

## Vocal Development in a Beluga Calf (*Delphinapterus leucas*)

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### Abstract

Acoustic communication is central to the socioecology of cetaceans. Knowledge of the ontogeny of their extensive repertoires is scant, and even less is known about the role of learning in vocal development. To examine these issues, the development of calls of one male beluga (*Delphinapterus leucas*) calf was systematically studied at the Vancouver Aquarium throughout his first year of life and opportunistically through his second and third years. He vocalized within the first hour after birth, producing exclusively low energy, broadband pulse trains. Both the dominant frequency and the pulse repetition rate of the pulsed calls increased with age. He acquired rudimentary whistles at 2 wks of age. During the second month, whistle production increased substantially. Whistle dominant frequency tended to increase with age, and at least in his first year, whistles did not attain full stereotypy. The calf started using mixed call types consistently at 4 mo. While some sounds tended to be more variable at later ages, his mixed calls progressively lost variability and increasingly resembled his mother's most predominant stereotyped mixed call type. By 20 mo, this call type was fully stereotyped. Six months after he was exposed to his father's sounds, he incorporated one of his father's call types into his repertoire. These findings are discussed in light of current theories of sound production mechanisms in odontocetes, developmental stages of vocal acquisition, and vocal learning.

**Key Words:** repertoire development, acoustic communication, vocal learning, cetacean, ontogeny, beluga, *Delphinapterus leucas*

### Introduction

The highly soniferous nature of many species of toothed whales and the importance of sound to mediate their complex social interactions are well known. Yet, knowledge of the ontogeny of odontocete sound production is scant, being

mostly limited to one species, the bottlenose dolphin (*Tursiops* sp.) (Caldwell & Caldwell, 1979; Lindhard, 1988; Reiss, 1988; McCowan & Reiss, 1995; Killebrew et al., 2001; Fripp et al., 2005), with the exception of a killer whale (*Orcinus orca*) study (Bowles et al., 1988) and a description of sound production in two neonate sperm whales (*Physeter macrocephalus*) (Madsen et al., 2003).

Parallels in vocal development in humans, other primate species, and songbirds have been amply documented. For instance, the "babbling" stage of human infants (Locke, 1993), consisting of adult-like segments that are not fully formed phonemes, is similar to a stage in infant marmosets' (*Cebuella pygmaea*) vocal maturation (Elowson et al., 1998; Snowdon & Elowson, 2001). In human infants, babbling is thought to provide necessary practice for language use and to increase social exchanges with caregivers (Locke, 1993; Elowson et al., 1998; Oller, 2000; Snowdon & Elowson, 2001). Similarly for marmosets, babbling might be a form of vocal practice and a way of attracting attention from group members (Snowdon & Elowson, 2001). The subsong of songbirds, characterized by long, irregular, and variable components, also is compared often to human babbling and is believed to help shape the stereotyped crystallized song (Marler & Peters, 1982). Bottlenose dolphin data are ambiguous as to whether they undergo an analogous phase to human babbling (McCowan & Reiss, 1995; Tyack, 1997).

The expression *vocal learning*, has traditionally been applied to the concept of production learning, whereby signals are modified *in form* through experience with those of other individuals, leading to signals that are either similar or dissimilar to the model (Janik & Slater, 1997). It is, thus, one aspect of social learning (whereby animals learn from each other how to behave). Its importance in the development of human speech (e.g., Locke & Snow, 1997) has striking parallels in other vocal systems (e.g., songbirds: Marler & Mundinger, 1971; vervet monkeys [*Cercopithecus aethiops*]: Seyfarth & Cheney, 1986; bottlenose dolphins: McCowan & Reiss, 1995; Tyack, 1997). For

instance, vocal learning is an important factor in the ontogeny of signature whistles (Sayigh, 1992; Tyack, 1997) and of other whistle types (McCowan & Reiss, 1995) in bottlenose dolphins.

Janik & Slater (2000) divided vocal learning into production learning, defined above, and contextual learning. Contextual learning affects usage and comprehension of sounds, and refers to cases where an individual associates signals already present in their repertoire with different contexts based on experiences of other individuals' use of such signals (Janik & Slater, 1997, 2000). Both forms of vocal learning can play key functions in the development of an ability to interact vocally with conspecifics.

The beluga (*Delphinapterus leucas*) is a long-lived, highly gregarious, circumpolar odontocete that migrates from overwintering areas of broken pack ice to spring and summer calving and feeding areas, which are usually shallow river estuaries (Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2004). A clear understanding of its sociality continues to be elusive. Some authors (e.g., Recchia, 1994) assert that scant knowledge of the beluga's social behavior points towards some similarity to bottlenose dolphins or sperm whales in terms of fission-fusion patterns of association. It is known, however, that it is the most soniferous odontocete species, producing highly varied communication calls (Schevill & Lawrence, 1949; Fish & Mowbray, 1962; Sjare & Smith, 1986a, 1986b; Karlsen et al., 2002) as well as possessing an unparalleled echolocation system (Au et al., 1985; Turl et al., 1987, 1991). This species uses the two predominant sound types among toothed whales: (1) whistles, or narrow-band, frequency modulated vocalizations, believed to be social signals, and (2) pulsed sounds, or trains of broadband pulses, including those used for echolocation. Some researchers (e.g., Karlsen et al., 2002) identified mixed calls for belugas, consisting of both a whistle and a pulsed component in the same discrete vocalization.

The vocal repertoire of belugas has been described as "graded," with general call types shifting into each other, at least to human perception (Sjare & Smith, 1986a; Recchia, 1994; Karlsen et al., 2002). Furthermore, the distinction between echolocation clicks and pulsed sounds that are used socially may be arbitrary—one type of beluga signal may merge into the other. In most odontocetes, click trains used for echolocation have an inter-click interval that is longer than the time for the signal to travel from the animal and back. But belugas are capable of emitting *packets* of clicks with inter-click intervals less than the round trip travel time to the sonar target (Turl & Penner, 1989).

There is much to be gained by understanding how beluga acoustic development maps onto what is known of the acquisition of sound repertoires in other mammals and in birds, especially the role of vocal learning in repertoire development. Descriptions of repertoire ontogeny may illuminate the role of learning in the development of calls and also should provide clues about the physical mechanisms of sound production in odontocetes—an unresolved area of inquiry (Cranford, 2000a).

To examine the issues outlined above, a longitudinal study of the vocal development of a male beluga calf, Tuvaq (ID #990692), was performed at the Vancouver Aquarium from the moment of his birth, throughout his first year of life, and opportunistically through his second and third years of life, providing the first account of the sequencing and timing of vocal acquisition in a beluga whale. The authors identify his mother's predominant mixed call type, used primarily to maintain contact with her calf, and document the calf's gradual development of the same call type.

Disentangling learning from other mechanisms in the development of the acoustic repertoire can be challenging. Robust evidence of vocal learning requires quantification of the acoustic environments and social settings of more than one infant to determine how variation in these characteristics affects vocal development (e.g., Fripp, 1999). This was not possible in the current study. However, two adult belugas, one of them the calf's father, Imaq (ID #103007), who produced unique sounds never recorded from the rest of the adults, were introduced into the calf's social group 18 mo after his birth. In view of the genetic relatedness of father and son, changes in the calf's calls in relation to his new auditory contact with his father may not be enough to invoke production learning but would at least indicate usage learning.

Thus, the authors also asked whether Tuvaq adjusted his sounds to increase their similarity to his father's sounds. Given that beluga society displays qualities known to be requisites of social learning such as mixed age-class groups, long-term but fluid relationships, long lives and delayed sexual maturity, strong mother-infant bonds with long lactation periods, cooperation, and marked behavioral variability (Drinnan & Sadleir, 1981; Bel'kovitch & Sh'ekotov, 1993; Martin, 1996), the authors predicted that Tuvaq would learn to use his father's call types.

## Materials and Methods

### *Social Group*

The main subject of this study was a male beluga calf, Tuvaq, born on 20 July 2002 at the Vancouver

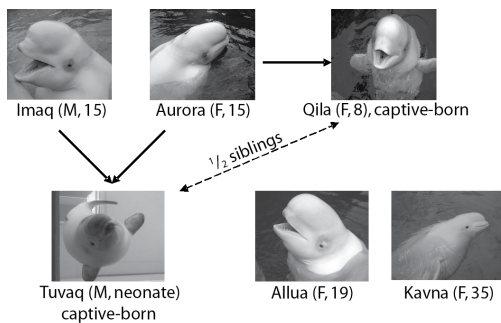
Aquarium in Canada. Tuvaq was an immature animal throughout the duration of this study. At the last sampling session at 32 mo of age, he was 2.83 m long, far from achieving full size (belugas grow to an average length of 4.57 m, and males are larger than females), had the uniform grey coloration typical of calves, and was still nursing frequently.

Tuvaq was housed with his 15-y-old mother, Aurora (ID #103006, captive since 1990), until his third month of life, when two other females, Qila (ID #103008, captive-born, Aurora's 8-y-old daughter and half-sibling to Tuvaq) and Allua (ID #103003, captive since 1985, unrelated, 19 y old) were reintroduced into the group. Tuvaq's father, Imaq (ID #103007, captive since 1990, 15 y old), and a 35-y-old unrelated female, Kavna (ID #040376, captive since 1976), were kept in a separate pool at the facility (acoustically isolated from the main pool) for husbandry reasons. Imaq and Kavna were introduced into Tuvaq's social group when he was 18 mo old. Except for Tuvaq and Qila, who were captive-born, all the Vancouver Aquarium belugas originate from Hudson Bay, Churchill, Manitoba. Figure 1 illustrates the genealogy of the Vancouver Aquarium belugas.

#### Sampling Regime and Observation Area

The animals were kept in an outdoor pool (18 m × 29 m; depth 6 m) connected to an adjacent 3-m deep, smaller medical holding pool (3 m × 3 m). They were observed and recorded from an underwater window with a good view of the entire larger pool, and occasionally from a smaller window with a view of the medical holding pool (Figure 2).

We performed 14 h of continuous recording and observation immediately after birth. Thereafter, sessions were 3 to 4 h long at least 3 times a week for the first 2 mo, and later 1 to 3 h twice a week



**Figure 1.** Genealogy of the Vancouver Aquarium belugas; between brackets are the sex and the age of each individual at the time when Tuvaq was born. Thick black arrows indicate "parent-offspring," and the broken arrow indicates half-sibling.

at variable times of day. After month 12, sessions in the larger pool were less regular, and the calf was recorded opportunistically whenever he was in voluntary or involuntary isolation in the medical holding pool (see below).

#### Acoustic Recordings

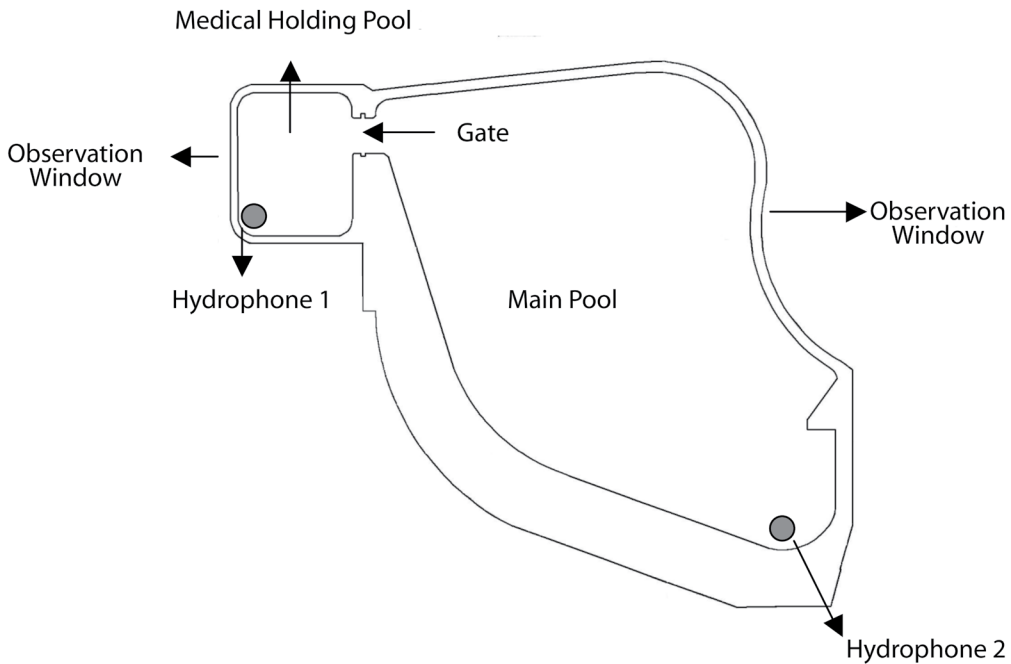
Underwater audio recordings were made using two hydrophones, which were installed permanently in the adjacent pools (Figure 2): (1) an Offshore Acoustics hydrophone (Offshore Acoustics, 5454 Indian River Drive, North Vancouver, BC) in the main pool and (2) a Brüel & Kjær 8101 hydrophone (Brüel & Kjær, DK-2850 Nærum, Denmark) in the medical holding pool. The calls were recorded digitally on two Pentium IV computers (each connected to a hydrophone) using *Avisoft SASlab Pro* software (Avisoft Bioacoustics) and *Cool Edit 2000* at a sampling rate of 44.1 kHz. The system had a frequency response of 0.02 kHz to 22.0 kHz + 1 dB. The authors occasionally had access to a sound card that sampled at 96.0 kHz (giving a recording bandwidth of 48.0 kHz), which assisted in determining whether high-frequency components were being missed in the 44.1 kHz recordings. The noises of the pool filtration system sometimes masked the frequencies below 2.0 kHz. This did not affect the narrow-band whistle recordings since only two whistles had a dominant frequency below 2.0 kHz. For the broad-band pulse trains and mixed calls, only the energy above 2.0 kHz was measured for the analysis of energy distribution.

Recordings were made throughout the length of the observation sessions, and all records were saved for later analysis. The time of the sound, its social and behavioral context, and the identity of the vocalizer, if possible, were simultaneously dictated on a mini-cassette recorder. The sounds were detected aurally via the speakers and visually by looking at the running sonograms on both computers.

#### Identification of Sound-Producing Individuals

Since cetaceans do not always produce visible signs when they make sounds, it is difficult to identify the phonating individual. This problem was circumvented in the following ways:

1. *Sound Source Localization*—Both hydrophones recorded simultaneously, so it was often possible to discern if a sound originated in the main pool or in the medical holding pool by comparing the amplitude of the same sound on the real-time spectrograms on the two computers because sounds originating in one of the pools were extremely attenuated, or even inaudible, from the other pool's hydrophone. This allowed for occasional identification



**Figure 2.** Diagram of the beluga pool and the adjacent medical holding pool at the Vancouver Aquarium; a narrow shallow passageway connects both pools, and the animals can voluntarily swim from one to the other. A rope gate (that allows visual and acoustic contact) is used when an animal needs to be temporarily isolated in the medical holding pool.

of the sound-producing individual when the animal was alone in one of the pools. Sounds originating near the passageway between the pools were often clearly audible from both hydrophones, however, and thus we excluded any identification of an individual in these sounds.

2. *Bubble-streams*—Emissions of streams of bubbles concurrent with sound production in bottlenose dolphin calves facilitated research on vocal development (McCowan & Reiss, 1995). They occur most frequently in infants, perhaps due to a lack of full control over the sound-producing apparatus, although the physiological mechanisms underlying them are inadequately understood. The beluga calf in this study also initially consistently emitted streams of bubbles while producing sounds. Fripp (2005) identified several problems associated with using bubble-streams and cautioned that whistles associated with bubble-streams do not adequately represent a dolphin's full whistle repertoire. Considering this caveat, we used bubble-streams in conjunction with other methods, and we do not assume that we documented the entire repertoire. We view this study as probing the development of the known rather than the full repertoire.

During the first few months, concurrent bubble-streams allowed identification of the calf's sounds. His sounds also were identified in the following circumstances: (1) when he swam alone in a pool; (2) when he was isolated in the medical holding pool for husbandry reasons; and (3) when the adults had their heads out of the water while being fed by trainers, but Tuvaq continued to swim around the pool (the adults were generally silent when being fed, and we were notified by the trainers if any sound had been produced above the water that could have been picked up by our recording system). As he learned to produce sounds without emitting bubbles, we relied more on the other methods of identification and, therefore, analyzed fewer vocalizations in later months.

Aurora was the only adult in the pool during the first 3 mo of her calf's life, thus it was easy to discern her vocalizations by their acoustic quality (from 2 mo of baseline recordings prior to the birth of the calf, during which time the remaining four adults were in the pool) or by her location in the tank relative to the two hydrophones. When the rest of the animals were introduced, the only adult sounds analyzed were produced in voluntary or forced isolation.

### Acoustic Analysis

Spectrograms are displayed here with *Avisoft SASlab Pro* (Avisoft Bioacoustics), using an FFT-size of 512 (for pulse trains) or 1,024 points (for whistles and mixed calls), a frame-size of 100% with a 75% overlap between frames, and a Hamming window. Call parameters were measured automatically with *Raven 1.2* (Cornell Lab of Ornithology). Sounds were classified into four major categories: (1) pulsed calls, (2) whistles, (3) mixed calls, and (4) variable calls.

**Pulsed Calls**—Due to the large number recorded, 20 pulsed calls/mo were randomly subsampled for analysis. To obtain an estimate of relative changes in pulse repetition rate (PRR) with age, PRR was estimated from the number of pulses in the middle 0.2 s of each call, multiplied by 5 to give pulses/s. When PRR was so high that pulses did not resolve into vertical bars on a spectrogram, the parameter was estimated from the sideband interval (Watkins, 1967). The energy content of the pulse trains at different ages also was examined to evaluate whether high-frequency components were more prevalent later in life. This analysis was limited to the frequencies above 2.0 kHz to account for the noise of the filtration system, and below 22.0 kHz due to the frequency response of our recording system. The estimate of dominant frequency was that of peak energy in the power spectrum (*Raven* displays the average power spectrum of a selected portion of a sound, computed over its duration). If this occurred at more than one frequency, the lowest frequency at which peak energy occurred was considered.

**Whistles**—All whistles that were unclear were excluded from the analysis. The estimate of dominant whistle frequency was, as for the pulse trains above, that of peak energy in the average power spectrum of the call, verified in the whistle contour itself, where intensity was the highest. To measure parameters such as duration, and maximum and minimum frequency, only the fundamental carrying the dominant frequency was considered.

**Mixed Calls**—Mixed calls consisted of both a whistle and a pulsed component, overlapping in the same sound. Some parameters of those calls that acoustically resembled Aurora's stereotyped mixed call type (type A1, described later) were measured to help understand Tuvaq's development of these calls over time. The parameters were PRR of the pulsed component, duration, dominant and beginning frequencies of the whistle component, and number of inflection points along the whistle component as a measure of its steadiness. These parameters were also measured in 51 calls of type A1 attributable to Aurora (recorded in different observation sessions from 20 July 2002 to 23 October 2002).

**Variable Calls**—Unstereotyped chirps, trills, and noisy calls (signals having no discernible fundamental frequency and harmonics structure) were assigned to the variable category.

### Vocal Learning

Through the calf's second year, his vocal learning was examined in relation to the introduction of new poolmates with different acoustic repertoires. Eleven recording sessions were conducted of the two adults that were kept in another pool, 7 to 5 mo before their introduction into Tuvaq's social group, to identify any call types that had not been recorded from the calf's acoustic environment. After their introduction when Tuvaq was 18 mo old, Tuvaq's father, Imaq, was recorded during six husbandry isolation sessions in the medical holding pool, lasting from 20 min to 2 h, to confirm any stereotyped vocalizations attributable to him alone (Kavna, the other new adult, was never isolated during this study). Figure 3 illustrates the different compositions of Tuvaq's social group during this study, and the husbandry isolation events during which Tuvaq or his father were recorded.

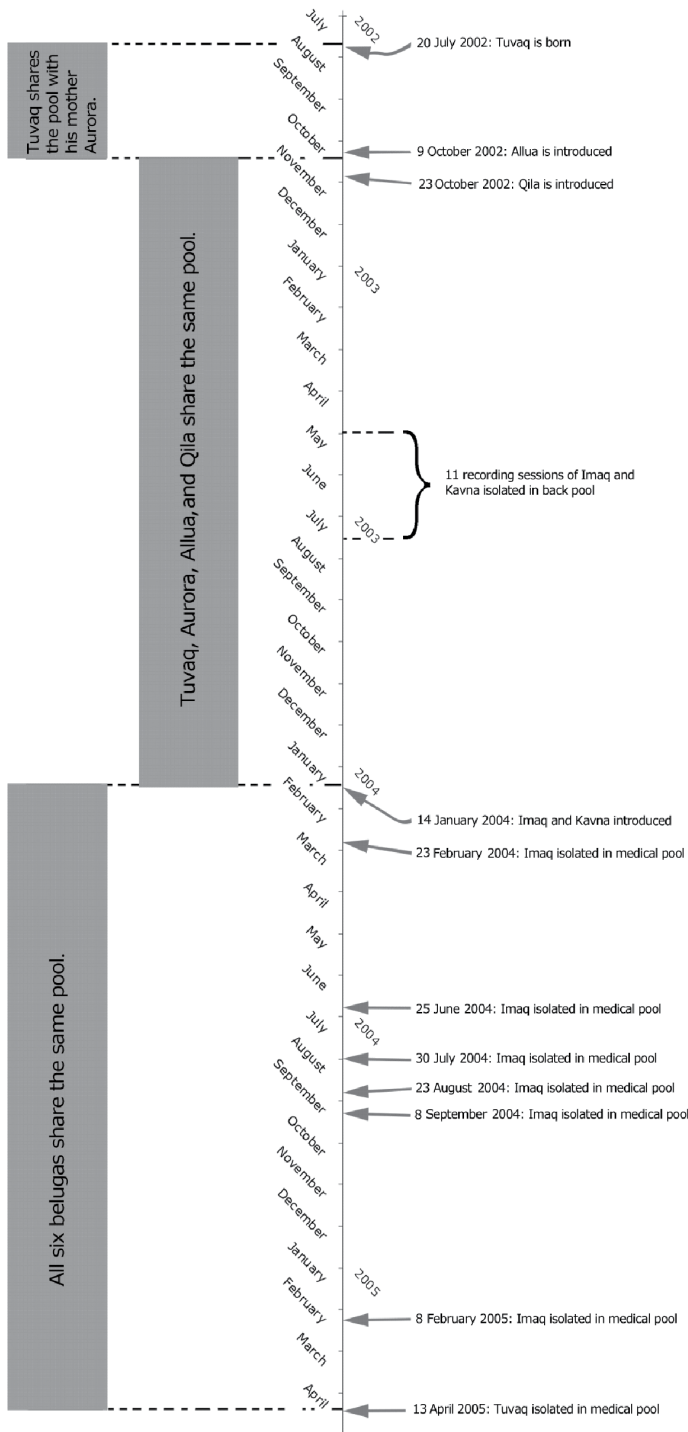
### Statistical Analyses

Statistical analyses were performed with *SPSS*, Version 14.0 (SPSS, Chicago, Illinois, USA). All tests were two-tailed. Measurements were reported as mean  $\pm$  SD, except for the number of inflection points in the whistle component of mixed calls, which were reported as median and quartile distance because the number of inflection points constitutes a discrete variable. The similarity of Aurora and Tuvaq's mixed call type A1 was assessed by discriminant function analysis (DFA) using a randomly selected 70% of the data set and crossvalidating the results with the remaining 30%. The DFA also extracted the parameters that best predicted assigning call type A1 to the appropriate animal.

## Results

### General Vocalization Types

A total of 2,185 sounds were recorded from the calf during his first year of life (1,385 pulsed calls, 359 whistles, 350 mixed calls, and 91 variable calls; Figure 4). He produced mostly pulse trains during his first month; his whistle production increased substantially during his second month; and he began to use mixed calls consistently at four months. Tuvaq's acoustic repertoire broadened as he aged, and nonstereotyped chirps, trills, and noisy calls were recognized and assigned to the "Variable Calls" category. Although rare, mixed calls in which two pulsed components of drastically different pulse repetition rates overlapped



**Figure 3.** Time line of the different compositions of the Vancouver Aquarium calf’s social group throughout the duration of this study, and the husbandry isolation events during which the calf, Tuvaq, or his father, Imaq, were recorded

in the same utterance were characterized. Due to their scarcity in the record (4 during 9 mo of age, and 2 during 12 mo of age), these were not represented in Figure 4.

*Pulsed Call Development*

Tuvaq’s first recorded sounds were 30 min after his birth. These were barely audible, and bubble-streams were not apparent (but the calls were easily distinguishable from Aurora’s loud, continuous, stereotyped calling; see below). They were low-energy pulse trains (Figure 5) with a mean PRR of  $17.5 \pm 4.2$  pulses/s and a variable duration with a mean of  $2.2 \pm 1.7$  s ( $n = 10$ ). The low PRR characterized all the earlier pulse trains. There was a significant increase in mean PRR with age ( $R^2 = 0.30, n = 89, p < 0.0001$ ; Figure 6). The calls progressively acquired the buzz-like aural quality

of the adult pulsed calls. The variability of PRR in the pulsed calls, which translates into variability in their aural qualities, also increased with age as reflected by the larger SD in later months.

During the first few days of his life, there was often no visible energy above 10.0 kHz. The pulse trains increased in bandwidth through the first month until their energy was distributed relatively uniformly across the frequency range of the recording system. An analysis of the energy content of the pulse trains at different ages showed an increase in the mean dominant frequency of the pulsed trains per recording session during the first 12 mo of Tuvaq’s life ( $R^2 = 0.45, n = 89, p < 0.0001$ ; Figure 7). The bandwidth of dominant frequencies also increased with age, from 3.4 kHz (Month 1) to 18.6 kHz (Month 8½). In fact, the variability was consistently higher after 5½ mo

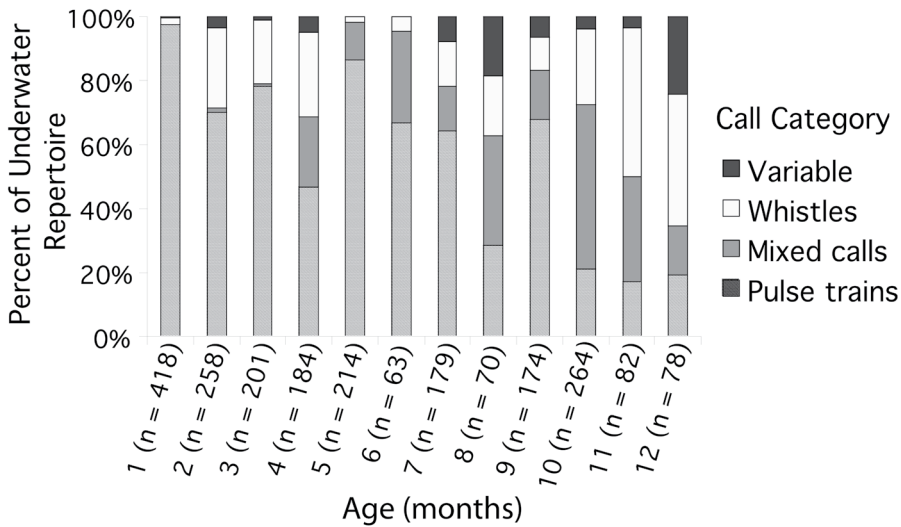


Figure 4. Beluga calf’s monthly usage of major vocalization types ( $n = 2,185$ ) at the Vancouver Aquarium

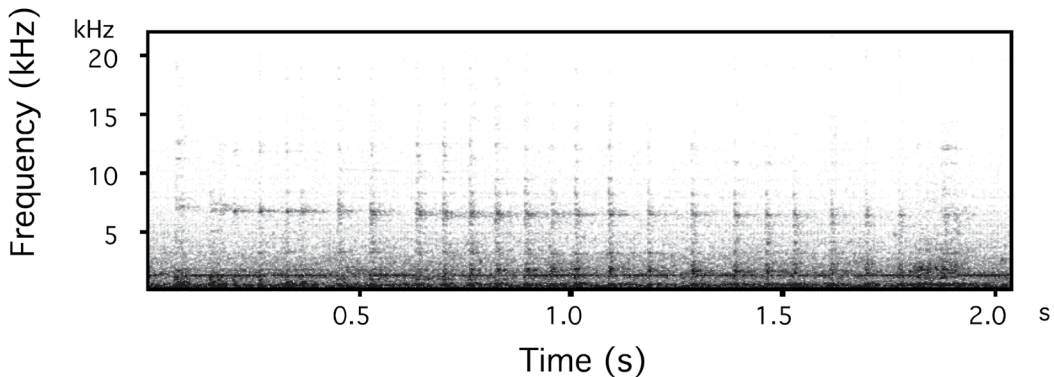
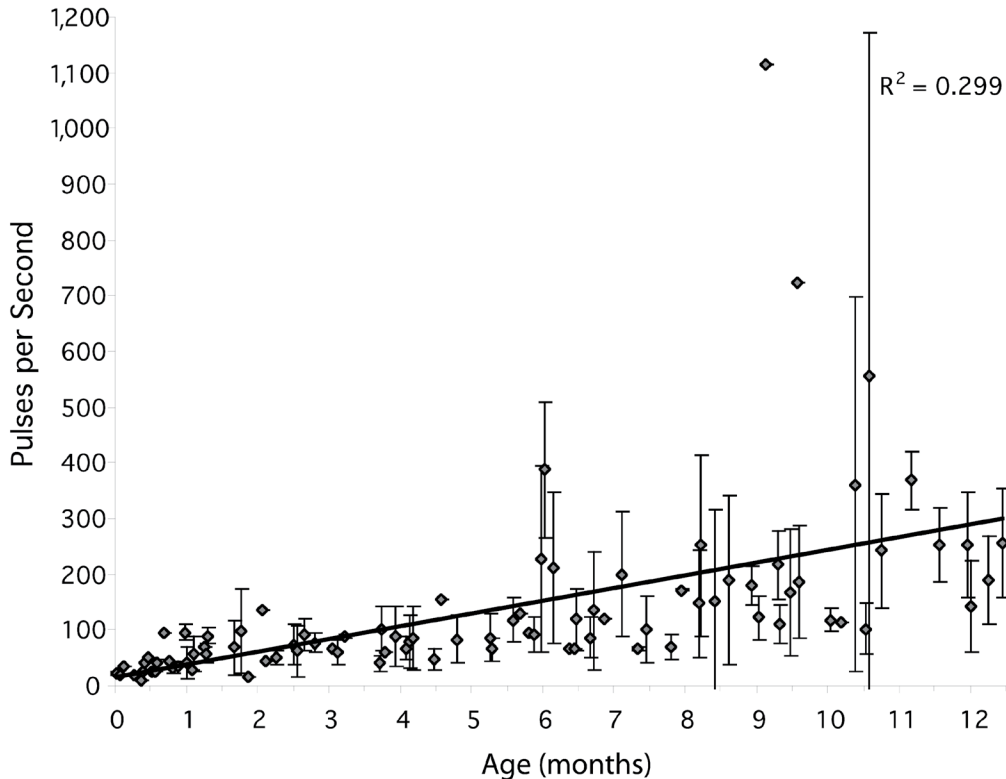


Figure 5. Example of a pulse train (FFT length, 512; window: Hamming; frame size, 100%; bandwidth, 112 Hz) emitted during the first day of life of a beluga calf at the Vancouver Aquarium



**Figure 6.** Mean pulse repetition rate per session ( $\pm$  SD) in the pulsed calls of a beluga calf at the Vancouver Aquarium, plotted as a function of age; data points represent the average of each session (some sessions had only one subsampled pulsed call).

of age. As this analysis was limited to frequencies below 22.0 kHz, real dominant frequencies, at least for older ages (more than 5 mo), may be well above 22.0 kHz.

#### Whistle Development

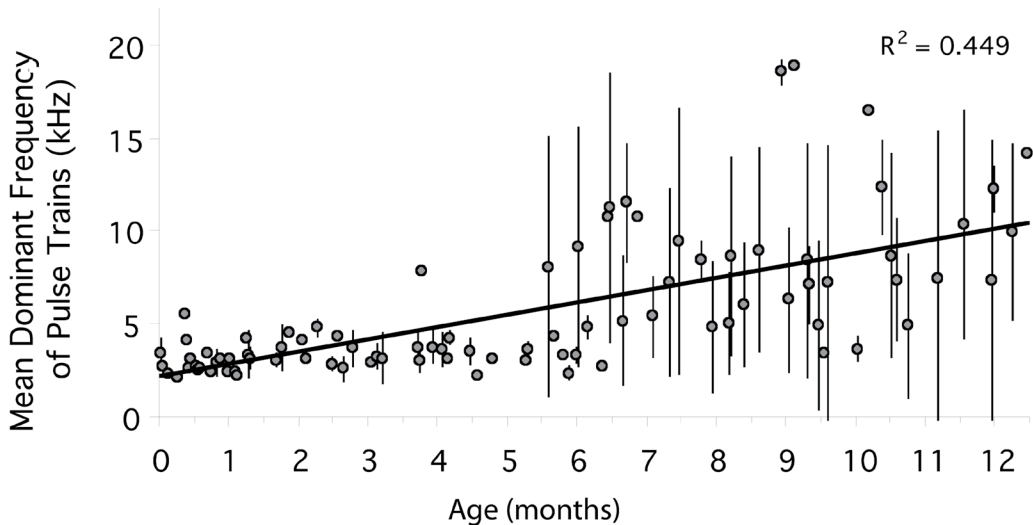
Thirteen days after birth, Tuvaq began producing faint whistle-like elements immediately preceding or following his pulse trains (Figure 8). These whistles were not clearly audible until Day 23. Tuvaq may have produced whistle-like elements before Day 13 which could have gone unnoticed. However, given the intensive recording schedule during Tuvaq's first month, we feel this to be unlikely.

Figure 9 illustrates whistle development with representative spectrograms. Tuvaq's initial whistles had a low mean dominant frequency ( $4.34 \text{ kHz} \pm 1.88$ ,  $n = 9$ ) relative to his whistles in later months and were quivery and lacking a regular frequency modulation. There was a weak positive relationship between the average dominant frequency of the whistles in a recording session and age during the first 12 mo of Tuvaq's life ( $R^2 =$

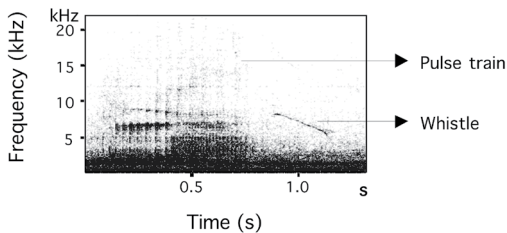
$0.10$ ,  $n = 55$ ,  $p = 0.016$ ) (Figure 10). However, this relationship was much stronger when considering only the first 5½ mo of life ( $R^2 = 0.81$ ,  $n = 28$ ,  $p < 0.0001$ ) (Figure 10) after which there is an unexplained drop in dominant frequency until Month 10. The larger SD in later months indicates that as Tuvaq aged, he continued to produce some low-frequency whistles, but he was also using a larger proportion of higher-frequency whistles.

Through his first year, Tuvaq's whistles remained unstereotyped. The authors' study on the proportional use of sounds in the pool in relation to social context and motivational state (Vergara & Barrett-Lennard, unpub. data) suggested that adult belugas in Tuvaq's social group typically produce a highly stereotyped series of short whistles during agonistic interactions (Figure 9, Adult) and unstereotyped, high-frequency whistles of longer duration during affiliative interactions or non-aggressive states. After his third month of life, Tuvaq's whistles were often produced in series (Figure 9), but not until 10 mo did the first series of whistles begin to resemble the stereotyped adult series (however, it was not produced,





**Figure 7.** Mean dominant frequency per session ( $\pm$  SD) of pulse trains emitted by a beluga calf at the Vancouver Aquarium, plotted against his age; data points represent the average of each session. For sessions with more than one subsampled call, the wide SD bars at Months 5½ to 12 reflect an increase, with age, of the bandwidth of dominant frequencies.



**Figure 8.** First recorded whistle at the end of a pulse train (FFT length, 512; window: Hamming; frame size, 100%; bandwidth, 112 Hz), produced on Day 13 of a beluga calf's life at the Vancouver Aquarium

as are the adult series, during aggression). After Month 10, it was not possible to record a fully stereotyped whistle series attributable with certainty to him, thus it remains unclear when he achieved full stereotypy in whistle production.

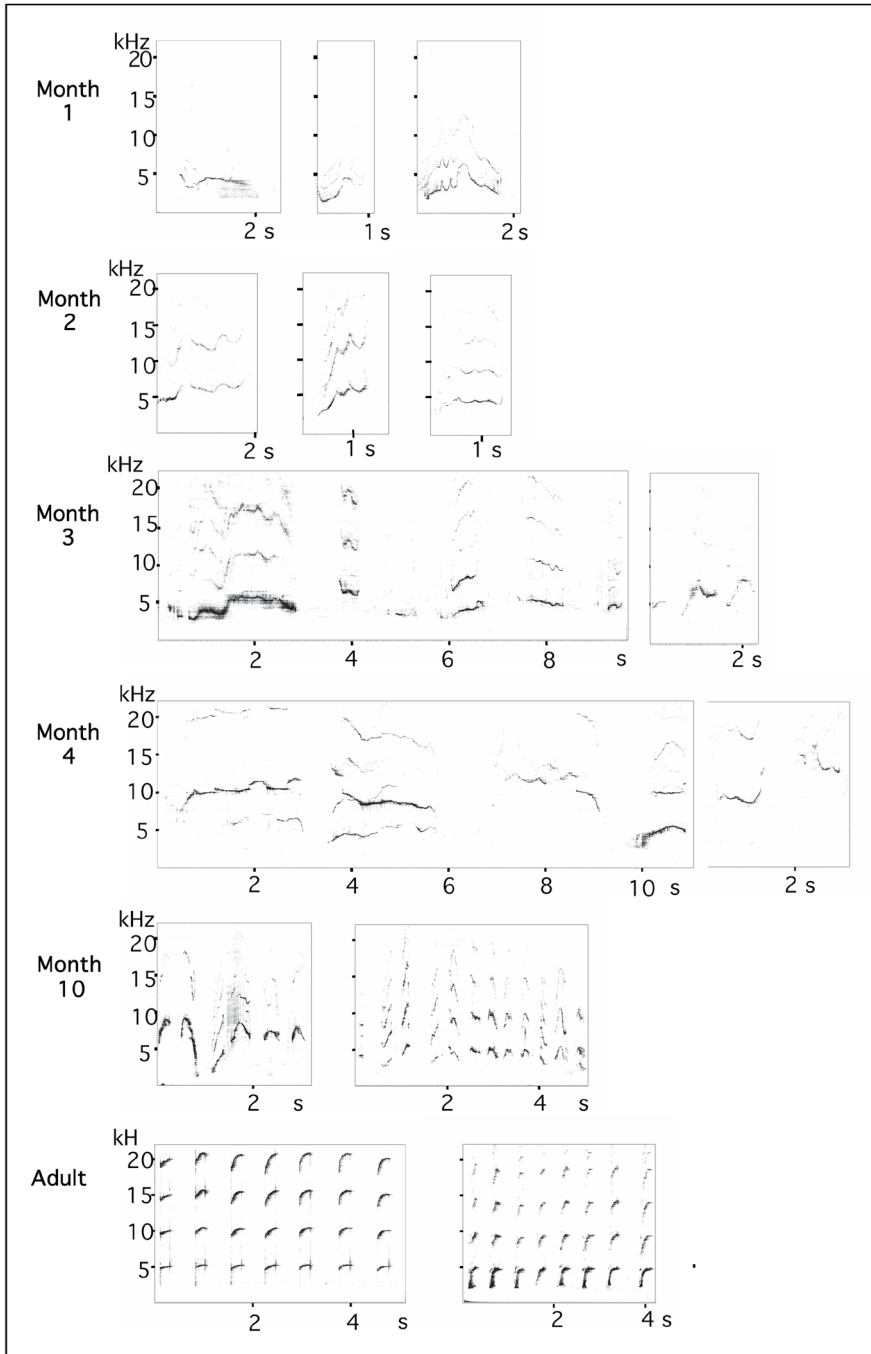
#### Mixed Calls

Tuvaq began incorporating a whistle overlapping a few of his pulse trains on his 20th day of life. However, mixed call production during his first 3 mo of life was minimal. At 4 mo, Tuvaq's mixed call production increased dramatically. Some of his mixed calls underwent a progressive resemblance to the predominant stereotyped mixed call of his mother, the "type A1" call, or whine, described below.

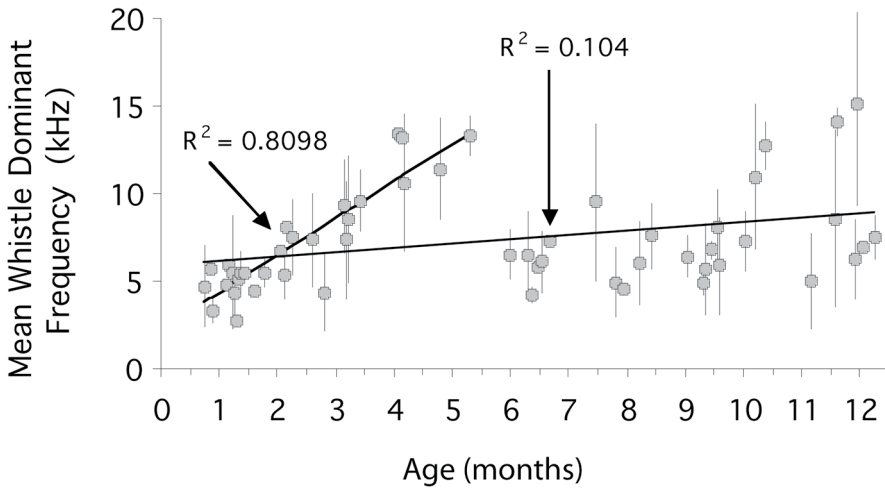
*Aurora's Stereotyped Call Type A1*—Tuvaq was frequently exposed to the mixed call type A1 of his mother, which she began to produce the day after Tuvaq's birth and later in every situation where

there was an apparent need to regain or maintain contact with him (e.g., forced or voluntary separation, divers in the tank), and in response to his calls (details in Vergara & Barrett-Lennard, unpub. data). Call type A1 aurally resembles a buzz, and it is characterized by a pulse train component with energy distributed more or less equally along the frequency range of the recording system and by an overlapping tonal component (Figure 11). There is little variability in the dominant frequency of the tonal component, with a mean of  $14.4 \pm 0.2$  kHz (CV: 1%;  $n = 51$ ). The whistle also shows little frequency modulation, with a simple contour that starts at a mean frequency of  $8.8 \pm 2.2$  kHz, followed by one shift to the dominant frequency of 14.4 kHz (in some renditions of the call, the whistle started directly at around 14.4 kHz). The number of inflection points (range: 0 to 2; median: 1) illustrates the steady quality of the whistle. Aurora tended to produce this call type A1 in bouts, sometimes in combination with acoustically similar call types lacking the whistle component: A2 and A3 (Figure 12).

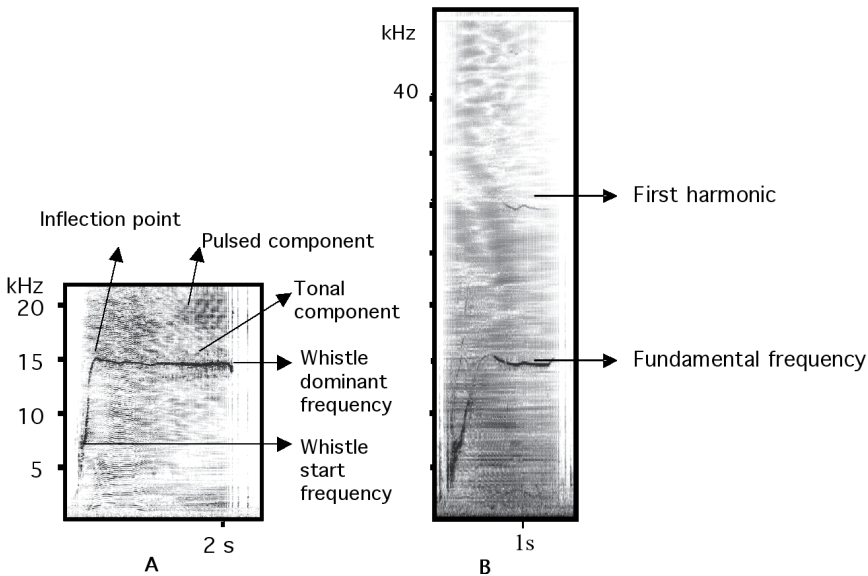
The calls A1, A2, and A3, collectively called "type A" calls or "whines" due to their acoustic quality, comprised 97% of Aurora's underwater sounds during the 3 mo between Tuvaq's birth and the reintroduction of the rest of the whales (i.e., when Tuvaq and his mother were alone in the pool). During the first 2 h immediately after the calf's birth, Aurora repeated the A3 pulsed call 588 times while echelon swimming with her calf. The next day she began to incorporate the other two variations, A1 and A2; and from the 3rd day after the birth until the reintroduction of the rest



**Figure 9.** Representative examples of whistle development in a beluga calf at the Vancouver Aquarium (FFT length, 1,024; window: Hamming; frame size, 100%, bandwidth, 56 Hz); two typical adult whistle series are shown for comparison. During the first two months of life, the whistles were low in frequency, of variable duration, and rarely produced in series. By Month 3, many of Tuvaq's whistles were produced in unstereotyped series. From Month 4 on, the series consisted of long ( $1.97 + 1.3$  s,  $n = 29$ ) variable whistles, a pattern that continued until Month 10 when we recorded the first whistle series that resembled the adults' stereotyped series.



**Figure 10.** Mean whistle dominant frequency per session ( $\pm$  SD) plotted against age of a beluga calf at the Vancouver Aquarium; data points represent the average of each recording session. Note the two trend lines: from birth to 12 months, the  $R^2$  is weak, but from birth to five months, the relationship between whistle frequency and age is much stronger.



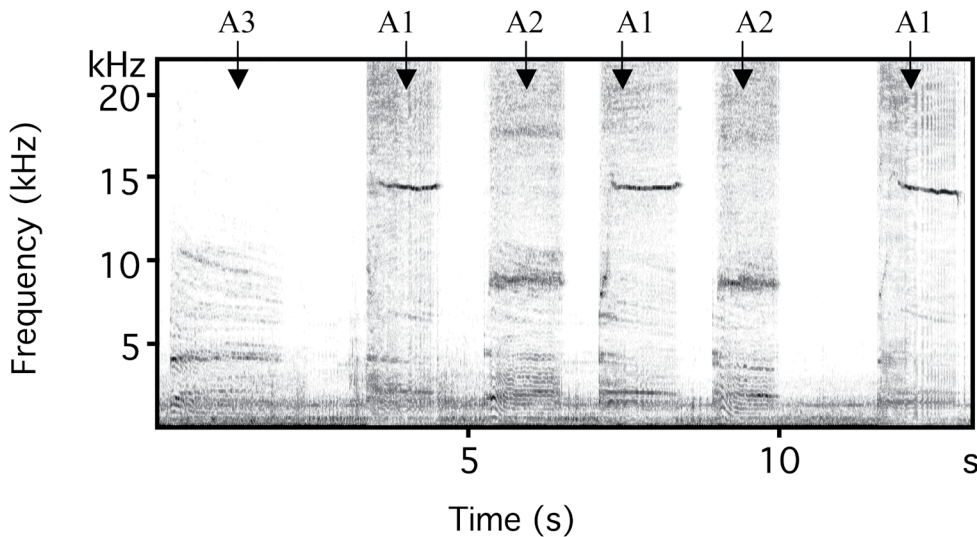
**Figure 11.** Examples of the stereotyped mixed call type A1 of the mother beluga, Aurora, at the Vancouver Aquarium recorded at 44.0 kHz (A) and at 96.0 kHz (B); the dark areas that span the entire frequency range of the spectrograms represent the pulsed component. The tonal component is clearly delineated at about 15.0 kHz overlapping the pulsed component. Note in B that there is little energy in the first harmonic of the fundamental frequency of the whistle.

of the social group, the mixed call type A1 comprised 66.7% of her sounds.

The call type A1 was not recorded during the 18 sessions (1 to 2 h in length) performed during the 2 mo preceding the birth when all five adults were in the pool, nor was it heard during the daily continuous monitoring of Aurora throughout the 5 d immediately before the birth when she was

in isolation (she was completely silent). This call type was also occasionally recorded from Tuvaq's half-sibling, Qila (dominant frequency of the tonal component:  $14.3 \pm 0.5$  kHz; 0 to 3 inflection points with a median of 1; whistle start frequency:  $8.2 \pm 3.3$  kHz,  $n = 18$ ).

*Development of Call Type A1*—The apparent function of the call type A1 as a contact call,



**Figure 12.** Example of a bout of the three classes of type A calls, or “whines,” produced by Aurora, the calf’s mother, at the Vancouver Aquarium; note the whistle component of the three type A1 mixed calls in this bout at nearly 15.0 kHz.

meaning that it was often used in isolation, made it methodologically easier to document its development since it was possible to record its production from Tuvaq well past the time when he stopped producing bubbles when vocalizing.

Figure 13 illustrates the development of Tuvaq’s renditions of call type A1. The reduction in variability with age was clearest for the inflection points in the whistle component and for its dominant frequency (Figure 14). The median of the number of inflection points per session decreased from Month 4 to Month 12 ( $R^2 = 0.34$ ,  $n = 33$ ,  $p = 0.0002$ ) until the whistle component attained the relatively constant frequency of his mother’s. The coefficient of variation in the dominant frequency of the whistle component also decreased with age ( $R^2 = 0.81$ ,  $n = 9$ ,  $p < 0.0001$ ), indicating progressive stereotypy. When Tuvaq was 20 mo old, a series of 12 calls of type A1 produced during a brief voluntary isolation in the medical holding pool was opportunistically recorded. These were stereotyped, with the contour of the whistle component clearly resembling that of his mother’s (see Figure 13) and little variability in its dominant frequency (1.2% CV), which matched his mother’s calls at  $14.35 \pm 0.2$  kHz.

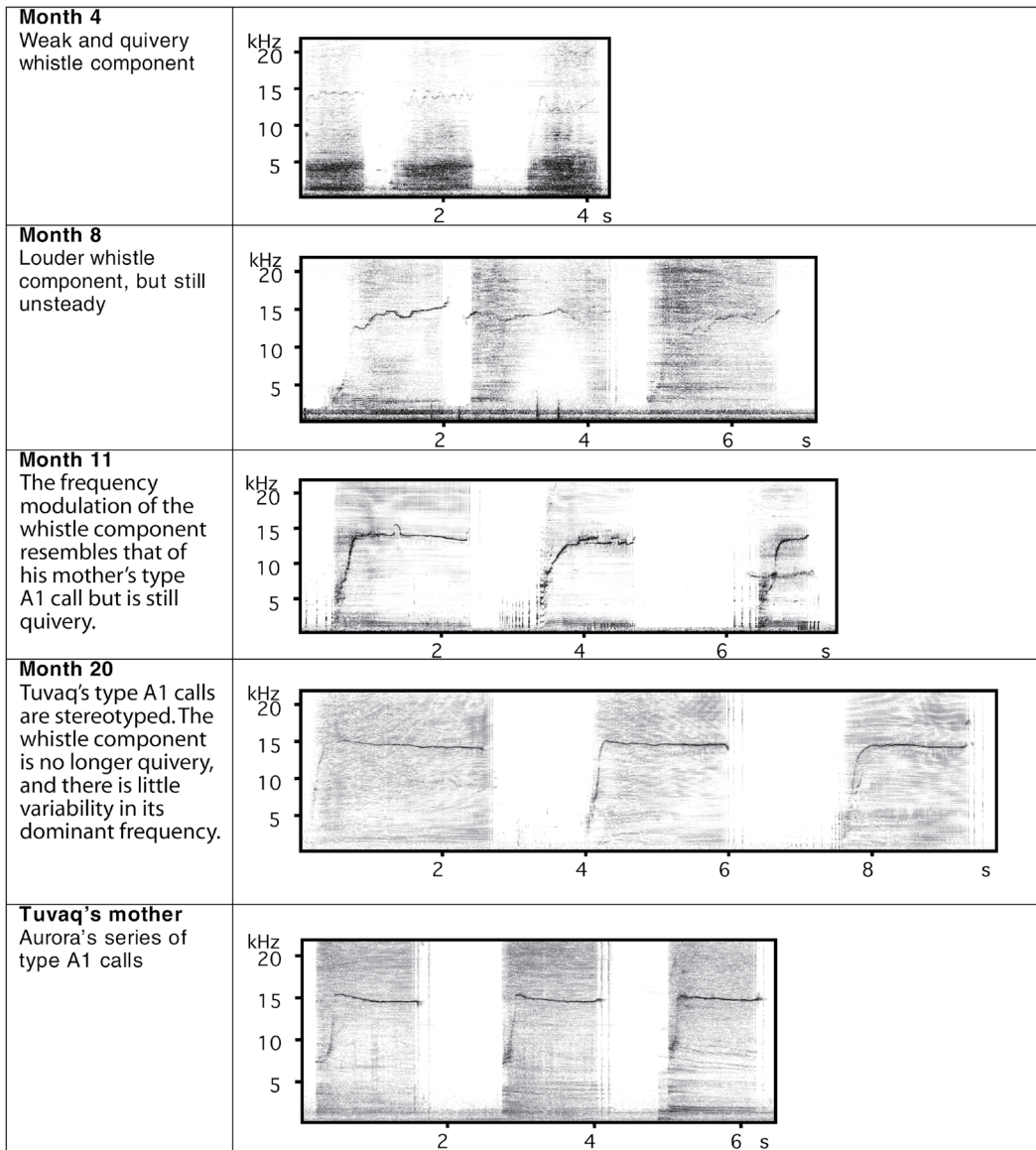
At 32 mo of age, Tuvaq was kept in isolation for veterinary procedures for a period of 2 h. He produced a series of 46 type A1 calls. The parameters of these fully developed calls are strikingly similar to those of his mother’s type A1 calls (Table 1). A discriminant function analysis was performed on Aurora’s 51 calls and Tuvaq’s 46 calls. The DFA was based on the following most obvious parameters that appropriately describe

the acoustic structure of this signal: PRR of the pulsed component of the mixed call, duration of the call, dominant frequency of the whistle component, and start frequency of the whistle component. A model with subset validation classified 83.3% of the calls correctly. The only variables with discriminant ability were the start frequency of the whistle (consistently lower for Tuvaq) and the call duration (consistently longer for Tuvaq). Removing these two variables, reclassification accuracy was much poorer (47.1%). This confirms that Tuvaq and Aurora’s calls are most similar in dominant frequency and PRR.

#### *Acquisition of a Novel Call*

The recordings of the two belugas kept in a separate pool during Tuvaq’s first 18 mo of life indicated that there were two distinct, stereotyped mixed vocalizations that had never been recorded from Tuvaq’s initial social group, labeled types B1 and B2 (Figure 15). After the reintroduction of Imaq and Kavna to the rest of the group, it was confirmed that these two call types were produced by Imaq, Tuvaq’s father. Twenty-one type B1 calls and 12 type B2 calls were recorded during three isolation events. Both mixed call types had an acoustically similar tonal component, which was a very audible trill, and an acoustically different pulsed component (that sounded like a trumpet in type B1, and like a clear train of pulses in type B2) (Figure 15).

Six months after the calf began to be exposed to Imaq’s calls, new sounds were recorded from him that were characterized by the most noticeable element of Imaq’s mixed call types: a trill



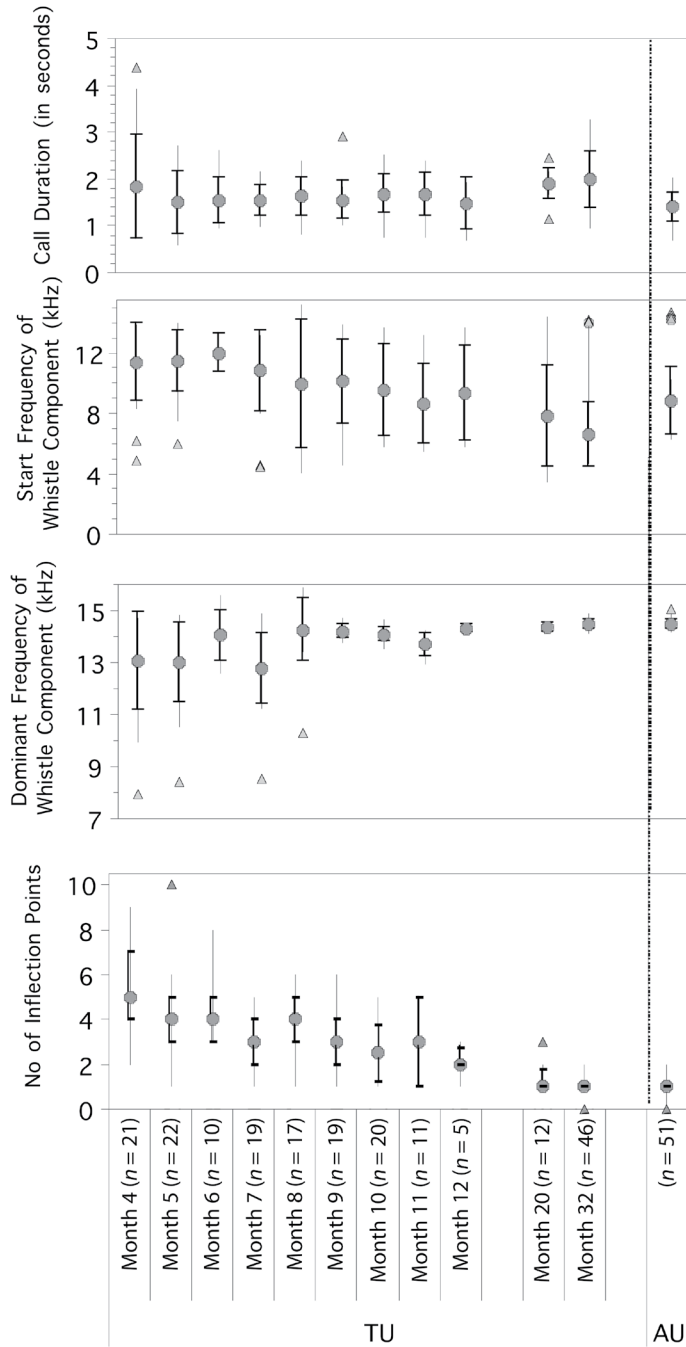
**Figure 13.** Natural sequences of three calls from a beluga calf at the Vancouver Aquarium, each a representative example of the development of the stereotyped mixed call type A1 (FFT length, 1,024; window: Hamming; frame size, 100%; bandwidth, 56 Hz). Note the similarity of the whistle contour between the calf, Tuvaq, at 20 months and his mother, Aurora.

component. Eighty-two of these calls, which were recorded during seven isolation events, acoustically and spectrographically resembled Imaq's type B2 calls (Figure 16). A random sample of 12 of these calls (to match the sample of Imaq's 12 calls) revealed that the dominant frequency of the trill component of these calls was the same as Imaq's ( $9.6 \text{ kHz} \pm 0.2$ ) with very little variability (Table 2). However, the trill was more tremulous than his father's, and the length of each

trill segment more irregular (CV 52.8%; Table 2). The remaining parameters also showed more variability (higher CVs) than Imaq's calls.

### Discussion

Four major questions guide the discussion of these results: (1) What is the significance of the changes that occur over the course of repertoire development? (2) Is early vocal production in belugas



**Figure 14.** Parameters of the mixed call type A1 for a beluga calf, Tuvaq (TU), at the ages when this call type was recorded, and for Aurora (AU), his mother, for comparison; for the dominant frequency, start frequency, and duration, the circles represent the means, the thick error bars represent SDs, and the thin bars represent the range, excluding the outliers which are shown as triangles outside the bars. For inflection points, which form a discrete distribution, the circles are the medians, the thick error bars represent the interquartile range, and the thin bars are the range.

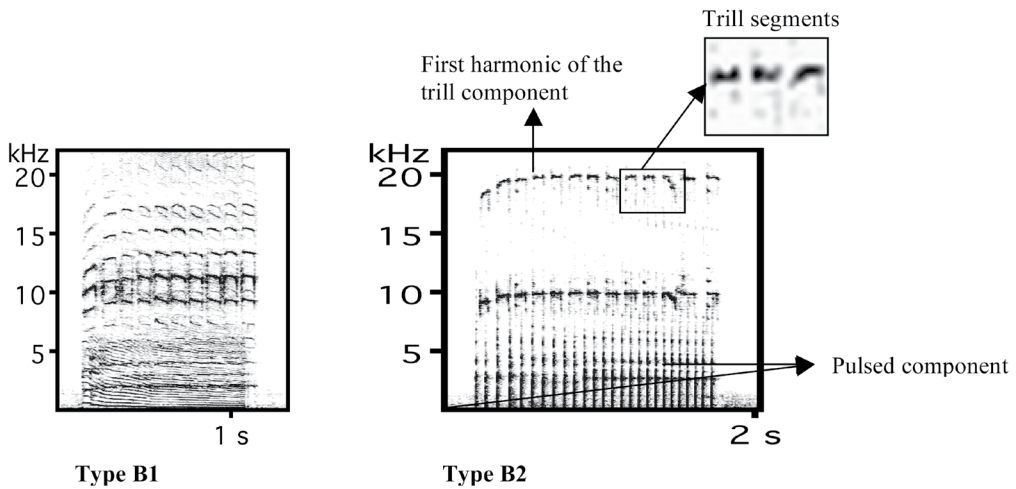


**Table 1.** Acoustic parameters of the beluga calf, Tuvaq’s, fully developed type A1 call at 32 months of age and of his mother, Aurora’s, type A1 call

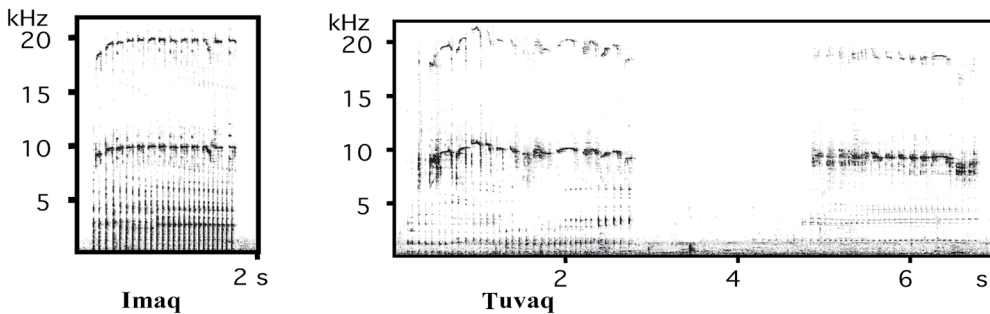
Parameters	Tuvaq <sup>a</sup>		Aurora <sup>b</sup>	
	Mean ± SD	CV	Mean ± SD	CV
Whistle dominant frequency (kHz)	14.5 ± 0.2	1.2%	14.4 ± 0.2	1.3%
Whistle start frequency (kHz)	6.6 ± 2.1	32.2%	8.8 ± 2.2	24.9%
Call duration (s)	1.9 ± 0.6	30.0%	1.4 ± 0.3	22.1%
PRR of pulsed component (pulses/s)	94.6 ± 14.1	14.9%	94.4 ± 12.7	13.8%
Number of inflection points in the whistle component	Median: 1 (Range: 1-2)		Median: 1 (Range: 0-2)	

<sup>a</sup>n = 46

<sup>b</sup>n = 51



**Figure 15.** Two beluga call types from Imaq, Tuvaq’s father, at the Vancouver Aquarium (FFT length, 1,024; window: Hamming; frame size, 100%; bandwidth, 56 Hz); types B1 and B2 were occasionally produced in series of two or three, with irregular inter-call intervals.



**Figure 16.** The father beluga, Imaq’s, type B2 call, and a randomly selected example of the calf, Tuvaq’s, two consecutive renditions of the same call six months after Imaq’s reintroduction (FFT length, 1,024; window: Hamming; bandwidth, 56 Hz)

**Table 2.** Acoustic parameters of call type B2 produced by a beluga calf, Tuvaq, and by his father, Imaq, at the Vancouver Aquarium

Parameters	Tuvaq <sup>a</sup>		Imaq <sup>b</sup>	
	Mean ± SD	CV	Mean ± SD	CV
Trill dominant frequency (kHz)	9.60 ± 0.20	2.1%	9.60 ± 0.40	4.2%
Trill segment length (s)	0.12 ± 0.06	52.8%	0.08 ± 0.01	12.5%
PRR of pulsed component (pulses/s)	31.40 ± 20.90	66.9%	58.30 ± 19.80	33.9%
Call duration (s)	1.60 ± 0.70	42.0%	0.77 ± 0.29	37.9%

<sup>a</sup>*n* = 12<sup>b</sup>*n* = 12

analogous to babbling in humans and other primates or subsong in birds? (3) What is the role of physical maturation of the vocal apparatus in the structural development of the calls? and (4) How might learning mediate vocal development?

#### *Early Vocalizations and Repertoire Development*

Tuvaq produced only pulse trains before he acquired rudimentary whistles at 2 wks of age. Similarly, sound production of a neonate captive beluga whale born in 2006 at L'Océanogràfic, Spain, consisted exclusively of low-frequency, short duration broadband pulse trains (Castellote et al., 2007). Despite differences in populations of origin (Canada vs Russia), in captive facilities, in health (the L'Océanogràfic calf was never vigorous and died at 1 mo of age), and in acoustic context, the sound production observed in these two neonate whales suggests a species-specific pattern of developmental stages in sound acquisition.

Burst pulse sounds were also the first vocalizations by a captive bottlenose dolphin (Killebrew et al., 2001). Bottlenose dolphins are capable of emitting whistles at birth (Caldwell & Caldwell, 1979), but some individuals may not produce them until a few days after birth (Killebrew et al., 2001). Caldwell & Caldwell (1979) and Reiss (1988) described infant bottlenose dolphin whistles as tremulous and lacking a regular frequency modulation. These descriptors also apply to Tuvaq, who did not whistle during his first 2 wks. Also like bottlenose dolphins (Killebrew et al., 2001), Tuvaq placed his first whistle-like elements at the beginning or end of pulse trains.

Little is known of the development of species-specific stereotyped calls in most cetaceans. Neonate bottlenose dolphins (Caldwell & Caldwell, 1979), sperm whales (Madsen et al., 2003), and killer whales (Bowles et al., 1988) produce unstereotyped sounds that are very different from the stereotyped calls of juveniles and adults. Production of stereotyped signature whistles by bottlenose dolphins can occur as early as 1 to 2 mo after birth, or as late as 17 mo (reviewed in Tyack,

1997). This study suggests that beluga calves also progress towards more stereotyped calling.

Bowles et al. (1988) reported that the first adult-like calls of a captive killer whale female calf resembled the most common call type produced by her mother. Similarly, in this study, the earliest call that structurally resembled an adult stereotyped call type was one of Tuvaq's mother's most frequent call types. In the resident population of dolphins in Sarasota, Florida, female bottlenose dolphin calves tend to develop stereotyped signature whistles different from those of their mothers, while males' whistles tend to be like their mothers', perhaps reflecting the different social roles of males and females in dolphin communities (Sayigh et al., 1990, 1995). Unlike bottlenose dolphins, Tuvaq's female sibling, Qila, also produced calls identical to her mother's.

By 32 mo, the type A1 calls of Tuvaq were practically identical to those of his mother in the dominant frequency of the whistle component and in the PRR of the pulsed component. Only the start frequency of their whistles and the duration of their calls discriminated them successfully. Thus, the most important identity information in the type A1 call appears to be in the frequency of the whistle component and in the duration of the call. However, a number of more subtle differences were also apparent such as the rounder inflection point of Tuvaq's whistle component of this mixed call type. It is also possible that identity information can be found in the PRR pattern and pulse power spectrum of the call, which are not quantified in this study.

Call type A1 may play an important functional role in mother-offspring recognition, highlighting the value of its early acquisition. Tyack (2003) pointed out that the combination of early mobility and extended dependence in bottlenose dolphin calves generates a strong need for early development of a mother-offspring recognition system. Signature whistles are believed to be important in maintaining contact between bottlenose dolphin mothers and calves (Tyack, 1997). Perhaps



call type A1 functions similarly in the belugas in this study. Mother-calf bonds are probably as strong and long lasting in belugas as in bottlenose dolphins. Lactation may last 24 mo in the wild (Brodie, 1971; Drinnan & Sadleir, 1981) and longer in captivity. At the Vancouver Aquarium, Qila, half-sibling of Tuvaq, nursed until she was 6 y old (B. Sheehan, Vancouver Aquarium, pers. comm.). Tuvaq nursed until he was 3 y old, not only from his mother but also from Qila and from an unrelated female, Allua, both of whom began lactating despite not having calves of their own.

Van Parijs et al. (2003) recorded sounds produced by belugas during capture events in Storfjorden, Svalbard. Only the youngest sub-adult, a solitary calf, and a mother-calf pair produced sounds. The calf from the pair occasionally produced frequency-modulated sounds within click trains (i.e., mixed calls) that look remarkably similar in their spectrogram to the type A calls reported here. Van Parijs et al. speculate that the fact that only young animals produced sounds during capture suggests that these may be contact calls between mothers and dependent young.

The following observations hint at the mother-calf recognition role of call type A1: (1) it was one of three acoustically similar call types that Aurora produced repeatedly during the first 24 h after Tuvaq's birth, suggesting the possibility of strong acoustic imprinting by the calf; (2) it was used predominantly when the two were separated, during tight synchronous swimming when disturbances occurred in the tank, and in response to each other's calls; and (3) Tuvaq's longest, fully stereotyped series of this call type was produced in involuntary isolation. The authors are currently investigating the context-specific variation in the vocalizations of the six captive belugas at the Vancouver Aquarium and examining in further detail the contextual uses of call type A1 (Vergara & Barrett-Lennard, unpub. data).

#### *Vocal Babbling*

Strong evidence of babbling exists for taxa as diverse as bats (e.g., Knörnschild et al., 2006), primates (e.g., Elowson et al., 1998), and birds (e.g., bird subsong; Marler & Peters, 1982), all highly vocal species, suggesting that babbling behavior may have evolved in species in which juveniles must acquire complex vocal repertoires (Knörnschild et al., 2006). Given the importance of babbling in other vocal systems, it is reasonable to consider whether the first stage of vocal development in belugas might be analogous to babbling by humans and some other primates or to the subsong of birds. As some of Tuvaq's calls were becoming stereotyped, he was also widening his repertoire by including a larger variety of sounds. Trills, chirp series, noisy

calls, and other sounds became more prominent as he aged, hinting at a similarity between beluga vocal development and that of bottlenose dolphins. While the variability of some dolphin whistles is reduced as the young develop a stereotyped signature whistle, there is also an increase of highly variable sounds with age (Tyack, 1997, 2003).

Tyack (2003) noted that this pattern is dissimilar to the babbling and subsong stages of other taxa, which consist of a progressive narrowing of an initially overproduced repertoire. McCowan & Reiss (1995), on the other hand, postulated that whistle development in bottlenose dolphins could be reasonably compared to the ontogeny of human and bird vocalizations since out of an unstereotyped repertoire emerges a subset of vocalizations. Similarly, in this study, if babbling in belugas is akin to human babbling, which consists of a subset of the phonetic units of adult speech (Oller & Eilers, 1988), then it is possible that Tuvaq's initial unstereotyped pulse calls were a form of babbling. As is the case for other vocal species (e.g., marmosets; Snowdon & Elowson, 2001), babbling may be functionally important in belugas in order to practice for adult vocal behavior and to maintain acoustic contact with or attract the attention of other group members. During the first month of life, Tuvaq's unstereotyped pulse trains often elicited an approach and a vocal response from his mother (Vergara & Barrett-Lennard, unpub. data).

Despite Tuvaq's variable repertoire at 12 mo, we are unsure about the possibility of attrition later on because we do not have systematic month-to-month data after the 1-y mark. Moreover, like bottlenose dolphins, belugas are long-lived, slow-maturing animals, and, accordingly, the vocal development stages in this species may be lengthier than documented here. These data suggest that in belugas, as in bottlenose dolphins (McCowan & Reiss, 1995), acoustic development likely continues well past their first year of life.

#### *Maturation Processes*

Determining the role of maturation of the vocal apparatus in vocal development is challenging. This is exacerbated by the fact that the precise mechanism of sound generation in odontocetes remains unclear, although much progress has been made in understanding it. Cranford et al. (1996) proposed a unified phonation mechanism for odontocetes. They described two structural complexes, each formed by a fatty bursa embedded in a pair of lips, which are associated with the upper nasal passages in all odontocetes (except sperm whales, which have only one). The most parsimonious working hypothesis is that sound is produced when air passes through the lips (termed "monkey lips"), causing them to open and slap together, creating vibrations in the monkey

lip/dorsal bursa (MLDB) complex. This periodic opening and closing of the lips determines the PRR, and may be regulated by muscle tension. It is likely that only the left lips generate whistles (Cranford et al., 1996; Cranford 2000a, 2000b)

Cranford et al. (1996) suggested that simultaneous use of the two MLDB complexes may be necessary to achieve the overlapping but distinct sounds common to several odontocete species. Mixed vocalizations with overlapping tonal and pulsed components, such as those reported here, have been described in killer whales (Schevill & Watkins, 1966), false killer whales (Murray et al., 1998), bottlenose dolphins (Killebrew et al., 2001), and spotted dolphins (*Stenella frontalis*) (Herzing, 2000).

A different type of mixed vocalization was occasionally recorded, consisting of two overlapping pulsed components of different PRRs. Karlsen et al. (2002) reported similar double-pulsed vocalizations in free-ranging belugas off Svalbard, Norway. This is consistent with strong evidence that bottlenose dolphins can generate acoustic pulses by both sets of phonic lips, independently and simultaneously (Cranford, 2000b).

In view of the current knowledge of sound generation in odontocetes, the observed patterns can be interpreted as follows: (1) the marked increase in mixed vocalizations at 4 mo suggests better control of the simultaneous use of the two hypothesized MLDB complexes at this age; (2) the increase in PRR with age may result from coordination of the muscles that control the monkey lips; (3) whistle production is thought to require greater nasal air pressure than does pulse generation (Cranford, 2000b)—the delay documented here in developing whistles supports the notion that whistle production may entail finer muscular control and greater muscle strength than the production of pulsed trains; and (4) finer muscle control may also be required to produce high-frequency pulse trains and whistles as suggested by the increase in dominant frequency of these vocalization types with age. For the whistle production, this relationship was quite strong for only the first 5 mo of Tuvaq's life.

Increased vocal control with age probably has a learned component, although it is likely that the sound-producing apparatus of beluga calves also matures physically in the first year. To support the idea that physical maturation of the vocal apparatus explains developmental changes in the calf's vocalizations would require demonstrating that more than one infant shows similar changes at similar times in their development. Strong inter-individual variability would support the existence of other mediating mechanisms. Such an approach revealed that changes in the "coo" vocalization of rhesus macaques (*Macaca mulatta*) during early

development are attributable mainly to physical maturation factors (Hammerschmidt et al., 2000).

#### Vocal Learning

It is well established that many songbirds learn at least some of their species-specific songs (Marler & Mundinger, 1971; Slater, 1989; Baptista, 1996). For nonhuman terrestrial mammals, on the other hand, robust evidence of production learning is limited to a handful of studies (Janik & Slater, 1997). In contrast, production learning has evolved independently in several lineages of marine mammals, providing an important comparative perspective (Tyack & Clark, 2000). There is growing evidence that humpback whales (*Megaptera novaeangliae*) (Payne & Payne, 1983), bottlenose dolphins (Caldwell & Caldwell, 1972; Reiss & McCowan, 1993; McCowan & Reiss, 1995; Sayigh et al., 1995), killer whales (Ford, 1991; Deecke et al., 2000), and several species of pinnipeds learn specific vocalizations (McCowan & Reiss, 1995).

Differentiating between learning and other processes in the development of acoustic repertoires can be challenging. There is growing consensus that most behavioral traits have a genetic component but are shaped to a smaller or larger degree by learning and experience. When infants develop vocalizations like those of their parents, it is difficult to separate the role of learning and genetic inheritance. The lack of his father's calls in Tuvaq's vocal repertoire before their first acoustic contact, and his incorporation of at least one of his father's calls after contact, strongly suggests production learning. Unfortunately, the close genetic relationship between the two animals introduces some doubt in this assertion, but these data certainly indicate that the calf had to learn to use the vocalization.

Tuvaq's type A1 call did not emerge suddenly but was slowly perfected towards full stereotypy. This gradual process suggests that production learning played a role. However, if the vocal apparatus matures slowly over time, then Tuvaq may not have been able to produce a perfect copy of this call until he reached a certain age. The slow maturation would explain equally well the gradual changes in call structure as discussed earlier. Thus, although Tuvaq's reproducing his mother's call is not compelling enough evidence that its production was entirely learned, it strongly suggests that at least its use has been learned because the call does not exist in Tuvaq's father's repertoire.

That learning plays some role in acoustic ontogeny in belugas would make sense in view of their life history and social parameters. In cetaceans, social learning coupled with a tendency for vocal plasticity is evident in species with certain characteristics: strong mother-infant bonds, extended

maturation period of the young, consistent social groupings where repeated interactions with the same individuals occur, long life spans, and multigenerational family groups (Brodie, 1969; Smolker et al., 1993; McCowan & Reiss, 1997; Boran & Heimlich, 1999; Mann & Smuts, 1999). The prevailing speculation is that vocal learning may facilitate individual or group recognition in aquatic environments (Janik & Slater, 1997), which is fundamental for the maintenance of the individual-specific social relationships common in social odontocetes (Tyack & Clark, 2000).

Furthermore, these animals seem capable of incorporating new sounds into their vocal repertoires as adults as indicated by anecdotal evidence of vocal imitation in belugas. According to Eaton (1979), a 15-y-old beluga at the Vancouver Aquarium produced utterances that resembled human speech. Another 9-y-old male beluga, held at San Diego Bay, imitated the sound of human conversations and did so with his head out of the water (Ridgway et al., 1985). This behavior occurred frequently enough that the trainers were able to solicit it with a fish reward so that his phonations could more easily be recorded and analyzed. The significance of anecdotes of marine mammals imitating human words rests on the fact that *they signal what may exist in the wild*. Tyack (1993) stated it quite clearly: "If an animal can imitate a sound that is not normally part of its repertoire, then it must have learned to modify its normal vocalizations to match the model. Animals that have evolved this rare capability may use it in developing their natural vocalizations" (p. 130).

In summary, it is unlikely that one mechanism alone completely explains developmental changes in repertoire variability and call characteristics. More likely, a combination of mechanisms mediates the ontogeny of calls, including maturational processes, social influences, and inheritance. As beluga births are becoming more common in captive facilities, studies of vocal development comparing more than one subject could validate the patterns observed here. Furthermore, careful descriptions of the ontogeny of usage and responses to sounds in relation to the social context will be required (e.g., Snowdon et al., 1997, for New World primates) before we can claim to understand the stages of vocal development in belugas and other cetacean species.

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#### Literature Cited

- Au, W. W. L., Carder, D. A., Penner, R. H., & Scronce, B. L. (1985). Demonstration of adaptation in beluga whale echolocation signals. *Journal of the Acoustical Society of America*, 77, 726-730.
- Baptista, L. F. (1996). Nature and its nurturing in avian vocal development. In D. E. Kroodsma & E. H. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 39-60). Ithaca, NY: Cornell University Press. 587 pp.
- Bel'kovitch, V. M., & Sh'ekotov, M. N. (1993). *The belukha whale: Natural behaviour and bioacoustics*. Woods Hole, MA: Woods Hole Oceanographic Institution.
- Boran, J. R., & Heimlich, S. L. (1999). Social learning in cetaceans: Hunting, hearing and hierarchies. In H. O. Box & K. R. Gibson (Eds.), *Mammalian social learning: Comparative and ecological perspectives* (pp. 283-307). Cambridge, UK: Cambridge University Press. 438 pp.
- Bowles, A. E., Young, W. G., & Asper, E. D. (1988). Ontogeny of stereotyped calling of a killer whale calf, *Orcinus orca*, during her first year. *Rit Fiskideildar*, 11, 251-275.
- Brodie, P. F. (1969). Duration of lactation in cetacea: An indicator of required learning. *American Midland Naturalist*, 1, 312-313.
- Brodie, P. F. (1971). A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island population. *Journal of the Fisheries Research Board of Canada*, 28, 1309-1318.
- Caldwell, M. C., & Caldwell, D. K. (1972). Vocal mimicry in the whistle mode by an Atlantic bottlenosed dolphin. *Cetology*, 9, 1-8.
- 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: Current perspectives in research* (Vol. 3, pp. 369-401). New York: Plenum Press. 458 pp.
- Castellote, M., Vergara, V., Barrett-Lennard, L. G., & Esteban, J. A. (2007). Sound production of neonate captive beluga whales. *Proceedings of the 21st Conference of the European Cetacean Society*. San Sebastian, Spain.
- Committee on the Status of Endangered Wildlife in Canada (COSEWIC). (2004). *Assessment and update status report on the beluga whale Delphinapterus leucas in Canada*. Ottawa, Canada: Author. 70 pp. Retrieved 20

- March 2007 from [www.sararegistry.gc.ca/virtual\\_sara/files/cosewic/sr\\_beluga\\_whale\\_e.pdf](http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_beluga_whale_e.pdf).
- Cranford, T. W. (2000a). 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* (Vol. 12, pp. 109-155). New York: Springer-Verlag. 485 pp.
- Cranford, T. W. (2000b). Two independent sonar signal generators in the bottlenose dolphin: Physiologic evidence and implications. *Journal of the Acoustical Society of America*, *108*, 2613-2614.
- 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.
- Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales (*Orcinus orca*): Implications for vocal learning and cultural transmission. *Animal Behaviour*, *60*, 629-638. (doi: 10.1006/anbe.2000.1454)
- Drinnan, R. L., & Sadleir, R. M. F. S. (1981). The suckling behavior of a captive beluga (*Delphinapterus leucas*) calf. *Applied Animal Ethology*, *7*, 179-185.
- Eaton, R. L. (1979). A beluga whale imitates human speech. *Carnivore*, *2*, 22-23.
- Elowson, A. M., Snowdon, C. T., & Lazaro-Perea, C. (1998). "Babbling" and social context in infant monkeys: Parallels to human infants. *Trends in Cognitive Sciences*, *2*, 31-37.
- Fish, M., & Mowbray, W. (1962). Production of underwater sounds by the white whale or beluga, *Delphinapterus leucas*. *Journal of Marine Research*, *20*, 149-162.
- Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia, Canada. *Canadian Journal of Zoology*, *69*, 1454-1483.
- Fripp, D. R. (1999). *Techniques for studying vocal learning in bottlenose dolphins, Tursiops truncatus*. Ph.D. dissertation, Woods Hole Oceanographic Institution and Massachusetts Institute of Technology, Woods Hole, MA. 349 pp.
- Fripp, D. R. (2005). Bubblestream whistles are not representative of a bottlenose dolphin's vocal repertoire. *Marine Mammal Science*, *21*, 29-44.
- Fripp, D. R., Owen, C., Quintana-Rizzo, E., Shapiro, A., Buckstaff, K., Jankowski, K., et al. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition*, *8*, 17-26.
- Hammerschmidt, K., Newman, J. D., Champoux, M., & Suomi, S. J. (2000). Changes in rhesus macaque "coo" vocalizations during early development. *Ethology*, *106*, 873-886.
- Herzing, D. L. (2000). Acoustic and social behavior of wild dolphins: Implications for a sound society. In W. W. L. Au, A. N. Popper, & R. R. Fay (Eds.), *Hearing by whales and dolphins* (pp. 225-272). New York: Springer-Verlag. 485 pp.
- Janik, V. M., & Slater, P. J. B. (1997). Vocal learning in mammals. *Advances in the Study of Behaviour*, *26*, 59-99.
- Janik, V. M., & Slater, P. J. B. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, *60*, 1-11. (doi: 10.1006/anbe.2000.1410)
- Karlsen, J. D., Bisther, A., Lydersen, C., Haug, T., & Kovacs, K. M. (2002). Summer vocalizations of adult male white whales (*Delphinapterus leucas*) in Svalbard, Norway. *Polar Biology*, *25*, 808-817.
- Killebrew, D. A., Mercado, E., III, Herman, L. M., & Pack, A. A. (2001). Sound production of a neonate bottlenose dolphin. *Aquatic Mammals*, *27*(1), 34-44.
- Knörnschild, M., Behr, O., & von Helversen, O. (2006). Babbling behavior in the sac-winged bat (*Saccopteryx bilineata*). *Naturwissenschaften*, *93*, 451-454.
- Lindhard, M. (1988). Apparent sonar clicks from a captive bottlenose dolphin, *Tursiops truncatus*, when 2, 7 and 38 weeks old. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar: Processes and performance* (pp. 109-113). New York: Plenum Press. 878 pp.
- Locke, J. L. (1993). Learning to speak. *Journal of Phonetics*, *21*, 141-146.
- Locke, J. L., & Snow, C. (1997). Vocal learning in human and non-human primates. In M. Hausberger (Ed.), *Social influences on vocal development* (pp. 274-292). Cambridge, UK: Cambridge University Press. 362 pp.
- Madsen, P. T., Carder, D. A., Au, W. W. L., Möhl, B., Nachtigall, P. E., & Ridgway, S. (2003). Sound production in neonate sperm whales (L). *Journal of the Acoustical Society of America*, *113*(6), 2988-2991. (doi: 10.1121/1.1572137)
- Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, *136*, 529-566.
- Marler, P., & Mundinger, P. (1971). Vocal learning in birds. In H. Moltz (Ed.), *The ontogeny of vertebrate behavior* (pp. 389-450). New York: Academic Press. 500 pp.
- Marler, P., & Peters, S. (1982). Subsong and plastic song: Their role in the vocal learning process. In D. E. Kroodsma & E. H. Miller (Eds.), *Acoustic communication in birds. Vol 2: Song learning and its consequences* (pp. 25-50). New York: Academic Press. 392 pp.
- Martin, T. (1996). *Beluga whales*. Stillwater, MN: Voyageur Press.
- McCowan, B., & Reiss, D. (1995). Whistle contour development in captive-born infant bottle-nosed dolphins (*Tursiops truncatus*): Role of learning. *Journal of Comparative Psychology*, *109*, 242-260.
- McCowan, B., & Reiss, D. (1997). Vocal learning in captive bottlenose dolphins: A comparison with humans and nonhuman animals. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 178-207). Cambridge, UK: Cambridge University Press. 362 pp.
- Murray, S. O., Mercado, E., & Roitblat, H. L. (1998). Characterizing the graded structure of false killer whale

- (*Pseudorca crassidens*) vocalizations. *Journal of the Acoustical Society of America*, 104, 1679-1688.
- Oller, D. K. (2000). *The emergence of the speech capacity*. Mahwah, NJ: Lawrence Erlbaum Associates.
- Oller, D. K., & Eilers, R. E. (1988). The role of audition in infant babbling. *Child Development*, 59, 441-449.
- Payne, K., & Payne, R. (1983). Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*). In R. Payne (Ed.), *Communication and behaviour of whales* (pp. 9-57). Boulder, CO: Westview Press. 643 pp.
- Recchia, C. (1994). *Social behaviour of captive belugas, Delphinapterus leucas*. Ph.D. dissertation, Woods Hole Oceanographic Institution and Massachusetts Institute of Technology, Woods Hole, MA. 206 pp.
- Reiss, D. (1988). Observations on the development of echolocation in young bottlenose dolphins. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar: Processes and performance* (pp. 121-127). New York: Plenum Press. 878 pp.
- Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning. *Journal of Comparative Psychology*, 107, 301-312.
- Ridgway, S. H., Carder, D. A., & Jeffries, M. M. (1985). Another "talking" male white whale. *Abstracts of the Sixth Biennial Conference on the Biology of Marine Mammals*, Vancouver, BC, Canada. 67 pp.
- Sayigh, L. S. (1992). *Development and function of signature whistles of free-ranging bottlenose dolphins, Tursiops truncatus*. Ph.D. dissertation, Woods Hole Oceanographic Institution and Massachusetts Institute of Technology, Woods Hole, MA. 127 pp.
- 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.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Scott, M. D., & Irvine, A. B. (1995). Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, 36, 171-177.
- Schevill, W. E., & Lawrence, B. (1949). Underwater listening to the white porpoise (*Delphinapterus leucas*). *Science*, 109, 143-144.
- Schevill, W. E., & Watkins, W. A. (1966). Sound structure and directionality in *Orcinus* (killer whale). *Zoologica*, 51, 70-76.
- Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, 34, 1640-1658.
- Sjare, B. L., & Smith, T. G. (1986a). The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. *Canadian Journal of Zoology*, 64, 2824-2831.
- Sjare, B. L., & Smith, T. G. (1986b). The vocal repertoire of white whales, *Delphinapterus leucas* summering in Cunningham Inlet, Northwest-Territories. *Canadian Journal of Zoology*, 64, 407-415.
- Slater, P. J. B. (1989). Bird song learning: Causes and consequences. *Ethology, Ecology and Evolution*, 1, 19-46.
- Smolker, R. A., Mann, J., & Smuts, B. B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioral Ecology and Sociobiology*, 33, 393-402.
- Snowdon, C. T., & Elowson, A. M. (2001). "Babbling" in pigmy marmosets: Development after infancy. *Behaviour*, 138, 1235-1248.
- Snowdon, C. T., Elowson, A. M., & Roush, R. S. (1997). Social influences on vocal development in New World primates. In C. T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 1-6). Cambridge, UK: Cambridge University Press. 362 pp.
- Turl, C. W., & Penner, R. H. (1989). Differences in echolocation click patterns of the beluga (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *Journal of the Acoustical Society of America*, 86, 497-502.
- Turl, C. W., Penner, R. H., & Au, W. W. L. (1987). Comparison of target detection capabilities of the beluga and bottlenose dolphin. *Journal of the Acoustical Society of America*, 85, 1487-1491.
- Turl, C. W., Skaar, D. J., & Au, W. W. L. (1991). The echolocation ability of the beluga (*Delphinapterus leucas*) to detect targets in clutter. *Journal of the Acoustical Society of America*, 89, 896-901.
- Tyack, P. L. (1993). Animal language research needs a broader comparative and evolutionary framework. In H. L. Roitblat, L. M. Herman, & P. E. Nachtigall (Eds.), *Language and communication: Comparative perspectives* (pp. 115-152). Hillsdale, NJ: Lawrence Erlbaum Associates. 520 pp.
- Tyack, P. L. (1997). Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. *Bioacoustics*, 8, 21-46.
- Tyack, P. L. (2003). Dolphins communicate about individually-specific social relationships. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 342-361). Cambridge, MA: Harvard University Press. 616 pp.
- Tyack P. L., & Clark C. W. (2000). Communication and acoustical behavior in dolphins and whales. In W. W. L. Au, A. N. Popper, & R. R. Fay (Eds.), *Hearing by whales and dolphins* (Vol. 12, pp. 156-224). New York: Springer-Verlag. 485 pp.
- Van Parijs, S. M., Lydersen, C., & Kovacs, K. M. (2003). Sounds produced by individual white whales, *Delphinapterus leucas*, from Svalbard during capture (L). *Journal of the Acoustical Society of America*, 113, 57-60.
- Watkins, W. A. (1967). The harmonic interval: Fact or artifact in spectral analysis of pulse trains. In W. N. Tavolga (Ed.), *Marine bio-acoustics* (Vol. 2, pp. 15-43). New York: Pergamon Press. 353 pp.