Trajectories of Vocal Repertoire Development in Beluga (*Delphinapterus leucas*) Calves: Insights from Studies a Decade Apart

Audra E. Ames[1, 2] and Valeria Vergara[3]

[1]*Fundación Oceanogràfic de la Comunitat Valenciana, Carrer d'Eduardo Primo Yúfera (Cientific) No. 1B, Valencia 46013, Spain*
E-mail: aames@oceanografic.org
[2]*School of Psychology, College of Education and Human Sciences, The University of Southern Mississippi,*
118 College Drive, Hattiesburg, MS 39406, USA
[3]*Marine Mammal Conservation Research Program, Ocean Wise Conservation Association,*
845 Avison Way, Vancouver, BC V6B 3X8, Canada

Abstract

There has been only one published study of beluga vocal development, despite the value of ontogenetic research for our understanding of sound-centered species. Findings from this seminal study were vital to understanding the beluga vocal repertoire, but further empirical study is necessary to determine if other calves follow similar trajectories in sound acquisition and development. Herein, we compare the two-year vocal progression of an additional calf, "Kylu," to the previous research. Additionally, we report on changes in acoustic energy distribution and source level of early calf sounds for the first time as part of a larger effort to understand the impacts of underwater noise on neonate vocalizations. From his day of birth, Kylu produced broadband pulse trains with upper-frequency limits above the study's Nyquist cutoff (128 kHz)—higher than what was reported by the previous study, which was limited by lower sampling rates. Pulsed signals were his most common sound type during his first year as in the previous study. Over Kylu's first month of life, pulse repetition rate, source level, and third quartile frequencies of the calf's pulse trains increased significantly. First and third quartile, center, and peak frequencies increased significantly over the first year as did pulse repetition rate and call duration. Mixed calls and tonal sounds were infrequent and not regularly produced until later in the first year of life. Calf acquisition of adult-like mixed call production appeared similarly between studies, while tonal acquisition appeared more variable. Kylu developed a contact call that was most similar to his mother's as found in the previous study, although slight variation in contact call acquisition was evident. By comparing beluga calves and employing new technology, we reveal species-specific parallels in development and provide new information about beluga calves.

Key Words: beluga, *Delphinapterus leucas*, calf, contact call, ontogeny, repertoire, vocalization, vocal development

Introduction

Beluga whales (*Delphinapterus leucas*) are considered to be one of the most vociferous cetacean species, yet there is a dearth of empirical studies pertaining to their communication system, including the ontogeny of their rich vocal repertoire. Beluga sounds fall along a continuous spectrum of tonal and pulsed emissions, although the beluga vocal repertoire can generally be classified into several primary *sound types* or *categories*. These include echolocation clicks and the more communicative signals: tonal sounds, pulsed sounds, and mixed calls. *Tonal sounds*, sometimes referred to as whistles, are narrowband, frequency-modulated signals. *Pulsed sounds* are generally comprised of broadband packets of non-echolocation clicks or pulses that are often classified based on pulse repetition rate, or the number of pulses per second (e.g., Sjare & Smith, 1986; Belikov & Bel'kovich, 2008; Chmelnitsky & Ferguson, 2012). *Mixed calls*, sometimes referred to as biphonations or combined calls, are sounds that commonly contain overlapped pulsed and tonal components; however, some mixed calls may also be characterized by other combinations of overlapping components such as two pulsed sounds of varying repetition rate produced simultaneously (Karlsen et al., 2002; Vergara et al., 2010; Vergara, 2011).

Beluga *call types* are comprised of the sounds described above but are generally stereotyped, contextually specific, and unique to the repertoires of

one or more individuals. For example, it has been established that some distinctive broadband long-duration pulsed sounds function as beluga contact calls or signals used to maintain or restore contact among conspecifics, including related individuals like mothers and calves (Van Parijs et al., 2003; Vergara et al., 2010). Contact calls are perhaps the most well-studied contextually specific call in the beluga vocal repertoire as these calls appear to serve a key biological purpose (Vergara et al., 2010; Morisaka et al., 2013; Mishima et al., 2015; Panova et al., 2017; Vergara & Mikus, 2019). Simple contact calls are comprised only of broadband pulses with no additional overlapping component (Vergara & Mikus, 2019) and have been described for captive beluga social groups (Morisaka et al., 2013; Mishima et al., 2015) and for a wild mother–calf pair (Van Parijs et al., 2003). Mixed contact calls, which contain two overlapping components, are referred to as complex contact calls (Vergara & Mikus, 2019) and, again, have been described for both captive (Panova et al., 2017) and wild (Van Parijs et al., 2003; Vergara & Mikus, 2019) belugas. The overlapping component of complex contact calls is believed to be a vocal signature that may encode individual or group identity (if shared with a few closely related animals; Vergara & Mikus, 2019).

To date, there is only a single ontogenetic study describing the development of the beluga vocal repertoire (Vergara & Barrett-Lennard, 2008; also see Vergara, 2011, for more details on two additional calves). Findings from this early work suggest that beluga calves do not immediately produce the large variety of call types and sound categories typical of adult belugas but that they acquire them gradually. This study also documented a progressive development of a beluga calf's complex contact call to match the complex contact call type of the mother (Vergara & Barrett-Lennard, 2008), thus indicating that at least in early life, some contact calls may be shared by the mother–calf dyad. Such a developmental trend may be explained by beluga social structure (Tyack, 1998) as related belugas appear to maintain close associations (Colbeck et al., 2013; O'Corry-Crowe et al., 2018) but still exhibit behaviors indicative of fission-fusion societies (Bel'kovitch & Sh'ekotov, 1993; Alekseeva et al., 2013; Krasnova et al., 2014). For calves in early life, production of the mother's contact call may facilitate maintenance of contact with kin while in large aggregates where group movement is fluid. Additional information on the vocal development of other beluga calves is lacking, however, so it is unknown whether other calves also develop their complex contact calls to match those of their mothers.

Studies of vocal ontogeny are an excellent source of information regarding complex animal communication systems. For example, it is likely that neonate vocal repertoires are initially comprised of sounds that are key to survival. Pulse trains (i.e., a series of pulses produced with a definable repetition rate) appear to be the only sound present in the beluga vocal repertoire at birth (Vergara & Barrett-Lennard, 2008; Vergara, 2011) and, thus, may function as rudimentary contact calls that are critical for calf survival. Early pulse train production may also provide the foundation for acquiring various sounds available in adult repertoires as they are produced exclusively before any other sound type (Vergara, 2011) and are often incorporated as components of multi-component signals. Parallel trajectories of sound acquisition and development in different beluga calves may highlight sensitive windows during which calves are physically able to produce elementary versions of sounds found in adult repertoires or alter sound parameters, which could be vital in determining when calves are able to compensate for noise in their environment. This is crucial in light of increasing anthropogenic underwater noise due to shipping, seismic exploration, offshore drilling, military operations, and construction in the circumpolar habitats of belugas (Erbe & Farmer, 1998; Erbe, 1999; Erbe et al., 2016). For example, anthropogenic noise has been identified as a main threat to the recovery of the endangered St. Lawrence beluga population (Fisheries and Oceans Canada [DFO], 2017), with the majority of animals exposed to commercial marine traffic consisting of females with calves and juveniles (Lesage et al., 2014a).

Following the progression of sound production in young animals can also elucidate processes fundamental to repertoire development like a species' ability to learn vocally. Vocal learning is a form of social learning by which animals' vocal development is influenced by the surrounding auditory environment (Nottebohm, 1972) and has likely evolved in gregarious species with complex communication and environmental constraints that disallow the maintenance of visual contact over periods of time (Janik, 2014). A theoretical framework regarding two key processes of vocal learning—(1) production learning and (2) contextual learning—has been widely established in the literature (e.g., Janik & Slater, 1997, 2000; Boughman & Moss, 2003). *Production learning* is the process by which an individual modifies an aspect of their vocal repertoire based on sounds that are available in the acoustic environment (Janik & Slater, 2000), while *contextual learning* involves the association of existing vocalizations with a particular function (Janik & Slater, 1997, 2000).

The importance of production learning in vocal development is evident through the acquisition of vocal signatures in some young animals. For

example, the acoustic environment seems to largely influence the development of signature whistles in bottlenose dolphin (*Tursiops truncatus*) calves (e.g., Caldwell & Caldwell, 1979; Sayigh, 1992; Tyack, 1997; Tyack & Sayigh, 1997; Bojanowski et al., 2000; Miksis et al., 2002; Fripp et al., 2005). Calves in managed care have been known to copy marking stimuli (e.g., whistles used by trainers to bridge a behavior prior to reinforcement; Sayigh, 1992; Tyack, 1997; Miksis et al., 2002), and calves in both managed care (Caldwell & Caldwell, 1979; Tyack & Sayigh, 1997) and the wild (Sayigh, 1992; Fripp et al., 2005) may produce whistles that resemble those of unrelated animals. While several cetacean species have shown the propensity to use sounds contextually (e.g., bottlenose dolphins [spp.]: Caldwell & Caldwell, 1965; Tyack, 1986; McCowan & Reiss, 1995a; Connor & Smolker, 1996; Janik & Slater, 1998; King & Janik, 2015; Vollmer et al., 2015; Ames et al., 2017; sperm whales [*Physeter macrocephalus*]: Watkins & Schevill, 1977; Schulz et al., 2008; belugas: Vergara et al., 2010), there is still little information regarding how young cetaceans learn to pair species-specific sounds with an appropriate context.

Herein, we provide the second longitudinal study on beluga vocal development to explore (1) potential maturational processes associated with physical sound production; (2) patterns in sound acquisition, use, and development; (3) calls that may be critical to neonate survival and the impacts of underwater noise on said calls; and (4) any underlying processes associated with repertoire development. By comparing beluga calves across studies, comparing calf repertoires to adult repertoires where possible, and employing new technology (i.e., digital hydrophones with high sampling rate capability), we illuminate potential species-specific trends in development and provide new information about this species.

Methods

Subjects and Sampling
The subjects of this study were three belugas housed at Oceanogràfic, a managed care facility in Valencia, Spain. These included "Kylu," a male calf born at Oceanogràfic (15 November 2016), Kylu's mother, "Yulka," and father, "Kairo." Yulka and Kairo are both wild-caught belugas of Russian origin, although it is unclear from which populations as there are gaps in the known histories of these animals prior to arriving at Oceanogràfic in 2003. At the time of this study, Yulka was estimated to be approximately 20 y of age, and Kairo was estimated to be in his mid-50s. Kairo was physically, but not acoustically, separated from Kylu until his eighth month

of life when physical introductions of Kairo and Kylu began. No additional belugas were housed at Oceanogràfic during the time of study.

Data for this study consisted of hydrophone recordings (see hydrophone details in "Acoustic Recordings") paired with simultaneous behavioral observations. During the *prepartum* period (10 September 2016 to the calf's birth on 15 November 2016), data were collected for 1 h in the morning and/or 1 h in the afternoon almost daily resulting in approximately 80 h of *prepartum* data. Data collection for the first and second years of life became more opportunistic depending on the location of the mother–calf dyad in relation to the hydrophone(s) and the ability of the observer to view underwater behavior. First year of life recordings began on the day of the calf's birth and continued until the calf's first birthday at which point recordings for the second year of life began. Special emphasis was placed on data collection during Kylu's first month of life as this period of development is of concern in regard to the potential impact of noise on neonate vocalizations (Lesage et al., 2014b). Thus, 79 h of data were recorded during the calf's first month of life, and an additional 129 h were recorded over the remaining 11 mo for a total of 208 h over the first year of life. A total of 54 h were recorded for the second year.

Acoustic Recordings
All sound analyses were conducted in *Raven Pro*, Version 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA) using a Hann window (window size: 1,024) with a Fourier Transform size of 1,024 points, an overlap of 50%, and 512 sample hop size. Underwater recordings were obtained with calibrated digital hydrophones. An icListen HF (Ocean Sonics, Great Village, Nova Scotia, Canada) was the primary hydrophone deployed for the entirety of the study, sampling at a rate of 256 kHz with 24-bit resolution and sensitivity of -171 dBV re 1 µPa. During the course of the study, the icListen was deployed in a semi-permanent installation in the main beluga pool or in the reproduction pool, depending on the location of the calf. Figure 1 illustrates the dimensions of the beluga pools at Oceanogràfic with the semi-permanent installations clearly marked. All pools in the habitat are 5 m deep, except for the medical pool which is 2 m deep.

A second calibrated digital hydrophone was sporadically available for use over the course of the study. Simultaneous deployment of a SoundTrap HF300 (Ocean Instruments, Auckland, New Zealand) occurred over several periods, allowing for increased accuracy in localization of vocalizing individuals. The SoundTrap was deployed at a sampling rate of 288 kHz with 16-bit resolution and a clip level of 172 dB re 1 µPa.
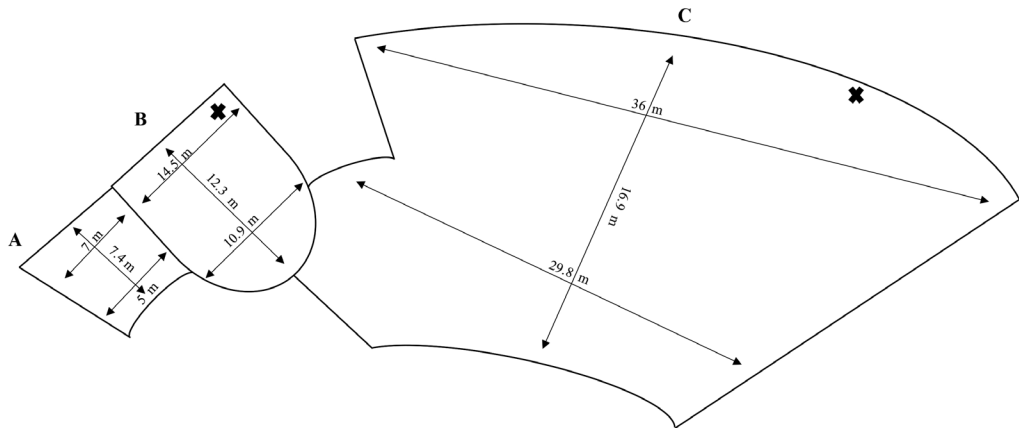
Figure 1. Pool layout of Oceanogràfic's beluga (*Delphinapterus leucas*) habitat: (A) the medical pool, (B) the reproduction pool, and (C) the main pool. The "X"s mark the semi-permanent hydrophone installations.

Localizing Vocalizations

Bubble stream methodology was employed during the calf's early life when bubble streams often coincided with simultaneous sound production. This method has been consistently employed in studies of vocal development in young odontocetes (McBride & Kritzler, 1951; Reiss, 1988; McCowan & Reiss, 1995b; Bojanowski et al., 2000; Killebrew et al., 2001; Miksis et al., 2002; Mello & Amundin, 2005; Morisaka et al., 2005a, 2005b; Hooper et al., 2006; Fripp & Tyack, 2008; Vergara & Barrett-Lennard, 2008; Gnone & Moriconi, 2010; Favaro et al., 2013) as calves seem to lack the musculature or motor ability to stop air flow from the vestibular air sacs by sealing the blowhole during underwater sound production. Bubble stream methodology was the only method employed for localizing calf calls in the first month of life. However, it should be noted that because some sound production could occur without simultaneous bubble release, the sounds identified may not represent the calf's full vocal repertoire (Fripp, 2005; Vergara & Barrett-Lennard, 2008).

Additional methods for localizing all adult calls and calf calls after the first month were used opportunistically. These methods became increasingly important as the calf aged, and bubble stream methodology became less applicable due to a decrease in bubble stream emission concurrently with the calf's call production over time. These methods include

- calls produced when an animal was in isolation.

- calf calls produced during periods when adults were participating in training sessions with their

melons above the water surface. The melon is the structure through which odontocetes are believed to direct sound (e.g., Cranford et al., 1996; Cranford, 2000; Madsen et al., 2010, 2013); therefore, if a beluga's melon was not in the water, underwater sound production was not associated with that beluga.

- calls produced underwater that were audible and localizable from the surface.

- calls produced at the surface.

- visual comparisons of the acoustic energy (i.e., dark coloration indicating the "loudness" of a sound) of calls on spectrograms if the animals' positions in the pool were known. These visual inspections could easily be done when both hydrophones were deployed; however, it was also possible during single hydrophone deployment given the size of the beluga habitat and small number of individuals in the social group. For example, if a beluga vocalized while swimming in the main beluga pool (Figure 1), this sound would lose much of its intensity before being recorded by the hydrophone deployed in the reproduction pool and vice versa. Moreover, if a beluga produced a call that could be positively attributed to them through one of the other methods listed here, and additional calls of similar visible energy appeared on the spectrogram shortly prior to or shortly after the call with the positive identification, it could be reasonably assumed that the identified beluga also produced the additional sounds if there were no other animals in near proximity.

- comparisons of call acoustic energy on spectrograms if animals were calling together and at least two of the animals' pool positions were known. Similar to the method listed above, if calls could be positively attributed to belugas through the distance of the animals from the hydrophone or through another method listed here, and animals were continually exchanging vocals (i.e., one animal would call and another would respond shortly thereafter), it could be reasonably assumed that calls of similar energy belonged to the same animal for the duration of the vocal exchange.

All localization information and animal behaviors that were relevant to localizing individuals (e.g., calf bubble stream emission, animal orientation and distance relevant to the position of the hydrophone, beginning and end periods of separations or sessions, vocal information when animals could be heard from or at the surface, etc.) were recorded using Timestamped Field Notes, an iPhone application that applies the time (h, min, and s) to an entered observation. The time codes for both digital hydrophones were synced with the time displayed by the iPhone prior to deploying the hydrophones so that the time stamps of the underwater recordings and the behavioral observations would be the same.

Calf Sound Classification Catalog

Vocalizations that were positively identified as Kylu's were included in a sound classification catalog used to determine sound acquisition (i.e., first recorded instances of sounds) and proportions of sound use in his vocal repertoire. One author (AEA) reviewed all acoustic and behavioral data in creation of the sound classification catalog, while the second author (VV) reviewed the catalog for agreement. Kylu's vocalizations were first classified based on four general sound categories known to be produced by belugas and other delphinoid species: (1) tonal, (2) pulsed (including burst pulses, pulse tones, noisy calls, and pulse trains), (3) mixed pulses, and (4) mixed calls. It should be noted that mixed pulses are considered mixed calls given that both sound types are biphonations with overlapping elements. For clarity, mixed pulses were treated as their own category, while the mixed call category refers to pulsed sounds with overlapping tonal elements. Likewise, pulse trains are also pulsed sounds, but given the depth of analysis and discussion of this sound type in the current study, they were described separately from other pulsed sounds.

The four general sound categories listed above were further classified into 14 subcategories based on variations within each sound type. Subcategories were created based on the visual and auditory characteristics of sounds in the recordings, with new subcategories defined if Kylu produced a call that could not be classified as an already occurring subcategory. Sound acquisition was investigated through the calf's first emission of each sound subcategory, while the calf's proportional use of sound was based on the four general categories. Table 1 summarizes the operational definitions of sound categories and subcategories.

Complex Contact Call Classification

Beluga contact call identification is straightforward as these calls are distinctive, pulsed, highly stereotyped, long in duration, broadband, and produced during contexts of separation (i.e., contexts of isolation, birth, death, the presence of external stressors, and group reunions; Vergara & Barret-Lennard, 2008; Vergara et al., 2010; Vergara & Mikus, 2019). Contact calls were classified through visual and aural inspection of spectrograms, a technique that has been used in other studies of beluga contact calls (e.g., Vergara & Barrett-Lennard, 2008; Vergara et al., 2010; Panova et al., 2017; Vergara & Mikus, 2019) and widely accepted as a reliable method in classifying the sounds of cetaceans (Deecke et al., 1999; Janik, 1999; Sayigh et al., 2007).

A complex contact call was considered to be a specific call type if at least five emissions of the call occurred in separation contexts across two different recording days. Contact call types were further classified into subtypes if enough variation among calls within a broad call type existed so that subtypes were distinguishable but still more similar to each other vs calls in different call types. A call was considered a subtype of a contact call if the variation appeared to be highly stereotyped with at least five emissions across two different recording days as well. As with calf sounds, one author (AEA) reviewed all acoustic and behavioral data, classifying contact calls along these criteria, while the second author (VV) reviewed the call type and subtype classifications for agreement.

Parameter Extraction

For further analyses of Kylu's repertoire development, parameters were extracted from calf sounds in the first year of life (again, with special emphasis on the first month) and complex contact calls. Vocalizations were included for parameter extraction if (1) no ambiguity existed in determining the signaling beluga; (2) there was no overlap of noise or other vocalizations; and (3) calls had a high signal-to-noise ratio with clear, definable elements. Parameters extracted for each sound category or call type and their operational definitions are listed in Table 2.

Table 1. Operational definitions of beluga (*Delphinapterus leucas*) calf sound categories and subcategories

Category	Subcategory	Definition
Pulsed	Noisy	Buzz-like sounds that have undefinable characteristics and no clearly visible pulses so that pulse repetition rate (PRR) cannot be assessed
	Burst pulse	Pulse packet with 100 to 1,000 pulses/s
	Pulse tone	Aurally tonal burst pulse sound with clear harmonic structure or sideband intervals (SBI) (Watkins, 1967) that indicates a PRR of 1,000 to 4,000 pulses/s
	Pulse trains	A series of pulses produced with definable PRR of < 100 pulses/s
Mixed pulse	Mixed pulse trains	Overlapping pulse trains that have two different PRRs
	Pulse train with pulse tone or burst pulse	Pulse train overlapped by pulsed sound with high PRR; burst pulses in this capacity had > 200 pulses/s
	Pulse train with noisy	Pulse train overlapped by pulsed sound with undefinable characteristics
	Burst pulse or noisy with pulse tone	Pulse tone overlapping an additional pulsed sound
Mixed call	Pulse tone with tonal component	A pulse tone overlapped by a tonal sound
	Pulse train with tonal component	A pulse train overlapped by a tonal sound
	Burst pulse or noisy with tonal component	Additional pulsed sound types overlapped by a tonal sound
Tonal	Whistles	Narrowband, frequency-modulated tonal sounds with clear contour and harmonic structure; fundamental frequency and harmonic integer interval were often > 4 kHz
	Tonal elements	Frequency-modulated tonal sounds that were less clear in contour shape and were often wider bandwidth than whistles (~1 to 3 kHz)
	Abbreviated tonal sweep series (ATSS)	A series of truncated tonal sounds (~6 to 11 ms) with upsweep contours

Pulse repetition rate (PRR) was determined by counting all pulses in a sound and dividing by the delta time (i.e., duration) of the sound when pulses were so few they could easily be counted, or when PRR was visibly high on the spectrogram, 10 pulses from the sound's duration midpoint (i.e., 5 pulses from both sides of the midpoint) were highlighted in *Raven Pro*, divided by their delta time, and used as a measure of center PRR. For pulsed sounds with individual pulses that were not readily apparent (e.g., burst pulses or pulse tones), PRR was measured from sideband intervals (Watkins, 1967).

Parameters of acoustic energy distribution were derived from the power spectrum of a sound in *Raven Pro*. To reduce influence of pool filtration noise on these parameters, measures were integrated between 500 Hz and 128 kHz. Precise minimum, maximum, and delta frequencies were discarded from analyses as a result, although it was clear that the delta frequency of complex contact calls and the calf's pulsed sounds encompassed the bandwidth of the recording system. Additionally, if a sound's peak frequency was less than or equal to 2 kHz, this peak was discarded to avoid the possible influence of the pool filtration noise, and the second peak in the power spectrum of the sound was extracted instead.

Finally, as part of an additional study investigating the impacts of vessel noise on neonate calf calls (Vergara et al., unpub. data), we measured the change in apparent source levels (i.e., the sound pressure level of a signal 1 m away from its source) of Kylu's pulse trains produced over his first month of life. Apparent source levels were calculated from the received levels of Kylu's pulse trains produced at known distances and orientations to the hydrophone, integrated from 500 Hz to 100 kHz, and by using cylindrical spreading to approximate transmission loss.

Table 2. Operational definitions of parameters with sounds[a] for which they were extracted (as indicated by asterisks)

Parameter	Definition	Burst pulse/ pulse trains	Mixed calls[b]
Minimum frequency	The lowest frequency of a sound		
Maximum frequency	The highest frequency of a sound		
Delta frequency	The frequency range of a sound (i.e., the difference between the minimum and maximum frequencies)		
First quartile frequency	Frequency of the 25th percentile of the acoustic energy distribution	*	*
Center frequency	Frequency of the 50th percentile of the acoustic energy distribution	*	*
Third quartile frequency	Frequency of the 75th percentile of the acoustic energy distribution	*	*
Peak frequency	The peak energy of a sound in the power spectrum	*	*
Delta time	Sound duration (s)	*	*
Pulse repetition rate (PRR)	The number of pulses/s	*	*
Dominant tonal frequency	Harmonic of a tonal sound containing the peak energy		*
Dominant tonal frequency beginning	Beginning frequency of the dominant tonal element		*
Dominant tonal frequency end	End frequency of the dominant tonal element		*
Fundamental frequency	First harmonic of a tonal sound; if the first harmonic also contained the peak energy of the tonal sound, the fundamental and dominant tonal frequency were considered the same		*
Inflection points[c]	The point in a tonal sound in which the slope of the sound changes direction (i.e., increasing to decreasing or vice versa)		*
Noisy tonal bandwidth[d]	The delta frequency of the type Y tonal element (i.e., noisy tonal band), which is characterized by a bandwidth wider than a pure tonal or pulse tone sound		*

[a]Sounds less common in the calf's repertoire are not listed here.
[b]Mixed calls include calf sounds and complex contact calls.
[c]Parameter not included in statistical analyses listed below.
[d]Parameter only included in the type Y discriminant function analyses (DFA).

Statistical Analyses

Linear regression analyses of changes in calf sound parameters over the first year of life were conducted in *Microsoft Excel*, Version 16.20. Parameters extracted for regression analyses varied for each sound subcategory analyzed (Table 2). Each day of recording was treated as a single event. A mean for each event (i.e., each day of life) was generated for each parameter extracted for sound subcategories. These means per day were then used in the regression analyses as individual data points. For linear regression analyses of PRR, burst pulse and pulse train PRR were combined. Burst pulses are analogous to high repetition pulse trains. While the two pulse signals were treated as separate sound types for evaluating sound type acquisition, analyses converged on PRR to determine if age was

a significant predictor of increased PRR, which could be expected given the increased motor control that may come with maturity. A linear regression analysis was also run on the apparent source levels of Kylu's pulse trains.

Discriminant function analyses (DFA) were completed in *SPSS*, Version 21, for the statistical classification of complex contact calls. For comparison of the adult complex contact calls, 50 calls from the most prominent call type emitted by each adult during the first month of life (i.e., period with most consistent involuntary mother–calf separations) were randomly selected. Parameters that were included in complex contact call DFAs are also listed in Table 2. Inflection points were not included in statistical analyses. Since they are a discrete variable, they are reported briefly below (see "Complex Contact Call Development") as median values.

Results

Sound Acquisition and Use

A total of 2,014 calf vocalizations were included in the calf sound classification catalog. The proportional use of each sound category in the calf's recorded repertoire within each month of life is given in Figure 2. As expected, Kylu began to produce low PRR, broadband pulse trains within a few hours of his birth (Figure 3). The upper-frequency limits of these pulse trains reached the Nyquist cutoff (128 kHz) of the study's sampling rate on this first day of life. Pulse trains comprised the majority of the calf's repertoire over the first month of life, and pulsed sounds (i.e., burst pulses, pulse tones, noisy calls, and pulse trains) was the most commonly recorded category over the first year.

A few additional sound subcategories began to appear in Kylu's recorded repertoire in the days following his birth. Noisy calls were first recorded on the calf's third day of life and appeared regularly in the calf's recorded repertoire until the ninth month. Two mixed calls were recorded on the calf's sixth day of life. These calls were characterized by low PRR pulse trains overlapped by a tonal element at the end of the train that trailed off independently of continued pulse production

(Figure 4). An additional mixed call in which the tonal element was embedded within the pulse train appeared on the calf's 19th day of life (Figure 4). Mixed calls that appeared adult-like in structure (i.e., clearly prominent overlapping pulsed and tonal elements) appeared in the calf's fifth month of life at which point the calf began to produce these sounds regularly (Figure 4). Burst pulses or noisy sounds with overlapping pulse tones appeared in the second and third months of life but were also not prominently produced until the fifth month.

The 26th day of life was marked by the first recordings of pulse tones and several mixed pulse subcategories, including mixed pulse trains and pulse trains with either (1) an overlapping noisy component, (2) an overlapping pulse tone, or (3) a burst pulse with high PRR resulting in a visible harmonic structure or sideband intervals. Burst pulses that were not mixed (i.e., not overlapped by another element in the same vocalization) appeared towards the end of the calf's third month of life (82nd day).

Finally, Kylu began to produce tonal sounds independent of pulsed components during his fourth month of life (94th day). These tonal sounds were similar to whistles produced by adult belugas but were produced infrequently and did not appear
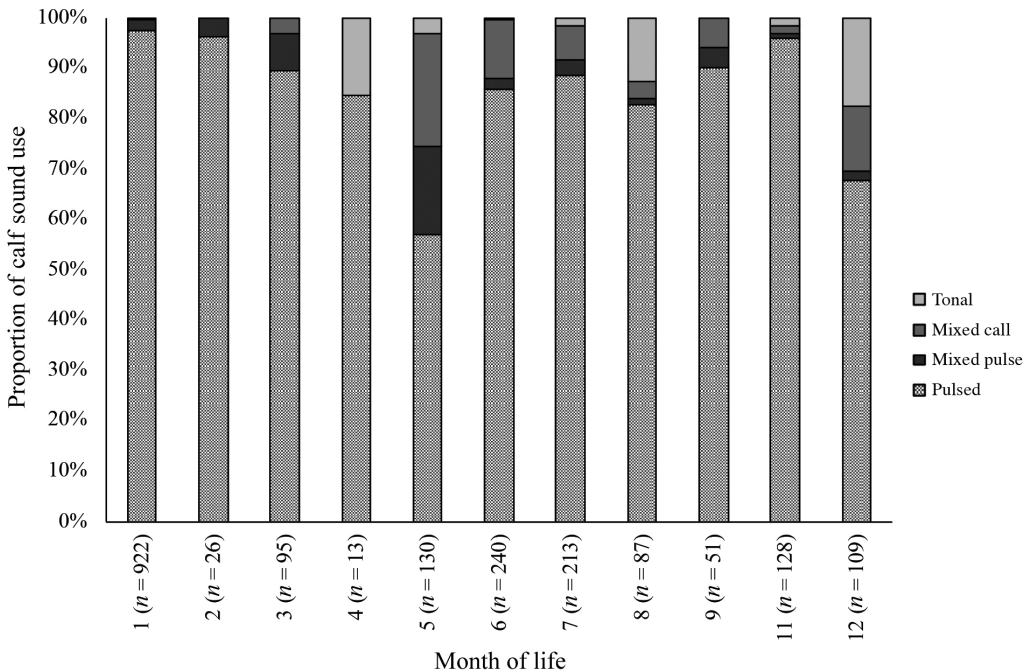

Figure 2. Proportional use of each of the four general sound categories in Kylu's repertoire per month (*n* = 2,014 total calls over the first year); note that no data were collected during the 10th month of life.
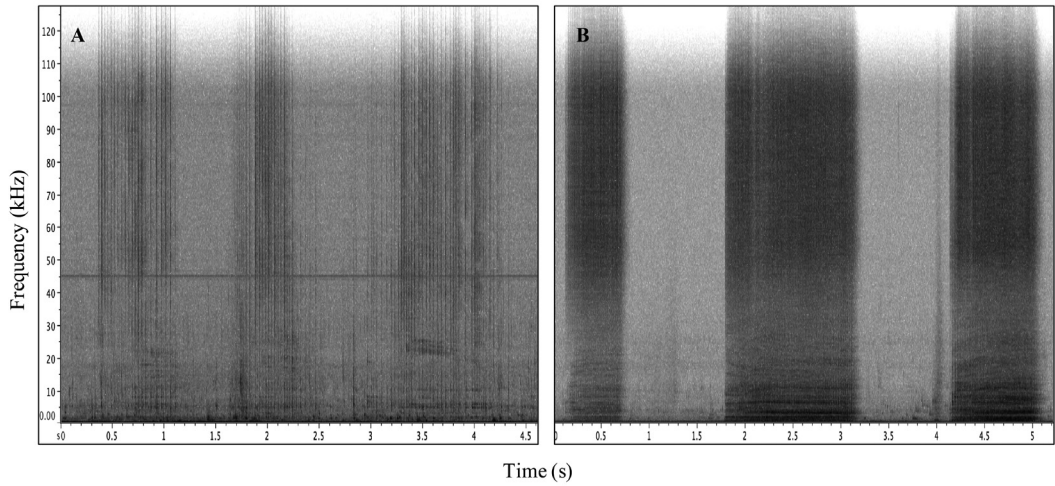
Figure 3. Sample pulse trains extracted from Kylu's first month of life: (A) a pulse train series from the day of Kylu's birth (note the extension of the upper-frequency limits past 128 kHz in addition to the low acoustic energy compared to the later pulse trains), and (B) a pulse train series from Kylu's 28th day of life. Spectrogram parameters: DFT 1,024, overlap 50%, 512 sample hop size, and Hann window.
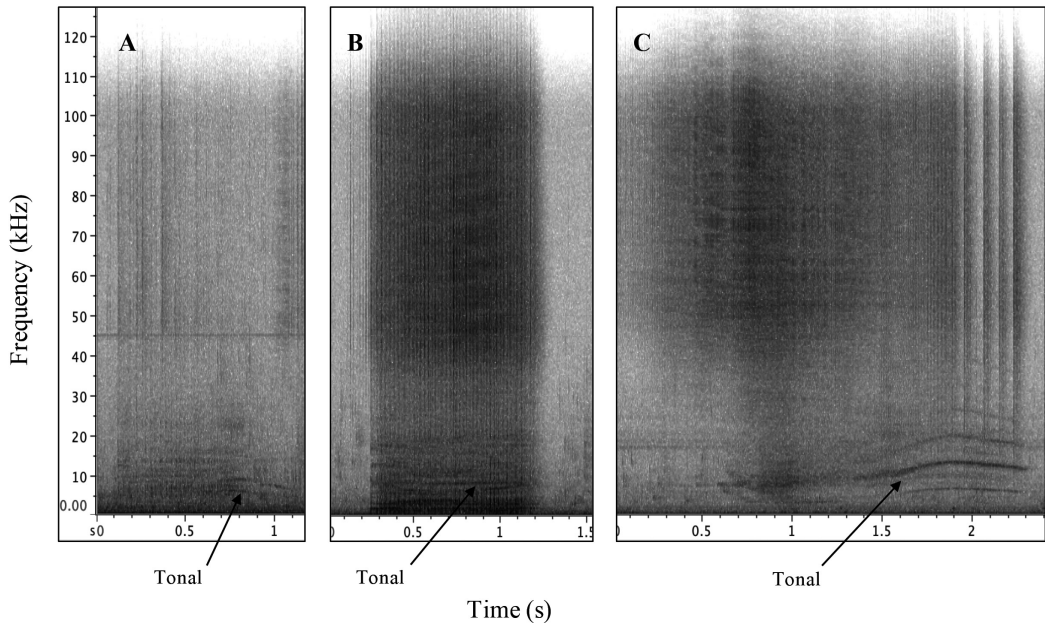

Figure 4. Kylu's mixed calls: (A) a mixed call from Kylu's sixth day of life with the overlapping tonal element at the end of the sound, (B) a mixed call emitted on Kylu's 19th day of life with the tonal element embedded within the sound, and (C) an "adult-like" mixed call emitted in Kylu's fifth month of life. Spectrogram parameters: DFT 1,024, overlap 50%, 512 sample hop size, and Hann window.

to become stereotyped over Kylu's first year. During his first year of life, Kylu also produced what we have termed *abbreviated tonal sweep series* (ATSS), but this subcategory did not appear in the recordings until his eighth month of life (221st day), and overall production of this sound was rare as well. All tonal sounds comprised only 2.1% of recorded sounds in the first year.

Burst Pulse and Mixed Call Development
Of the sound subcategories, pulse trains (see "Pulse Train Development"), burst pulses ($n = 64$), and mixed calls ($n = 29$) were the only sound types that met inclusion criteria for parameter extraction frequently enough to warrant analyses of changes in these sounds over time. All other sound subcategories were too rare.

Mixed calls during the first year were highly variable and unstereotyped. As such, age was not a significant predictor for any parameter changes related to mixed calls over the first year of life. For burst pulses, all parameters of acoustic energy distribution (i.e., peak, first and third quartile, and center frequencies) significantly increased over the first year (see Table 3 for *p* values and descriptive and regression statistics for burst pulses and mixed calls over the first year of life).

Pulse Train Development
First Month—Parameters were extracted from 329 of Kylu's pulse trains in the first month of life. PRR increased significantly over the first month of life (Table 4). Mean PRR ($\pm$ SD) on the first day of life (17.8 ± 13.8 pulses/s) was much lower when compared to mean PRR ($\pm$ SD) towards the end of the calf's first month (28th day: 59.3 ± 8.9 pulses/s; Figure 3). The third quartile frequency and apparent source levels (Table 4) of the calf's pulse trains also increased significantly during this time period (Figure 3). The mean source level ($\pm$ SD) estimated for pulse trains emitted during the week following Kylu's birth (120.0 ± 5.8 dB re 1 μPa rms) was lower when compared to the mean source level for the remainder of the month (132.7 ± 5.1 dB re 1 μPa rms). Table 4 details the *p* values and descriptive and regression statistics for pulse trains in the first month and the first year of Kylu's life.

First Year—An additional 81 pulse trains were used for parameter extraction over the remaining 11 mo of the first year for a total of 410 pulse trains. Over the calf's first year of life, linear regression analyses indicated that age was a

Table 3. *p* values[a] of linear regression analyses and descriptive statistics[a] for the calf's burst pulses and mixed calls over the first year of life

Call type	Parameter	Mean ± SD	R^2	*p*
Burst pulse	First quartile frequency (kHz)	18.5 ± 21.6	0.35	< 0.001
	Center frequency (kHz)	43.1 ± 34.0	0.24	< 0.001
	Third quartile frequency (kHz)	28.9 ± 28.0	0.20	< 0.001
	Peak frequency (kHz)	19.9 ± 25.0	0.34	< 0.001
	Delta time (s)	1.1 ± 0.6	0.19	0.21
	PRR[b] (pulses/s)	420.6 ± 209.5	--	--
Mixed call	First quartile frequency (kHz)	41.2 ± 19.8	0.05	0.45
	Center frequency (kHz)	52.2 ± 22.3	0.06	0.39
	Third quartile frequency (kHz)	70.4 ± 22.0	0.04	0.52
	Peak frequency (kHz)	46.6 ± 27.4	0.04	0.51
	Delta time (s)	1.6 ± 0.8	0.04	0.50
	PRR (pulses/s)	167.8 ± 188.1	0.11	0.24
	Dominant tonal frequency (kHz)	8.6 ± 3.5	0.34	0.23
	Dominant tonal frequency beginning (kHz)	7.3 ± 3.1	0.08	0.33
	Dominant tonal frequency end (kHz)	8.8 ± 3.3	0.15	0.18
	Fundamental frequency (kHz)	6.7 ± 2.0	0.09	0.29

[a]Mean ± SD values were calculated from the raw data ($n = 64$ burst pulses; $n = 29$ mixed calls). R^2 and *p* values were calculated based on the method outlined for linear regression analyses ($n = 10$ d from which burst pulse parameters were extracted; $n = 12$ d for mixed calls).
[b]R^2 and *p* value were not available for burst pulse pulse repetition rate (PRR) because this parameter was combined with pulse train PRR in the linear regression analysis of PRR over the calf's first year.

Table 4. *p* values[a] of linear regression analyses and descriptive statistics[a] for the calf's pulse trains over the first month and first year of life

Time period	Parameter	Mean ± SD	R^2	*p*
First month	First quartile frequency (kHz)	8.8 ± 13.1	0.20	0.09
	Center frequency (kHz)	23.8 ± 22.6	0.15	0.15
	Third quartile frequency (kHz)	48.1 ± 25.5	0.28	0.04
	Peak frequency (kHz)	7.4 ± 14.0	0.18	0.11
	Delta time (s)	0.8 ± 0.5	0.12	0.20
	PRR (pulses/s)	41.2 ± 13.1	0.65	< 0.001
	Source level (dB re 1 µPa rms)	126.7 ± 8.4	0.78	< 0.001
First year	First quartile frequency (kHz)	13.1 ± 17.0	0.58	< 0.001
	Center frequency (kHz)	29.0 ± 24.5	0.40	< 0.001
	Third quartile frequency (kHz)	52.4 ± 25.8	0.33	< 0.001
	Peak frequency (kHz)	12.0 ± 20.1	0.42	< 0.001
	Delta time (s)	0.9 ± 0.5	0.33	< 0.001
	PRR (pulses/s)	99.1 ± 150.3	0.13	0.03

[a]Mean ± SD values were calculated from the raw data (*n* = 329 pulse trains for all first month parameters excluding source level, *n* = 65; *n* = 410 pulse trains for all first year parameters). R^2 and *p* values were calculated based on the method outlined for linear regression analyses (*n* = 15 d for the first month; *n* = 33 d for the first year).

significant predictor for all parameters (Table 4). First and third quartiles, and center and peak frequencies significantly increased over this time period, indicating shifts in all acoustic energy distribution towards upper-frequency limits of the calf's pulse trains in the first year. Delta time also increased significantly over the calf's first year of life.

Significant increases in the PRR of pulsed sounds occurred ($R^2 = 0.13$, *n* = 33, *p* = 0.03); however, the low R^2 value indicates that age was not a strong predictor of PRR, and the large SD indicates high variability in this parameter. There appeared to be high variability across many of the parameters extracted from Kylu's sounds as SD values were often large. This variability may have been due to the low number of days from which mean parameter values could be extracted from the first month (*n* = 15) and first year (*n* = 33) of life or may be representative of a high degree of variation in Kylu's sounds as they developed. Figure 5 provides regression plots of these parameters.

Complex Contact Call Development
Adult Contact Calls—Yulka's individual contact call (type Y) was identified during involuntary separations of the dyad during Kylu's first month of life. During these separations, Yulka emitted a

particular subtype (Y1) of the type Y call exclusively. Kairo also produced complex contact calls (type K) during these periods of involuntary separations of the dyad. A subtype of the type K call (K1) was the most commonly recorded complex contact call produced by Kairo in the first month of life. To investigate individual specificity in the adults' contact call types, Y1 and K1 calls were compared (Figure 6). A DFA classified 100% of Y1 and K1 calls correctly, indicating a high degree of difference in these two call types. Except for call duration (*p* = 0.190), all parameters were highly discriminant (*p* < 0.05).

It should be noted that Yulka used Y1 calls and an additional subtype, Y2 (Figure 7), during the 2 mo of recording prior to Kylu's birth, but Y2 emissions were sparse in the first year of life. After the first month of Kylu's life, Yulka's type Y production occurred rarely; however, when she did produce complex contact calls, she predominantly used Y1. Yulka's complex contact call production was relatively absent in the second year of life, except for the days during which Kylu was medically isolated in his 23rd month, further discussed below.

Kylu's Type Y Call Development—Kylu was recorded producing only simple contact calls during separation contexts until his 16th month of life, during which three unstereotyped type Y calls were recorded on a single day. Thus, Kylu's
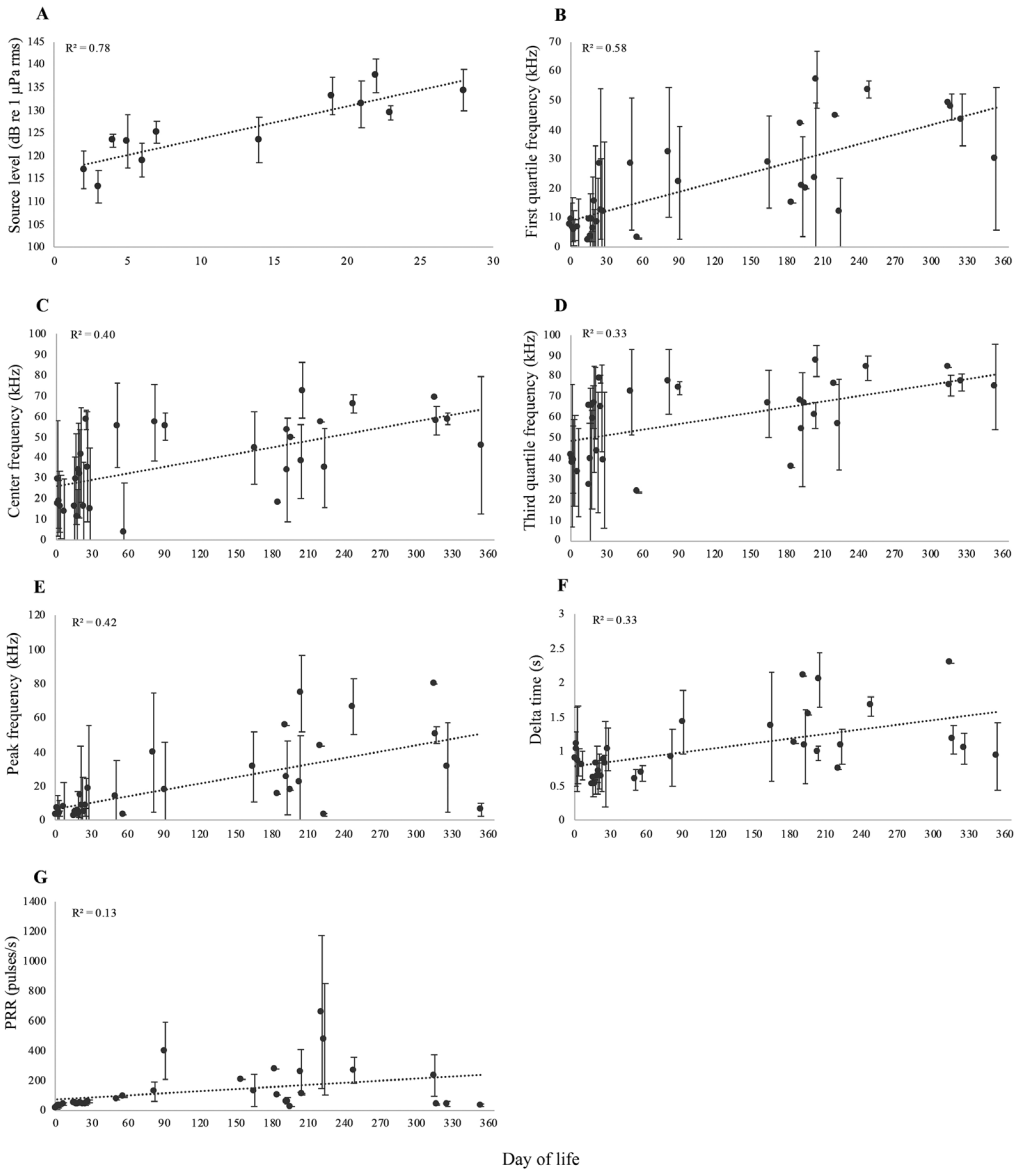
Figure 5. Significant changes in Kylu's pulse train parameters: (A) apparent source levels over the first month, (B) first quartile frequency over the first year, (C) center frequency over the first year, (D) third quartile frequency over the first year, (E) peak frequency over the first year, (F) delta time over the first year, and (G) PRR over the first year. Data points represent daily means (error bars: ± SD).

complex contact calls could not be adequately evaluated until his 23rd month of life, during which Kylu was involuntarily isolated in the medical pool for husbandry procedures on two separate days. During these medical separations, Kylu produced calls similar to his mother's type Y2 contact call. Yulka was also recorded using the Y2 subtype more prominently than the Y1 subtype during these same isolation sessions. Approximately 30 Y2 calls that could be positively attributed to Kylu over the two observation periods met parameter extraction criteria. The calf's Y2 calls were then compared to the first 30 Y2 calls produced by Yulka during these sessions that also met criteria for parameter extraction.
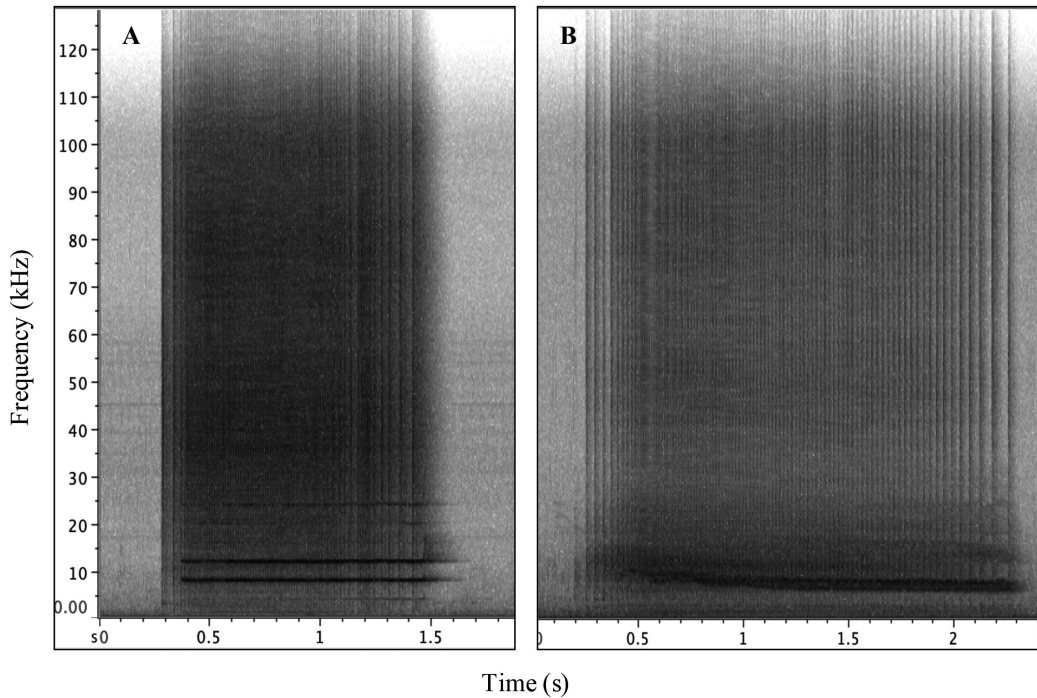
Figure 6. The most predominant complex contact calls produced by the adults during Kylu's first month of life: (A) Kairo's K1 call and (B) Yulka's Y1 call. Spectrogram parameters: DFT 1,024, overlap 50%, 512 sample hop size, and Hann window.

A DFA classified 80% of Kylu and Yulka's Y2 calls correctly. Parameters that had high discriminant ability ($p < 0.05$) included the calls' first quartile and peak frequencies and the beginning and end frequency of the *noisy tonal band* (i.e., the overlapping tonal element characteristic of the Y2 call type). In addition, the dominant tonal frequency was a parameter with high discriminant ability as Kylu still appeared to have an overall lack of stereotypy in the dominant frequency of his Y2 noisy tonal band. This was apparent when comparing the variability of the noisy tonal dominant frequency of Kylu's Y2 calls (20.7% CV) to the variability of Yulka's Y2 noisy tonal dominant frequency (5.3% CV). Kylu's Y2 dominant tonal component was also a bit more tremulous in inflection. While the median value for number of inflection points was the same for both Yulka and Kylu (median of 0), Yulka's Y2 dominant tonal did not have any inflection, whereas the number of inflection points in Kylu's Y2 dominant tonal was more variable (range from 0 to 2). Call parameters that were similar across the two animals' Y2 calls included center and third quartile frequencies, call duration, fundamental frequency, bandwidth of the noisy tonal element, and PRR. Kylu and Yulka's Y2 calls are illustrated in Figure 8. The descriptive statistics of parameters

extracted from Kylu's Y2 calls, Yulka's Y1 and Y2 calls, and Kairo's K1 calls are detailed in Table 5.

A DFA of Kylu's Y2 and Yulka's Y1 calls was more accurate in assigning Y2 and Y1 calls to the correct classification, with 98.8% of cases classified correctly. The dominant frequency and noisy tonal bandwidth were the only parameters that did not have discriminant ability. All other parameters were significantly dissimilar ($p < 0.05$). A DFA of Kylu's Y2 calls, Yulka's Y1 calls, and Kairo's K1 calls classified 96.2% of calls correctly. All parameters had high discriminant ability ($p < 0.001$).

Discussion

Sound Acquisition
Kylu produced pulse trains exclusively on his first day of life, which were characterized by low energy and low PRR relative to later pulse trains. This is consistent with findings based on three other beluga calves (Vergara, 2011). Kylu began to produce other pulsed sounds within his first month of life. Altogether, pulsed signals were the most commonly produced sound over his first year.

Kylu's tonal sound production appeared to occur later in life than what was reported for two calves born at the Vancouver Aquarium. "Tuvaq,"
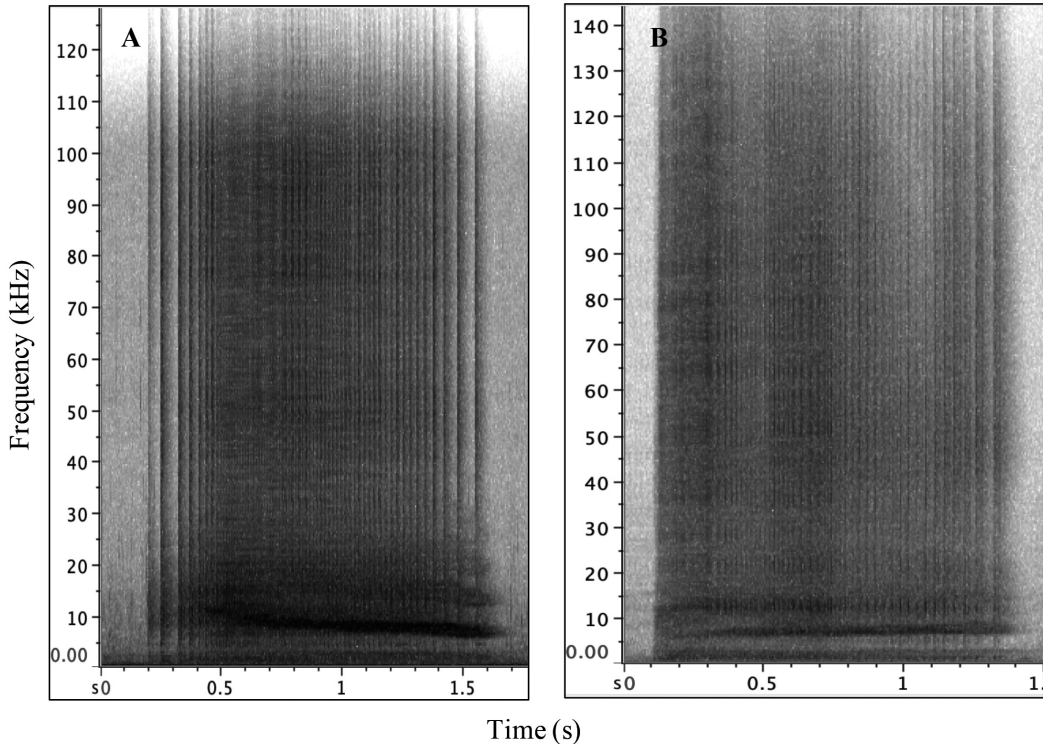
Figure 7. Comparison of the subtypes of Yulka's type Y calls: (A) the Y1 call, characterized by a downsweeping contour and slow PRR, and (B) the Y2 call, characterized by a constant contour and higher initial PRR. (A) was recorded on the icListen HF at a sampling rate of 256 kHz, and (B) was recorded by the SoundTrap HF300 at a sampling rate of 288 kHz. Spectrogram parameters: DFT 1,024, overlap 50%, 512 sample hop size, and Hann window.

the focal calf in Vergara & Barret-Lennard's (2008) study, began producing whistles on his 13th day; and "Tiqa," a female calf born several years after Tuvaq, began whistle production on Day 50 (MacLeod, 2009; Vergara, 2011). Tonal emissions preceded adult-like mixed call production in both Tuvaq and Kylu (unknown for Tiqa); however, Kylu produced far fewer tonal sounds over his first year when compared to Tuvaq.

Kylu produced mixed calls a few days after birth, a little earlier than Tuvaq who produced his first mixed calls on Day 20. Both calves' initial mixed calls were unstereotyped and not akin to adult beluga mixed calls. Furthermore, these early mixed calls were quite rare as both calves began producing adult-like mixed calls more consistently later in the first year (fourth month for Tuvaq and fifth month for Kylu). Kylu's earliest mixed calls, characterized by pulse trains that trailed off into whistles, were reminiscent of Tuvaq's early whistles, which immediately followed pulse train emissions (Vergara, 2011).

Given the rarity and unstereotyped nature of neonate mixed calls, it is likely that the tonal components overlapping these signals are an artifact of poor motor control or underdevelopment in the vocal structures belugas use to produce sound (Killebrew et al., 2001). All odontocete species (with the exception of sperm whales) possess two pairs of phonic lips (i.e., the vibrating vocal structure within the melon; Cranford et al., 1996; Cranford, 2000), both of which are believed to be simultaneously actuated during mixed call production (Brill & Harder, 1991; Murray et al., 1998; Cranford et al., 2000, 2011; Madsen et al., 2013). Neonate mixed calls are likely a byproduct of inadvertently actuating both phonic lip pairs through increasing air pressure as changes in air pressure occur concurrently in both nasal cavities (Cranford et al., 2000). Additionally, the delay in regular adult-like mixed call and tonal production likely stems from an inability to pneumatically drive whistle production as this appears to require greater air pressure than the production of pulses (Cranford et al., 2000).
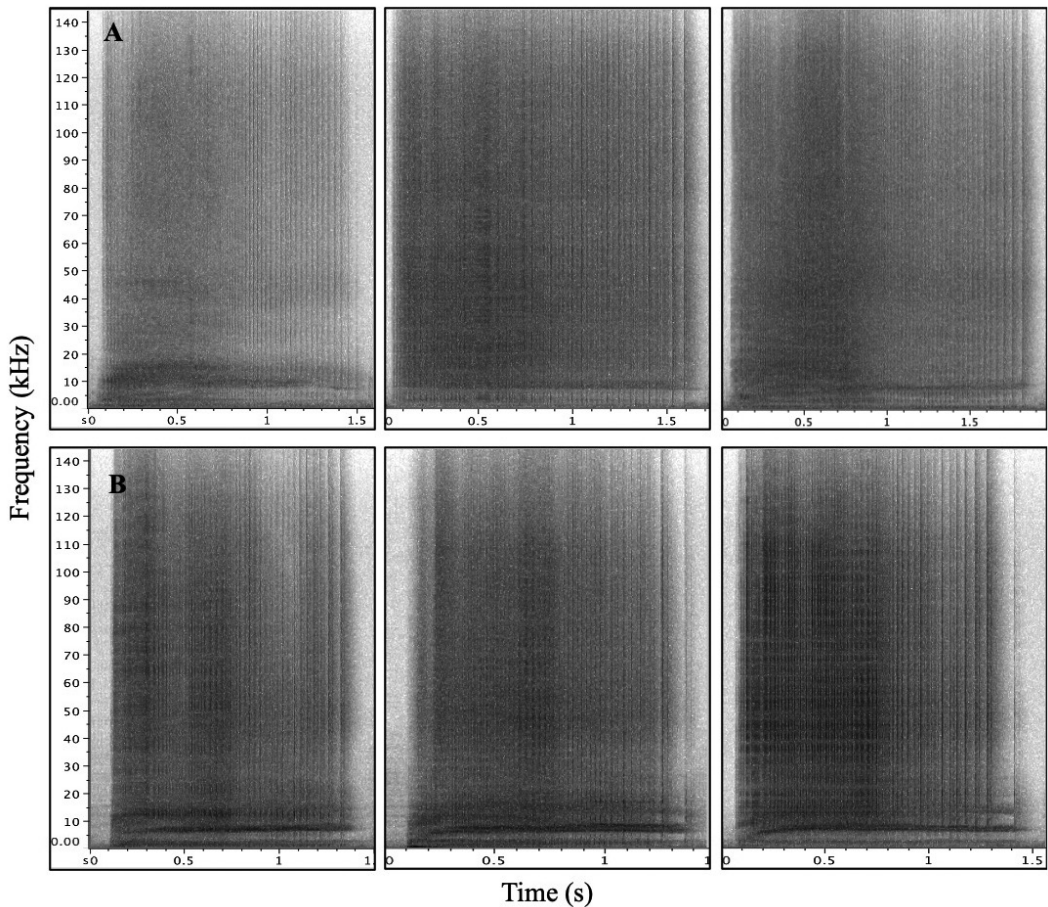
Figure 8. Three examples of (A) Kylu's and (B) Yulka's Y2 calls. Each call example was randomly selected from the representative group of 30 calls chosen for parameter extraction and subsequent DFAs. Spectrogram parameters: DFT 1,024, overlap 50%, 512 sample hop size, and Hann window.

Pulse Train Development

Pulse trains are salient to the repertoire of beluga calves, perhaps because they appear to function as rudimentary contact calls. The upper-frequency limits of Kylu's calls from birth indicate that beluga neonates are capable of much broader bandwidth sounds than reported by the previous study of beluga vocal ontogeny, which was limited by lower sampling rates (Vergara & Barrett-Lennard, 2008). During the first month of Kylu's life, the third quartile frequency of his pulse trains increased significantly, indicating a shift in pulse train energy distribution towards the upper-frequency limits of these sounds. In addition, his calls became louder as indicated by a significant increase in source levels. This may have aided the described shift in acoustic energy distribution as increases in source level are correlated with a shift of acoustic energy towards

higher frequencies (i.e., center frequency; Madsen et al., 2013).

Over the first year of life, changes in PRR and peak frequency occurred similarly for Kylu and Tuvaq as both parameters increased significantly with age. Pulse trains with increased PRR began to aurally and visually resemble more adult-like pulsed trains (e.g., some simple contact call types; Morisaka et al., 2013; Mishima et al., 2015) for both calves (Vergara & Barrett-Lennard, 2008). Vergara & Barrett-Lennard (2008) hypothesized that the peak frequencies of Tuvaq's pulse trains (which they termed "dominant frequency"; see pp. 129-130) were likely higher as the calf aged than what the authors were able to report given the limitations in sampling rate of the study. This is corroborated by the current study in that beginning in Kylu's third month of life, the peak frequencies of his pulse trains tended to be greater than 22 kHz, the Nyquist frequency reported

Table 5. Descriptive statistics for each parameter of type Y and type K calls

Parameter	Kylu/Y2 Mean ± SD	Yulka/Y1 Mean ± SD	Yulka/Y2 Mean ± SD	Kairo/K1 Mean ± SD
First quartile frequency (kHz)	21.7 ± 14.6	9.5 ± 4.1	13.4 ± 9.8	19.9 ± 10.4
Center frequency (kHz)	36.8 ± 17.7	18.1 ± 12.8	31.4 ± 15.3	31.1 ± 13.7
Third quartile frequency (kHz)	60.4 ± 20.4	36.7 ± 19.7	56.1 ± 13.2	43.9 ± 15.0
Peak frequency (kHz)	22.1 ± 18.0	9.3 ± 7.0	9.5 ± 9.1	12.9 ± 9.9
Delta time (s)	1.1 ± 0.3	1.5 ± 0.2	1.2 ± 0.2	1.4 ± 0.3
PRR (pulses/s)	149.1 ± 50.7	67.8 ± 13.8	163.3 ± 61.3	95.4 ± 7.0
Dominant tonal frequency (kHz)	7.6 ± 1.6	7.8 ± 0.6	6.8 ± 0.4	10.1 ± 2.0
Dominant tonal frequency beginning (kHz)	7.2 ± 1.9	11.5 ± 0.7	6.0 ± 0.7	10.5 ± 2.1
Dominant tonal frequency end (kHz)	7.4 ± 1.4	5.9 ± 0.3	8.2 ± 1.2	11.2 ± 2.3
Fundamental frequency (kHz)	7.2 ± 1.9	7.8 ± 0.6	6.8 ± 0.4	4.7 ± 1.4
Noisy tonal bandwidth (kHz)	2.7 ± 1.8	2.7 ± 0.5	2.4 ± 0.5	--

by Vergara & Barrett-Lennard (2008). First and third quartile and center frequencies also increased significantly over Kylu's first year of life. As with sound acquisition, changes in the measured parameters discussed herein may have at least been partially due to increased motor control and changes in physical development as the calf aged.

Impacts of Noise on Neonate Pulse Trains
Vessel noise is the primary source of anthropogenic noise in the marine environment (Hildebrand, 2009). While the maximum output for large vessels tends to be below 1 kHz (Croll et al., 2001; Clark et al., 2009), vessel noise has been demonstrated to extend well into the ultrasonic range (i.e., 20+ kHz) when vessels are in close proximity (Gervaise et al., 2012; Hermannsen et al., 2014; Veirs et al., 2016). The ability to increase acoustic energy at ultrasonic frequencies to compensate for some vessel noise may be useful for odontocete species that use these frequencies for signaling. Adult belugas, for example, may mitigate some effects of masking (i.e., the interference of noise with an animal's ability to detect or discriminate sounds of interest; Erbe et al., 2016) by shifting the peak frequencies of their sounds (Au et al., 1985; Lesage et al., 1999).

It is unknown when calves learn to alter signal energy to compensate for noise; however, the physical ability to produce higher peak frequencies is likely a precursor to this process. Starting in Kylu's third month of life, the mean peak frequency of his pulse trains was near 40 kHz, indicating a potential age at which beluga calves may be able to compensate for some vessel noise even in the ultrasonic frequency range (Veirs et al., 2016). Calf signaling may be particularly vulnerable to masking until sometime around this age as a result. This is especially true for pulse trains emitted during the first few weeks of a calf's life given the low apparent source levels reported herein and relatively low peak frequencies of these sounds.

Complex Contact Call Development
The primary complex contact calls emitted by Yulka and Kairo during Kylu's first month of life were individually distinct contact call types, providing further evidence for potential vocal signatures in beluga contact calls (Vergara & Mikus, 2019). The complex contact calls produced by Kylu during the medical isolations in his 23rd month were consistently most similar to his mother's type Y2 contact calls. Kylu did not appear to have incorporated a stereotyped version of Yulka's Y1 call into his vocal repertoire by the end of the second year.

Interestingly, Yulka's own Y2 emission was rarely recorded during Kylu's first 2 y of life, with the exception of his medical isolations during the 23rd month. However, Yulka did produce both Y1 and Y2 calls regularly during the *prepartum* recording period, contrary to "Aurora," Tuvaq's mother, who did not produce contact calls at all during the *prepartum* period (Vergara & Barrett-Lennard, 2008). Kylu's exposure to his mother's Y2 call may have begun during the *prepartum* period as has been implicated for whistle learning in dolphins (Tyack & Sayigh, 1997) and voice

recognition in humans (e.g., DeCasper & Fifer, 1980; Partanen et al., 2013). It is also likely that Kylu was exposed to his mother's Y2 call outside of recording periods for the current study.

Kylu produced fewer mixed calls overall in his first year of life in comparison to Tuvaq (Vergara & Barrett-Lennard, 2008), which could explain the delayed stereotypy of Kylu's Y2 call. Tuvaq had reached full stereotypy in the production of his type A1 calls by his 20th month, but Kylu did not reach full stereotypy in his Y2 production within the scope of this study. As of the 23rd month of life, the variability in dominant tonal frequency of Kylu's calls was still considerably higher than Yulka's. At 20 months, the CVs of the Vancouver belugas' A1 dominant tonal frequency were substantially smaller and almost identical for Tuvaq and Aurora (Vergara, 2011). Moreover, we do not have evidence of Kylu emitting any calls resembling his mother's Y2 call during his first year, unlike Tuvaq's production of rudimentary versions of his mother's A1 call beginning at 4 mo.

It is not surprising that the two calves differed in their complex contact call development as variability in timing of signature whistle acquisition occurs in bottlenose dolphin calves (e.g., Caldwell & Caldwell, 1979; Sayigh, 1992; Tyack & Sayigh, 1997; Fripp et al., 2005). Unlike the beluga calves discussed here, however, bottlenose dolphin calves generally appear to develop signature whistles that are dissimilar to those of their mothers (e.g., Caldwell & Caldwell, 1979; Sayigh, 1992; Tyack, 1997; Tyack & Sayigh, 1997; Bojanowski et al., 2000; Miksis et al., 2002; Fripp et al., 2005), although in instances when dolphin calves do model their signature whistle after their mothers, the calves tend to be male (Sayigh et al., 1990, 1995). Beluga calves may still model their mother's complex contact call regardless of calf sex, however, as Vergara & Barrett-Lennard (2008) reported that Tuvaq's older half-sister, "Qila," also produced their mother's call type. Additional research on vocal development in female beluga calves is necessary to adequately assess this hypothesis.

If calves develop contact calls that are similar to their mothers, and these call types remain stable in the vocal repertoires of these animals, then some beluga calls may be used for long-term kin identification. Beluga contact call development is likely influenced by the species' social structure (Tyack, 1998). In some wild populations, kin appear to maintain close associations along migratory routes and within summering areas (Colbeck et al., 2013; O'Corry-Crowe et al., 2018) where site fidelity has been observed in related individuals that return to the same summering habitats for up to 20 y (O'Corry-Crowe et al., 2018). A number of matrilineal units of females, calves, and older female offspring form large summering herds (Smith et al., 1994; Palsbøll et al., 2002); and, periodically, individuals from these units mingle, separating and rejoining, thus creating some temporary fluctuations in group composition typical of fission-fusion societies (Bel'kovitch & Sh'ekotov, 1993; Alekseeva et al., 2013; Krasnova et al., 2014). Maintaining associations with kin while group membership oscillates among matrilineal units may require sharing some contact calls so that these calls are readily identifiable to related individuals when produced among a large number of conspecifics. Sharing the mother's complex contact call type at least in early life may allow calves to maintain contact with kin in an aquatic environment where animals may quickly lose sight of one another.

Species-Specific Trends in Development

Pulse trains are consistently reported as the first calls produced by beluga calves (Vergara & Barrett-Lennard, 2008; Vergara, 2011) and may be rudimentary contact calls. These sounds may also provide the foundation for many of the sounds produced by adult belugas as they are produced exclusively prior to other sound types and are often incorporated into more complex signaling. PRR and peak frequency of these sounds are initially low (this work and Vergara, 2011), and changes in these parameters behave similarly over time. Remaining sound type acquisition seems to vary somewhat between individual calves but still follow a similar pattern. For example, Kylu's whistle production was delayed when compared to the two Vancouver aquarium calves (MacLeod, 2009; Vergara, 2011), but whistle emission still preceded the regular production of mixed calls in both Tuvaq and Kylu. Regular production of more adult-like mixed calls began around the same time for Tuvaq and Kylu, but, again, Kylu was a bit more delayed in reaching this milestone when compared to Tuvaq. Consequently, there appear to be stages of sound acquisition that occur within a window of time (i.e., 1 to 3 mo for whistle emergence and 4 to 5 mo for adult-like mixed calls). Delays in Kylu's acquisition of some sounds may have been influenced by the sounds available to him in his sound environment. The lack of whistle production in the vocal repertoires of the adult belugas, for example, may have contributed to the delay in the production of this sound in Kylu. Moreover, Kylu's social group was unique in that it only comprised his parents, while Tuvaq matured in a more complex social grouping with multiple whales, both related and unrelated, with more opportunities for social (or vocal) learning. Yulka's vocal repertoire could also be described as comparably stunted to Kairo's repertoire (and

documented wild beluga repertoires; e.g., Belikov & Bel'kovich, 2008; Chmelnitsky & Ferguson, 2012; Garland et al., 2015), possibly due to being wild-caught at approximately 2 y of age, while Kairo was believed to have been caught in his mid-20s. Thus, some of Kylu's delays may be attributable to his unique social situation and mother's own stunted repertoire. Unfortunately, it was impossible to directly compare more of Kylu's repertoire to the repertoires of his parents as many of Kylu's sound types remained unstereotyped (i.e., did not progress into specific call types) by the end of his first year.

Unstereotyped mixed calls were a precursor to the development of complex contact calls in both calves but with great individual variation in the acquisition of complex contact calls. These do appear to approach full stereotypy towards the end of calves' second year of life. The prevalence of a mother's contact call subtype in the first month of life may not influence a calf's incorporation of that subtype in later life, but, ultimately, beluga calves appear to develop contact calls that are similar to their mothers. These contact calls may be shared with related animals and may be important for long-term kin recognition. Further research is essential in determining whether some complex contact calls remain stable in the beluga vocal repertoire over time or if belugas alter characteristics of their contact calls once they mature and separate from their mothers.

Influences on Beluga Vocal Development: Genetics or Learning?

It is difficult to tease apart the roles of genetics and learning in ontogenetic studies when offspring develop sounds that are similar to their kin as has been the case with beluga complex contact call development in managed care. Still, it is likely that vocal learning processes influence the development of these calls based on what is known regarding this species. Belugas are highly social and mobile aquatic mammals, capable of maintaining long-term associations with kin across large distances. Vocal learning appears to coincide with the development of complex signaling in other gregarious species (e.g., Australian magpie [*Gymnorhina tibicen*], American crow [*Corvus brachyrhynchos*], and budgerigar [*Melopsittacus undulates*]: reviewed in Brown & Farabaugh, 1997; killer whales [*Orcinus orca*]: Deecke et al., 2000; Crance et al., 2014; and bottlenose dolphins: Janik & Sayigh, 2013), and this is especially true for species with environments in which visual acuity may be limited but contact with conspecifics is critical.

The ability of a species to imitate sounds outside the bounds of its normal vocal repertoire is perhaps the strongest evidence for production learning (Janik & Slater, 1997; Tyack, 2019). Some anecdotal (Eaton, 1979; Ridgway et al., 2012) and empirical (Murayama et al., 2014) evidence of belugas imitating human speech as well as synthetic sounds (Murayama et al., 2014) suggest that this species may have evolved this ability. Imitation of synthetic sounds has been successfully demonstrated in bottlenose dolphins (e.g., Richards et al., 1984), and calves even incorporate synthetic sounds as signature whistles (Miksis et al., 2002). Studies of beluga calves in managed care reared in the absence of their mothers would be valuable in determining whether the mother's call is an innate template or whether such calves depend on sounds from the acoustic environment as models for contact calls.

Differences in contact call development between calves may also be attributable to learning as calves would likely develop contact calls along a similar inherent trajectory should they be genetically predisposed. Tuvaq and Kylu showed different progressions of contact call development and influence in the acquisition of one of their mother's subtypes. Other areas of calf development progress variably across calves (e.g., Hill, 2009; Hill et al., 2013) and are heavily influenced by social learning as neonates appear to lack a multitude of innate behaviors or skills (Krasnova et al., 2009). For example, young calves appear to develop social and motor skills first through imitation of the mother and later through imitation of conspecifics (Krasnova et al., 2009). A similar trend may occur with complex contact call acquisition in which calves first develop contact calls that are similar to their mothers but later incorporate contact calls of other social group members. Tuvaq later incorporated his father's contact call only after the physical re-introduction of his father to the habitat 18 mo after Tuvaq's birth (Vergara & Barrett-Lennard, 2008). While suggesting that this may support production learning by beluga calves, Vergara & Barrett-Lennard (2008) were still hesitant to rule out genetics as a potential mechanism underlying Tuvaq's incorporation of his father's call. In the wild, it would be unusual for fathers to be present for the development of their calves (e.g., Loseto et al., 2006; Hauser et al., 2017; O'Corry-Crowe et al., 2018).

Conclusions and Future Directions

Vocal development studies are sparse in the literature for many animal species. In cetaceans, this is partially due to the fact that long-term study of vocal development in wild cetacean calves would be logistically difficult if not impossible. Yet, studies of vocal ontogeny are fundamental to understanding sound-centered species that rely on sound

to survive and to maintain social ties with conspecifics. This second longitudinal study on beluga vocal development under managed care has illuminated some important species-specific trends in ontogeny. This study was also the first to use high sampling rates to evaluate beluga vocal development. Given the broad bandwidth of beluga vocalizations, additional studies would help corroborate how the parameters of acoustic energy distribution of beluga broadband calls change with age. In addition, future studies in larger social groupings would aid in disentangling maturational processes, genetic inheritance, and learning.

Acknowledgments

Literature Cited

Alekseeva, Y. I., Panova, E. M., & Bel'kovich, V. M. (2013). Behavioral and acoustical characteristics of the reproductive gathering of beluga whales (*Delphinapterus leucas*) in the vicinity of Myagostrov, Golyi Sosnovets, and Roganka Islands (Onega Bay, the White Sea). *Biology Bulletin*, *40*, 307-317. https://doi.org/10.1134/S1062359013030023

Ames, A. E., Zapetis, M. E., Witlicki, K. L., Wielandt, S. J., Cameron, D. M., Walker, R. T., & Kuczaj III, S. A. (2017). Thunks: Evidence for graded harmonic structure in an Atlantic bottlenose dolphin (*Tursiops truncatus*) sound. *International Journal of Comparative Psychology*, *30*.

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

Belikov, R. A., & Bel'kovich, V. M. (2008). Communicative pulsed signals of beluga whales in the reproductive gathering off Solovetskii Island in the White Sea.

Acoustical Physics, *54*, 115-123. https://doi.org/10.1134/S1063771008010168

Bel'kovitch, V. M., & Sh'ekotov, M. N. (1993). *The belukha whale: Natural behavior and bioacoustics* (M. A. Svanidze, Trans.). Woods Hole Oceanographic Institution. https://doi.org/10.1575/1912/75

Bojanowski, E., Veit, F., & Todt, D. (2000). The development of a bivocal signature whistle in a bottlenose dolphin calf. *European Research on Cetaceans*, *14*, 70-74.

Boughman, J. W., & Moss, C. F. (2003). Social sounds: Vocal learning and development of mammal and bird calls. In A. M. Simmons, A. N. Popper, & R. R. Fay (Eds.), *Acoustic communication* (pp. 138-224). Springer-Verlag. https://doi.org/10.1007/0-387-22762-8_4

Brill, L. R., & Harder, P. J. (1991). The effects of attenuating returning echolocation signals at the lower jaw of a dolphin (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, *89*, 2851-2857. https://doi.org/10.1121/1.400723

Brown, E. D., & Farabaugh, S. M. (1997). What birds with complex social relationships can tell us about vocal learning: Vocal sharing in avian groups. In C. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 98-127). Cambridge University Press. https://doi.org/10.1017/CBO9780511758843.007

Caldwell, M. C., & Caldwell, D. K. (1965). Individualized whistle contours in bottle-nosed dolphins (*Tursiops truncatus*). *Nature*, *207*(4995), 434-435. https://doi.org/10.1038/207434a0

Caldwell, M. C., & Caldwell, D. K. (1979). The whistle of the Atlantic bottlenosed dolphin *(Tursiops truncatus)* –Ontogeny. In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine animals* (Vol. 3, pp. 369-401). Plenum Press. https://doi.org/10.1007/978-1-4684-2985-5_11

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*, 4821-4835. https://doi.org/10.1121/1.4707501

Clark, C. W., Ellison, W. T., Southall, B. L., Hatch, L., Van Parijs, S. M., Frankel, A., & Ponirakis, D. (2009). Acoustic masking in marine ecosystems: Intuitions, analysis, and implication. *Marine Ecology Progress Series*, *395*, 201-222. https://doi.org/10.3354/meps08402

Colbeck, G. J., Duchesne, P., Postma, L. D., Lesage, V., Hammill, M. O., & Turgeon, J. (2013). Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*, 20122552. https://doi.org/10.1098/rspb.2012.2552

Connor, R. C., & Smolker, R. A. (1996). "Pop" goes the dolphin: A vocalization male bottlenose dolphins produce during consortships. *Behaviour*, *133*, 643-662. https://doi.org/10.1163/156853996X00404

Crance, J. L., Bowles, A. E., & Garver, A. (2014). Evidence for vocal learning in juvenile male killer whales, *Orcinus orca*, from an adventitious cross-socializing

experiment. *Journal of Experimental Biology*, *217*, 1229-1237. https://doi.org/10.1242/jeb.094300

Cranford, T. W. (2000). In search of impulse sound sources in odontocetes. In W. W. L. Au, A. N. Popper, & R. R. Fay (Eds.), *Hearing by whales and dolphins* (pp. 109-155). Springer-Verlag. https://doi.org/10.1007/978-1-4612-1150-1_3

Cranford, T. W., Amundin, M., & Norris, K. S. (1996). Functional morphology and homology in the odontocete nasal complex: Implications for sound generation. *Journal of Morphology*, *228*, 223-285. https://doi.org/10.1002/(SICI)1097-4687(199606)228:3<223::AID-JMOR1>3.0.CO;2-3

Cranford, T. W., Elsberry, W. R., Van Bonn, W. G., Jeffress, J. A., Chaplin, M. S., Blackwood, D. J., Carder, D. A., Kamolnick, T., Todd, M. A., & Ridgway, S. H. (2011). Observation and analysis of sonar signal generation in the bottlenose dolphin (*Tursiops truncatus*): Evidence for two sonar sources. *Journal of Experimental Marine Biology and Ecology*, *407*, 81-96. https://doi.org/10.1016/j.jembe.2011.07.010

Cranford, T. W., Elsberry W. R., Blackwood, D. J., Carr, J. A., Kamolnick, T., Todd, M., Van Bonn, W. G., Carder, D. A., Ridgway, S. H., Bozlinski, D. M., & Decker, E. C. (2000). Two independent sonar signal generators in the bottlenose dolphin: Physiologic evidence and implications. *The Journal of the Acoustical Society of America*, *108*(5), 2613-2614. https://doi.org/10.1121/1.4743727

Croll, D. A., Clark, C. W., Calambokidis, J., Ellison, W. T., & Tershy, B. R. (2001). Effect of anthropogenic low-frequency noise on the foraging ecology of *Balaenoptera* whales. *Animal Conservation*, *4*(1), 13-27. https://doi.org/10.1017/S1367943001001020

DeCasper, A., & Fifer, W. (1980). Of human bonding: Infants prefer their mother's voices. *Science*, *208*, 1174-1176. https://doi.org/10.1126/science.7375928

Deecke, V. B., Ford, J. K. B., & Spong, P. (1999). Quantifying complex patterns of bioacoustics variation: Use of a neural network to compare killer whale (*Orcinus orca*) dialects. *The Journal of the Acoustical Society of America*, *105*(4), 2499-2507. https://doi.org/10.1121/1.426853

Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *Animal Behaviour*, *60*, 629-638. https://doi.org/10.1006/anbe.2000.1454

Eaton, R. L. (1979). A beluga whale imitates human speech. *Carnivore*, *2*, 22-23.

Erbe, C. (1999). The effects of anthropogenic noise on Canadian marine mammals. *Canadian Acoustics*, *27*, 10-11.

Erbe, C., & Farmer, D. M. (1998). Masked hearing thresholds of a beluga whale (*Delphinapterus leucas*) in icebreaker noise. *Deep Sea Research Part II: Topical Studies in Oceanography*, *45*, 1373-1388. https://doi.org/10.1016/S0967-0645(98)00027-7

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine Pollution Bulletin*, *103*, 15-38. https://doi.org/10.1016/j.marpolbul.2015.12.007

Favaro, L., Gnone, G., & Pessani, D. (2013). Postnatal development of echolocation abilities in a bottlenose dolphin (*Tursiops truncatus*): Temporal organization. *Zoo Biology*, *32*, 210-215. https://doi.org/10.1002/zoo.21056

Fisheries and Oceans Canada (DFO). (2017). *St. Lawrence Estuary beluga: A science based review of recovery actions for three at-risk whale populations*. DFO.

Fripp, D. (2005). Bubblestream whistles are not representative of a bottlenose dolphin's vocal repertoire. *Marine Mammal Science*, *21*, 29-44. https://doi.org/10.1111/j.1748-7692.2005.tb01206.x

Fripp, D., & Tyack, P. (2008). Postpartum whistle production in bottlenose dolphins. *Marine Mammal Science*, *24*, 479-502. https://doi.org/10.1111/j.1748-7692.2008.00195.x

Fripp, D., Owen, C., Quintana-Rizzo, E., Shapiro, A., Buckstaff, K., Jankowski, K., Wells, R., & Tyack, P. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition*, *8*, 17-26. https://doi.org/10.1007/s10071-004-0225-z

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*, *137*(6), 3054-3067. https://doi.org/10.1121/1.4919338

Gervaise, C., Simard, Y., Roy, N., Kinda, B., & Ménard, N. (2012). Shipping noise in whale habitat: Characteristics, sources, budget, and impact on beluga in Saguenay–St. Lawrence Marine Park hub. *The Journal of the Acoustical Society of America*, *132*, 76-89. https://doi.org/10.1121/1.4728190

Gnone, G., & Moriconi, T. (2010). Use and function of distinctive whistle-like signals in bottlenose dolphin (*Tursiops truncatus*) mother-calf pair. In A. G. Pearce & L. M. Correa (Eds.), *Dolphins: Anatomy, behavior and threats* (pp. 149-167). Nova Science Publishers.

Hauser, D. D., Laidre, K. L., Stern, H. L., Moore, S. E., Suydam, R. S., & Richard, P. R. (2017). Habitat selection by two beluga whale populations in the Chukchi and Beaufort Seas. *PLOS ONE*, *12*(2), e0172755. https://doi.org/10.1371/journal.pone.0172755

Hermannsen, L., Beedholm, K., Tougaard, J., & Madsen, P. T. (2014). High frequency components of ship noise in shallow water with a discussion of implications for harbor porpoises (*Phocoena phocoena*). *The Journal of the Acoustical Society of America*, *136*(4), 1640-1653. https://doi.org/10.1121/1.4893908

Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, *395*, 5-20. https://doi.org/10.3354/meps08353

Hill, H. M. (2009). The behavioral development of two beluga calves during the first year of life. *International Journal of Comparative Psychology*, *22*(4).

Hill, H. M., Campbell, C., Dalton, L., & Osborn, S. (2013). The first year of behavioral development and maternal care of beluga (*Delphinapterus leucas*) calves in

human care. *Zoo Biology*, *32*(5), 565-570. https://doi.org/10.1002/zoo.21093

Hooper, S., Reiss, D., Carter, M., & McCowan, B. (2006). Importance of contextual saliency on vocal imitation by bottlenose dolphins. *International Journal of Comparative Psychology*, *19*(1).

Janik, V. M. (1999). Pitfalls in the categorization of behaviour: A comparison of dolphin whistle classification methods. *Animal Behaviour*, *57*, 133-143. https://doi.org/10.1006/anbe.1998.0923

Janik, V. M. (2014). Cetacean vocal learning and communication. *Current Opinion in Neurobiology*, *28*, 60-65. https://doi.org/10.1016/j.conb.2014.06.010

Janik, V. M., & Sayigh, L. S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. *Journal of Comparative Physiology A*, *199*, 479-489. https://doi.org/10.1007/s00359-013-0817-7

Janik, V. M., & Slater, P. J. (1997). Vocal learning in mammals. *Advances in the Study of Behaviour*, *26*, 59-100. https://doi.org/10.1016/S0065-3454(08)60377-0

Janik, V. M., & Slater P. J. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, *56*, 829-838. https://doi.org/10.1006/anbe.1998.0881

Janik, V. M., & Slater, P. J. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*, 1-11. https://doi.org/10.1006/anbe.2000.1410

Karlsen, J., Bisther, A., Lydersen, C., Haug, T., & Kovacs, K. (2002). Summer vocalisations of adult male white whales (*Delphinapterus leucas*) in Svalbard, Norway. *Polar Biology*, *25*, 808-817. https://doi.org/10.1007/s00300-002-0415-6

Killebrew, D., Mercado, E., Herman, L., & Pack, A. (2001). Sound production of a neonate bottlenose dolphin. *Aquatic Mammals*, *27*(1), 34-44.

King, S. L., & Janik, V. M. (2015). Come dine with me: Food-associated social signaling in wild bottlenose dolphins (*Tursiops truncatus*). *Animal Cognition*, *18*, 969-974. https://doi.org/10.1007/s10071-015-0851-7

Krasnova, V. V., Bel'kovich, V. M., & Chernetskii, A. D. (2009). Formation of behavior in the White Sea beluga calf, *Delphinapterus leucas*, during early postnatal ontogenesis. *Russian Journal of Marine Biology*, *35*(1), 53-59. https://doi.org/10.1134/S1063074009010088

Krasnova, V. V., Chernetsky, A. D., Zheludkova, A. I., & Bel'kovich, V. M. (2014). Parental behavior of the beluga whale (*Delphinapterus leucas*) in natural environment. *Biology Bulletin*, *41*, 349-356. https://doi.org/10.1134/S1062359014040062

Lesage, V., Barrette, C., Kingsley, M., & Sjare, B. (1999). The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River Estuary, Canada. *Marine Mammal Science*, *15*(1), 65-84. https://doi.org/10.1111/j.1748-7692.1999.tb00782.x

Lesage, V., McQuinn, I. H., Carrier, D., Gosselin, J. F., & Mosnier, A. (2014a). *Exposure of the beluga (*Delphinapterus leucas*) to marine traffic under various scenarios of transit route diversion in the St. Lawrence Estuary* (DFO Canadian Science Advisory Secretariat Research Document 2013/125). Fisheries and Oceans Canada.

Lesage, V., Measures, L. N., Mosnier, A., Lair, S., Michaud, R., & Béland, P. (2014b). *Mortality patterns in St. Lawrence Estuary beluga (*Delphinapterus leucas*), inferred from the carcass recovery data, 1983-2012* (DFO Canadian Science Advisory Secretariat Research Document 2013/118). Fisheries and Oceans Canada.

Loseto, L. L., Richard, P., Stern, G. A., Orr, J., & Ferguson, S. H. (2006). Segregation of Beaufort Sea beluga whales during the open-water season. *Canadian Journal of Zoology*, *84*(12), 1743-1751. https://doi.org/10.1139/z06-160

MacLeod, C. D. (2009). *Vocal learning in a captive beluga calf (*Delphinapterus leucas*)* (Bachelor's thesis). University of British Columbia, Vancouver, Canada.

Madsen, P. T., Wisniewska, D., & Beedholm, K. (2010). Single source sound production and dynamic beam formation in echolocating harbour porpoises (*Phocoena phocoena*). *Journal of Experimental Biology*, *213*, 3105-3110. https://doi.org/10.1242/jeb.044420

Madsen, P. T., Lammers, M., Wisniewska, D., & Beedholm, K. (2013). Nasal sound production in echolocating delphinids (*Tursiops truncatus* and *Pseudorca crassidens*) is dynamic, but unilateral: Clicking on the right side and whistling on the left side. *Journal of Experimental Biology*, *216*, 4091-4102. https://doi.org/10.1242/jeb.091306

McBride, A., & Kritzler, H. (1951). Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. *Journal of Mammalogy*, *32*, 251-266. https://doi.org/10.2307/1375657

McCowan, B., & Reiss, D. (1995a). Maternal aggressive contact vocalizations in captive bottlenose dolphins (*Tursiops truncatus*): Wide-band, low-frequency signals during mother/aunt-infant interactions. *Zoo Biology*, *14*, 293-309. https://doi.org/10.1002/zoo.1430140402

McCowan, B., & Reiss, D. (1995b). Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): Role of learning. *Journal of Comparative Psychology*, *109*, 242-260. https://doi.org/10.1037/0735-7036.109.3.242

Mello, I., & Amundin, M. (2005). Whistle production pre- and post-partum in bottlenose dolphins (*Tursiops truncatus*) in human care. *Aquatic Mammals*, *31*(2), 169-175. https://doi.org/10.1578/AM.31.2.2005.169

Miksis, J., Tyack, P., & Buck, J. (2002). Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. *The Journal of the Acoustical Society of America*, *112*, 728-739. https://doi.org/10.1121/1.1496079

Mishima, Y., Morisaka, T., Itoh, M., Matsuo, I., Sakaguchi, A., & Miyamoto, Y. (2015). Individuality embedded in the isolation calls of captive beluga whales (*Delphinapterus leucas*). *Zoological Letters*, *1*. https://doi.org/10.1186/s40851-015-0028-x

Morisaka, T., Shinohara, M., & Taki, M. (2005a). Underwater sounds produced by neonatal bottlenose dolphins (*Tursiops*

truncatus): I. Acoustic characteristics. *Aquatic Mammals*, *31*(2), 248-257. https://doi.org/10.1578/AM.31.2.2005.248

Morisaka, T., Shinohara, M., & Taki, M. (2005b). Underwater sounds produced by neonatal bottlenose dolphins (*Tursiops truncatus*): II. Potential function. *Aquatic Mammals*, *31*(2), 258-265. https://doi.org/10.1578/AM.31.2.2005.258

Morisaka, T., Yoshida, Y., Akune, Y., Mishima, H., & Nishimoto, S. (2013). Exchange of "signature" calls in captive belugas (*Delphinapterus leucas*). *Journal of Ethology*, *31*, 141-149. https://doi.org/10.1007/s10164-013-0358-0

Murayama, T., Iijima, S., Katsumata, H., & Arai, K. (2014). Vocal imitation of human speech, synthetic sounds and beluga sounds, by a beluga (*Delphinapterus leucas*). *International Journal of Comparative Psychology*, *27*(3).

Murray, S. O., Mercado, E., & Roitblat, H. L. (1998). Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations. *The Journal of the Acoustical Society of America*, *104*(3), 1679-1688. https://doi.org/10.1121/1.424380

Nottebohm, F. (1972). The origins of vocal learning. *The American Naturalist*, *106*, 116-140. https://doi.org/10.1086/282756

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., Ferrer, T., Citta, J., Burkanov, V., Frost, K., & Mahoney, B. (2018). Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLOS ONE*, *13*, e0194201. https://doi.org/10.1371/journal.pone.0194201

Palsbøll, P. J., Heide-Jørgensen, M. P., & Bérubé, M. (2002). Analysis of mitochondrial control region nucleotide sequences from Baffin Bay beluga (*Delphinapterus leucas*): Detecting pods or sub-populations? *NAMMCO Scientific Publications*, *4*, 39-50. https://doi.org/10.7557/3.2836

Panova, E., Agafonov, A., Belikov, R., & Melnikova, F. (2017). Vocalizations of captive beluga whales, *Delphinapterus leucas*: Additional evidence for contact signature "mixed" calls in belugas. *Marine Mammal Science*, *33*, 889-903. https://doi.org/10.1111/mms.123933

Partanen, E., Kujala, A., Tervaniemi, M., & Huotilainen, M. (2013). Prenatal music exposure induces long-term neural effects. *PLOS ONE*, *8*, e78946. https://doi.org/10.1371/journal.pone.0078946

Reiss, D. (1988). Observations on the development of echo-location in young bottlenose dolphins. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar* (pp. 121-127). Plenum Publishing. https://doi.org/10.1007/978-1-4684-7493-0_14

Richards, D. G., Wolz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *Journal of Comparative Psychology*, *98*(1), 10-28. https://doi.org/10.1037/0735-7036.98.1.10

Ridgway, S., Carder, D., Jeffries, M., & Todd, M. (2012). Spontaneous human speech mimicry by a cetacean. *Current Biology*, *22*(20), R860-R861. https://doi.org/10.1016/j.cub.2012.08.044

Sayigh, L. S. (1992). *Development and functions of signature whistles of free-ranging bottlenose dolphins,* Tursiops truncatus (Doctoral dissertation). Massachusetts Institute of Technology, Cambridge. https://apps.dtic.mil/dtic/tr/fulltext/u2/a259362.pdf

Sayigh, L. S., Esch, H. C., Wells, R. S., & Janik, V. M. (2007). Facts about signature whistles of bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, *74*, 1631-1642. https://doi.org/10.1016/j.anbehav.2007.02.018

Sayigh, L. S., Tyack, P. L., Wells, R. S., & Scott, M. D. (1990). Signature whistles of free ranging bottlenose dolphins *Tursiops truncatus*: Stability and mother offspring comparisons. *Behavioral Ecology and Sociobiology*, *26*, 247-260. https://doi.org/10.1007/BF00178318

Sayigh, L., Tyack, P., Wells, R., Scott, M., & Irvine, A. (1995). Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, *36*, 171-177. https://doi.org/10.1007/BF00177793

Schulz, T. M., Whitehead, H., Gero, S., & Rendell, L. (2008). Overlapping and matching of codas in vocal interactions between sperm whales: Insights into communication function. *Animal Behaviour*, *76*, 1977-1988. https://doi.org/10.1016/j.anbehav.2008.07.032

Sjare, B. L., & Smith, T. G. (1986). The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. *Canadian Journal of Zoology*, *64*, 2824-2831. https://doi.org/10.1139/z86-406

Smith, T. G., Hammill, M. O., & Martin, A. R. (1994). Herd composition and behavior of white whales (*Delphinapterus leucas*) in two Canadian arctic estuaries. *Meddelelser om Grønland Bioscience*, *39*, 175-184.

Tyack, P. L. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: Mimicry of signature whistles? *Behavioral Ecology and Sociobiology*, *18*, 251-257. https://doi.org/10.1007/BF00300001

Tyack, P. L. (1997). Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. *Bioacoustics*, *8*, 21-46. https://doi.org/10.1080/09524622.1997.9753352

Tyack, P. L. (1998). Acoustic communication under the sea. In S. L. Hopp, M. J. Owren, & S. C. Evans (Eds.), *Animal acoustic communication – Sound analysis and research methods* (pp. 163-220). Springer-Verlag. https://doi.org/10.1007/978-3-642-76220-8_6

Tyack, P. L. (2019). A taxonomy for vocal learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1789), 20180406. https://doi.org/10.1098/rstb.2018.0406

Tyack, P. L., & Sayigh, L. S. (1997). Vocal learning in cetaceans. In C. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 208-233). Cambridge University Press. https://doi.org/10.1017/CBO9780511758843.011

Van Parijs, S. M., Lydersen, C., & Kovacs, K. M. (2003). Sounds produced by individual white whales, *Delphinapterus leucas*, from Svalbard during capture.

The Journal of the Acoustical Society of America, *113*, 57-60. https://doi.org/10.1121/1.1528931

Veirs, S., Veirs, V., & Wood, J. D. (2016). Ship noise extends to frequencies used for echolocation by endangered killer whales. *PeerJ*, *4*, e1657. https://doi.org/10.7717/peerj.1657

Vergara, V. (2011). *Acoustic communication and vocal learning in belugas (*Delphinapterus leucas*)* (Doctoral dissertation). University of British Columbia, Vancouver, Canada. https://doi.org/10.14288/1.0071602

Vergara, V., & Barrett-Lennard, L. G. (2008). Vocal development in a beluga calf (*Delphinapterus leucas*). *Aquatic Mammals*, *34*(1), 123-143. https://doi.org/10.1578/AM.34.1.2008.123

Vergara, V., & Mikus, M. A. (2019). Contact call diversity in natural beluga entrapments in an Arctic estuary: Preliminary evidence of vocal signatures in wild belugas. *Marine Mammal Science*, *35*, 434-465. https://doi.org/10.1111/mms.12538

Vergara, V., Michaud, R., & Barrett-Lennard, L. (2010). What can captive whales tell us about their wild counterparts? Identification, usage, and ontogeny of contact calls in belugas (*Delphinapterus leucas*). *International Journal of Comparative Psychology*, *23*(3).

Vollmer, N. L., Hayek, L. A. C., Heithaus, M. R., & Connor, R. C. (2015). Further evidence of a context-specific agonistic signal in bottlenose dolphins: The influence of consortships and group size on the pop vocalization. *Behaviour*, *152*, 1979-2000. https://doi.org/10.1163/1568539X-00003311

Watkins, W. A. (1967). The harmonic interval: Fact or artifact in spectral analysis of pulse trains. In W. N. Tavolga (Ed.), *Marine bioacoustics* (pp. 15-43). Pergamon Press. https://doi.org/10.1575/1912/2726

Watkins, W. A., & Schevill, W. E. (1977). Sperm whale codas. *The Journal of the Acoustical Society of America*, *62*, 1485-1490. https://doi.org/10.1121/1.381678