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What can Captive Whales tell us About their Wild Counterparts? Identification, Usage, and Ontogeny of Contact Calls in Belugas (*Delphinapterus leucas*)

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Contact calls are ubiquitous in social birds and mammals. Belugas are among the most vocal of cetaceans, but the function of their calls is poorly understood. In a previous study we hypothesized that a broad band pulsed call type labeled "Type A," serves as a contact call between mothers and their calves. Here we examined context-specific use of call types recorded from a captive beluga social group at the Vancouver Aquarium, and found that the Type A call comprised 24% to 97% of the vocalizations during isolation, births, death of a calf, presence of external stressors, and re-union of animals after separation. In contrast it comprised 4.4% of the vocalizations produced during regular sessions. We grouped 2835 Type A calls into five variants, A1 to A5. A discriminant function analysis classified 87% of calls in the same groupings that we assigned them to by ear and visual examination of spectrograms. The variants do not represent individual signatures. One variant, A1, was used by three related individuals: an adult female, her male calf and his juvenile half-sister. Our previous research documented the gradual development of the A1 variant by the male calf, until at 20 months he was producing stereotyped renditions of his mother and sister's A1. We used our findings to generate testable predictions about the usage of these signals by wild belugas. We verified the existence of signals with the same distinctive features as the contact calls found in captivity in the repertoire of St. Lawrence Estuary herds, and documented their usage by two wild individuals from different populations. In the St. Lawrence, these were emitted by a female calling after a dead-calf. In Hudson Bay, by a temporarily restrained juvenile. We propose that these calls function in nature, as in captivity, to maintain group cohesion, and that the variants shared by related animals are used for mother-calf recognition.

Belugas (*Delphinapterus leucas*), nicknamed "sea canaries," are among the most soniferous cetaceans, producing what has been suitably described as a bewildering array of sounds (Finley, Miller, Davis, & Greene, 1990). These resemble the predominant sounds used by other toothed whales, and fall into two acoustic categories: whistles, or narrow band frequency modulated vocalizations, and pulsed sounds, or trains of broad band pulses. The latter can in turn be divided into two functional categories: click trains, used largely for echolocation, and burst pulse sounds (bursts of pulses with rapid pulse repetition rates), believed to be

social signals, which may sound to the human ear like grunts, squawks, screams, whines and even whistles. In belugas, one type of signal may merge into the other. Some researchers (e.g., Karlsen, Bisther, Lydersen, Haug, & Kovacs, 2002; Vergara & Barrett-Lennard, 2008) identified mixed calls for belugas, consisting of either a whistle and a pulsed component, or two pulsed sounds with different pulse repetition rates, produced synchronously in the same vocalization.

There have been a number of attempts to classify the vocal repertoire of belugas (Angiel, 1997; Belikov & Bel'kovich, 2003, 2006, 2007, 2008; Bel'kovitch & Sh'ekotov, 1993; Faucher, 1988; Fish & Mowbray, 1962; Karlsen et al., 2002; Morgan, 1979; Recchia, 1994; Sjare & Smith, 1986). This body of data provides some indication that the sounds vary with behavioral and group context, and suggests geographic variation in signal use among populations. In general, however, the studies have been primarily descriptive, with no major efforts to provide a functional analysis of the calls.

The inquiry into the acoustic system of belugas is not exempted from two intimately related problems that are persistent stumbling blocks in the study of animal communication: First, great variability in the physical features of the sounds, with general call types grading into each other (e.g., Recchia, 1994) introduces great uncertainty in the categorization schemes. Secondly, it is inherently difficulty to categorize sounds that are biologically meaningful without testing how belugas themselves perceive or use them (Tyack & Clark, 2000). To exacerbate these problems, belugas, like all cetaceans, rarely produce visible signs when they make sounds, making the identification of the phonating individual in a group, so necessary for the study of function, problematic.

How, then, do we begin to understand the function of the calls produced by so loquacious an animal? One approach is to look for call types that are predictably produced in particular, identifiable circumstances. The signals commonly referred to as "contact calls," ubiquitous in social birds and mammals, are a good place to start because we can predict the circumstances when we would hear them. These signals are used to mediate group cohesion and coordinate movements in social animals, when animals are losing or have lost contact with one another – in which case they are sometimes termed "isolation calls" (Tyack, 2000) and to facilitate contact between particular social companions, including mothers and dependent young. They are particularly advantageous in mobile species that inhabit environments where conspecifics can easily lose sight of one another, such as the marine environment.

Contact calls have been widely studied in birds (e.g., several parrot species: Bradbury, 2003; orange-fronted parakeets, *Aratinga canicularis*: Cortopassi & Bradbury, 2006; budgerigars, *Melopsitacus undulates:* Farabaugh, Linzenbold, & Dooling, 1994; communal nesting long-tailed tit, *Aegithalos caudatus*: Sharp & Hatchwell, 2006), terrestrial mammals (e.g., vampire bats, *Diaemus youngi*: Carter, Skowronski, Faure, & Fenton, 2008; marmosets, *Callithrix jacchus*: Chen, Kaplan, & Rogers, 2009; baboons, *Papio cynocephalus*: Cheney, Seyfarth, & Palombit, 1996; African elephants, *Loxodonta africana*: McComb, Reby, Baker, Moss, & Sayialel, 2003), and marine mammals (e.g., killer

whales, *Orcinus orca*: Ford, 1989; bottlenose dolphins, *Tursiops truncatus*: Janik & Slater, 1998; Sayigh, Tyack, Wells, & Scott, 1990). Depending upon the species' social system, it may suffice for those calls to be shared at the level of the group, or they may need to be individually distinctive (Tyack, 2000; Tyack & Clark, 2000). A system of reliable, individually distinctive vocal signatures would make it easier for animals to keep track of one another in species with high mobility and long-term yet fluid relationships in an aquatic environment (Tyack, 2003). This is, indeed, the case for bottlenose dolphins (Caldwell & Caldwell, 1965; Caldwell, Caldwell, & Tyack, 1990; Sayigh et al., 1998; Tyack, 2003; Watwood, Owen, Tyack, & Wells, 2005; *cf.* McCowan & Reiss, 2001) which are known to live in fission-fusion societies in which group composition may change moment to moment, but with strong and stable bonds between individuals (Connor, Wells, Mann, & Read, 2000; Tyack & Clark, 2000; Wells, Scott, & Irvine, 1987).

What do we know about beluga society? They are long lived, highly gregarious, circumpolar odontocetes that migrate from overwintering areas of broken pack ice to spring and summer calving and feeding areas, usually shallow river estuaries (COSEWIC, 2004). Genetic evidence indicates strong philopatry of females and their calves (Brennin, Murray, Friesen, Maiers, Clayton, & White, 1997), with longitudinal data on cow-calf pairs remaining together for many years (Michaud, unpublished data). Summer aggregations are in general separated into herds of males and large nursery groups of females, calves, and juveniles occupying slightly different areas (Michaud, 1993; Smith, Hammill, & Martin, 1994; Smith & Martin, 1994). A long term photo-identification study of the St. Lawrence estuary belugas in their summering range has provided the first detailed portrait of their social structure and behavior, revealing a fission-fusion grouping pattern, and long-lasting male-male associations and alliances (Michaud, 2005).

As a species with high mobility and long-term associations between individuals, we would expect belugas to use a system of discrete contact calls. Furthermore, given their fission-fusion social system, we might expect selection to have favored individually distinctive recognition signals. In our previous study of the vocal development of a beluga calf (Vergara & Barrett-Lennard, 2008), we identified three variants of a broadband, pulsed call type labeled "Type A," used predominantly by the mother after a birthing event. We hypothesized that at least one of the variants, A1, produced by the mother, her juvenile daughter, and gradually developed by a male calf, is a contact call that may play an important functional role in mother-offspring recognition.

The present paper further investigates the context-specific use of the Type A call in a captive beluga social group at the Vancouver Aquarium to ascertain its function as a contact call. We predicted that Type A calls would be recorded more often in situations that would elicit a need to regain or maintain contact, such as the presence of external stressors (divers), changes in the group composition (re-introductions, separations, births, deaths), and forced or voluntary isolation – the latter ameliorating the problem of identifying the individual vocalizer. This is important as a first step in understanding the functional significance of beluga

signals, and to aid in the categorization of sounds that are biologically meaningful to these animals

Despite the obvious differences between the captive environment and that of wild belugas, the former provides opportunities such as uninterrupted observations of social interactions at close range and the sampling of continuous sequences of behavior concurrent with sound recordings, along with knowledge of the ages, sex, and social relationships between the animals, affording in this way a more transparent window into the function of beluga calls. However, there always remains the question of whether their wild counterparts behave the same way. In this study we use analyses of signal structure and usage in captivity to construct testable hypotheses to guide investigations of sound usage in wild belugas. We then use opportunistic recordings from the wild environment as a field test of some of the hypotheses derived from the captive study. The "umbrella" objective of our work is thus to evaluate if studying vocal usage in captive belugas is relevant to understanding how these animals use vocal signals in their natural environment.

Study Approach

Our general study approach has been to exploit the ease with which the animals can be observed underwater in a captive setting in order to begin to investigate call function, and then use the results and ideas generated from this research as a springboard for guiding research in the wild. We will thus first present the methodology and results of the captive component of the study; we will then outline a set of hypotheses and predictions about wild belugas generated from our captive work, and finally describe two opportunistic studies in the wild environment to shed light on these hypotheses. We will discuss the captive and wild results jointly.

Captive Component: Methods

Time frame and social group

This study took place at the Vancouver Aquarium (British Columbia, Canada) between 2002 and 2006, with additional data collected during two beluga births in 2008 and 2009, and one death in 2010. A total of 8 captive belugas, four captive born, and four captured in Hudson Bay (Churchill, Canada), have been observed and recorded since 2002. Their social group had varying compositions throughout the length of this study. Figure 1 illustrates the genealogy of the studied animals. Their ages at the time of writing, whether captive-born or wild-caught, and the periods when they were observed and recorded are summarized in Table 1.
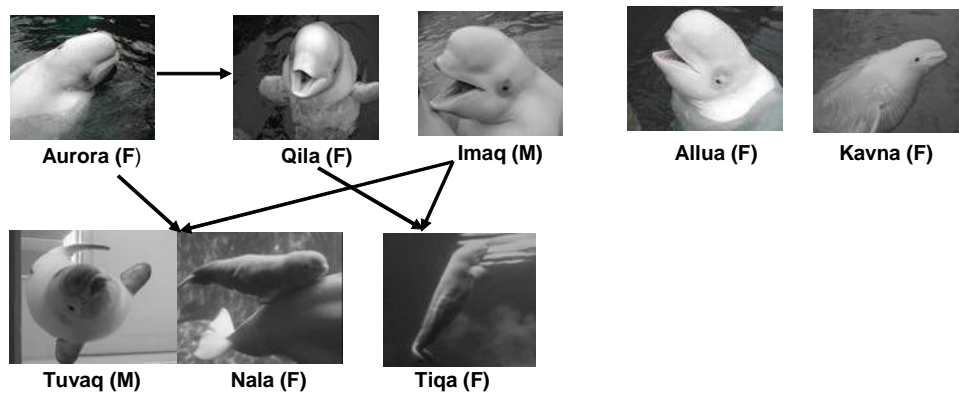
Figure 1. Genealogy of the Vancouver Aquarium belugas. Black arrows indicate "parent-offspring." Ages of the animals and whether captive-born or wild caught on Table 1.

Table 1
Ages, sex, and period of study for the belugas at the Vancouver Aquarium

Animal	Wild-caught or captive born?	Year	Age and Sex	Observed and Recorded
Aurora	Wild caught	1990	23 year-old F	2002-2006, 2008, 2009
Imaq	Wild caught	1990	23 year-old M	2002-2006 [a]
Allua	Wild caught	1985	27 year-old F	2002-2005 [b, c]
Kavna	Wild caught	1976	43 year-old F	2002-2006 [a]
Qila	Captive born	1995	15 year-old F	2002-2006, 2008, 2009[c]
Tuvaq	Captive born	2002	Died at 3 years, M	2002-2005 [d]
Tiqa	Captive born	2008	2 year-old F	June-July 2008 [e]
Nala	Captive born	2009	Died at 1 year, F	June 2009 [f]

a.   Imaq and Kavna were transferred to another pool from July 2002 (Tuvaq's birth) until January 2004, when both animals were re-introduced with the rest of the social group. Both were re-transferred in June 2008 (Tiqa's birth) and they remain in a separate pool at the time of writing.
b.   Allua was transferred to another aquarium in January 2005.
c.   Allua and Qila were transferred to another pool in July 2002 (Tuvaq's birth) and re-introduced in October 2002.
d.   Tuvaq died at 3 years of age, in July 2005.
e.   Tiqa is currently a subject of an ongoing vocal development study. Only data related to her mother's vocalizations during her first month of life are included here.
f.   Nala was a subject of an ongoing vocal development study. We only include here data related to her mother's vocalizations during the 2 hours after her birth, and during a 1 hour session after her death in June 2010.

Sampling regime and observation area

   The animals were kept in an outdoor pool (18 m x 29 m; depth 6 m) connected to an adjacent 3 m deep smaller medical holding pool (3 m x 3 m). A netted gate that allowed acoustic and visual contact between the whales occasionally separated both pools. We observed and recorded the animals 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 pool.

Observation/recording sessions varied in length from 15 min to 2 h (and longer for the initial 2 months of the vocal development study, see Vergara & Barrett-Lennard, 2008) at variable times of day. The frequency of the observation sessions was variable throughout the entire study period, occurring as often as three times weekly, and as infrequently as once per month, depending on the time allocated to other aspects of the beluga research.

Acoustic recordings

We made underwater audio recordings throughout the length of each observation session using two hydrophones installed permanently in the adjacent pools: an Offshore Acoustics hydrophone in the main pool and a Brüel & Kjaer 8101 hydrophone in the medical pool. The calls were recorded digitally on two Pentium IV computers (each connected to a hydrophone) using Avisoft SASlab Pro software (Avisoft Bioacoustics), Cool Edit 2000, and, since 2004, Raven (Cornell Lab of Ornithology) at a sampling rate of 44.1 kHz. The system had a frequency response of 0.02 kHz – 22.0 kHz + 1 dB. The recording of the 2010 session following the death of a calf was made with a Marantz PMD660 solid state recorder at a sampling rate of 48 kHz, each hydrophone connected to one channel of the device. We occasionally had access to a sound card that sampled at 96 kHz (giving a recording bandwidth of 48 kHz), which assisted in determining whether high frequency components were being missed in the 44.1 kHz recordings.

Since both hydrophones recorded simultaneously, it was often possible to identify the individual vocalizer by comparing the amplitude of the same recorded sound on the two computers (or stereo channels).

Spectrograms are displayed here with Avisoft SASlab Pro (Avisoft Bioacoustics). Call parameters were measured automatically with Raven 1.3.

Call type categorization

Given that the efficacy of sound categorization methods that rely on aural and spectrographic comparisons is well demonstrated (e.g., Deecke et al., 1999; Ford, 1984; Janik, 1999), we categorized call types by ear and by visual inspection of spectrograms. We considered each discrete phonation that was found five or more times in the repertoire a distinct call type. Phonations that were unstereotyped or presented a 'graded' structure (borders hard to define, unable to tell when a vocalization ended and another started) were assigned to the "variable" category. Following the categorization of beluga calls by Rechia (1994), vocalizations that were intermediate in structure and did not clearly fall into any of the categories, or that were rare (less than five) were assigned to a category labeled "other".

Call categorization based on observer consensus (Sayigh, Tyack, Wells, Scott, & Irvine, 1995; Watwood, Tyack, & Wells, 2004), or on automated methods (Deecke & Janik, 2006) was beyond the scope of this study, and categorization was instead performed by a single experienced observer (Vergara). Of relevance here is the distinctiveness of the Type A call in relation to the overall repertoire of 28 call types. Several of these call types have variants that aurally fall into the same general call category but that show some spectrographical differences in duration, energy distribution, or pulse repetition rate. In this paper we consider only the five variants of the Type A call, A1-A5.

Discriminant function analysis (DFA)

We used a DFA to verify our subjective classification of the five variant types of the Type A call, A1 to A5, using SPSS, version 16.0 (SPSS, Chicago, Illinois, USA). For this purpose, we randomly selected 60 cases of each variant from a total of 2835 cases. The DFA is a classification procedure that assigns each call case either correctly to its appropriate variant type, or incorrectly to another type, based on combinations of those acoustic parameters that best separate the groups of cases. We used subset validation, whereby a random subsample of 40 cases of each variant type (for a total of 200 cases) was used to create the model, setting the remaining 100 unselected cases aside to

validate the analysis. To subsample the cases of each variant type for the measurement of acoustic parameters, we used "Research Randomizer" (http://www.randomizer.org/form.htm).

Acoustic parameters for the DFA. The DFA was based on the following acoustic parameters measured for each of the 60 randomly selected exemplars of each of the five variant types of the Type A call: maximum power (in dB re 1 dimensionless sample units), average power (the value of the spectrogram's power spectral density in each bin of the spectrogram averaged over the entire call), peak frequency (the frequency at which maximum power occurs, which, for the A1 mixed variant, coincides most often with the whistle component), duration, and three measurements of pulse repetition rate (number of pulses per second, henceforth abbreviated PRR) along the time axis of each call: initial PRR, middle PRR and end PRR.

We used these three measurements of pulse repetition rate to describe the 'inflection' of the five pulsed variants. These measurements were obtained by counting the pulses in the 0.2 seconds at the beginning, middle, and end of each call, and multiplying each count by 5 for an estimate of pulses per second at three locations of each call (Fig. 2). The mean PRR of a call was estimated by averaging these three numbers. We used an analyzing filter bandwidth of 200 Hz and a DFT size of 512 samples in order to discriminate pulses more readily. We also counted the pulses by ear, to corroborate the visual counts, by playing back each 0.2 seconds clip at 3% to 10% of the original speed.

The PRR of some pulsed sounds can be high enough to confer a tonal character to the call (generally classified as burst pulsed sounds), with harmonically related frequency sidebands on a spectrogram (Watkins, 1967). When the PRR was too rapid to discriminate individual pulses, it was estimated through this harmonic interval, as described in Watkins (1967). Thus, we measured the frequency of two harmonic bands at the same three locations on the time axis of the call (i.e., beginning, middle, end), and subtracted one from the other to obtain the number of cycles per second, or PRR, at each location. In such cases we reduced the filter bandwidth to 50-70 Hz, increasing the DFT to 1024-2048 samples, for better resolution of the harmonic bands.
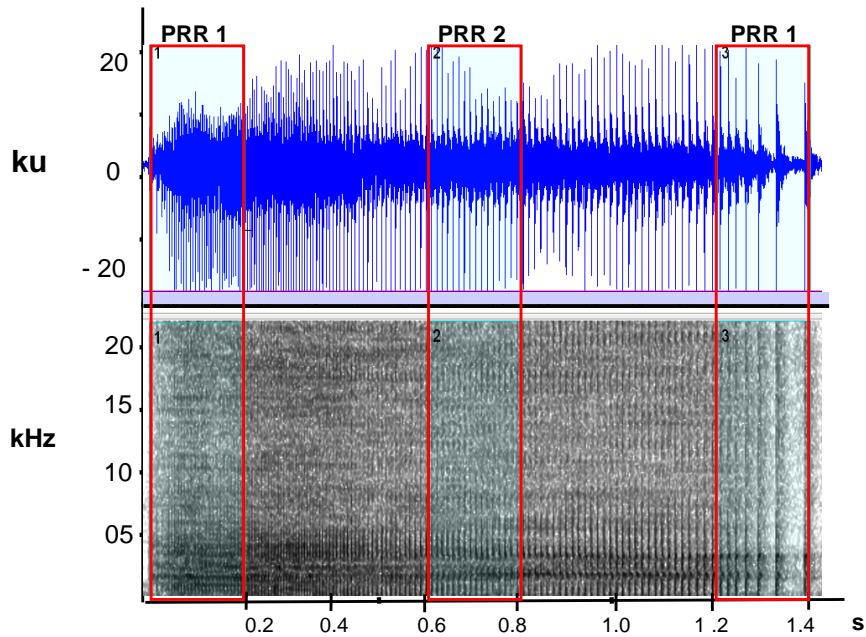

Figure 2. Example of the pulse repetition rate measurements at the beginning, middle, and end of a call. The bottom graph is a spectrogram and the top a waveform.

Contextual use

We examined both the overall proportional usage of the Type A call in relation to all other recorded call types (including variable calls) and the call rate (call number/individual/hour) during recording sessions where maintaining contact was presumed to be important to the animals, termed for simplification purposes "special sessions" (described below), and during regular sessions (sessions where no isolation events, external stressors, separations and reunions, births, or deaths were taking place). We sub-sampled 18 regular sessions from the multi-year study using a random date generator (http://www.lrs.org/interactive/randomdate.php). The special sessions were the following:

A. *Births.* We considered the 2 hours immediately following each of three beluga births at the Vancouver Aquarium "birth sessions": 1) On July 20, 2002, Aurora gave birth to a male calf, Tuvaq. She was alone in the pool. No animals were held in the contiguous medical pool. 2) On June 9, 2008, Qila, captive-born daughter of Aurora, gave birth to a female calf, Tiqa. Aurora, was held in the contiguous medical pool, from where she could see and hear the birthing mother and the newborn calf. 3) On June 7, 2009, Aurora gave birth to a female calf, Nala. Qila and Tiqa (Aurora's daughter and granddaughter) were held in the medical pool during the birth. For both the 2008 and 2009 births, only the vocalizations produced in the main pool were considered.

B. *Isolation of mother and calf.* Twelve sessions when Aurora was vocal, out of 27 recording sessions when Aurora and her calf Tuvaq were isolated from all other animals (from birth to 3 months of age).

C. *Separation of females.* Eleven sessions when Qila and Aurora were in the two contiguous pools, separated by a netted gate, within visual (although somewhat obstructed, since the aperture between the two pools is small) and acoustic contact. Qila was in the larger of the two pools with her newborn calf, Tiqa, and Aurora was kept in the smaller pool for 1 month.

D. *Re-introduction.* Two sessions when first Allua (October 9, 2002) and then Qila (October 23, 2002) were re-introduced into the pool with Aurora and her calf, after 3 months of complete separation (visual and acoustic).

E. *Divers.* Seven sessions when 2 or more divers entered the pool for cleaning and maintenance purposes.

F. *Husbandry procedures.* Six husbandry procedures involving temporary isolation in the medical pool (termed "gating") and/or restraint of an adult, a calf, or an adult-calf pair (for the purpose of weighing, taking blood samples, etc). The gated animals were always within acoustic contact of the rest of the group.

G. *Voluntary isolation.* Four sessions when a particular animal spent 80% or more of the session alone in one of the two pools. This could have occurred by active exclusion by the other animals. For example on July 3, 2003, Qila was prevented from entering the medical pool by the rest of the animals, who jointly rebuffed all her attempts to enter. "Voluntary" then, is relative, and is used here in the sense of an isolation event not imposed on by humans locking a gate.

H. *Death of a calf.* On June 22, 2010, at 10:15 pm, Nala, Aurora's one-year old calf, died suddenly of respiratory failure. We conducted a 1 hour recording session 2 hours after her death, once her body had been retrieved from the pool.[1] At the time of this recording the only animals in the two contiguous pools were Aurora, Qila, and 2-year old Tiqa.

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[1]Since Nala's death occurred when the present paper had been accepted for publication, we added these important data to the contextual analysis, but did not include these additional vocalizations in the analysis of variant types nor in the vocal matching analysis.

Call matching exchanges

We considered two in-sequence Type A calls by different individuals produced within 2 seconds of one another a "call matching exchange." We assumed that 2 calls were from different individuals if they originated from the two contiguous pools. We chose the 2 s cutoff based on the distribution of the time differences between adjacent Type A calls made by different whales, which shows that most occurred within 2 s of each other (Fig. 3) (see Schulz, Whitehead, Gero, & Rendell, 2008).

A second-in-sequence Type A call was considered a potential answer to an initial Type A call if the onset occurred after the onset but before the termination of a preceding Type A call, termed "overlapping call" or if it occurred within 2 s but after the termination of the preceding Type A call, termed "adjacent call" (see Soltis, Leong, & Savage, 2005).

The three 2-hour birth sessions were not considered in the calculation of adult call matching exchanges.

Vocal development

A longitudinal study of the vocal development of a male beluga calf, Tuvaq was performed at the Vancouver Aquarium, from birth, throughout his first year of life and opportunistically through his second and third. The ontogeny of one of the contact call variants that we describe in the present paper is an aspect of that study. For details on the methodology, refer to Vergara and Barrett-Lennard (2008).
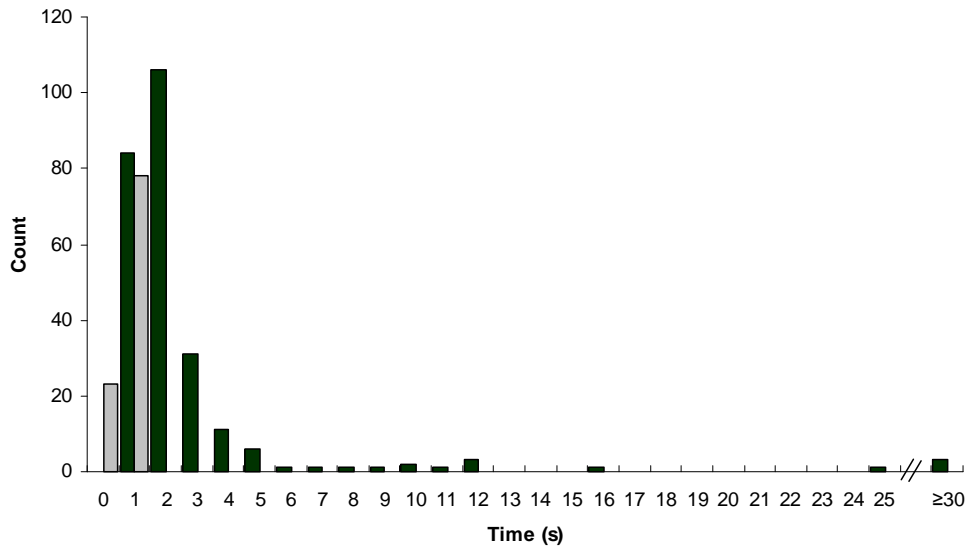
Figure 3. Histogram of the time intervals between adjacent (black bars) and overlapping (grey bars) Type A calls made by different whales.

Captive Component: Results

Context specific use of the Type A call

Figure 4 represents the context specific use of call types (both discrete and variable) for a total of 8,214 recorded calls. The Type A call was clearly the predominant type during births, isolation of mother and calf, separation of females, re-introduction, divers in pool, veterinarian or husbandry procedures (forced isolation), voluntary isolation, and death of a calf, collectively termed "special sessions." It comprised 24% to 97% of the vocalizations during those sessions. In contrast it composed 4.4 % of the vocalizations produced during regular sessions.

Figure 5 illustrates the average vocalization rate per individual per hour, for each session type, for the Type A, and for all other call types combined - to standardize for number of animals in the pool and length of the observation session. There was a strong association between the frequency of use of the Type A call and special sessions, ($\chi^2 = 1253.262$, $n = 2858$, $p < 0.0001$). Even during those special sessions when the animals vocalized little, such as isolation of mother and calf or separation of adult females (bars B and C of Fig. 5), when they did vocalize they favored Type A calls. Conversely, during regular sessions (bar I of Fig. 5) the animals rarely produced Type A calls.

Both the highest overall vocalization rate and the highest frequency of Type A calling occurred after the death of a calf and after the birthing events. Aurora was the animal producing the majority of the calls during the recording session immediately after her year-old daughter's death. She spent the majority of this session by herself in one of the contiguous pools, which permitted the attribution of her calls by comparing amplitudes. Out of the 586 recorded calls, 404 were Aurora's, and were almost entirely (99%) Type A calls.

During the re-introduction and diving sessions, the Type A call production occurred while the animals swam rapidly around the pool in a tight and synchronous formation.
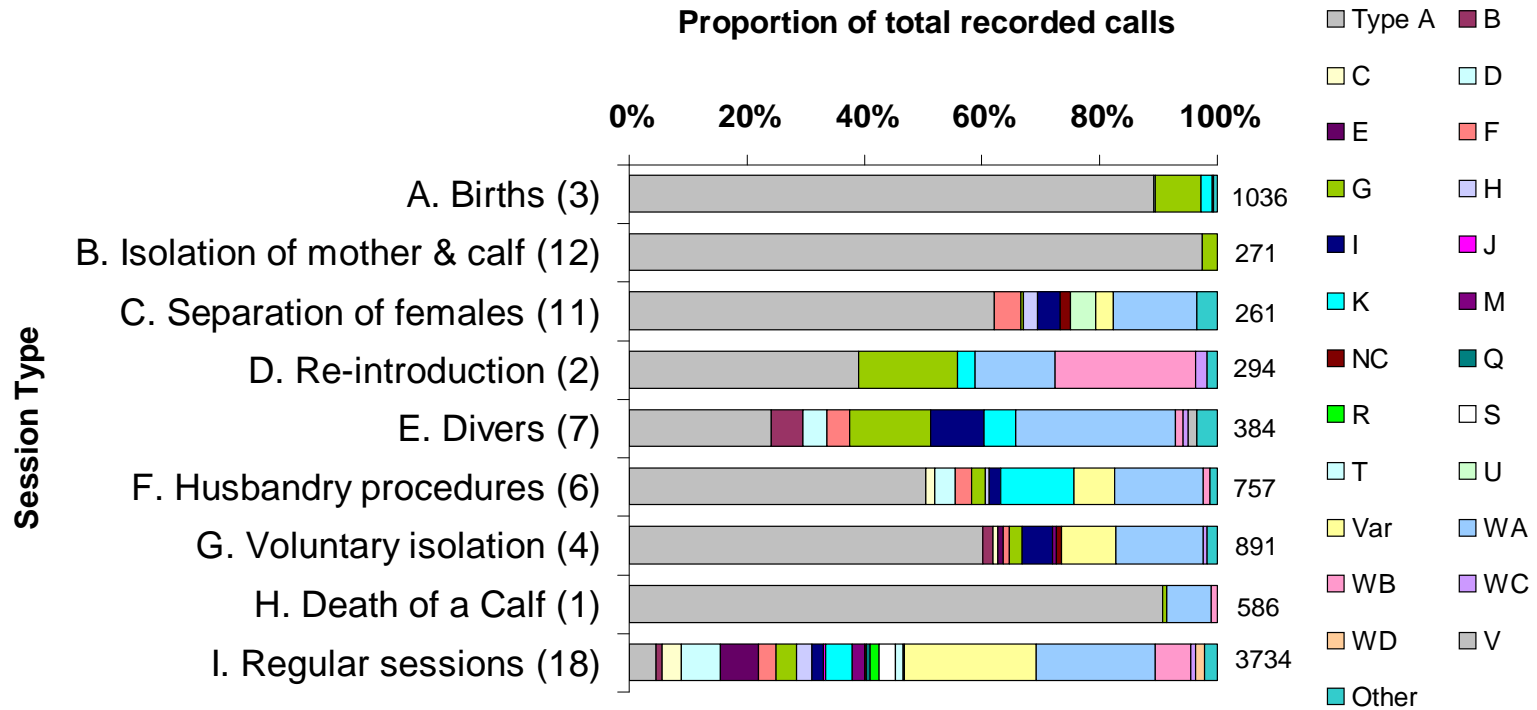
Figure 4. Context specific use of all calls (discrete and variable) recorded at the Vancouver Aquarium during special sessions (bars A to H) and regular sessions (I). The numbers between brackets indicate the number of observation sessions for that session type. The total number of vocalizations recorded for each session type is shown to the right of the respective bar. During separation of adult females (C), some diving events (E), and husbandry procedures (F), the animals were separated by an acoustically transparent net, i.e., they could see each other and hear each other while being held in different pools.
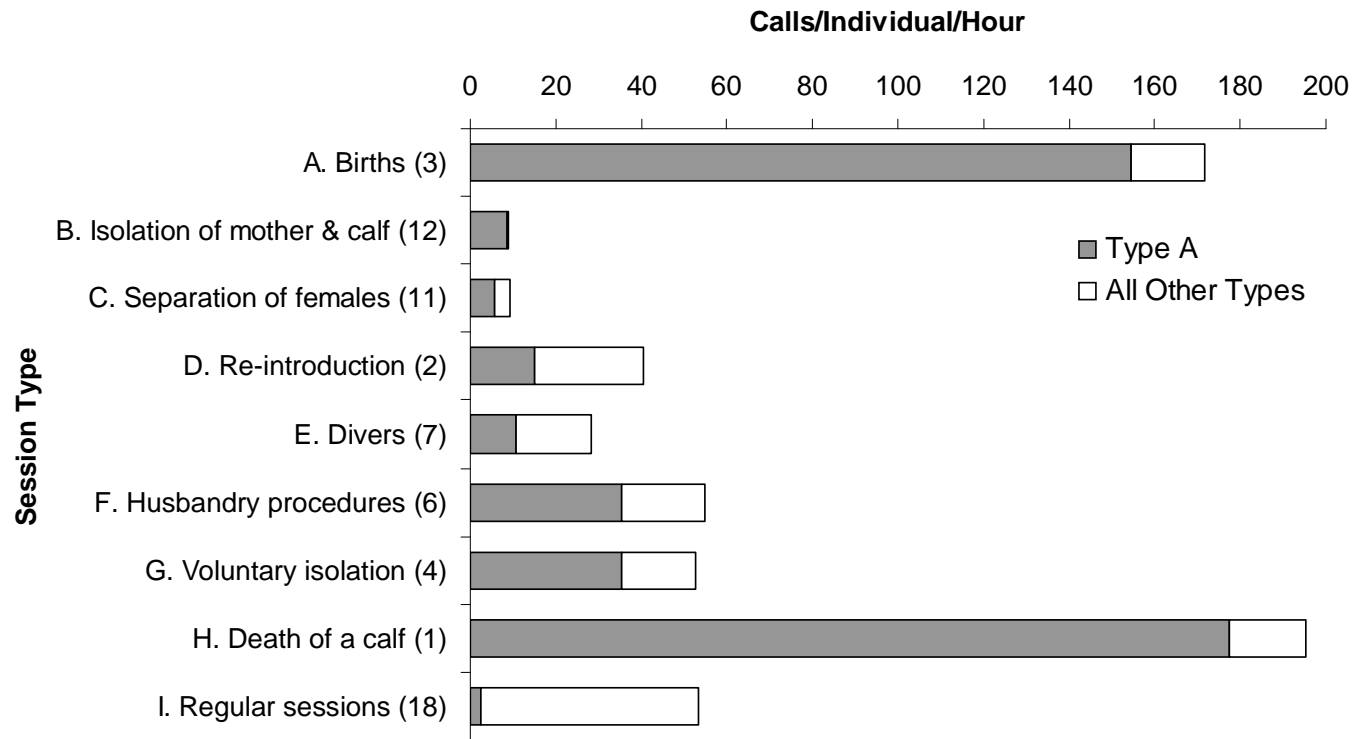
Figure 5. Average frequency (number per individual per hour) of Type A calls and of all other call types combined during special sessions (A through H) and regular sessions (I). The numbers between brackets indicate the number of observation sessions for that session type.

Vocal exchanges

Call matching exchanges. Of 1115 assigned Type A calls, 38 % occurred in call matching exchanges (Fig. 6), whereby two or more adults produced Type A calls in an antiphonal manner, using either the same or structurally different variants (described later). Considering only the second-in-sequence calls, a total of 20% of the assigned Type A calls occurred in the 2 s following the onset of a Type A call by a different whale, often overlapping.

Mother-calf vocal exchanges. During the first three months of Tuvaq's life, when he and his mother (Aurora) were isolated from all other animals, 50% of Aurora's Type A calls ($n = 264$) were preceded or followed by a calf's call (an unstereotyped pulsed train) within 2 s. Thus, considering the dyadic vocal exchange as the unit of analysis, 50% of Aurora's Type A calls were produced in vocal exchanges with her calf. This is a conservative estimate, as it does not take into account that the response unit may be an entire bout of several Type A calls, rather than one individual call; 29% of the maternal responses that occurred in the 2 s following the onset of a calf's call were not isolated Type A calls, but bouts of 2 to 10 consecutive Type A calls within 2 s of each other.
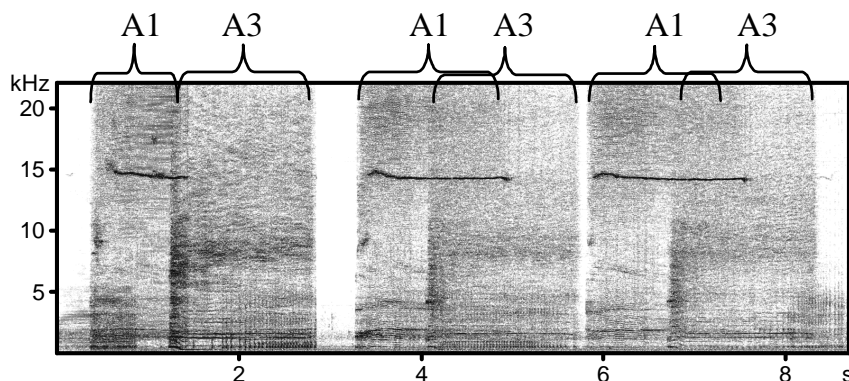

Figure 6. Spectrogram illustrating a call matching exchange between Aurora, in this case producing A1 variants (see next section), and Qila, producing overlapping A3 variants (FFT length: 1024, frame size: 100%, window: hamming, bandwidth: 56 Hz, overlap: 75%).

Variants of the Type A call

We grouped 2835 Type A calls into five acoustically different variants within a common template, labeled A1 to A5 (Fig. 7). All five variants were typically produced in bouts, and consisted of a broad-band rapid pulse-train (the dark bands that span the frequency range of the spectrograms) of relatively long duration (1.2 to 1.9 seconds), but they differed in the pulse repetition rates and in their energy distribution, translating into slightly different aural qualities. Variation in PRR along the time axis of a call confers each call variant a particular inflection (Fig. 8). Types A1 and A4 overlap closely in this pattern of PRR, with an average PRR of 94.6 ± 13.0 and 115.0 ± 26.1 pulses per second respectively, and they

sound practically the same to our human ears - a loud buzz much like a door creaking, with a somewhat crooning intonation. A2, A3 and A5 have more of a bleating quality to their sound, and are closer to each other than to A1 and A4 in PRR pattern, with average PRRs of 328.9 $\pm$ 36.4 for A2, 306.4 $\pm$ 42.4 for A3, and 371.8 $\pm$ 40.3 for A5, falling into the burst pulsed sound category demarcated by Au and Hastings (2008): trains of pulses characterized by a pulse repetition rate higher than 300 pulses per second.

Although, as noted above, there are no clear audible differences (to our human ears) between A1 and A4, there is different structural information in the calls: A1 is a mixed pulsed/tonal call, with a narrow band tonal component consistently at 14.6 $+$ 0.6 kHz (n = 559) overlapping the pulse-train, while A4 lacks the tonal component. A3 can also be a combined call, sometimes having a synchronous, slower pulse train of the same duration. All variants may begin or end with a series of a few discrete pulses. We obtained recordings of three of the variants (A1, A4, and A5) with a 96 kHz sound card, and the broadband pulse train still spans the frequency range of the system, with strong energy at 48 kHz in all three variants.
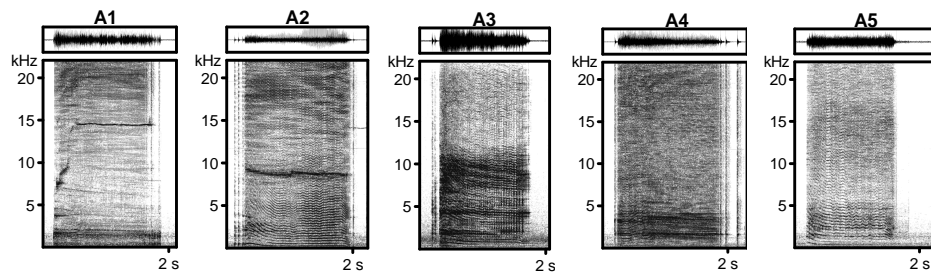

Figure 7. Representative spectrograms (bottom) and oscillograms (top) of the five variants of the Type A call (FFT length: 1024, frame size: 100%, window: hamming, bandwidth: 56 Hz, overlap: 75 %). The only mixed pulsed/tonal variant is A1 (note the overlapping whistle). The dark band across A2 is not tonal (as it can be resolved into pulses when manipulating the spectrogram FFT length), but a strong (and consistent) concentration of energy at 8 kHz. Variant A3 has two overlapping pulse trains of different PRR, one much more rapid than the other.

The DFA correctly classified 83% of the original grouped cases selected to create the model and 87 % of the cases that were not selected to create the model (i.e., the cases left aside for validation). The model assigned to the correct category 100 % of the unselected A1 cases, 100 % of the A2 cases, 75% of the A3 cases, 75% of the A4, and 84% of the A5 cases. The only variable that had no significant effect on the model was average power. The remaining variables contributed to the model, but maximum power and duration were the least likely variables to discriminate between groups. Predictably, the acoustic parameters that best describe these variants were: peak frequency and initial PRR, middle PRR and end PRR. For a visual representation of the discriminant space see Figure 9. The PRR pattern, represented by Function 1 on Figure 9, was better than peak frequency at overall discrimination between groups, and coincides with the pattern illustrated in Figure 8.
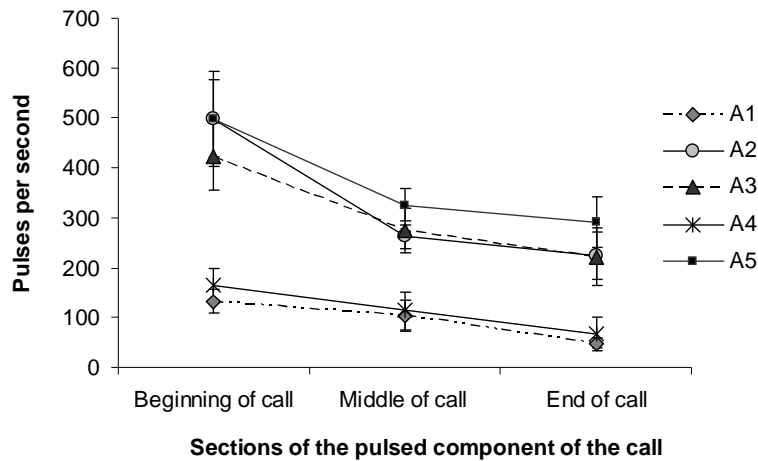
Figure 8. PRR pattern for each of the 5 variants of the Type A call. The two clear groups coincide with the aural similarity of these call variants. The PRR is much more rapid for A3, A2, and A5 than for A1 and A4.
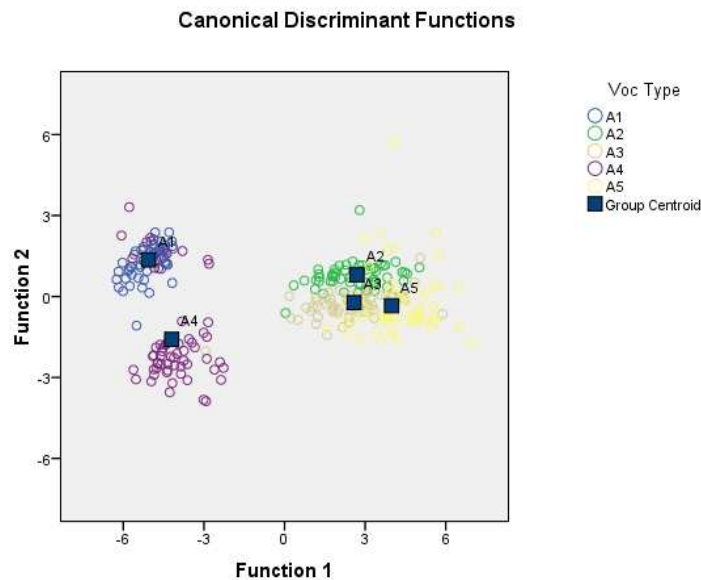

Figure 9. Discriminant function plot. The two axes are the two discriminant functions that represent the most powerful differentiating dimensions. Function 1 represents the repetition rate pattern (initial PRR, middle PRR and end PRR were highly correlated with this function) and Function 2 represents peak frequency (strongly correlated with function 2). The farther apart one point is from another on the plot, the more the dimension represented by that axis differentiates those two groups. Type A1 and A4 tend to be at one end of Function 1 and A2, A3 and A5 at the opposite end, which means that PRR differentiates A1 and A4 from the other 3 vocal types. Although A1 and A4 are hard to distinguish from each other by their PRR only, A1 tends to be higher on dimension 2 (peak frequency) than A4. This makes sense, given that peak frequency often coincides with the tonal component of A1.

Usage of the Type A variants in isolation

We examined the use of these variants by each of 4 belugas recorded in isolation (mostly forced isolation, occasionally voluntary) in one of the contiguous pools (Fig. 10). All four belugas favored the Type A call over other call types when in isolation, using one or more of its variants. Allua, an unrelated female, used only variant A5. Aurora and her two offspring, Qila and Tuvaq, used three, four, and two of the remaining variants respectively, including A1 (the only mixed pulsed/tonal variant). Aurora and Qila used predominantly A3, and Tuvaq used predominantly A1. Data presented for Tuvaq are based on only two isolation events, recorded at 20 and 32 months of age, shortly after his Type A calls had developed full stereotypy (Vergara & Barrett-Lennard, 2008).

Although Aurora's Type A calls as a whole composed 93% of her phonations during 26 isolation events from 2002 to 2010, the A1 variant accounted for only 18.6% of such calls. However, this mixed variant played a more predominant role during most of the vocal sessions when Aurora was alone with her calf after the 2002 birth. From the third day after Tuvaq's birth until the reintroduction of the rest of the social group into the pool 3 months later, A1 comprised 67% of Aurora's phonations (Vergara & Barrett-Lennard, 2008). After the death of her year-old calf Nala, Aurora produced the same variants (A1, A2, A3) as immediately after the birth of her calves, favouring A3, but at over double the rate.

Two or more variants could be produced in the same bout by one animal (Vergara & Barrett-Lennard, 2008), and vocal matching exchanges of the Type A call between two animals consisted of up to 4 different variants in a short (12 s) exchange.
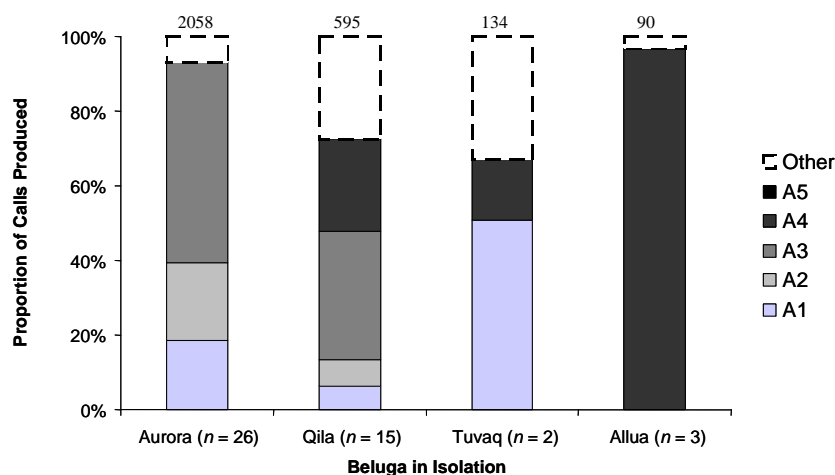

Figure 10. Proportional use of Type A variants and of all other call types combined (white) for each beluga that was recorded in forced or voluntary isolation. The "*n*" between brackets on the X axis is the number of isolation events when the animals were vocal. The numbers above the bars represent the total vocalization count for that individual in isolation.

Development of the Type A1 variant

　　　　Our study on the vocal development of a beluga calf, Tuvaq, from the time of his birth until 3 years of age (Vergara & Barrett-Lennard, 2008) addressed the ontogeny of the pulsed/tonal mixed variant A1. Tuvaq´s mixed call production was minimal during the first three months of his life, and increased dramatically at four months of age. Some of his mixed calls increasingly resembled the stereotyped mixed call A1 of his mother Aurora (Fig. 11). Both the number of inflection points along the whistle component of his mixed calls and its dominant frequency showed a reduction in variability with age (Fig. 12a), indicating progressive stereotypy. Opportunistic recordings of Tuvaq during 2 isolation events at 20 months and 32 months of age revealed that he was producing stereotyped Type A1 calls with parameters strikingly similar to those of his mother and half sister's A1 calls (for further details, refer to Vergara & Barrett-Lennard, 2008).
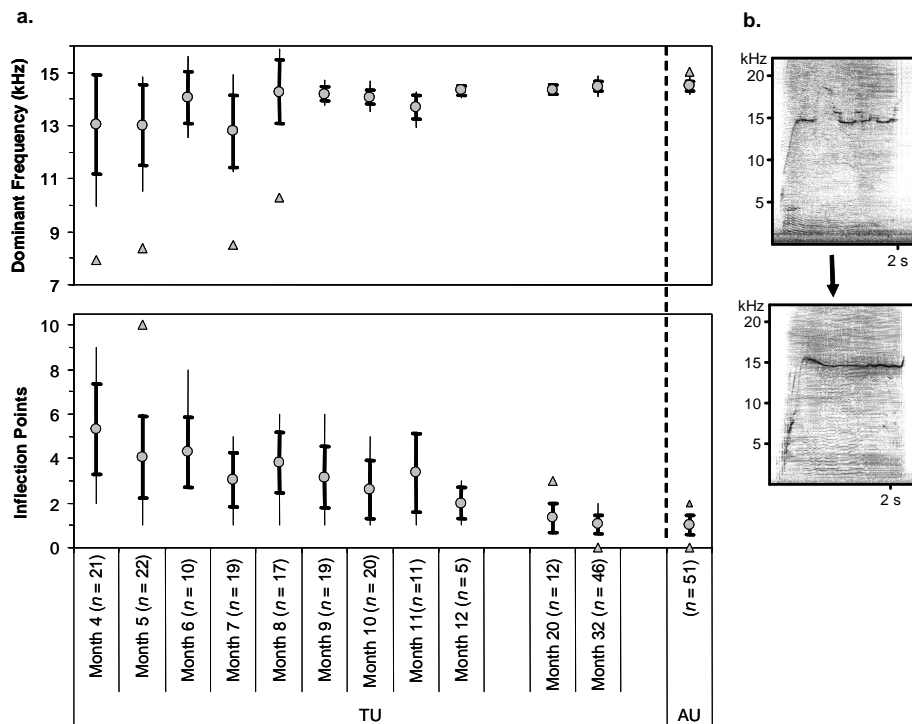
Figure 11. Ontogeny of the Type A1 call. a. Dominant frequency and number of inflection points of the whistle component of the A1 variant for the calf Tuvaq (TU), at the ages when this call type was recorded from him, and for Aurora (AU), his mother, for comparison. For the dominant frequency, the circles represent the means, the thick error bars represent the standard deviations, and the thin bars 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 (adapted with permission from Vergara and Barrett-Lennard, 2008). b. Spectrograms illustrating an immature Type A call produced at 8 months of age (top), with an unsteady whistle component, compared to a mature call at 20 months.

Wild Component

Overview

The captive work described here has generated the following hypotheses about what we might expect in the wild environment: a) wild belugas utilize a specific broadband call type (a "contact call") to maintain contact between individuals and promote group cohesion, and b) females and their offspring may share specific contact call variants which serve a recognition function in large aggregations. Some test predictions include the following: a) the use of contact calls increases when beluga groups are disturbed, broken-up, or when individuals are separated from the group, and b) all other factors being equal, contact call use is highest in nursery groups where it serves to maintain mother-calf contact.

General approaches to testing these hypotheses include recording the vocalizations produced by belugas temporarily isolated from the rest of the social group during trapping and satellite tagging operations, analyzing recordings from wild beluga social groups, and utilizing the playback technique to further investigate the function and mechanisms of these calls. We will next describe two brief, opportunistic studies to validate the existence and function of this call type in wild beluga populations. The first study tests the disturbance/separation prediction. The second confirms the existence of contact calls in wild nursery groups, without formally testing the prediction that this call type is predominant in such groups (the data examined were not collected with this test in mind).

Nelson River Estuary

The use of satellite telemetry and pectoral flipper band tags to study movements and diving behavior of belugas in the last decade has required the temporary live capture and release of a considerable number of animals (Orr, Joe, & Evic, 2001). Operations involving capturing and tagging of wild belugas offer an ideal situation to address questions about contact calls: a controlled behavioral context (temporary restraint and separation from the group), a known primary variable (stress), and information on the sex and estimated age of the isolated individuals. The latter is key in light of the fact that the major challenge for studying the contact calls of free ranging cetaceans rests on the difficulty of identifying the individual vocalizer.

With this in mind, one of us (Vergara) joined a Department of Fisheries and Oceans (Canada) research team to record the isolation calls of temporarily restrained wild belugas in the Nelson River Estuary, Western Hudson Bay (Manitoba, Canada, 57 ° 02' N, 92 ° 28' W), between July 15 – August 2, 2005.

Belugas were captured by herding a small group into shallow water (about 2 m deep) using two zodiacs, and then deploying a seine net from a fast moving jet boat so that it surrounded one whale. The animal was quickly disentangled from the seine net, a hoop net (1.2 m diameter) and a tail rope were placed on it, and the whale was taken carefully to water shallow enough for the capture team to handle

and instrument it. The time elapsed from capture to release ranged from 20 to 35 min. For further details of the capture procedure, see Orr et al. (2001).

Acoustic recordings were made with an Offshore Acoustics hydrophone and a Sony TCD-D100 Digital Audio Tape recorder (this system has a frequency response of 0.02 Hz – 22 KHz + 1 dB). We recorded continuously during the handling and release of each captured whale by placing a hydrophone about 0.5 m deep in the water approximately 2 m from the restrained animal. Simultaneous voice notes were dictated onto a mini-voice recorder.

Two of 6 restrained belugas vocalized, both producing only broad band pulsed calls that sounded to human listeners much like the Type A call described for the captive belugas. Both were 2-3 year old juveniles, a male and a female. We obtained a successful recording of one of the two, the juvenile female, which produced 43 broadband vocalizations in 21 min. Like the captive Type A calls, these signals consisted of loud broadband rapid pulse-trains with a mean duration of 1.8 ± 0.5 s and an average PRR of 103.5 ± 15 pulses per second (average of the PRR at the three locations of each call, see methods). Although the energy was distributed more or less equally throughout the frequency range of the spectrogram, there was average peak energy at 3.18 ± 1.6 kHz ($n = 43$). The interval between calls ranged from 0.7 to 24.1 s, with an average of 4.3 ± 5.9 s. Figure 12 shows an exemplar of one of these calls.
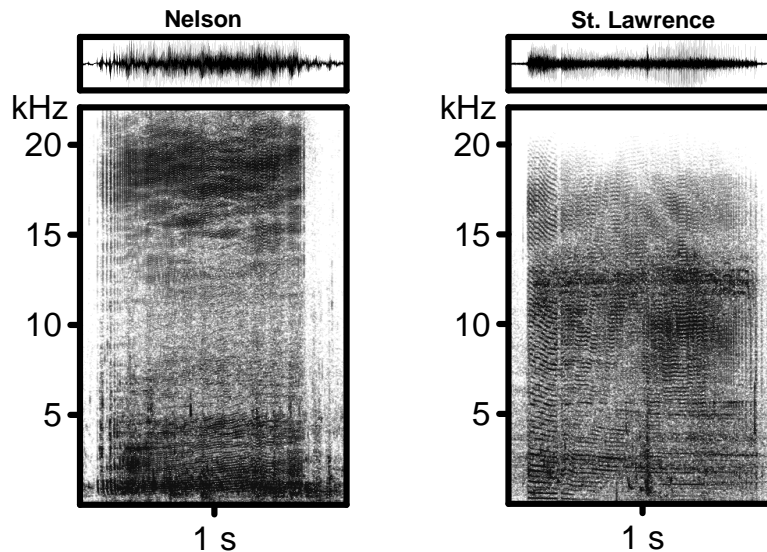

Figure 12. Sample spectrograms (bottom) and oscillograms (top) of the broadband pulsed calls that resemble the captive contact calls both in structure and context, identified in two different wild beluga populations: Nelson River estuary (left) and St Lawrence estuary (right) (FFT length: 1024, frame size: 100%, window: hamming, bandwidth: 56 Hz, overlap: 75 %).

St. Lawrence Estuary

The St. Lawrence Estuary beluga population, recently estimated at 1100 individuals (Hammill, Measures, Gosselin, & Lesage, 2007) is genetically and geographically isolated from other populations (Brennin et al., 1997) and is at the southernmost limit of the species' range. Summer aggregations are separated into herds of males and large nursery groups of females, calves, and juveniles occupying slightly different areas (Michaud, 1993).

To verify whether the Type A call described in captivity is used in wild nursery groups, we reviewed recordings from St. Lawrence beluga social groups of both females and young and adult males obtained in June-September 1999 and June-September 2000. The 1999 recordings were made with an NRD-Q2 omnidirectional, long line hydrophone with a flat response from 0-60 kHz, and a Sony TCD-D10 Pro II digital audio tape (DAT) recorder with a frequency response of 20-22,000 Hz ($\pm$ 1.0 dB). In 2000, recordings were made with Vemco VHLF omnidirectional hydrophone with a flat response from 20 Hz to 22 kHz, and the same Sony digital tape recorder. Acoustic samples were recorded onto the DAT every 30 min for a duration of 3 min in 1999 and 5 min in 2000, as long as whales were sighted within 300 meters from the research platform. We reviewed 112 three-minute sessions and 344 five-minute sessions, for a total of 34 h of recordings.

This call type is easily recognizable both by ear and in spectrograms. The tapes were reviewed by listening while examining the real-time spectrograms in 30 second segments, using Raven 1.3 (Cornell Lab of Ornithology), and this process was performed "blind": the reviewer (Vergara) did not know the contextual behavioral details of the calls during the review process.

We identified 16 events, for a total of 89 calls that resembled, acoustically and spectrographically, the contact calls described for the captive animals. We defined as an "event" the presence of at least one Type A call in a 5-min (2000) or a 3-min (1999) recording session. Overall, Type A calls were identified in 12 out of 299 recording sessions of female and young herds (4%), in 1 of 106 recording sessions of adult male herds (1.9%), and in 1 out of 45 recording sessions of large mixed herds (adult males, females, and young) (2.2%). One event (of one call) was recorded in a session for which herd type was not noted.

Specific behavioral details beyond group composition existed only for one of the 16 events, identified in a 1999 recording of a herd of females and young. This event consisted of a series of 17 calls that had been produced by an adult female swimming around a dead calf and pushing it along (Fig. 13). DNA signatures of both animals are awaiting testing and will reveal if the female was the calf's mother. Her Type A calls had a mean duration of 1.7 $\pm$ 0.3 s, an average pulse repetition rate of 188. 6 $\pm$ 7.6 pulses per second, and average peak energy at 10.6 $\pm$ 2.6 kHz (n = 17). The inter-call interval ranged from 3.4 to 77.6 s, with an average of 20.1 $\pm$ 18.7 s (see Fig. 12).
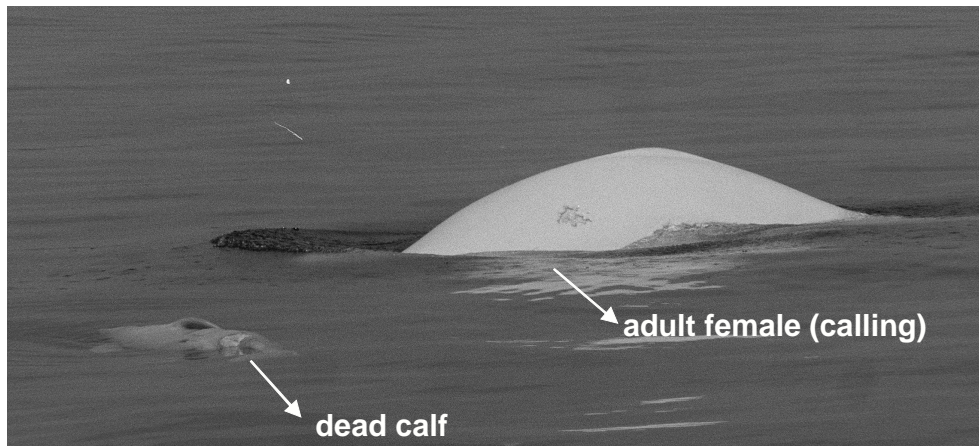
Figure 13. Adult female and dead calf in the St. Lawrence estuary, 1999. A series of 17 Type A calls were recorded from this female as she was staying close to the calf. Photo courtesy of GREMM.

Discussion

This study shows that captive belugas at the Vancouver Aquarium use a particular broadband pulsed call type, referred to as Type A, predominantly during isolation, husbandry and pool-cleaning procedures, re-union of animals after separation, immediately after births and deaths, and in mother-calf vocal exchanges. It is also used in vocal matching exchanges between adults and in some situations (divers in the pool, reunion of animals) during tight synchronous swimming. In other words, this call type appears to be favored in situations where establishing contact and group cohesion are important to the whales. There were variants of this call type within a common template, some of which were shared only by one mother and her two offspring. One of these offspring, the male calf, progressively developed the combined pulsed/tonal contact variant of his mother and older half sister, decreasing variability and increasing stereotypy with age (Vergara & Barrett-Lennard, 2008).

Although our findings about the acoustic behaviour of captive belugas should be interpreted with caution given the small sample size, they warrant some hypotheses about the usage of these signals by their wild counterparts, critical to understanding how these animals function in the vocal domain. They suggest that wild belugas utilize stereotyped broadband pulsed vocalizations as contact calls, that females and their offspring share variants that can serve for long-term recognition, and that calves slowly develop such variants. These hypotheses set the stage for future studies in the wild environment. We initiated such research by verifying the existence of this call type in the repertoire of groups of females and young and adult males in the St. Lawrence River estuary, and documenting its usage by two wild individual belugas from different populations, Hudson Bay and St. Lawrence Estuary, in contexts that further ascertain its function as a contact call.

In identifying the general function of the Type A call as a contact call we can be relatively confident that this category of sound is not a meaningless construct of an arbitrary human categorization scheme, but that it is a category important to belugas. This assertion is reinforced by the fact that Type A calls often occur in adult reciprocal call matching exchanges that fit the description of antiphonal calling for other species (e.g., cotton-top tamarins, *Saguinus oedipus*: Ghazanfar, Smith-Rohrberg, Pollen, & Hauser, 2002; Miller, Iguina, & Hauser, 2005; sperm whales, *Physeter macrocephalus*: Schulz et al., 2008; African elephants: Soltis et al., 2005). The vocal response to a contact call is classified as antiphonal if it consists of the same type of vocalization occurring within a few seconds of receiving the eliciting vocalization (Miller et al., 2005). Since by definition, a sound must be recognized as a specific type of conspecific vocal signal to elicit an antiphonal response (Miller et al., 2005), this behavior further points to the categorical perception of this call type by belugas. There is, however, one caveat: temporally associated signals are not necessarily communicative events (Soltis et al., 2005). Further testing using more formal methods such as randomization techniques (e.g., Miller, Shapiro, Tyack, & Solow, 2004 for killer whales; Schulz et al., 2008 for sperm whales) are underway to determine if Type A calls of different adults are adjacent or overlapping by chance alone, or if an adult is indeed more likely to produce a Type A call after a conspecific call of the same type (Vergara and Barrett-Lennard, in preparation).

This call type may have similar functional significance in other beluga populations. Van Parijs, Lydersen, & Kovacs (2003) recorded sounds produced by belugas during capture events in Storfjorden, Svalbard. The sounds produced by the mother of a captured mother-calf pair were spectrographically similar to the contact calls described here (Van Parijs et al., 2003). We listened to audio files kindly provided by Van Parijs, and confirmed an aural similarity between the broad band pulsed calls emitted by their restrained mother (see Fig. 2 in Van Parijs et al., 2003) and the contact calls we describe here, particularly those produced by the St Lawrence female. A cursory analysis of the first 10 good quality maternal calls from Van Parijs et al. unpublished data (their 2003 paper does not provide parameters specific to these maternal broad band calls in particular, but only in combination with a click train, a different call type), revealed that these were, as our described contact calls, of long duration (1.6 ± 0.6 s), had and an average pulse repetition rate of 145.9 ± 7.6 pulses per second, and energy distributed throughout the entire frequency range of the spectrogram (band limited to 22 kHz, the upper limit of the recording equipment), with average peak energy at 5.7 ± 3.2 kHz (Van Parijs, unpublished data).

The broadband, pulsed structure of beluga contact calls differs from the tonal signals that serve as cohesion calls in bottlenose dolphins, the well studied signature whistles, recorded from captive (e.g., Caldwell & Caldwell, 1965; Janik & Slater, 1998), wild (e.g., Smolker, Mann, & Smuts, 1993) and temporarily restrained animals (Sayigh, Esch, Wells, & Janik, 2007). On the other hand, there is recent preliminary evidence of broadband combined pulsed/tonal contact calls in narwhals, *Monodon monoceros*. Shapiro (2006) recorded the phonations of two

adult male narwhals immediately upon their return to deep water after they had been separated from their groups during a brief period of capture. They both produced broadband combined tonal/pulsed signals, in addition to whistles, that were individually distinctive and may have facilitated their reunion with group members. Shapiro's published spectrograms and parameters of these signals reveal the same general template as the beluga contact calls identified here, although with longer inter-call intervals (A. Shapiro, personal communication, November 30, 2009). Sound clips provided by Shapiro allowed us to verify by ear that the pulsed/tonal signal types produced in particular by one of the animals (individual mm226 in Shapiro, 2006) sound, at least to the human ear, similar to the combined Type A1 call described here, but with a more audible tonal component overlapping the pulse-train. Shapiro reports that these signals had a mean duration of 1.2 s and were characterized by broad band pulses (48 kHz) with PRR of between 148 and 180 pulses per second, and an overlapping tonal component at a lower frequency than our Type A1 call, which is why it is more audible to the human ear.

That narwhals and belugas would favor similarly structured contact calls is not surprising, given the shared environment they evolved in. It has long been known that the structure of signals should reflect selection to facilitate effective transmission in the habitats that they have evolved to function in (e.g., Blumstein & Turner, 2005; Morton, 1975; Richards & Wiley, 1980). The ice filled waters of the arctic create a highly noisy and reverberant environment. The clutter produced by the echoes might make sound perception difficult, reducing a signal's active space, a concept that describes the area in which an individual can detect the calls of a conspecific (Brenowitz, 1982). Some features of the call may have evolved to increase this active space. For instance, the persistent energy at a wide frequency band may help to minimize masking by ambient noise.

The mixed (tonal/pulsed or pulsed/pulsed) structure of some beluga contact call variants - likely produced with the twin phonating apparatuses described by Cranford, Amundin, and Norris (1996) - might enable an individual to distinguish the signal of a familiar individual from signals of other conspecifics in this clutter and in the bustling acoustic environment of the herd. This capacity in relation to the specific structure of contact calls has been well studied in several penguin species (e.g., Aubin, 2004; Jouventin & Aubin, 2002; Lengagne, Aubin, Jouventin, & Lauga, 2000; Robisson, 1992; Robisson, Aubin, & Bremond, 1993). Of most relevance here is the finding that two non-nesting species of penguin, the emperor penguin (*Aptenodytes forsteri*) and the king penguin (*A. patagonicus*), which rely solely on acoustic cues, and not on landmarks, to reunite with their mate in a noisy colony of thousands of mobile birds, use their two-voice system to recognize each other (Aubin, Jouventin, & Hildebrand, 2000; Lengagne, Lauga, & Aubin, 2001).

In addition, vocal behavior and signal design should reflect a trade-off between maximizing signal efficacy while minimizing conspicuousness to eavesdroppers (Bayly & Evans, 2003). The risk of being overheard by their acoustically sensitive predators, killer whales *(Orcinus orca)*, may also reflect on the features of beluga contact calls. There is evidence from two cetacean species

that higher frequency elements of calls are more directional than lower frequency components (Lammers & Au, 2003 for spinner dolphins; Miller, 2002 for killer whales). The relatively high frequency tonal component of the pulsed/tonal variant A1 might provide directional cues so that individuals could efficiently locate each other over short distances, but, since the higher the frequency the more rapid the attenuation of sound in water (Au & Hastings, 2009), it would attenuate quickly, decreasing the chances of eavesdropping by distant killer whales. However, without proper propagation experiments, speculating further on the possible advantages of the kind of contact call structure we have described for belugas would be premature at this point.

Lastly, it is important to take into account that a considerable portion of the beluga vocal production consists of whistles. In fact, several studies from different geographical areas that have classified the beluga repertoire found that whistles were the most common signal type (Bristol Bay, Alaska: Angiel, 1997; White Sea, Russia: Belikov & Bel'kovich, 2007; Svalbard, Norway: Karlsen et al., 2002; Cunningham Inlet, Canada: Sjare & Smith, 1986). The contact calls we identified in this study are pulsed, but the possibility that the signal type described here is just one of several phonation types that might play a role as cohesion calls should remain open.

Let us now turn to our finding that contact calls comprise clearly identifiable variants. This is in line with evidence of contact call variants in other species. For example, orange-fronted parakeets and budgerigars produce several different contact call variants, but favor one or two dominant types per bird (Cortopassi & Bradbury, 2006; Farabaugh et al., 1994). Bottlenose dolphins are also known to produce more than one signature whistle type per dolphin. The prevailing explanation for this phenomenon, at least for male dolphins, is that individuals will share whistle types with closely allied social partners (Smolker & Pepper, 1999; Watwood et al., 2004).

The five variants of the Type A call identified in this study do not appear to have an individual signature function. Only one animal, Allua, an unrelated female, adhered to one variant type alone, but she was only recorded in isolation three times, so this is inconclusive. The remaining variants were shared between the three related individuals. The possibility remains, of course, that even if each particular variant per se is not an individual signature, each variant could have identity coding based on some parameters. We have not yet explored this possibility.

Why, then, these variants? Are they biologically meaningful? The common thread of the situations when Type A calls were favored was a need to establish or maintain contact. However, a number of different variables could have called for different messages or elicited different levels of arousal, such as the distress induced by the death of a calf (wild and captive) or by live-captures (wild) and veterinarian procedures (captive), alarm at the intrusion of divers in the tank, or the need for rapidly forging an acoustic bond with a newborn calf in an aquatic environment. There is evidence that species vary the rate or number of times a particular call type is emitted, its intensity and even its acoustic structure in

response to different degrees of risk or predator types (e.g., alarm calls of three marmot species, *Marmota* sp.: Blumstein, 1999; of white-browed scrubwren, *Sericornis frontalis*: Leavesley & Magrath, 2005; and of suricates, *Suricata suricatta*: Manser, 2001), stress (e.g., signature whistles of bottlenose dolphins: Esch, Sayigh, Blum, & Wells, 2009), or need (e.g., separation calls of domestic piglets: Weary & Fraser, 1995). It is conceivable that variant types and repetition rates of beluga contact calls are associated with urgency, distress, need, or alarm. Aurora produced the same variant types after the death of her year-old calf Nala as after the births of the same and an earlier calf, but at double the rate. The acoustic dimension made a critical difference in our perception of maternal distress (there was nothing particularly obvious in her non-acoustic behaviour that indicated distress).

As previously proposed (Vergara & Barrett-Lennard, 2008), the pulsed/tonal variant, A1, may play an important functional role in mother-offspring recognition. Aurora used this variant predominantly when she was alone with her calf Tuvaq from the 3rd day after his birth until the re-introduction of the rest of the whales 3 months later (Vergara & Barrett-Lennard, 2008). Tuvaq and his half-sister Qila shared this mixed variant, and we have documented its clear ontogeny. Tuvaq did not emit these stereotyped contact calls at birth, but rather produced unstereotyped pulse trains and rudimentary whistles (Vergara & Barrett-Lennard, 2008). Additional data on two calves born at the Vancouver Aquarium in 2008 and 2009 confirm that calves are not born "knowing" these contact calls (McKillop, Vergara, & Barrett-Lennard, unpublished data), and must learn them. A1 was the first call for which we documented full stereotypy, past a year of age.

The combination of early mobility and extended dependence, invoked to account for the development of a mother-offspring recognition system in bottlenose dolphins (Tyack, 2003), might generate the same strong need in belugas. Indicative of the long-lasting mother-calf bond in belugas is the prolonged lactation period, which may last 24 months in the wild (Brodie, 1971; Drinnan & Sadleir, 1981), and longer in captivity. At the Vancouver Aquarium, Tuvaq nursed from his mother until he was three years old, and also from his half sibling and from an unrelated female, both of whom began lactating despite not having calves of their own (Leung, Vergara, & Barrett-Lennard, 2010). The maternally-directed philopatry evidenced by genetic studies (Brennin et al., 1997) is also indicative of the long-lasting mother-calf bond. It may be important for young belugas to travel with their mothers for a period of several years to learn the migration route, the overwinter areas, where to eat, and where to spend the summer (Brennin, 1992), amongst other skills (e.g., maternal skills). In view of this, our captive findings suggest that wild beluga mothers and their offspring may share contact call variants that could serve for long-term acoustic recognition amongst large aggregations of females and young, a testable hypothesis.

A final, but not least important, consideration regarding contact call variants is the captive observation that one animal could produce up to three of these variants in the same vocal bout, or that four variants were produced in a brief (e.g., 12 s) vocal exchange between two animals. This greatly exacerbates the

problem of assigning context to the variants, and hints at the possibility that these within-category distinctions may not be biologically meaningful. Perceptual experiments are essential to answer whether these variants are perceived categorically by the whales; playback experiments of these variants might reveal functional differences if they elicit sufficiently different responses (see Teixidor & Byrne, 1999).

Future research

Although we successfully recorded only one temporarily restrained wild beluga, her unequivocal vocal response not only validated the captive results, but is also in agreement with a similar study on temporarily restrained whales by Van Parijs et al. (2003). Given the prevalent use of satellite telemetry, there is much to be gained by ensuring that acoustic recordings are a standard protocol of beluga tagging operations, especially those operations that take place in the same area year after year. An example of this approach is the excellent body of data on signature whistles that resulted from acoustic recordings of temporarily restrained dolphins in Sarasota, Florida (Esch et al., 2009; Fripp et al., 2005; Sayigh et al., 1990, 1995, 1998, 2007; Watwood et al., 2004, 2005). For example, based on our captive data, we predicted that females and their calves may share specific contact call variants used for recognition. The sort of data needed to test this prediction could be obtained by recording temporarily restrained mother-calf pairs, or temporarily restrained mothers whose calves are swimming near-by, as is often the case during these operations (J. Orr, personal communication, July 2005).

Jointly, results from the captive and wild components of this study have provided reasonable certainty about the structure of beluga contact calls. Simply put: we now know what beluga contact calls sound like, and we may begin to refine the details of their function. The playback technique has been widely used to study specific aspects of contact calls, such as whether kin selectively answer each other's contact call barks in baboons, (Cheney et al., 1996), long term vocal recognition in fur seals, *Callorhinus ursinus* (Insley, 2000), responses to family vs. strangers' infrasonic contact calls in African elephants (McComb, Moss, Sayialel, & Baker, 2000), and individual recognition in bottlenose dolphins (Sayigh et al., 1998). The tendency, in captivity, for the Type A calls to elicit calls of the same type from conspecifics makes them ideal candidates to utilize a playback technique in order to further investigate the function and mechanisms of such calls in the wild. To our knowledge, only one playback study exists that broadcasted beluga calls to free-ranging belugas (Morgan, 1979). A two-week pilot study in the summer of 2008 in the St. Lawrence Estuary helped us begin to elucidate the appropriate and realistic design required for playback studies with free ranging belugas (Vergara, Michaud, & Barrett-Lennard, 2009, unpublished manuscript).

Lastly, propagation experiments of this signal type and an evaluation of how habitat acoustics might be related to the transmission of these signals are needed (e.g., Lammers & Au, 2003 for spinner dolphins; Mercado & Frazer, 1999; Mercado et al., 2007 for humpback whales). This species evolved in the arctic

environment. In their recent review of signal propagation in the Arctic, Au and Hastings (2009) emphasized that the uniqueness of the environmental conditions in the Arctic reflect on unique sound propagation characteristics. In addition, proper testing of the propagation properties of the Type A calls would require wider band recordings, since our findings are mostly band-limited to 22 kHz (48 kHz for A1, A4, and A5, see results).

In many locations, belugas and other marine mammals are faced with alarming degrees of noise pollution from human activities. It is difficult to evaluate the consequences of the interference of noise on sound production and reception without understanding the specific function of such sounds, and this understanding has been enhanced by captive work. By continuing to shed light on the characteristics and functions of beluga calls, we may use changes in the type and rate at which such vocalizations are emitted to evaluate not only how the whales respond to various kinds of human disturbances, but also to assist such things as assessments of group composition. For instance, the notable predominance of the contact calls described here during all three captive births and their role in mother-calf vocal exchanges – coupled with our recent an ongoing familiarity with what beluga calves sound like, might enable us to predict the presence of young calves in a group simply through bioacoustic monitoring. By the same token, captive work means little if we do not validate the results with "real life" data – as we attempted to do here. In sum, it is clear that a fluid exchange between captive and wild research is crucial for a more integrated picture of beluga communication.

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