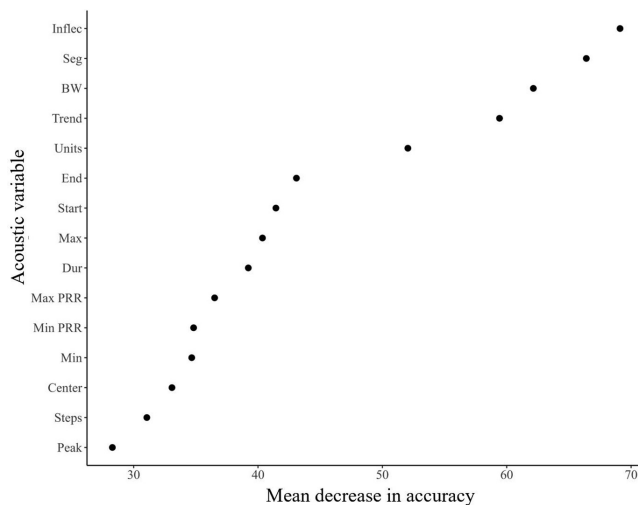


FIG. 7. Mean decrease in out-of-bag accuracy caused by excluding individual acoustic variables from the Random Forest model. Acoustic variables are listed in order of descending importance.

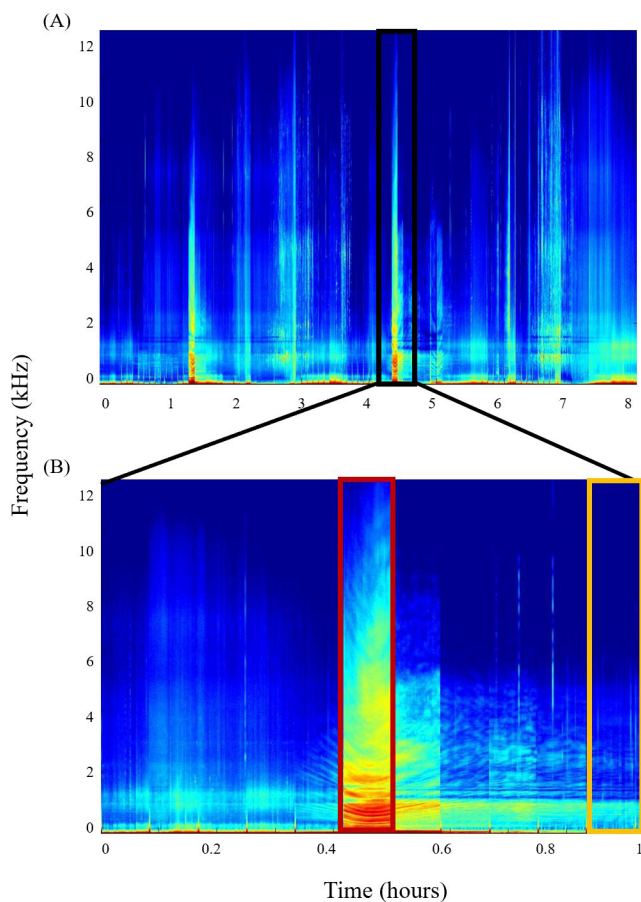


FIG. 8. (Color online) Commercial ship noise recorded at Susitna. (A) LTSA of 24 h (8 h of duty-cycled data) with beluga acoustic encounters and commercial ship noise. The commercial ship encounter used in masking analysis is shown in black outline. (B) Zoomed in spectrogram of 3 h (1 h of duty-cycled data) of the commercial ship encounter. The two 5 min sections shown in bolded outline represent the center (shown in red) and edge (shown in yellow) of the ship's acoustic footprint.

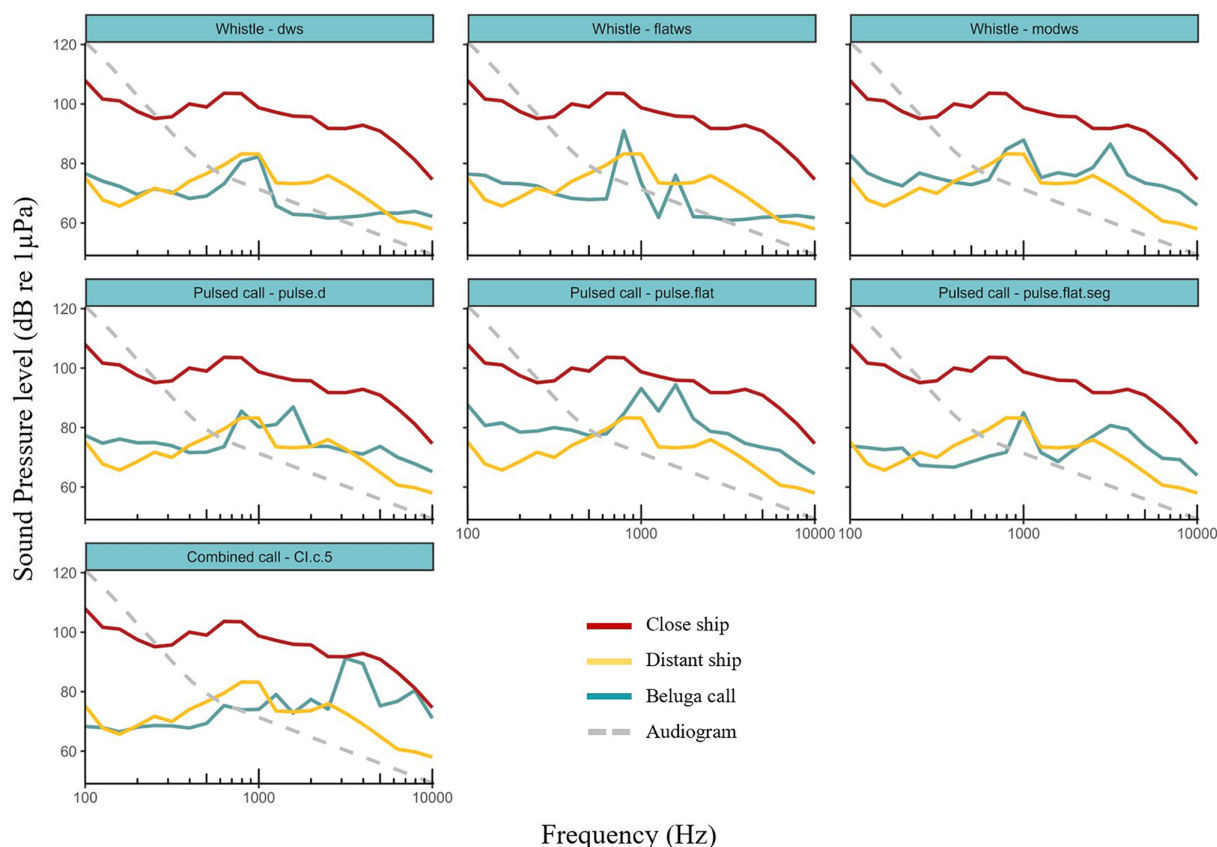


FIG. 9. (Color online) One-third octave band frequency spectral levels of common CIB call types (blue), and commercial ship noise at close (red) and distant (yellow) conditions received at the Susitna acoustic recorder. The audiogram (dashed gray) is the smoothed minimum beluga whale audiogram, also in one-third octave bands (from Erbe *et al.*, 2016). Whenever any portion of the call type signal is below the audiogram, hearing is audiogram limited and the signal is inaudible. Whenever any portion of the call type signal is above the audiogram, hearing is noise-limited and masking occurs when any portion of the call type signal is below the commercial ship noise.

exhibit larger and more complex social units show greater communicative complexity and these complex communication systems can express a wide range of emotional and motivational states between group members (Freeberg *et al.*, 2012).

It has been hypothesized that some pulsed and/or combined calls may aid in group cohesion. Calls used for this specific purpose are referred to as contact calls, some of which may possibly encode individual or group identity (Vergara and Mikus, 2019). The use of contact calls between group members has been studied in belugas in both aquaria and the wild (Mishima *et al.*, 2015; Mishima *et al.*, 2018; Morisaka *et al.*, 2013; Panova *et al.*, 2017; Panova and Agafonov, 2023; Van Parijs *et al.*, 2003; Vergara *et al.*, 2010; Vergara and Mikus, 2019). The use of individual identity and group cohesion calls has been extensively studied in delphinids, particularly in bottlenose dolphins, which are known to produce highly stereotyped signature whistles containing individual identity and broadcast information about the caller (Caldwell and Caldwell, 1965; Janik *et al.*, 2006; Janik and Slater, 1998; Sayigh *et al.*, 1999). In killer whales, pods exhibit unique calls that are thought to function as contact signals to maintain group cohesion (Ford, 1989; Yurk *et al.*, 2002). Narwhals (*Monodon monoceros*),

which are the closest living relative to the beluga and only other species in the family Monodontidae, have also been shown to exhibit evidence of signature contact calls in both adults (Shapiro, 2006) and mother-calf pairs (Ames *et al.*, 2021).

Belugas are highly social cetaceans and the CIB population in particular live in an extremely turbid environment in which acoustic signaling is the most effective form of sensory modality. Identification calls at the level of the individual or group could aid in group cohesion efforts during periods of isolation or separation via predator presence, tidal influence, or anthropogenic disturbance. In Cook Inlet, we documented several pulsed and combined calls that may serve as contact calls given their structure (e.g., pulse.flat, pulse.flat.seg, CI.c.6, CI.c.7). Though this study was not able to investigate contact call use, we hope the classification of these calls will be useful for future studies that aim to investigate beluga contact calls in Cook Inlet.

B. Comparisons among beluga vocal repertoires worldwide

Geographic variation in vocal repertoires among beluga populations can occur through drift or active social learning and may be a reliable indicator of divergence and population

structure among groups. In this study, we were not able to conduct a formal, quantitative geographic variation analysis; however, we have expanded on the call type comparison table from [Garland *et al.* \(2015\)](#) to include call types documented in Cook Inlet and their relation to other beluga populations (Table III). Our study shows that the CIB population exhibits a number of unique call types and it is likely that the divergence of the CIB vocal repertoire is due to the population's long-term geographic and genetic isolation from other beluga populations ([O'Corry-Crowe *et al.*, 1997](#)).

Among whistles, multiple call types have been documented across all eight populations studied, including ascending, descending, flat, modulated, n-shaped, and u-shaped whistles. Overall, flat whistles appear to be a dominant call type across beluga populations, being either the most common or second most common call type across all eight populations studied. In Cook Inlet, flat whistles (flatws) comprised 20% of the vocal repertoire, which was the second most common call type. Descending whistles, the most common call type in Cook Inlet (dws, 22.1%), were also the most common call type in the eastern Beaufort Sea population ([Garland *et al.*, 2015](#)). Segmented whistles (aws.seg, dws.seg, flatws.seg, modws.seg, modws.m.seg, modws.seg.t, nws.seg) were present in Cook Inlet, primarily modulated segmented whistles (modws.seg, 4.7%) and were also documented in the eastern Beaufort Sea ([Garland *et al.*, 2015](#)), Svalbard ([Karlsen *et al.*, 2002](#)), Bristol Bay ([Angiel, 1997](#)), St. Lawrence ([Faucher, 1988](#)), and Cunningham Inlet ([Sjare and Smith, 1986](#)) populations. Whistles in sequences (aws.seq, dws.seq, dws.seq.t, modws.sa.seq, nws.seq, uws.seq) were also present in Cook Inlet, primarily descending whistle sequence (dws.seq, 4.9%), which was also documented in the White Sea population ([Belikov and Bel'kovich, 2007](#)). Trills were documented in Cook Inlet (3%) and also occurred in the eastern Beaufort Sea ([Garland *et al.*, 2015](#)), Svalbard ([Karlsen *et al.*, 2002](#)), St. Lawrence ([Faucher, 1988](#)), and Cunningham Inlet ([Sjare and Smith, 1986](#)) populations while dotted trills (0.2%) were only documented in Cook Inlet.

Among Cook Inlet pulsed call types, only flat pulsed calls were documented in all other populations. Along with flat whistles, flat pulsed calls seem to be a universal call type among all beluga populations studied thus far. Flat pulsed calls (pulse.flat, 7%) were the most common pulsed call type in Cook Inlet, and second most common call types in Svalbard ([Karlsen *et al.*, 2002](#)) and Bristol Bay ([Angiel, 1997](#)). Segmented pulsed calls (pulse.d.seg, pulse.flat.seg, pulse.flat.seg.1-4, pulse.mod.seg) were present in Cook Inlet, primarily flat segmented pulsed calls (pulse.flat.seg, 4%), which were the second most common pulsed call type. This call type was also documented in the White Sea ([Belikov and Bel'kovich, 2008](#)) and Cunningham Inlet ([Sjare and Smith, 1986](#)). The third most common pulsed call type in Cook Inlet was descending pulsed call (pulse.d, 2.6%) which was also documented in the eastern Beaufort Sea ([Garland *et al.*, 2015](#)), White Sea ([Belikov and](#)

[Bel'kovich, 2008](#)), Bristol Bay ([Angiel, 1997](#)), and Cunningham Inlet ([Sjare and Smith, 1986](#)) populations. No combined calls found in Cook Inlet were documented elsewhere.

Due to the lack of standardization among beluga vocal repertoire studies, one important caveat to highlight is that differences in repertoires could potentially be in part due to non-comparable recording effort across studies (e.g., number of days recorded, single season, and single location sampling, effect of human and vessel presence on beluga vocal behavior when collecting recordings, recorder sampling rate, and duty cycle). In this study, our analysis was based on 1633 calls, other studies varied from 460 calls in St. Lawrence, Canada ([Faucher, 1988](#)) to 2839 calls across three studies in the White Sea, Russia ([Belikov and Bel'kovich, 2006, 2007, 2008](#)). Because our study is the only one to use a rarefaction curve to assess vocal repertoire richness and completeness, it is unclear how complete the vocal repertoire is for other beluga populations.

C. Anthropogenic noise masking

In the presence of vessel noise, belugas have been shown to reduce their overall calling rate and increase repetition of specific calls, as well as shift the frequency range of their calls upward ([Lesage *et al.*, 1999](#)). [Vergara *et al.* \(2021\)](#) modeled the communication range of various age classes of belugas in the presence of vessel noise in the St. Lawrence Estuary and showed that communication ranges of young belugas were significantly reduced in the presence of noise, which can have particularly detrimental effects on mothers and dependent calves as it may prevent maintaining contact with one another. Another study in St. Lawrence showed that belugas vary vocalization levels as a function of noise, indicating a Lombard vocal response ([Lombard, 1911](#); [Scheifele *et al.*, 2005](#)).

In Cook Inlet, previous studies have documented the occurrence and potential impacts of anthropogenic noise ([Castellote *et al.*, 2018](#); [Mooney *et al.*, 2020](#); [Polasek, 2021](#); [Small *et al.*, 2017](#)), which has been listed as a high level concern for the recovery of the CIB population ([National Marine Fisheries Service, 2016](#)). In particular, commercial shipping noise has been found to be the most prevalent anthropogenic noise source within Cook Inlet, showing a wide spatial distribution and temporal duration ([Castellote *et al.*, 2018](#)). Because of this, communication masking by commercial shipping noise has been highlighted as a potential concern ([Castellote *et al.*, 2018](#)). The masking of communication signals can be problematic for a species that relies heavily on acoustic communication, rather than vision for navigation, foraging, group cohesion, and predator avoidance. Our study provides empirical support that all seven of the most common call types in the CIB vocal repertoire were partially masked by distant commercial ship noise and completely masked by close commercial ship noise in the frequency range up to 12 kHz. Auditory masking occurs when one sound interferes with an individual's ability to not

only detect, but also discriminate and recognize another sound (Branstetter and Sills, 2022; Erbe *et al.*, 2016). While some beluga calls can have acoustic energy above 12 kHz, the crucial components of the calls below 12 kHz will be masked and the animal's ability to discriminate, recognize, and process the encoded information will be impacted.

This region of Susitna is in the core of the CIB critical habitat and within 2000 m of the Port of Alaska commercial shipping lanes. We consider these results a conservative measure of masking of beluga communication in other areas of the critical habitat along the commercial shipping lanes (shown in Fig. 1). Due to the shallow nature and high glacial sediment load of Cook Inlet (Sharma and Burrell, 1970), sound propagation in this environment is strongly attenuated (Au and Hastings, 2008). Therefore, the sound levels for the commercial ship footprint reported 2000 m away would likely occur at greater distances in the deeper waters of the CIB critical habitat.

It has been estimated that roughly 486 commercial ships use the Port of Alaska annually, with an average of 8–10 ships per week (Eley, 2006). Our results suggest that every time a commercial vessel transits through the Port of Alaska commercial shipping lanes, CIB communication is heavily impacted within their core habitat. Our study fills a critical research gap in which we quantify masking levels as they relate to commonly used CIB call types. We recommend that future research use acoustic tags on CIB to further investigate the effect of masking by anthropogenic noise on the behavior of individuals in the population, in particular in areas of their critical habitat encroached by commercial shipping noise, such as the Susitna Delta or lower Knik Arm.

V. CONCLUSION

We have provided the first description of CIB vocal repertoire, which complements previous studies of vocal repertoire in other beluga populations, providing a critical baseline framework that can be built upon to quantify geographic variability in vocal repertoire among populations, or context-specific acoustic behavior within the Cook Inlet population. We have also provided a quantification of call masking by commercial ship noise for the most commonly used CIB call types in the frequency range of 0–12 kHz. Our masking analysis results indicate that, in the Susitna area, beluga communication is heavily impacted during each commercial ship passage, with all seven of the most commonly used call types being partially or fully masked during this noise disturbance.

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¹See supplementary material at <https://doi.org/10.1121/10.0022516> for a beluga call type comparison table; CART figure; the Random Forest confusion matrix and call type error rates.

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