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A STUDY OF BELUGA (DELPHINAPTERUS LEUCAS) VOCAL ONTOGENY

by

Audra Elizabeth Ames

A Dissertation Submitted to the Graduate School, the College of Education and Human Sciences and the School of Psychology at The University of Southern Mississippi in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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ABSTRACT

There is a shortage of literature regarding beluga (Delphinapterus leucas) vocal ontogeny, as presently, there has only been one published study on the vocal development of beluga calves, despite the value of ontogenetic studies for our understanding of sound-centered species. Here I offer the second longitudinal study of beluga vocal development. Using a calibrated digital hydrophone with a sampling rate of 256 kHz, I studied the vocal progression of a male beluga calf in early life. From his first day, the calf produced broadband pulse trains with upper frequency limits extending past the study's Nyquist frequency (128 kHz); higher than what was initially reported in studies limited by lower sampling rates. Pulse signals were the most common sound type in the calf's vocal repertoire during his first year. Mixed calls were produced in month one but were rare overall and not regularly produced until the calf's fifth month of life. Tonal production was also infrequent and not apparent until month four. Over the calf's first month of life, pulse repetition rate, source level, and third quartile frequencies of the calf's pulse trains increased significantly. First and third quartile, center, and peak frequencies increased significantly over the first year, as did pulse repetition rate and call duration. In his second year of life, the calf developed a contact call that was most similar to his mother's, analogous to the contact call acquisition of other beluga calves. Parallel findings from this and previous studies imply species-specific trends in vocal development.

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DEDICATION

In memory of Dr. Stan Kuczaj, my friend and mentor. You are truly missed.

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LIST OF ABBREVIATIONS

ATSS	Abbreviated tonal sweep series
PRR	Pulse repetition rate
SLE	St. Lawrence River Estuaries

CHAPTER I - INTRODUCTION

The beluga vocal repertoire

Beluga whales (*Delphinapterus leucas*) are considered one of the most vociferous cetacean species. Yet despite their known vocal nature, there is a dearth of literature across many areas of information pertaining to the beluga communication system. Descriptive studies of beluga signals encompass much of our current understanding of beluga communication (e.g., Belikov & Bel'kovich, 2006, 2007, 2008; Chmelnitsky & Ferguson, 2012; Fish & Mowbray, 1962; Garland, Castellote, & Berchok, 2015; Karlsen, Bisther, Lydersen, Haug, & Kovacs, 2002; Panova, Belikov, Agafonov, & Bel'kovich, 2012; Schevill & Lawrence, 1949; Sjare & Smith, 1986a). These studies, however, tend to lack information regarding the functional significance of the calls they describe.

Beluga emissions fall along a continuous spectrum of tonal and pulse sounds although the beluga vocal repertoire can generally be classified into several primary sound categories. These include echolocation clicks, or the sonar signals belugas use to navigate their environment and capture prey, and the more communicative signals: 1) tonal sounds, 2) pulse sounds, and 3) mixed calls. Tonal sounds (often referred to as whistles) are narrowband, frequency modulated signals that are generally used in social contexts. Sjare and Smith (1986b) noted that beluga tonal sounds were more common in contexts of rest, travel, or social interaction as opposed to situations of alarm. Some tonal sound types are believed to be used for short distance communication while others are believed to be used over longer distances (Belikov & Bel'kovich, 2006; Panova et al., 2012). Karlsen et al. (2002) found instances of both whistles and pulse calls in contexts of travel or social interaction. Pulse sounds are generally comprised of broadband packets of non-echolocation clicks or pulses that are often classified based on pulse repetition rate, or number of pulses per second (e.g., Belikov & Bel'kovich, 2008; Chmelnitsky & Ferguson, 2012; Sjare & Smith, 1986b). Mixed calls, sometimes referred to as biphonations or combined calls, are sounds that commonly contain overlapped pulse and tonal components. However, some mixed calls may also be characterized by other combinations of overlapping components such as two pulse sounds of varying repetition rate produced simultaneously (Karlsen et al., 2002; Vergara, 2011; Vergara, Michaud, & Barrett-Lennard, 2010).

It has been established that some distinctive broadband long-duration pulsed calls are beluga contact calls, or signals used to maintain or restore contact between conspecifics, including related individuals like mother-calf dyads (Van Parijs, Lydersen & Kovacs, 2003; Vergara et al 2010). Contact calls are perhaps the most well-studied contextually specific call in the beluga vocal repertoire as these calls appear to serve key biological functions (Mishima et al., 2015; Morisaka, Yoshida, Akune, Mishima, & Nishimoto, 2013; Panova, Belikov, Agafonov, & Bel'kovic, 2017; Vergara & Mikus, 2018). Simple contact calls are comprised only of broadband pulses with no additional overlapping component (Vergara & Mikus, 2018) and have been described for captive beluga social groups (Mishima et al., 2015; Morisaka et al., 2013) and for a wild mothercalf pair (Van Parijs et al., 2003). Additionally, Van Parijs et al. (2003) described a mixed contact call that contained both pulse and tonal components. These mixed contact calls are referred to as complex contact calls (Vergara & Mikus, 2018) and again, have been described for both captive (Panova et al., 2017) and wild belugas (Vergara & Mikus, 2018).

There is a growing body of literature evaluating the potential for individual specificity embedded in contact calls through voice cues (Mishima et al., 2015; Morisaka

et al., 2013) or vocal signatures (Panova et al., 2017; Vergara & Mikus, 2018). Examples of individuality related to voice cues are evident in the subtle distinctions of simple contact calls (i.e., pulse repetition rate, Mishima et al., 2015; Morisaka et al., 2013), likely a result of morphological differences between whales producing these sounds (Boughman & Moss, 2003; Vergara & Mikus, 2018). The overlapping component of complex contact calls is a more obvious individual specifier and believed to be a vocal signature that may encode identity individually or shared with closely related animals (Vergara & Mikus, 2018).

What can ontogenetic studies tell us?

To date, there is only a single ontogenetic study describing the development of the beluga vocal repertoire (Vergara & Barrett-Lennard, 2008). Vergara and Barrett-Lennard (2008) studied the vocal development of a male beluga calf (Tuvaq) throughout his first year of life, and opportunistically thereafter until the calf's 32nd month. Findings generated from such seminal works are vital in establishing human understanding of cetacean communication systems and are often the base of knowledge for future research. For example, Vergara and Barrett-Lennard (2008) noted contextual cues associated with a call (type A) produced by the study's focal mother, Aurora. Later, this call type was reviewed in greater detail (Vergara et al., 2010), and determined to be a contact call based on its use in contexts of isolation, birth, death, the presence of external stressors, and group reunions. Similar contact calls have been identified in wild populations during analogous contexts (Churchill River, Canada, Chmelnitsky & Ferguson, 2012; Storfjorden, Svalbard, Van Parijs et al., 2003; Nelson River and St. Lawrence Estuaries, Canada, Vergara et al., 2010).

Vergara and Barrett-Lennard's (2008) contextual association of the type A call during their study of vocal ontogeny was fundamental in elucidating the function of this biologically critical call. Studies of vocal ontogeny are an excellent source of information regarding aspects of sound that are salient to the more verbose animal taxa. For example, it is likely that the vocal repertoires of neonates are initially comprised of sounds that are key to survival. Moreover, following the progression of sound production in young animals may illuminate a species' ability to vocally learn.

Vocal learning is a form of social learning by which animals' vocal development is influenced by the surrounding auditory environment (Nottebohm, 1972), and has likely evolved in gregarious species with complex communication and environmental constraints that disallow the maintenance of visual contact over periods of time (Janik, 2014). Theoretical framework regarding two key processes of vocal learning, vocal production and contextual learning, has been widely established in the literature (Boughman & Moss, 2003; Janik & Slater, 1997, 2000). Production learning is the process by which an individual modifies an aspect of their vocal repertoire based on sounds that are available in the acoustic environment (Janik & Slater, 2000). Production learning has been abundantly described in the human and bird literature (for review, see Boughman & Moss, 2003; Kroodsma & Baylis, 1982; Soha & Peters, 2015; Tyack, 2016). In nonhuman mammals, it has been noted in African savannah elephants (Loxodonta africana Poole, Tyack, Stoeger-Horwath, & Watwood, 2005), Indian elephants (*Elephas maximus indicus*; Holden, 2006), primate species (e.g., chimpanzees, Pan troglodytes, Crockford, Herbinger, Vigilant, & Boesch, 2004; orangutans, Pongo spp., Wich et al., 2009), pinnipeds (for review, see Reichmuth & Casey, 2014), bats (for review, see Knörnschild, 2014) and cetaceans. Evidence of production learning ascribed

to cetaceans includes the humpback whale song (*Megaptera novaeangliae*, Janik & Slater, 1997, 2000; Tyack, 2008; Tyack & Sayigh, 1997), spontaneous mimicry in belugas (Eaton, 1979; Ridgway, Carder, Jefferies, & Todd, 2012), incorporation of novel sounds in bottlenose dolphin (*Tursiops truncatus*) repertoires (e.g., Caldwell & Caldwell, 1972; Reiss & McCowan, 1993; Richards, Wolz, & Herman, 1984), and cross dialectchanges (Crance, Bowles, & Garver, 2014) and mimicry (Foote et al., 2006) in killer whale (*Orcinus orca*) calls. Vergara and Barrett-Lennard (2008) cautiously provided evidence of beluga production learning through Tuvaq's adaptation of his father's calls once his father was re-introduced to the social group. The authors could not entirely rule out genetic relatedness and maturational process in the acquisition of this novel call, however.

The importance of production learning in vocal development is evident through the acquisition of vocal signatures in some young animals. For example, the acoustic environment seems to largely influence the development of signature whistles in bottlenose dolphin calves (e.g., Caldwell & Caldwell, 1979; Fripp et al., 2005; Miksis, Tyack, & Buck, 2002; Sayigh, 1992; Tyack & Sayigh, 1997; Tyack, 1997). Often, dolphin calves develop signature whistles that resemble other sounds in their environment (Bojanowski et al., 2000; Caldwell & Caldwell, 1979; Fripp et al., 2005; Miksis et al., 2002; Tyack, 1997; Sayigh, 1992; Tyack & Sayigh, 1997) as calves in managed-care have been known to model marking stimuli (e.g., whistles used by trainers to bridge a behavior prior to reinforcement, Miksis et al., 2002; Sayigh, 1992; Tyack, 1997) or sounds produced by unrelated social group members (Caldwell & Caldwell, 1979; Tyack & Sayigh, 1997). When other acoustic models are available in a dolphin calf's environment, calves often incorporate that model over developing signature whistles that are similar to their mothers (Fripp et al., 2005; Sayigh, 1992; Tyack, 1997). The inclusion of sounds from alternative stimuli or non-related conspecifics into a calf's repertoire is a distinguishing factor in determining the influence of production learning on call development.

Contextual learning involves learning to associate existing vocalizations with a particular function (Janik & Slater, 1997, 2000), and is somewhat difficult to study in underwater species as identifying the function of a sound requires a researcher's ability to associate behaviors of a signaler and recipient during a sounds' production. Several cetacean species have shown the propensity to use sounds contextually. For example, as reviewed above, belugas produce contact calls in separation contexts (Vergara et al., 2010). Likewise, sperm whales (*Physeter macroephalus*) use codas (stereotyped click patterns) to maintain contact with conspecifics. (Schulz, Whitehead, Gero, & Rendell, 2008; Watkins & Schevill, 1977). Bottlenose dolphins produce signature whistles in order to maintain group cohesion (Caldwell & Caldwell, 1965; Tyack, 1986; Janik & Slater, 1998), brays during foraging (Tursiops truncatus, King & Janik, 2015), pops when herding (Tursiops aduncus: Connor & Smolker, 1996; Vollmer, Hayek, Heithaus, & Connor, 2015), and thunks during mother-calf separations and/or discipline events (Tursiops truncatus: Ames et al., 2017; McCowan & Reiss, 1995a). While these are strong cases for cetacean ability to contextually use sound, there is still little information regarding how young cetaceans learn to pair species-specific sounds with an appropriate context.

Vocal learning studies in more controlled settings offer some insight into the contextual learning process. For example, preliminary evidence of object/signal association in a beluga indicate that the species can be trained to understand the

relationship between context and sound (Murayama et al., 2012). Shapiro, Slater, and Janik (2004) demonstrated clear contextual learning in grey seals (*Halichoerus grypus*) by showing that two young animals could be trained to produce a call type in accordance with presented stimuli. Grey parrots (*Psittacus erithacus*) can also be trained to use novel sounds (e.g., human speech) referentially (for review, see Pepperberg, 2010). Training in experimental settings implies that animals are reinforced for correct effort, and thus may contextually learn through a reward system. It is unclear whether some type of social reward is present in natural interactions with conspecifics that may shape a signal's contextual association for a young animal, especially in the aquatic setting. But, longterm studies of vocal ontogeny in controlled environments where animals can be observed interacting present key opportunities to study these processes more in depth.

Species-specific patterns of development

Given that there is only one existing published study on beluga vocal development (Vergara and Barrett-Lennard, 2008), we know very little about speciesspecific trends in vocal ontogeny and sound acquisition. Behaviorally, beluga calves follow similar trends in development, although there are individual differences between calves (Hill, 2009; Hill, Campbell, Dalton, & Osborn, 2013). It would be useful to determine if the original findings by Vergara and Barrett-Lennard (2008) indicate species-specific vocal ontogenesis by comparing sound acquisition and development of the study's focal calf (Tuvaq) to the vocal development of additional beluga calves.

Moreover, additional information is required in order to adequately assess contact call development in belugas. The ontogeny of Tuvaq's complex contact call suggested that beluga calves develop contact calls that are similar to their mothers (Vergara and Barrett-Lennard, 2008). Tuvaq began to produce rudimentary versions of his mother's A1 call in his fourth month of life, continually developing the call until it was fully incorporated into his repertoire in month 20. However, it is unknown whether all beluga calves begin to acquire complex contact calls in the first year of life and if all calves first develop contact calls that resemble the call types of their mothers.

Belugas are highly social animals, with variation in movement and group membership in wild populations (Colbeck et al., 2013; O'Corry-Crowe, Suydam, Rosenberg, Frost, & Dizon, 1997). They may travel great distances between seasons, migrating to and from summering and wintering sites (e.g., Colbeck et al., 2013; Hobbs, Laidre, Mahony, & Eagleton, 2005; Suydam, Lowry, Frost, O'Corry-Crowe, & Pikok, 2001). Site-fidelity has been observed across related whales that return to the same summering habitats for up to 20 years (O'Corry-Crowe et al. 2018). Related belugas appear to maintain close associations along migration routes and within summering areas (Colbeck et al., 2013; O'Corry-Crowe et al. 2018), and matrilineal units of females, calves, and older female offspring constitute the large summering herds (Palsbøll, Heide-Jørgensen, & Bérubé, 2002; Smith, Hammill, & Martin, 1994). Periodically, individuals separate or rejoin social groups, creating some fluctuation in group composition (Alekseeva, Panova, & Bel'kovich, 2013; Bel'kovitch & Sh'ekotov 1993; Krasnova, Chernetsky, Zheludkova, & Bel'kovich, 2014), indicative of a fission-fusion society. Belugas are an aquatic species, which means that individuals must be able to communicate over great distances or when visual acuity is otherwise limited in order to facilitate reunions with kin. In the presence of other animals, it may be easy for important signals to get lost in noise (Janik, 2005). Consequently, belugas may develop some call types that allow them to maintain social bonds across large distances and identify kin among a number of conspecifics.

8

Beluga calves and anthropogenic noise

Arguably a critical piece to our understanding of beluga vocal development concerns characteristics of calls that may be vital to calf survival; namely, changes in call parameters that may indicate when young belugas can compensate for noise in their environment. Beluga populations inhabit Arctic and sub-Arctic waters. Anthropogenic, or human-made, noise continues to increase in these environments due to shipping, seismic exploration, offshore drilling, military operations, and construction (Erbe, 1999; Erbe, Reichmuth, Cunninham, Lucke, & Dooling, 2015; Erbe & Farmer, 1998), and is a pervasive concern regarding the welfare of marine life that reside in or use affected habitats. Noise can alter animal behavior (for review, see Nowacek, Thorne, Johnston, & Tyack, 2007), impact animal physiology (e.g., Rolland et al., 2012), and interfere with sounds marine mammals use to forage, navigate and communicate (Clark et al., 2009). Thus, noise can have deleterious consequences for the acoustic systems of marine mammals, and specifically, vessel noise has been a target of interest in the cetacean literature due to the severe impact of vessel noise on these sound-centered species.

Current study

Studies of beluga vocal development can provide valuable insight regarding species-specific ontogenetic trends and the development of biologically critical vocalizations. We can determine similarities in sound acquisition, parameter changes, and contact call development through comparing the focal calves of different studies. Furthermore, we can glean insights into more pervasive issues affecting wild belugas, like the effects of noise on neonate calls. In addition, the original study on beluga vocal ontogeny (Vergara and Barrett-Lennard, 2008) was limited to the lower sampling rates of the equipment available at the time of the study. More recent investigations of vocal development that are able to employ new technologies and subsequently, higher sampling rates, are thus necessary in order to explore the upper frequency limits of odontocete calf calls that may extend past predominant vessel noise frequency bands.

The aim of the proposed study was to build on the current vocal ontogeny literature by further exploration of the above topics as they relate to beluga vocal development. Specifically, the current report sought to answer the following questions: 1) what can we infer regarding the beluga communication system through studying and comparing the vocal development of beluga calves? 2) What more can we understand regarding complex contact calls? 3) Finally, how are the calls of beluga neonates affected by noise? I sought to answer these questions by conducting the second long-term observational study of beluga vocal development, beginning prior to the birth of a calf and continuing through his first two years of life.

CHAPTER II - METHODOLOGY

Subjects and Sampling

The subjects of this study were three belugas housed at Oceanogràfic, a managed care facility in Valencia, Spain. The subjects included Kylu, a calf born at Oceanogràfic on November 15th, 2016, Kylu's mother, Yulka, and father, Kairo. Yulka and Kairo are both wild-caught belugas of Russian origin, although it is unclear which populations as there are gaps in the known histories of these animals prior to arriving to Oceanogràfic in 2003. Presently, Yulka is believed to be around 20 years of age and Kairo is believed to be in his mid-fifties. Kairo was separated from the calf until the eighth month of life when physical introductions of Kairo and Kylu began.

Data recorded for this study consisted of underwater hydrophone recordings (see hydrophone details below) paired with simultaneous behavioral observations. Pre-partum data were recorded from September 10th, 2016 to the calf's birth on November 15th, 2016. Approximately 80 hours of data were recorded for this period. First year of life recordings began on the day of the calf's birth and continued until the calf's first birthday, at which point recordings for the second year of life began. Special emphasis was placed on data collection during Kylu's first month of life as this period of development is critical to the survival of beluga infants. As such, 79 hours of data were recorded during the calf's first month of life. An additional 129 hours were recorded over the remaining 11 months, for a total of 208 hours over the first year of life. Roughly 54 hours were recorded for the second year. See Figure 1 for a timeline of important dates related to the study. Complex contact call production in the pre-partum period and second year of life were included in this study, however the current study primarily focuses on sound production and development in the first year of Kylu's life. The Institutional Animal Care and Use Committee's approval (The University of Southern Mississippi, protocol number: 16041402) and approval from the Animal Care and Welfare Committee (project reference OCE-9-16, OCE-14-18) relating to the application for use of animals at Oceanogràfic were obtained for the completion of this study.



Figure 1. Timeline of key study dates.

Acoustic Recordings

All sound analyses were conducted in Raven Pro 1.5, 64-bit version (Cornell Lab of Ornithology) using a Fourier Transform size of 1024 points, an overlap of 50%, 1024 samples, and Hann window. Underwater recordings were obtained with calibrated digital hydrophones. An icListen HF (Ocean Sonics, Great Village, N.S., Canada) was the primary hydrophone deployed for the entirety of the study, sampling at a rate of 256 kHz with 24-bit resolution and sensitivity of -171 dBV re 1 µPa. During the course of the study, the icListen was deployed in a semi-permanent installation in the main beluga pool or in the reproduction pool, depending on the location of the calf. Figure 2 illustrates the dimensions of the beluga pools at Oceanogràfic with the semi-permanent installations

clearly marked. All pools in the habitat are five meters deep, except for the medical pool which is two meters deep.

A second calibrated digital hydrophone became available sporadically for use over the course of the study. Simultaneous deployment of a SoundTrap HF300 (Ocean Instruments, Auckland, New Zealand) occurred over several periods, allowing for more frequent localization of the vocalizing individuals. The SoundTrap was deployed at a sampling rate of 288 kHz with 16-bit resolution and a clip level of 172 dB re 1 μ Pa. During these periods of simultaneous deployment, the icListen was deployed in the main beluga pool while the SoundTrap was deployed in the reproduction pool. The timeline illustrated in Figure 1 includes the periods during the calf's first year of life when the two hydrophones were deployed together.



Figure 2. Oceanogràfic's beluga habitat pools.

The red "X" marks the semi-permanent hydrophone installations. The remaining features include: A) The poolside observation areas, B) the trainer's office, C) the medical pool, D) the reproduction pool, E) the main beluga pool, F) the public viewing area, G) training platforms (jet floats), and H) decorative rock features in the pool. Values in red are pool dimensions in meters.

Behavioral Observations

All behavioral observations were recorded in Timestamped Field Notes, an iPhone application that applies the time in hours, minutes, and seconds to an entered observation. The time codes for both digital hydrophones were synced with the time displayed by the iPhone prior to deploying the hydrophones so that the time stamps of the underwater recordings and the behavioral observations would be the same. Detailed behavioral observations could be generally grouped into one the following categories:

1) Animal orientation and distance relevant to the position of the

hydrophone(s). Pool position and orientation of the belugas were consistently noted so that vocalizing individuals could later be identified. Distance of an individual from the hydrophone was also included when deemed necessary (e.g., when an animal was at source level distance, or 1 m, from the hydrophone).

- Vocal information. This included observation of bubble stream emission from the calf and signaler identification when calls could be heard from the surface and localized to a beluga.
- 3) Separations. Both voluntary and involuntary separations were recorded. Voluntary separations occurred when either the calf or the mother left the dyad for a period of time. Involuntary separations included the gating, or removal of an individual to another pool, including the medical pool for medical procedures, or the temporary restraint of a beluga by animal care staff. Temporary restraint by trainers occurred frequently during Kylu's early life as he was hand-raised, requiring several daily feedings during which he needed to be held. When any type of separation occurred, the beluga(s) that

was being separated or that was responsible for the separation was recorded in addition to the duration of the separation and the animal responsible for the reunion if the separation was voluntary.

- On session. When any of the animals were in training sessions, the belugas involved and start, and end time of the session were recorded.
- 5) Play. All instances and types of play were recorded for both Kylu and Yulka (Kairo was not especially active or playful during the study given his age). This included:
 - a. Object play- when a beluga interacted with a toy in the pool or pool feature (e.g., training platforms, gates, hydrophone installations).
 - b. Bubble play- when a beluga could be seen visible producing bubbles and interacting with their own or another beluga's bubbles.
 - c. Motor play- when a beluga manipulated an aspect of its body. This manifested itself most commonly in contraction/release movements in the melon, mouth movements, bouncing the head up and down rapidly in a nodding motion, and breeching/porpoising.
 - d. Water play- when a beluga "spit" or splashed water.
 - e. Trainer play- when a beluga was in play or enrichment session with trainers.
 - f. Social play- when belugas were playing together or when Kylu would interact with harbor seals (*Phoca vitulina*) that were temporarily housed in the beluga habitat for some of Kylu's development.
 - g. Solitary play when Kylu was playing on his own.

- 6) Aggression/Aggravation. Obvious aggressive behaviors included jaw clapping, head jerking, open mouths, and chase/flee events. This also included aggressive instances of Yulka towards the trainers when the calf was first born, and the trainers attempted to separate the dyad for medical procedures or feeding sessions in addition to instances of calf discipline or herding by Yulka. Also, there were occasions when Yulka or the dyad would swim with high energy in stereotypical patterns. This would usually occur when the habitat grew noisy or sometimes prior to or after training sessions.
- Tactile. When a member of the dyad rubbed, bumped, or maintained physical contact with a body part of the other beluga. This also included affiliative mouthing.
- Sexual. Occasionally as Kylu matured, an erection could be seen while he swam with and/or was rubbing on his mother.
- 9) Nursing. This included changes in beluga swim positions or swim speed as the calf prepared to nurse, Kylu's "bumping" (Recchia, 1994) of Yulka's mammary region, and actual latched on behavior.
- 10) Swim position. These positions included:
 - a. Mother/calf position- when the calf would swim directly under the mother's peduncle.
 - b. Echelon position- when the calf would swim in the mother's slip stream above and to the side of her dorsal ridge.
 - c. Pair swim- in which the calf and mother were swimming together in an unspecified position, usually side by side.

d. Pair swim with contact- in which the mother and calf swam together while keeping some form of tactile contact.

Swim position also included periods of time when the dyad was swimming in stereotypical swim patterns or stationary together at the surface of the pool.

Video recordings were collected continuously in the pre-partum period and opportunistically until February 14th, 2017 at which point filming stopped as observations entered in the Timestamped Field Notes application proved to be more useful than referencing video recordings. However, video recording was re-introduced during physical introductions of the calf to Kairo on June 26th and 27th, 2017 as these sessions were marked by a flurry of activity in which detailed observations were difficult to obtain. All videos were recorded with a Canon Vixia HF R700, except for the medical isolations in Kylu's 23rd month of life (discussed further below) during which an iPhone 8 camera was used to record video. Again, this was due to increased activity of the whales that was better captured on video instead of observational notes. When video recordings were referenced in the study, a time stamp was applied to the video and linked to the corresponding time in the acoustic recordings.

Localization of vocalizing individuals

Bubble stream methodology was employed during the calf's early life when bubble streams often coincided with simultaneous sound production. This method has been consistently employed in studies of vocal development in young odontocetes (Bojanowski, Veit, & Todt, 2000; Bowles, Grebner, Musser, Nash, & Crance, 2015; Favaro, Gnone, and Pessani, 2013; Fripp & Tyack, 2008; Gnone & Moriconi, 2010; Hooper, Reiss, Carter, & McCowan, 2006; Killebrew, Mercado, Herman, & Pack, 2001; McBride & Kritzler, 1951; McCowan & Reiss, 1995; Mello & Amundin, 2005; Miksis et al., 2002; Morisaka, Shinoharam & Taki, 2005a, b; Reiss, 1988; Vergara & Barrett-Lennard, 2008) as calves seem to lack the musculature or motor ability to stop air flow from the vestibular air sacs by sealing the blowhole during underwater sound production. Bubble stream methodology was the only method employed in the first month of life. Additional methods for localizing calf calls after the first month and all adult calls were used opportunistically. For calf call localization, these methods became increasingly important as the calf aged, and bubble stream methodology became less applicable due to a decrease in bubble stream emission concurrently with the calf's call production over time. These methods included:

- 1) Calf or adult isolation.
- 2) Calf calls produced during periods when adults were participating in training sessions with their melons above the water surface. The melon is the structure through which odontocetes are believed to direct sound (e.g., Cranford, 2000; Cranford, Amundin, and Norris, 1996; Madsen, Wisniewska, & Beedholm, 2010; Madsen, Lammers, Wisniewska, & Beedholm, 2013), and therefore if a beluga's melon was not in the water, underwater sound production could not be associated with that beluga.
- 3) Underwater calls produced by the calf or adults that were audible from the surface during observations. This was often the case with Kairo's vocalizations and with Yulka's contact call production as these calls were often quite loud.
- 4) Calls produced at the surface by a beluga. The belugas would often open their blowholes when producing sounds at the surface with their melons either in or out of the water. Often when the melon was in the water during production of

sounds at the surface, the sound could be heard clearly at the surface while still appearing with high acoustic energy (i.e., dark coloration indicating the "loudness" of a sound) on spectrograms of the underwater recordings.

- 5) Comparisons of the acoustic energy of the calls on spectrograms if the animals' positions in the pool were known. This could easily be done when both hydrophones were deployed, however it was also possible during single hydrophone deployment given the size of the beluga habitat. For example, if a beluga vocalized while swimming in the main beluga pool, this sound would lose much of its intensity before being recorded by the hydrophone deployed in the reproduction pool and vice versa. Moreover, if a beluga produced a call that could be positively attributed to them through one of the other methods listed here, and additional calls of similar visible energy appeared on the spectrogram shortly prior to or shortly after the call with the positive identification, it could be reasonably assumed that the identified beluga also produced the additional sounds if there were no other animals in near proximity.
- 6) Comparisons of call acoustic energy on spectrograms if animals were calling together and at least two of the animals' pool positions were known. Similar to the method listed above, if calls could be positively attributed to belugas through the distance of the animals from the hydrophone or through another method listed here, and animals were continually exchanging vocals (i.e., one animal would call and another would respond shortly thereafter), it could be reasonably assumed that calls of similar energy belonged to the same animal for the duration of the vocal exchange. For example, if Yulka and Kylu could

be heard calling to each other from my observation position at the side of the pool, calls within the vocal exchange that were of similar energy to calls that could be attributed to either Yulka or Kylu were believed to also belong to the same animal. This method was often employed during mother-calf separations when all three animals would continually call (Kairo usually from the other pool).

All call information was time stamped on the Timestamped Field Notes application (see above) and synced to the underwater recordings for signal processing and analyses (e.g., if a note reflected a calf bubble stream or an audible beluga call at a given time, a call recorded by the hydrophone at the same time was attributed to that beluga).

Calf sound classification catalog

All calls positively identified as emitted by the calf were included in a sound classification catalog used to determine sound acquisition (i.e., first recorded instances of sounds) and proportions of sound emission in the calf's vocal repertoire. All calf calls were classified based on general sound categories known to be produced by belugas and other delphinoid species, i.e., tonal, pulse (including burst pulses, pulse tones, noisy calls, and pulse trains), mixed pulse, and mixed calls. It should be noted that mixed pulse calls are considered mixed calls, given that both sound types are biphonations with overlapping elements. For clarity, mixed pulses will be treated as their own category in this study. Likewise, pulse trains are also pulse sounds, but given the depth of analysis and discussion of this call type in the current study, they will be described separately of other pulse sounds.

Calls were further classified into 14 subcategories of the five general categories based on variations in sound types within each general classification. Subcategories were created based on the visual and auditory characteristics of sounds in the recordings, and new subcategories were created and defined if Kylu produced a call that could not be classified as an already occurring subcategory. See Table 1 for operational definitions of sound categories and subcategories. Sound acquisition was investigated through the calf's first emission of each sound subcategory, but the calf's proportional emission of sound is based on the five general categories.

Table 1

CATEGORY	SUBCATEGORY	DEFINITION
	Noisy	Buzz-like sounds that have undefinable characteristics and no clearly visible pulses so that pulse repetition rate cannot be assessed
	Burst pulse	Pulse packet with 100-1000 pulses per second
Pulse	Pulse tone	Aurally tonal burst pulse sound with clear harmonic structure, or sideband
		1968) that indicates a pulse repetition rate of 1000- 4000 pulses per second
	Pulse Trains	A series of pulses produced with definable pulse repetition rate <100 pulses per second

Operational definitions of calf sound categories and subcategories
Table 1 (continued)

	Mixed pulse trains	Overlapping pulse trains that have two different pulse repetition rates
	Pulse train with pulse tone or	Pulse train overlapped by
	burst pulse	pulse sound with high
	· · · · · · · · · · · · · · · · · · ·	pulse repetition rate: burst
Mixed Pulse		pulses in this capacity had
		>200 pulses per second
	Pulse train with noisy	Pulse train overlapped by
		pulse sound with
		undefinable characteristics
	Burst pulse or noisy with	Pulse tone overlapping an
	pulse tone	additional pulse sound
	Pulse tone with tonal	A pulse tone overlapped
Mixed Call	component	by a tonal sound
	Pulse train with tonal	A pulse train overlapped
	component	by a tonal sound
	Burst pulse or noisy with	Additional pulse call types
	tonal component	overlapped by a tonal
		sound
	Whistles	Narrowband, frequency
		modulated tonal sounds
		with clear contour and
		harmonic structure;
		fundamental frequency
		and harmonic integer
		interval were often >4 kHz
Tonal	Tonal elements	Frequency modulated
i onar		tonal sounds that were less
		clear in contour shape and
		were often wider
		bandwidth than whistles
		(~1-3 kHz)
	Abbreviated tonal sweep	A series of truncated tonal
	series (ATSS)	sounds (\sim 6-11 ms) with
		upsweep contours

Complex contact call classification

Beluga contact call identification is straightforward as these calls are distinctive, pulsed, highly stereotyped, long in duration, broadband, and produced during contexts of separation (Vergara and Lance Barret-Lennard, 2008; Vergara et al., 2010; Vergara and Mikus, 2018). Contact calls were classified through visual and aural inspection of spectrograms, a technique that has been used in other studies of beluga contact calls (e.g., Panova et al., 2017; Vergara & Barrett-Lennard, 2008; Vergara et al., 2010; Vergara and Mikus, 2018) and widely accepted as a reliable method in classifying the sounds of cetaceans (Deecke, Ford, & Spong, 1999; Janik, 1999a; Sayigh, Esch, Wells, & Janik, 2007).

A contact call was considered to be a specific type if at least five emissions of the call across two different recording days occurred. Contact call types were further classified into subtypes if enough variation between calls within a broad call type existed so that subtypes were distinguishable, but still more similar to each other versus calls in different call types. A call was considered a subtype of a contact call if the variation appeared to be highly stereotyped with at least five emissions across two different recording days as well.

Vocalization exclusion criteria

Calls were excluded from the study if:

- Any ambiguity existed in localizing calling belugas. For example, as the calf aged calf calls became more difficult to identify as they increased in similarity to the adult repertoires. Thus, if the dyad was in close proximity during call production, these calls were excluded.
- There was too much overlap with other calls so that the call could not be easily classified.
- Calls had a low signal to noise ratio, and thus were too faint to see clearly defined elements.

4) The calls were produced by a beluga during a training session (i.e., the beluga was asked to produce a call) or at the surface with the animal's melon out of the water as these calls were often too faint and given their production in air, it was believed that these calls would not be comparable to underwater sounds with complete accuracy.

Finally, chirps, or short duration tonal sounds (< 0.2 s, Recchia, 1994), were also excluded from this study as these calls were difficult to localize to an individual animal.

Parameter extraction criteria

Calls that did not meet any of the above criteria for exclusion and had a high signal to noise ratio with clear, definable elements were further analyzed through parameter extraction. Parameters extracted for each sound category or call type and their operational definitions are listed in Table 2. Pulse repetition rate (PRR) was determined as follows: 1) counting all pulses in a sound and dividing by the delta time of the sound when pulses were so few they could easily be counted, or 2) when pulse repetition rate was visibly high on the spectrogram, 10 pulses from the center of the sound were highlighted in Raven, divided by their delta time and used as a measure of center PRR. When PRR was so high (e.g., for burst pulses or pulse tones) that individual pulses were not readily apparent, PRR was measured from sideband intervals (Watkins, 1968). Parameters of acoustic energy distribution were derived from the power spectrum of the sound in Raven. The upper frequency limit of the noise band produced by the pool filtration system was most often around 2 kHz. Thus, peak frequencies that were less than or equal to 2 kHz were discarded and the second peak in the power spectrum of the sound was extracted instead. Other measures of acoustic energy distribution (i.e., center, first and third quartiles) were integrated between 500 Hz and 128 kHz. The minimum

frequency of calls was limited to 500 Hz to avoid including excess noise in the energy distribution of the call. Given that the true minimum frequency of some of the calf's calls was below 500 Hz, especially in early life, this parameter was ultimately discarded from analyses of calf calls. The maximum frequency parameter was also excluded from analyses as the upper frequency limit of an overwhelming majority of the calf's calls were above the Nyquist frequency of the recording system. Subsequently, precise delta frequency was discarded from analyses, although it was clear that the delta frequency of the adult contact calls and the calf's pulse calls encompassed the bandwidth of the recording system. Analyses of contact calls also excluded minimum, maximum, and delta frequencies.

Finally, received levels of Kylu's pulse trains produced in his first month of life at known distances and orientation of Kylu to the hydrophone were integrated from 500 Hz to 100 kHz and used to calculate apparent source levels of Kylu's calls using cylindrical spreading to approximate transmission loss (Vergara, Wood, Ames, Mikus, and Michaud, in prep.). These apparent source levels were used by the current study to analyze the change in source level of Kylu's pulse trains over his first month.

Table 2

PARAMETER	DEFINITION	BURST PULSE/PULSE TRAINS	MIXED CALLS
Minimum	The lowest frequency of a sound		
Frequency			
Maximum	The highest frequency of a sound		
Frequency			
Delta Frequency	The frequency range of a sound (i.e., the differences between the minimum and maximum frequencies)		

Operational definitions of parameters with sounds for which they were extracted

Table 2 (continued)

First Quartile	Frequency of the 25th percentile	*	*	
Frequency	of the acoustic energy distribution			
Contor Fraguenes	Frequency of the 50th percentile	*	*	
Center Frequency	of the acoustic energy distribution	·	·	
Third Quartile	Frequency of the 75th percentile	*	*	
Frequency	of the acoustic energy distribution			
Deals Energy on av	The peak energy of a sound in the	*	*	
reak rrequency	power spectrum	·	·	
Delta Time	Sound duration (s)	*	*	
Pulse Repetition	The number of pulses per second	*	*	
Rate (PRR)		·	·	
Dominant Tonal	Harmonic of a tonal sound		*	
Frequency	containing the peak energy		·	
Dominant Tonal	Beginning frequency of the			
Frequency	dominant tonal element		*	
Beginning				
Dominant Tonal	End frequency of the dominant		*	
Frequency End	tonal element			
	First harmonic of a tonal sound; if			
	the first harmonic also contained			
Fundamental	the peak energy of the tonal		*	
Frequency	sound, the fundamental and			
	dominant tonal frequency were			
	considered the same			
	The point in a tonal sound in			
Inflaction Daints	which the slope of the sound			
Innection Foints	changes direction (i.e., increasing			
	to decreasing or vice versa)			
	The tonal element within type Y			
	calls characterized by wider			
Noisy Tonal Band	bandwidth than pure tonal or		*	
-	pulse tone components of mixed			
	calls			

Note: Sounds less common in the calf's repertoire are not listed here.

Statistical analyses

Linear regression analyses of calf call parameter changes over the first month and first year of life were conducted in Microsoft Excel version 16.20. Parameters included in regression analyses varied for each sound category analyzed (Table 3). Each day of recording sessions was treated as a single event. A mean for each event (i.e., each day of life) was generated for each parameter included in each of the sound categories. These means per day were then used in the regression analyses as individual data points. The linear regression for PRR included the repetition rate of pulse trains and burst pulses. A linear regression analysis was also run on the apparent source levels of Kylu's calls, estimated for the recent study completed by Vergara and colleagues (in prep.).

Coefficients of variation (CV) were calculated for the acoustic energy distribution parameters of Kylu's pulse trains in addition to the dominant tonal frequency of the type Y2 calls (defined in *Complex contact call development* in the results section). For parameters of acoustic energy distribution, CVs were calculated over the calf's first year of life, however, only months that had a minimum of 11 pulse trains extracted for parameters were included. In order to compare the end of the first year of life to previous months, the 11th and 12th months were combined into a period titled "End".

Discriminant function analyses (DFA) were completed in SPSS version 21 for the statistical classification of complex contact calls analyzed here. For comparison of the adult complex contact calls, 50 calls were randomly selected for each adult from the first month of life. Parameters that were included in complex contact call DFAs are also listed in Table 3. The number of the inflection points of mixed call tonal components were considered a discrete variable, and as such, were not included in the listed analyses. Instead, inflection points are reported briefly below (see *Complex contact call development*) as median values.

Table 3

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Parameter	Pulse Train & Burst Pulse Regression	Mixed Call Regression	Type Y DFAs	Y1/K1 DFA	Type Y/K1 DFA
First	*	*	*	*	*
Quartile					
Frequency					
Center	*	*	*	*	*
Frequency					
Third	*	*	*	*	*
Quartile					
Frequency					
Peak	*	*	*	*	*
Frequency					
Delta Time	*	*	*	*	*
Pulse	*	*	*	*	*
Repetition					
Rate (PRR)					
Dominant		*	*	*	*
Tonal					
Frequency					
Dominant		*	*	*	*
Tonal					
Frequency					
Beginning					
Dominant		*	*	*	*
Tonal					
Frequency					
End					
Fundamental		*	*	*	*
Frequency					
Noisy Tonal			*		
Band					

CHAPTER III - RESULTS

Sound acquisition and use

A total of 2,014 calf calls were included in the calf's sound classification catalog. Figure 3 shows proportional use of each sound category in the calf's recorded repertoire within each month of life. As expected, the calf began to produce low pulse repetition rate (PRR), broadband pulse trains within a few hours of his birth (Figure 4). The upper frequency limits of these calls reached the Nyquist frequency (128 kHz) on this first day of life. Pulse trains comprised the majority of the calf's repertoire over the first month of life. Pulse calls (i.e., burst pulses, pulse tones, noisy calls, and pulse trains) were the most commonly recorded category over the first year.



Figure 3. Percentage of use for each general sound category in Kylu's repertoire per month.



Figure 4. Pulse trains extracted from Kylu's first month of life.

The three pulse trains on the left are a series from the day of Kylu's birth. The three pulse trains on the right are a series from Kylu's 28th day of life. Note the extension of the upper frequency limits of Kylu's day one pulse trains past 128 kHz. Spectrogram parameters: FFT 1024, Overlap 50%, 1024 Samples, Hann Window.

A few additional sound subcategories began to appear in the calf's recorded repertoire in the days following his birth. Noisy calls (Figure 5) were first recorded on the calf's third day of life and appeared regularly in the calf's recorded repertoire until the ninth month. Two mixed calls were recorded on the calf's sixth day of life. These calls were characterized by low pulse repetition rate pulse trains overlapped by a tonal element at the end of the train that trailed off independent of continued pulse production (Figure 6). An additional mixed call in which the tonal element was embedded within the pulse train appeared on the calf's 19th day of life (Figure 6). These mixed calls were unstereotyped and not akin to the mixed calls produced by adult belugas. Mixed calls that appeared adult-like in structure (i.e., clearly prominent overlapping pulse and tonal elements) appeared in the calf's fifth month of life at which point the calf began to produce these calls regularly (Figure 6). Mixed pulse calls with overlapping pulse tones appeared in the second and third months of life but were also not prominently produced until the fifth month of life (Figure 7).

The 26th day of life was marked by the first recordings of multiple mixed pulse and pulse sound subcategories produced by the calf. First emissions of pulse tones (Figure 5) and mixed pulse calls, including mixed pulse trains and pulse trains with either a 1) overlapping noisy component, 2) overlapping pulse tone, or 3) burst pulse with high pulse repetition rate (PRR) resulting in a visible harmonic structure, or side band intervals (Figure 7) occurred on this day. Burst pulses independent of overlap by pulse train appeared towards the end of the calf's third month of life (82nd day) (Figure 5).

Finally, Kylu began to produce tonal sounds (Figure 8) on their own, independent of pulse components, during his fourth month of life (94th day). These tonal sounds were similar to whistles produced by adult belugas, but they did not appear to become stereotyped over Kylu's first year as he produced these sounds infrequently. During his first year of life, Kylu also produced abbreviated tonal sweep series (ATSS) (Figure 8), but this subcategory did not appear in the recordings until his eighth month of life (221st day) and overall production of this sound was rare as well. All tonal sounds comprised only 2.1% of total calls in the sound classification catalog



Figure 5. Kylu's early pulse sounds (excluding pulse trains).

The noisy call was produced during Kylu's first month, the pulse tone was produced during the second, and the burst pulses were produced during the third month of life. Spectrogram parameters of the enlarged boxes above the noisy (1) and burst pulses (2): FFT 4096, Overlap 50%, 4096 Samples, Hann Window. Note the clear sideband intervals in box 2. Spectrogram parameters: FFT 1024, Overlap 50%, 1024 Samples, Hann Window.



Figure 6. Kylu's mixed calls.

Note the tonal element at the end of the day 6 mixed call and the tonal element embedded in the day 19 mixed call. Spectrogram parameters: FFT 1024, Overlap 50%, 1024 Samples, Hann Window.



Figure 7. Kylu's mixed pulse calls.

1) Mixed pulse train with a high frequency (HF) and low frequency (LF) component. The high frequency component has a higher PRR. 2) Pulse train with overlapping pulse tone. 3) Noisy with overlapping pulse tone. 4) Burst pulse overlapped by pulse train. The pulse train is low frequency (<10 kHz) and can be audibly deciphered from the broadband burst pulse. 5) Three individual pulses overlapped by a burst pulse with visible sideband intervals. 6) Pulse train with overlapping noisy component. Spectrogram parameters: FFT 1024, Overlap 50%, 1024 Samples, Hann Window.



Time (s)

Figure 8. Kylu's tonal sounds.

The whistle was produced during the sixth month and the ATSS was produced during the eighth month of life. The abbreviated tonal sweep series (ATSS) is overlapped by a jaw clap presumably produced by one of the adults. Spectrogram parameters: FFT 1024, Overlap 50%, 1024 Samples, Hann Window.

Burst pulse and mixed call development

Of the sound subcategories, pulse trains, burst pulses, and mixed calls (pulse trains or burst pulse sounds with overlapping tonal element) were the only sound types that met inclusion criteria for parameter extraction frequently enough to warrant analyses of changes in these sounds over time. All other sound subcategories were too rare. A total number of 64 burst pulses and 29 mixed calls met inclusion criteria for parameter extraction and subsequent linear regression analyses. Age was not a significant predictor for any parameter changes related to mixed calls over the first year of life. However, all parameters of acoustic energy distribution (i.e., peak, first and third quartile, and center frequencies) for burst pulses significantly increased over the first year. The PRR of burst pulses was combined with analysis of this parameter in pulse trains below. See Table 4 for p-values and descriptive and regression statistics for burst pulses and mixed calls over the first year of life.

Table 4

P-values of linear regression analyses and descriptive statistics for the calf's burst pulses and mixed calls over the first year of life

CALL TYPE	PARAMETER	Mean	SD	R ²	p-value
Burst pulse	First Quartile Frequency	18.50	21.56	0.35	<.001*
	Center Frequency	43.09	34.02	0.24	<.001*
	Third Quartile Frequency	28.87	28.00	0.20	<.001*
	Peak Frequency	19.94	25.04	0.34	<.001*
	Delta Time (s)	1.06	0.56	0.19	0.21
	PRR	420.63	209.48		
Mixed call	First Quartile Frequency	41.17	19.79	0.05	0.45
	Center Frequency	52.21	22.29	0.06	0.39
	Third Quartile Frequency	70.38	22.04	0.04	0.52
	Peak Frequency	46.62	27.41	0.04	0.51
	Delta Time (s)	1.58	0.79	0.04	0.50
	PRR	167.82	188.13	0.11	0.24
	Dominant Tonal Frequency	8.62	3.45	0.34	0.23
	Dominant Tonal Frequency Beginning	7.25	3.12	0.08	0.33
	Dominant Tonal Frequency End	8.79	3.32	0.15	0.18
	Fundamental Frequency	6.74	2.00	0.09	0.29

Note: Mean \pm SD are the only values available for burst pulse PRR because this parameter was combined with pulse train PRR in the linear regression analysis of PRR over the calf's first year. Means \pm SDs were calculated from the raw data. R² and p-values were calculated based on the method outlined for linear regression analyses. *Denotes significance.

Pulse train development

First Month

Parameters were extracted from 329 pulse trains in the first month of life. There were more useable calls for parameter extraction during the first month of Kylu's life due to the increased sampling effort during this period as it was of most concern given the relevance to questions of noise impact on neonate calls. Further, this data set was characterized by consistent separations between mother and calf for feedings and medical care. Linear regression analyses of pulse train parameters over the first month of Kylu's life showed that pulse repetition rate (PRR) increased significantly ($R^2 = 0.65$, n=15, p<.001). Mean PRR (M=17.77, SD=13.84) on the first day of life was much lower when compared to mean PRR towards the end of the calf's first month (28th day: M=59.32, SD=8.94) (Figure 4). Additionally, the third quartile frequency of his pulse trains increased significantly ($R^2 = 0.28$, n=15, p=0.04), demonstrating shifts in acoustic energy distribution towards upper frequency limits of the calf's broadband pulse trains. See Table 5 for a comparison of p-values and descriptive and regression statistics for pulse trains in the first month versus the first year of Kylu's life.

Apparent source levels of the calf's pulse trains in the first week of life were much lower than apparent source levels of the calf's pulse trains in weeks two through four (see Vergara et al., in prep). Furthermore, apparent source levels of the calf's calls in the first month of life were also much lower than apparent source levels estimated for the parents' contact calls during this same time period (Vergara et al., in prep). Source levels of the calf's pulse trains increased significantly over the first month of life (R^2 =0.81, n=11, p<.001). See Figure 4 for spectrograms of the calf's pulse trains on the first day of life versus at the end of the first month of life.

Table 5

P-values of linear regression analyses and descriptive statistics for the calf's pulse trains

TIME PERIOD	PARAMETER	Mean	SD	R ²	p-value
First Month	First Quartile Frequency	8.47	6.79	0.20	0.09
	Center Frequency	20.08	16.94	0.15	0.15
	Third Quartile Frequency	39.38	21.16	0.28	0.04*
	Peak Frequency	6.16	5.88	0.18	0.11
	Delta Time (s)	1.01	0.53	0.12	0.20
	PRR	23.18	8.82	0.65	<.001*
First Year	First Quartile Frequency	13.11	17.01	0.58	<.001*
	Center Frequency	29.01	24.51	0.40	<.001*
	Third Quartile Frequency	52.38	25.83	0.33	<.001*
	Peak Frequency	11.95	20.07	0.42	<.001*
	Delta Time (s)	0.88	0.50	0.33	<.001*
	PRR	99.05	150.32	0.13	0.03*

over the first month and first year of the life

Note: Means \pm SDs were calculated from the raw data. R^2 and p-values were calculated based on the method outlined for linear regression analyses. *Denotes significance.

First Year

An additional 81 pulse trains were used for parameter extraction over the remaining part of the first year for a total of 410 pulse trains from which parameters were extracted. Over the calf's first year of life, linear regression analyses indicated that age was a significant predictor for all parameters. First ($R^2 = 0.58$, n=33, p<.001) and third ($R^2 = 0.33$, n=33, p<.001) quartiles, center ($R^2 = 0.40$, n=33, p<.001) and peak ($R^2 = 0.42$, n=33, p<.001) frequencies significantly increased over this time period, indicating shifts in all acoustic energy distribution towards upper frequency limits of the calf's calls in the

first year. Delta time (i.e., call duration) also increased significantly ($R^2 = 0.50$, n=33, p<.001) over the calf's first year of life.

For linear regression analyses of pulse repetition rate (PRR), burst pulse and pulse train PRR were combined. Burst pulses are analogous to high repetition pulse trains. While the two pulse signals were treated as separate sound types for the rest of this study, analyses converged on PRR in order to determine if age was a significant predictor for changes in repetition rate. Significant increases in PRR occurred over the calf's first year of life ($R^2 = 0.13$, n=33, p=.03), however the low R^2 value indicates that age was not the best predictor for this model and the large SD indicates high variability in this parameter. There appeared to be high variability across many of the parameters extracted from Kylu's calls, as SD values were often large and R^2 values were low. It should be noted that variability in Kylu's call parameters may have been due to the low number of days from which mean parameter values could be extracted from the first month (n=15) and first year (n=33) of life or may be representative of a high degree of variation in Kylu's sounds as they developed. See Figure 9 for regression plots of these parameters.





Figure 9. Linear regression plots of Kylu's pulse train parameters over the first year of life.

Data points represent daily means (error bars: \pm SD).

Coefficients of variation (CV) for parameters of acoustic energy distribution were taken for comparison over the calf's first year in order to determine at which age in this time period, energy distribution of the calf's calls became less variable. Variability in acoustic energy distribution of the calf's pulse trains considerably decreased over the first year as variability was lowest in months 11 and 12 of life (Figure 10), however variability in peak frequency was still relatively high (85.4% CV) in this period in comparison to moderate variability in the remaining pulse train acoustic energy distribution parameters (Q1: 33.8% CV, Center: 28.6% CV, and Q3: 12.8% CV). See Table 6 for descriptive statistics of pulse train peak frequency in each month of Kylu's first year of life as they correspond with CVs below.



Figure 10. Coefficients of variation (CV) for parameters of acoustic energy distribution extracted from pulse trains.

The "End" period represents the 11th and 12th month of Kylu's life.

Table 6

Month	Mean	SD	n
1	7.38	14.02	329
2	12.16	19.11	11
3	36.30	34.40	23
6	31.20	20.52	14
7	37.25	29.04	13
End	32.31	27.58	12

Mean peak frequency of the calf's pulse trains per month

Note: Means \pm SDs were calculated from the raw data.

Complex contact call development

Adult Contact Calls

Yulka's individual contact call (type Y) was identified when Kylu was involuntarily separated from the dyad during the calf's first month of life. Type Y calls were complex and Yulka used a subtype of this call (Y1) repeatedly until Kylu was returned to the dyad. Yulka's type Y1 calls were easy to localize as they were audible from my observation position on the side of the pool. Additionally, Kairo was separated from the dyad during the majority of the calf's first month of life (there were a few instances where Kairo and Yulka were gated together for a short period of time so that Kairo was not consistently in isolation). Kairo also produced complex contact calls (type K) that were audible from the pool side and thus easily attributable to him during these periods when the calf was separated from the dyad. Involuntary separations of the dyad would often result in simultaneous calling by calf, mother, and father in which contact calls could easily be attributed to each of the three individuals. Table 7 describes the complex contact call types and subtypes identified and investigated in this study. To determine individual specificity in the adults' contact calls, the most prominent contact call types produced by each adult beluga in the calf's first month of life (type Y1 for Yulka and type K1 for Kairo) were compared (Figure 11). A discriminant function analysis classified 100% of Y1 and K1 calls correctly, indicating a high degree of difference in these two call types. Preliminary analyses have identified several additional contact call subtypes for each adult in the pre-partum period and first and second years of the calf's life. Yulka's Y2 subtype will be discussed below as it relates to Kylu's contact call development. However, analyses of remaining contact call subtypes are beyond the scope of this paper.

Table 7

Complex Contact Call	Definition
Y1	A subtype of Yulka's type Y calls produced by Yulka prominently during Kylu's first month of life. The call is characterized by a low PRR and overlapped by a down-sweeping noisy tonal band.
¥2	A subtype of Yulka's type Y calls produced by Yulka and Kylu in the 23rd month of life. The call is characterized by two pulse repetition rates; the first part of the call has a high PRR and the latter part of the call has a low PRR. The pulse component is overlapped by a noisy tonal band with a constant contour.
К1	A subtyped of Kairo's type K calls produced prominently in Kylu's first month of life. This call is characterized by a high PRR and overlapping constant tonal component with a slight upsweep at the end and/or slight down-sweep at the beginning.
A1	A subtype of the type A calls produced by Aurora, the beluga mother of the Vancouver aquarium. Tuvaq later incorporated this subtype as his own contact call (Vergara and Barrett-Lennard, 2008).

Operational definitions of the complex contact calls investigated by the current study



Time (s)

Figure 11. Kairo's K1 and Yulka's Y1 complex contact calls.

These subtypes represent the prominent complex contact call produced by Kairo and Yulka in Kylu's first month of life. Spectrogram parameters: FFT 1024, Overlap 50%, 1024 Samples, Hann Window.

Kylu's Type Y Call Development

Kylu was involuntarily isolated in the medical pool for blood draws on two separate days in his 23rd month of life. During these medical separations, he produced a subtype of his mother's type Y calls (type Y2). Yulka was also recorded using the Y2 subtype more prominently than the Y1 subtype during these same isolation sessions. Approximately 30 Y2 calls that could be positively attributed to the calf over the two observation periods met parameter extraction criteria. The calf's Y2 calls were then compared to the first 30 Y2 calls produced by Yulka that also met criteria for parameter extraction. A discriminant function analysis classified 80% of Kylu and Yulka's Y2 calls correctly (26.7% of Kylu's Y2 calls were classified as Yulka's and 13.3% of Yulka's Y2 calls were classified as Kylu's). Parameters that had high discriminant ability (p < 0.05) included the calls' first quartile and peak frequencies and the beginning and end frequency of the noisy tonal band. In addition, the dominant tonal frequency was a parameter with high discriminant ability as Kylu still appeared to have an overall lack of stereotypy in the dominant frequency of the noisy tonal band. This was apparent when comparing the variability of the dominant noisy tonal frequency of Kylu's Y2 calls (20.7% CV) to the variability of Yulka's Y2 noisy tonal dominant frequency (5.3% CV). Kylu's Y2 dominant tonal component was also a bit more tremulous in inflection. While the median value for number of inflection points was the same in both Yulka and Kylu (median=0), Yulka's Y2 dominant tonal did not have any inflection (range:0) whereas the number of inflection points in Kylu's Y2 dominant tonal was more variable (range: 0-2). Call parameters that were similar across the two animals' Y2 calls included center and third quartile frequencies, call duration, fundamental frequency, bandwidth of the noisy tonal element, and PRR. Figure 12 illustrates Kylu and Yulka's Y2 calls. See Table 8 for descriptive statistics of parameters extracted from Kylu's Y2 calls, Yulka's Y1 and Y2 calls, and Kairo's K1 calls.

A discriminant function analysis of Kylu's Y2 and Yulka's Y1 calls was more accurate in assigning Y2 and Y1 calls to the correct categories, with 98.8% of cases classified correctly (one case of Kylu's Y2 call was classified as Yulka's Y1). The dominant frequency and bandwidth of the noisy tonal were the only parameters that did not have discriminant ability. All other parameters were significantly dissimilar (p<0.05). Interestingly, a discriminant function analysis comparing Yulka's Y1 and Y2 calls classified 100% of cases correctly, indicating a high degree of difference in the call subtypes based on the parameters extracted. A discriminant function analyses of Kylu's Y2 calls, Yulka's Y1 calls, and Kairo's K1 calls classified 96.2% of calls correctly.



Kylu/Y2

Figure 12. Kylu and Yulka's Y2 calls.

Each call example was selected from the representative group of 30 calls chosen for parameter extraction and discriminant function analyses. Spectrogram parameters: FFT 1024, Overlap 50%, 1024 Samples, Hann Window.

Table 8

Beluga/	Daramatar	Moon	SD	Beluga/	Daramatar	Maan	SD
Contact	1 al ameter	Witali	50	Contact Call	1 al ameter	Ivican	50
	First Quartile Frequency	21.73	14.57		First Quartile Frequency	13.37	9.83
	Center Frequency	36.79	17.68		Center Frequency	31.37	15.27
	Third Quartile Frequency	60.37	20.42		Third Quartile Frequency	56.06	13.19
	Peak Frequency	22.09	17.97		Peak Frequency	9.46	9.08
	Delta Time (s)	1.13	0.25		Delta Time (s)	1.18	0.17
IZ1 (N/A	PRR	149.10	50.66		PRR	163.26	61.30
Kylu/ Y 2	Dominant Tonal Frequency	7.56	1.56	Y UIKA/Y Z	Dominant Tonal Frequency	6.84	0.36
	Dominant Tonal Frequency Beg	7.18	1.86		Dominant Tonal Frequency Beg	6.01	0.73
	Dominant Tonal Frequency End	7.40	1.39		Dominant Tonal Frequency End	8.15	1.16
	Fundamental Frequency	7.17	1.93		Fundamental Frequency	6.84	0.36
	Noisy Tonal Band	2.68	1.78		Noisy Tonal Band	2.42	0.53
	First Quartile Frequency	9.50	4.10		First Quartile Frequency	19.93	10.36
	Center Frequency	18.06	12.76		Center Frequency	31.12	13.70
	Third Quartile Frequency	36.69	19.74		Third Quartile Frequency	43.91	14.99
	Peak Frequency	9.32	7.03		Peak Frequency	12.89	9.92
	Delta Time (s)	1.52	0.22		Delta Time (s)	1.44	0.32
Valles /V1	PRR	67.79	13.80	Vaina/V1	PRR	95.40	6.95
Yulka/Y1	Dominant Tonal Frequency	7.83	0.56	Kairo/Ki	Dominant Tonal Frequency	10.11	2.04
	Dominant Tonal Frequency Beg	11.48	0.72		Dominant Tonal Frequency Beg	10.49	2.14
	Dominant Tonal Frequency End	5.90	0.30		Dominant Tonal Frequency End	11.19	2.29
	Fundamental Frequency	7.77	0.60		Fundamental Frequency	4.71	1.42
	Noisy Tonal Band	2.70	0.47				

Descriptive statistics for each parameter of type Y and type K calls

Note Dominant Tonal Frequency Beg=Dominant Tonal Frequency Beginning

CHAPTER IV – DISCUSSION

Sound acquisition

Kylu produced pulse trains exclusively on his first day of life with acquisition of other sounds occurring with age. This is consistent with findings based on other beluga calves (Castellote, Vergara, Barrett-Lennard, & Esteban, 2007; Vergara, 2011). Kylu began to produce other pulse sounds within his first month of life and altogether, pulse signals were the most commonly produced sound over his first year. Kylu's tonal sound production occurred later in life than what was reported for two calves born at the Vancouver Aquarium. Tuvaq, the focal calf in Vergara and Barret-Lennard's (2008) study, began producing whistles on his 13th day and Tiqa, a female calf born several years after Tuvaq (MacLeod, 2009; Vergara, 2011), began whistle production on day 50. Tonal production preceded adult-like mixed call production in both Tuvaq and Kylu (unknown for Tiqa), however Kylu produced far fewer tonal sounds over his first year when compared to Tuvaq.

Kylu produced mixed calls a few days after birth, a little earlier than Tuvaq who produced his first mixed calls on day 20. Both calves' initial mixed calls were unstereotyped and not akin to adult beluga mixed calls. Furthermore, these early mixed calls were quite rare as both calves began producing adult-like mixed calls more consistently later in the first year (month four for Tuvaq and month five for Kylu). Kylu's earliest mixed calls, characterized by pulse trains that trailed off into whistles, were reminiscent of Tuvaq's early whistles (Vergara, 2011) and the whistle-squawks of bottlenose dolphin neonates, which also have a pulse-like attribute (Killebrew et al., 2001).

In bottlenose dolphins, the squawky, tremulous nature of neonate whistles is believed to be caused by undeveloped vocal structures and/or lack of motor control (Killebrew et al., 2001). This is likely the case with beluga neonates as well. Given the rarity and unstereotyped nature of neonate mixed calls, it is likely that the tonal components overlapping these signals were an artifact of underdeveloped or poor motor control of the vocal structures belugas use to produce sound. Some of these early mixed calls may be produced if calves inadvertently actuate both pairs of phonic lips, the vibrating vocal structure within the melon of odontocete species (Cranford, 2000; Cranford et al., 1996), through increases in air pressure that occur concurrently in the nasal cavities (Cranford et al., 2000). All odontocete species (with the exception of sperm whales) possess two phonic lip pairs and both pairs are believed to be pneumatically actuated during biphonation (i.e., mixed call) production. This has been demonstrated in a recent study of beluga sound production (Ames, Beedholm, and Madsen, in prep.) and similar studies of other delphinoid species (bottlenose dolphins, Brill & Hader, 1991; Cranford et al., 2000; Cranford et al., 2011; Madsen et al., 2013, and false killer whales, Pseudorca crassidens, Murray, Mercado, & Roitblat, 1998; Madsen et al., 2013).

Each pair of phonic lips is situated on one side of the medial nasal midline so that one pair is on the left side of an animal's head and the other is on the right. The left phonic lips are smaller than the right in some delphinoid species (Cranford, 2000; Cranford et al., 2011) and are generally responsible for the tonal sounds produced by belugas (Ames et al., in prep.) and other delphinoids (bottlenose dolphins, Cranford et al., 2011; Dormer, 1979; MacKay & Liaw, 1981; Madsen et al., 2013, and false killer whales, Madsen et al., 2013). In beluga calves, the delay in regular mixed call and tonal production is likely due to an inability to pneumatically drive whistle production as this may require greater air pressure than the production of pulses (Cranford et al., 2000). Nothing is known regarding the development of vocal structures or related motor coordination in beluga infants, however some understanding can be inferred by vocal development studies of belugas and other odontocetes that highlight similarities in early sound production and development.

Pulse train development

Pulse trains are salient to the repertoire of beluga calves as these appear to function as rudimentary contact calls. The upper frequency limits of Kylu's calls from birth indicate that beluga neonates are capable of broader bandwidth sounds than previously reported by studies limited by lower sampling rates (Castellote et al., 2007; Vergara and Barrett-Lennard, 2008). During the first month of Kylu's life, source levels of his pulse trains increased significantly. All acoustic energy distribution parameters of the calf's calls increased throughout this period as well, although the third quartile frequency was the only to do so significantly. It is likely that the increasing source levels of Kylu's calls correlate with some changes in acoustic energy distribution. For example, higher source levels are related to increases in center frequency but do not appear to influence the peak frequency of sounds produced by other delphinoid species (Madsen et al., 2013). Increasing air pressure in the nasal cavities during sound production is related to increases in source level (Cranford et al., 2000), and given the correlation between source level and center frequency (Madsen et al., 2013), it is likely that as belugas gain the ability to increase air pressure with age, they also gain the ability to increase acoustic energy at higher frequencies.

The pulse repetition rate (PRR) of Kylu's pulse trains on his first day of life was nearly identical to the rate of Tuvaq's pulse trains on his first day (Tuvaq: M=17.5,

SD=4.2, Vergara and Barrett-Lennard, 2008). However, it appears that PRR was far more variable in Kylu's pulse trains, as indicated by a larger standard deviation in this parameter. Pulse repetition rate increased significantly with age for both calves.

Findings from Tuvaq, Kylu, and the only other calf born to Yulka (born at Oceanogràfic in 2006, Castellote et al., 2007), indicated that the month one pulse trains of all three calves had low mean peak frequencies in comparison to calls produced by older animals. The pulse trains produced by Yulka's first calf during the first month of life were very similar to Kylu's in mean peak frequency (Yulka's first calf: M=6.72, SD=1.9 kHz, Castellote et al., 2007), although again, Kylu showed much more variability in this parameter. Peak frequencies of Tuvaq's first month pulse trains (2.5 to 5 kHz, Vergara and Barrett-Lennard, 2008) were slightly lower than the two Oceanogràfic calves.

Pulse train peak frequency (termed dominant frequency in Vergara & Barrett-Lennard, 2008) increased significantly over the first year of life in both Tuvaq and Kylu. Vergara and Barrett-Lennard (2008) hypothesized that peak frequencies in Tuvaq were likely higher as the calf aged than what the authors were able to initially report given the limitations in sampling rate of the study. This is corroborated by the current study: beginning in Kylu's third month of life, the peak frequencies of his pulse trains tended to be greater than 22 kHz, the Nyquist frequency in Vergara and Barrett-Lennard's study (2008). Additional parameters of energy distribution (first and third quartile, and center frequencies) increased significantly over Kylu's first year of life. As with sound acquisition, changes in any of the measured parameters discussed here were likely due to increased motor control and changes in physical development as the calf aged.

Complex contact call development

A discriminant function analysis (DFA) confirmed that the primary complex contact calls emitted by Yulka and Kairo during Kylu's first month of life were distinct contact-call types, providing further evidence for vocal signatures in beluga contact calls (Vergara and Mikus 2018). As expected, the complex contact call produced by Kylu during the medical isolations in his 23rd month was most similar to a subtype of his mother's type Y contact calls. Kylu produced calls that were more consistent with the Y2 subtype, which Yulka also produced during these separations. He had not appeared to incorporate a version of Yulka's Y1 call, which she prominently produced during Kylu's first month of life, into his vocal repertoire by the end of the second year. This development was contrary to Tuvaq, who adapted the call used predominantly by his mother in the first and subsequent months of his life. In order to determine how Yulka's Y2 production might have influenced the development of Kylu's Y2 calls, further analyses of the adult calls throughout Kylu's first year of life are needed to asses if and when Yulka began to produce more Y2 calls.

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

It is not surprising that the two calves differed in their complex contact call development, as variability in timing of call acquisition occurs in other delphinoid species. For example, bottlenose dolphin calves produce whistles on the first day of life (Morisaka et al., 2005a), and most calves have refined their signature whistle by 17 months (Caldwell & Caldwell, 1979; Fripp et al., 2005; Tyack & Sayigh, 1997). Bottlenose dolphin calves are not known to produce their own signature whistle until they are at least a few months old (Caldwell & Caldwell, 1979; Fripp et al., 2005; Tyack & Sayigh, 1997), but some appear to produce discernable signature whistles within the first few days of life and these whistles remain stable signatures throughout the calves' development (Sayigh, 1992; Tyack & Sayigh, 1997).

Bottlenose dolphin calves generally appear to develop signature whistles that are dissimilar to those of their mothers (e.g., Bojanowski et al., 2000; Caldwell & Caldwell, 1979; Fripp et al., 2005; Miksis et al., 2002; Tyack, 1997; Sayigh, 1992; Tyack & Sayigh, 1997). However, in instances when calves do model their signature whistle after the mother, calf sex may be of influence. In wild populations, male bottlenose dolphin calves have shown a tendency to produce signature whistles similar to their mothers, whereas females develop more distinctive whistles (Sayigh, Tyack, Wells, & Scott, 1990; Sayigh, Tyack, Wells, Scott, & Irvine, 1995). Sex differences in signature whistle modeling are likely a result of greater selective pressure on female calves as related females maintain close associations (Sayigh et al., 1990, 1995). As such, it may be necessary for females to develop distinctive whistles in order to maintain individuality among kin. The development of signature whistles in male calves may be less restrictive, and males that

develop signature whistles similar to their mothers may be more readily identifiable to kin after separating from the mother-calf dyad (Sayigh et al., 1995).

Beluga calves may first develop complex contact calls most similar to the contact calls of their mothers regardless of calf sex, as evident in the contact call types incorporated by Kylu, Tuvaq, and Tuvaq's half-sister, Qila, in early life (Vergara and Barrett-Lennard, 2008). However, additional research of vocal development in female beluga calves is necessary to adequately assess this hypothesis. If calves develop contact calls that are similar to their mothers and these call types remain stable in the vocal repertoires of these animals, then some beluga calls may be used for long-term kin identification. As previously discussed, similarity between mother and calf contact call repertoires may have important implications regarding the longevity of affiliation with related individuals. These calls may have a critical function in the reunion of related individuals along migratory routes or in summering areas as they may allow for kin identification from a long distance or within a large number of conspecifics.

Individual identity information may be encoded in parameters with discriminant ability, which could aid in conspecific recognition when related individuals produce the same contact call type. For example, some reports of killer whale communication calls have shown the importance of call parameters in differentiating the same call type in the vocal repertoires of matrilineal units (Miller & Bain, 2000) and communities or clans (Riesch, Ford, & Thomsen, 2006). Likewise, parameters with discriminant ability that are similar across beluga contact call types may be indicative of species-specific call characteristics that encode individual identity.

For the complex contact calls described by Vergara (2011) and here, the beginning frequency of the dominant tonal element was an important parameter in

determining the individual producing the call. Thus, it may be that belugas use differences such as this in tonal or other overlapping signature elements (Vergara and Mikus, 2018) in order to code identity information (Vergara and Barrett-Lennard, 2008). In killer whale whistles, the beginning tonal frequency was also a differentiating parameter when comparing whistles produced by communities or clans (Riesch et al., 2006), although individual differences in call type production were not assessed. Future playback studies should investigate the salience of parameters with discriminant ability in order to determine whether the characteristics used to classify calls in statistical analyses are biologically important in identifying related individuals.

Comparison of maternal contact call production

Yulka and Aurora, the mother in the earlier study, both produced their contact calls in similar contexts of separation, when a diver was present in their respective habitats, and in response to their calf's own contact calls, which supports the contextual specificity of contact calls highlighted by previous reports (Vergara and Barrett-Lennard, 2008; Vergara et al., 2010). Yulka produced her type Y1 call on the day of Kylu's birth and continuously in the first month of Kylu's life, unlike Aurora who produced a different subtype of her contact call on the day of Tuvaq's birth, beginning the production of other subtypes the following day (Vergara and Barrett-Lennard, 2008). Additionally, Vergara and Barrett-Lennard (2008) reported that Aurora did not use her type A calls prepartum, but preliminary analyses of data collected in the pre-partum period of the current study revealed the presence of both Yulka's Y1 and Y2 calls within the few months prior to Kylu's birth. It is likely that the variation in rates of contact call production and use of different subtypes are due to individual differences in the mothers. Similar variations in pre-partum signature whistle production in bottlenose dolphin mothers have been noted. For example, two studies (Mello and Amundin, 2005; Ames, 2016) found that dolphin mothers increase their signature whistle production prior to their calf's birth, although the timing of this increase varied. Fripp and Tyack (2008) found that no such pre-partum increase occurred in their study. Ames and colleagues (2017) also discussed differences in maternal use of an additional dolphin contact call termed "thunk" emitted in one population of captive bottlenose dolphin females. Variations in rates of family specific call production also exist between Northern Resident killer whale matrilines during the post-partum period (Weiß, Ladich, Spong, & Symonds, 2006). Thus, it is likely that individual beluga mothers differ in their emission of contact call subtypes during the pre and post-partum periods, although contextual use of these sounds appears more rigid.

Given that Kylu did not ultimately incorporate the Y1 subtype and did not produce complex contact calls until his second year, it is likely that beluga mothers are responsible for the development and maintenance of early recognition systems in the mother-calf dyad, similar to bottlenose dolphins (for review, see Ames, 2016). Furthermore, as Aurora did not produce type A calls in the months prior to Tuvaq's birth, this early recognition system may begin to be established after a beluga calf's birth, and not sometime in the pre-partum period as has been implied for dolphins (Tyack & Sayigh, 1997) and humans (e.g., DeCasper & Fifer, 1980; Partanen, Kujala, Tervaniemi, & Huotilainen, 2013). Beluga calves are precocial at birth, so some established recognition system would likely be useful to calf survival. However, it is currently difficult to ascertain when this system would likely be established due to the differences between studies in the timing of maternal contact call production.
Playing with sound: evidence of beluga babbling?

One period of data collection at the end of the calf's first month of life was remarkable in that the calf produced several sounds types that had previously not been identified in his repertoire. On the 26th day of Kylu's life, he produced pulse tones and several types of mixed pulse calls. As previously discussed, this may be indicative of increased motor control or development of the phonic lips or associated vocal structures, allowing the simultaneous production of pulses with increased repetition rate. Communication pulses have been shown to be produced in both the left and right phonic lip sets in belugas (Ames et al., in prep.), so it is likely that both pairs were used in mixed pulse production. Two other reports (Karlsen et al., 2002; Vergara, 2011) have indicated mixed pulse production in beluga whales, so it was not unusual that these sounds appear in Kylu's repertoire. It was curious, however, that all of these sounds would appear within the same recording session.

Behavioral observations on this day revealed that during periods when Kylu produced these novel sound types, he was not physically interacting with his parents, but playfully interacting with his trainers or playing on his own. Hence, Kylu may have been practicing or quite literally playing with sound during this recording session. Human children play with language and it has been hypothesized that solitary play has a role in the development of contextually flexible communication for humans and animals (Kuczaj & Makecha, 2008). Furthermore, Kuczaj (1998) postulated that species with flexible communication systems are more likely to play with their sounds. Perhaps the most tangible evidence of sound play is babbling.

Babbling may be an integral part of development in species that use a wide range of sounds for communication (Knörnschild, Behr, & von Helversen, 2006). For example,

in non-human animals babbling has been ascribed to birds (e.g., Goldstein, King, & West, 2003; Hultsch & Todt, 2004; Marler & Peters, 1982a, b), giant otters (Pteronura brasiliensis, Mumm & Knörnschild, 2014), marmosets (pygmy marmosets, Cebuella pygmaea, Elowson, Snowdon, & Lazaro-Perea, 1998a, b; Snowdon & Elowson, 2001; Snowdon, Elowson, & Roush, 1997, and common marmosets, Callithrix jacchus, Takahashi et al., 2015), and bats (Knörnschild et al., 2006; Monroy, Carter, Miller, & Covey, 2011), in addition to belugas (Vergara and Barrett-Lennard, 2008). It is possible that there is a relationship between play and babbling in beluga infants, just as there appears to be a relationship between single-object play and babbling with later symbolic and linguistic development in humans (Orr & Geva, 2015). Play and novel sound production may be a feature in the development in other delphinoid species as well. An eight-month-old female killer whale calf purportedly produced a wide variety of sounds at a newly deployed hydrophone that seemed to peak her interest (Bowles, Young, & Asper, 1998). This variety in sound production continued for the entire hour the hydrophone was deployed and showed increased variability in the calf's repertoire when compared to an early recording period. Likewise, Kylu would often turn his attention to a submerged platform in the beluga pool the trainers used for feeding and play sessions with the calf. The platform was hinged to a ladder that extended over the wall of the pool, and when the belugas were not on session (i.e., trainers were not on the platform), Kylu would continually push the platform up in a flurry of bubbles and vocalizations. Attention to the hydrophone for the killer whale calf and continued interaction with the training platform for Kylu could represent some type of single object play, and as such, this type of solitary play may serve as a critical function in the development of odontocete communication.

Babbling is thought to invoke parental response in some species (e.g., giant otters, Mumm & Knörnschild, 2014, and pygmy marmosets, Elowson et al., 1998a, b; Snowdon & Elowson, 2001), but this may not be reflective of babbling in beluga calves if novel sound production does not result in an interaction with conspecifics. Yulka did not respond to Kylu's sound production during this event at the end of his first month, or during later solitary play events when Kylu continually emitted several sound types. The absence of Yulka's response may actually allow for some building blocks of contextual learning to take root, as sound play may facilitate contextual learning in addition to signal acquisition (Kuczaj & Makecha, 2008). Adult sac-winged bats (Saccopteryx bilineata) do not respond to the babbling of their pups (Knörnschild et al., 2006). When bat pups babble, they string together sounds adults use in specific contexts, juxtaposing sounds that have different contextual applications in the same bout (Knörnschild et al., 2006). Later, these sounds are applied to the appropriate context, suggesting that pups first practice sounds, perfecting their production, before applying them contextually. Likewise, beluga calves may first practice sound through solitary play in order to perfect a vocalization before applying it to the appropriate context.

Over Kylu's first year of life, sound acquisition and attrition were fluid as he acquired sound types as quickly as they disappeared from his repertoire. Many of the calls first recorded on his 26th day were not prominent in later months; especially as earlier sounds gave way to more sophisticated sound production. Bottlenose dolphins refine their signature whistles gradually, but also continue to increase their vocal repertoires over time (Tyack, 2003) as bottlenose dolphins vocally learn throughout their lifetime (King, Sayigh, Wells, Fellner, & Janik, 2013; Richards et al., 1984; Tyack & Sayigh, 1997). The continued inclusion of new sounds in a species' adult repertoire is

inconsistent from babbling behavior in other species wherein babbling leads from an overproduction of sounds to a more polished repertoire. For example, in bird species, the babbling stages of subsong and plastic song (Goldstein, King, & West, 2003) lead to crystallized full song through attrition (Hultsch & Todt, 2004; Marler, & Peters, 1982b).

With human babbling, infants produce an assortment of sounds that will not appear in the language eventually learned by the child (Kuczaj & Makecha, 2008). But it is important to consider that, while language itself may represent a refinement in the vocal repertoires of humans, adults are still capable of learning, imitating, and incorporating new sounds (e.g., new languages). The contrary is true for the babbling behavior of pygmy marmosets (Snowden et al., 1997) and bats (Knörnschild et al., 2006) that appear to begin life with almost a complete adult vocal repertoire, but no understanding of contextual application. Furthermore, it has been sufficiently demonstrated that the adult vocal repertoire emerges from unstereotyped sounds produced by beluga (Vergara and Barrett-Lennard, 2008) and dolphin (McCowan & Reiss, 1995) calves. Thus, it is likely that babbling is manifested somewhat differently between highly communicative species, and variability in a species' developed repertoire should be treated as evidence for the vocal flexibility of the species, especially if newly incorporated sounds in an adult's repertoire are adult-like in their initial production and have contextual significance.

Species-specific developmental trajectory

Pulse trains are consistently the first calls produced by beluga calves, as reported for 5 beluga calves (2 born at Oceanogràfic including Kylu; 3 born at the Vancouver aquarium, Vergara, 2011). These calls consistently appear in beluga calves' vocal repertoires in early life and are understood to be preliminary contact calls. Pulse train PRR and peak frequency are initially low in all beluga calves (see findings in Castellote et al., 2007 and Vergara, 2011), and changes in these parameters behave similarly over time. Parallels in the development of acoustic energy parameters in calves may indicate the stage in development at which belugas may be able to compensate for noise in their sound environments (further discussed below).

Remaining sound type acquisition varied but still followed a similar pattern in the beluga calves. For example, Kylu was more delayed in whistle production when compared to the two Vancouver aquarium calves (MacLeod, 2009; Vergara, 2011), but whistle emission still preceded the regular production of mixed calls in both Tuvaq and Kylu. Regular, more adult-like mixed call production began around the same time for Tuvaq and Kylu, but again, Kylu was a bit more delayed in reaching this milestone when compared to Tuvaq. Consequently, there appear to be stages of sound acquisition that occur within a window of time (i.e., 1-3 months for whistle emergence and 4-5 months for adult-like mixed calls). Delays in Kylu's acquisition of some sounds may have been influenced by the sounds available to him in his sound environment. For example, a lack of whistle production in the vocal repertoires of the adult belugas may have contributed to the delay in the production of this sound in Kylu. Continued analyses of adult calls produced during the calf's first year of life may shed light on factors contributing to the delays in Kylu's sound acquisition. Moreover, it should also be noted that Kylu's social group was unique in that it only comprised his parents. Tuvaq developed alongside multiple whales, both related and unrelated, so some of Kylu's delays may be attributable to his unique social situation.

Unstereotyped mixed calls were a precursor to the development of complex contact calls in both calves, but with great individual variation in developmental

trajectory. Furthermore, the prevalence of a mother's contact-call subtype in the first month of life may not influence a calf's incorporation of that subtype in later life, as is evident by Kylu's use of his mother's alternative subtype, Y2, at 23 months of age. Ultimately, beluga calves appear to develop contact calls that are similar to their mothers, which may be group specific and important for long-term kin recognition. These calls appear to approach full stereotypy towards the end of calves' second year of life. Further research is necessary in order to determine whether beluga contact calls are stable over time, or if calves alter characteristics of their contact calls once they mature and separate from their mothers.

Influences on beluga vocal development: Genetics or learning?

It can be difficult to tease apart the influence of learning processes from genetic predisposition in ontogenetic studies, especially when offspring develop sounds that are similar to their kin. For example, killer whales are known vocal production learners (Crance et al., 2014; Foote et al., 2006), but biological influence cannot be discounted in calves that develop calls that are similar to their mothers (Bowles et al., 1988), especially when killer whale societies are formed of matrilineal units that have family specific calls. The current study was not designed to thoroughly evaluate the roles of genetics and learning in the development of Kylu's complex contact call (discussed further in *Limitations*) as Kylu developed a call type that was similar to his mother's. Perhaps if Kylu had modeled his contact call based on another acoustic signal in his sound environment, more could be said re the learning processes associated with beluga vocal development.

Some arguments do support the influence of vocal learning in the development of complex contact calls, however. For example, if beluga calves are genetically

predisposed to develop the contact calls of their mothers, it should be expected that complex contact call development would follow the same inherent trajectory across calves. Tuvaq and Kylu showed slight differences in the influence of their mother's subtype, as Kylu incorporated a subtype that was not acoustically abundant early in his life. Furthermore, the progression of Tuvaq's contact call could be described as a slow perfection over time in comparison to the potentially more abrupt and less stereotyped emergence of Kylu's contact call at the end of his second year. It should be noted that it is possible Kylu began producing his contact call sometime prior to its emission during the 23rd month of life. Further analyses of data recorded in the second year may be able to illuminate more on the development of Kylu's Y2 call, but it's likely that, given the more opportunistic nature of data collection in the second year, some earlier versions of Kylu's Y2 call were not recorded.

As previously discussed, vocal learning likely evolved in highly gregarious mammals as a means of developing complex signals that allow conspecifics to maintain social bonds in visually limited environments. This is especially true for the development of contact calls for use in the aquatic environment where conspecifics may be separated by large distances, as sounds can transmit farther and faster in water than in air (Janik, 2014). Belugas are highly social and mobile aquatic mammals, capable of maintaining long-term associations with related individuals while traversing large migratory distances. Belugas may share specific complex contact calls with related individuals in order to facilitate contact with kin, and it is likely that individual identity is embedded within these shared vocal signatures. As reviewed above, there is a growing body of support for the existence of vocal signatures in the form of beluga complex contact calls (Panova et al., 2017; Vergara & Mikus, 2018), however it may be possible that some vocal signatures are shared by related individuals. If some contact calls function as kin identifiers, variations in shared vocal signatures may be key in distinguishing individuals using the same call type, although the extent of the variation in the signature would need to be able to withstand certain environmental pressures. It is doubtful that voice cues would be sufficient in encoding identity information in calls used by cetaceans as under pressure, voice cues are likely altered due to changes in the vocal tract of diving animals (Tyack, 1991), and the noisy nature of the underwater environment may easily interfere in the transmission of subtle identity information (Janik, 1999b). In contrast, variations in vocal signatures could potentially allow belugas to convey identity information despite the constraints of the aquatic environment (Janik, 2014; Vergara & Mikus, 2018). Vocal signatures appear to be heavily influenced by vocal learning and the learning of group specific calls likely promote individual variation in shared vocal signatures through copying errors (Boughman & Moss, 2003). Thus, it would be more useful for complex contact calls to be learned and incorporated into the vocal repertoires of beluga calves, rather than genetically predisposed.

Neonate calf calls and noise

A component of this study focused on the changes in pulse train parameters during the first month of Kylu's life. Understanding the structure of the vocalizations produced by newborn calves during the first few weeks of life is important in light of increased mortality rates of newborns in the St. Lawrence in recent years (Lesage, Mosnier, Measures, Lair, & Béland, 2014) and pulse trains are the primary call type used by beluga calves during this period critical to calf survival. Anthropogenic noise is one of the various factors hypothesized to play a role to high calf mortality rates in the St. Lawrence Estuary belugas (DFO, 2017), and mothers and calves are exposed to vessel noise daily (Lesage, McQuinn, Carrier, Gosselin, & Mosnier, 2014).

In the Pacific Northwest, a study of vessel noise integrated from 11.5 Hz to 40 kHz from various ship types found that underwater noise emanated from vessels extended into the ultrasonic frequency range when ships were within a distance of three kilometers (Veirs, Veirs, & Wood, 2016). The findings from this study have detrimental implications for the many odontocete species that send or receive signals within this frequency range, as sounds that are critical to the survival of these species may experience masking (i.e., the interference of noise with an animal's ability to detect or recognize a sound of interest, Erbe et al., 2015). Gervaise, Simard, Roy, Kinda, and Menard (2012) estimated source levels of ship noise in the Saguenay-St. Lawrence area integrated from 10 Hz-20 kHz. The authors postulated potential serious effects of anthropogenic noise on the upper frequencies of beluga whale sounds, but presently, no studies have thoroughly investigated vessel noise at ultrasonic frequencies in the SLE. Furthermore, many studies of beluga whale communication signals drastically underestimate the upper frequency limits of these sounds.

The mean peak frequency of Kylu's pulse trains in his first month of life was less than 10 kHz, demonstrating the vulnerability of these early calf calls to shipping noise. Additionally, calf calls produced in the first few weeks of life have much lower source levels than adult belugas (Vergara et al., in prep). Lower source levels coupled with peak frequencies that may easily be masked by vessel noise may make it challenging for beluga mothers of especially young calves to detect their calf's calls in noisy environments. Whether beluga mothers can hear these calls however may be dependent on the distance the mother is from her calf, as findings from the recent study by Vergara and colleagues (in prep.) showed that the active space of calf calls is dramatically reduced in noisy conditions. Thus, if a separation between a beluga mother and her calf occurs, the mother may not be able to reunite with her calf if conditions in the environment are too noisy and/or the distance of the separation becomes too great.

Cetaceans (see Erbe, 2016 for review), bats (Hage, Berquist, Feng, & Metzner, 2013) and birds (e.g., Francis, Ortega, Cruz, & 2010; Hanna, Blouin-Demers, Wilson, & Mennill, 2011; Nemeth et al., 2013) appear to compensate for noise by actively shifting the amplitude and/or acoustic energy distribution of their calls. In the presence of increased environmental noise, dolphin species have been shown to alter minimum or maximum whistle frequencies (Papale, Gamba, Perez-Gil, Martin, & Giacoma, 2015), reduce frequency modulations, or alter the frequencies at which whistles were produced (Morisaka, Shinohara, Nakahara, & Akamatsu, 2005). Belugas are capable of shifts in call peak frequency in order to compensate for noise. Au, Carder, Penner, and Scronce (1985) showed that a beluga whale in managed care shifted the peak frequency of its echolocation clicks when it was moved to a new semi-captive facility with a sound environment that included more biotic noise from snapping shrimp within the animal's previous echolocation frequency range. Lesage, Barrette, Kingsley, and Sjare (1999) found that belugas possess the ability to shift the peak frequencies of tonal calls to a higher frequency when near in proximity to vessels in the St. Lawrence.

As discussed above, peak frequency increased over Kylu's first year of life. This was particularly noticeable starting in his third month when the mean peak frequency of the calf's pulse trains was near 40 kHz. This trend in month three may indicate the period when beluga calves are able to naturally compensate for vessel noise through increased energy at the higher frequencies of their calls. It is currently unknown when calves learn

to shift peak frequencies as a response to noise. However, it is likely that the physical ability to produce higher peak frequencies is a precursor to this learned ability. Identifying the sensitive window in which calves are at least physically able to produce sounds at higher frequencies is possible through vocal development studies such as the current report that investigate changes in acoustic energy distribution. This report has highlighted several differences in calf developmental trajectory, so future studies of beluga vocal development are important to determine if the third month increases in peak frequency are consistent among calves.

Limitations

This study initially sought to investigate changes in minimum, maximum, and subsequently, delta frequencies, however due to the pool noise that was previously discussed, minimum frequencies could not be accurately assessed. In addition, maximum frequency was limited by the sampling rate of the IcListen in the calf's early life. It is likely that the upper frequency limits of the calf's calls from birth extended past the 128 kHz Nyquist frequency of this study. Because minimum and maximum frequencies could not be accurately assessed, delta frequency was not analyzed.

It should also be noted that an anti-aliasing filter occurring at 40% of the icListen's sampling rate may have affected energy distribution at the upper frequency limits of the calf's calls recorded on this hydrophone. However, despite some filtering of the upper frequencies, the overall trends showed that the calf's acoustic energy distribution increased with age; an indicator of the robustness of the findings presented here.

It should be noted that my findings are only limited to data in which I could positively identify the calf's calls. There may have been earlier instances of each sound that were either 1) not recorded within my data set or 2) could not be assigned to Kylu with certainty. At times, single hydrophone deployment made it difficult to localize individuals with 100% accuracy. However, given the size of the pools in the beluga habitat and the ease with which other methods could be employed instead, the use of two hydrophones was not necessary in the localization of calling individuals a majority of the time.

Finally, this study was not designed to decipher whether beluga call development occurs from a biological template or through production learning. Vergara and Barrett-Lennard (2008) provided tentative evidence for vocal production learning in beluga calves through the acquisition of a novel sound when Tuvaq, who had previously been acoustically isolated from his father, Imaq, began to produce Imaq's contact calls once he was introduced to Tuvaq's sound environment. The current study cannot offer further insight on this phenomenon as the gates in the beluga habitat at Oceanogràfic are not acoustically opaque and as such, Kairo was never acoustically separated from the dyad. Even if Kairo had been separated acoustically from the dyad, Kylu may still have been predisposed to produce his father's calls as he matured, even without exposure (Vergara & Barrett-Lennard, 2008).

Conclusions

Studies of vocal development are crucial in understanding the communication of species that heavily rely on sound to survive and maintain social ties with conspecifics. It was my objective to complete a study that added to the literature and furthered the scientific understanding of beluga calves through the development of Kylu's vocal repertoire. As was emphasized above, the aim of this research was to answer the following questions: 1) what can we infer regarding the beluga communication system

through studying and comparing the vocal development of beluga calves? 2) What more can we understand regarding complex contact calls? And 3) how are the calls of beluga neonates affected by noise?

Findings in the current report provide evidence in support of species-specific stages in sound acquisition and changes in parameters of beluga calf sounds also follow similar developmental trajectories. A detailed investigation into the changes of calf call acoustic energy distribution over the first year of life is also provided here. Furthermore, it appears that male beluga calves first develop contact calls that are similar to their mother's contact call type, though not identical as evident through DFA classification. Finally, analyses of pulse train source levels and parameters of acoustic energy distribution in the calf's first month of life are useful to shed light on the extent to which vessel noise in the SLE and other noisy beluga habitats impacts effective mother-calf communication. Future research will seek to further our understanding of beluga contact call usage in addition to elucidating the function of other contextually specific calls.

There is still much to be learned regarding the communication systems of the loquacious beluga whale. Continuing studies of vocal development can tell us a good deal about highly communicative animal species in regard to the sounds that are salient to the species, learning processes or genetic predispositions that shape vocal repertoires over time, and how changes in characteristics of vocalizations interact with the environment, especially when animals are forced to respond to environmental changes that may be influenced by humans. Vocal development studies are sparse in the literature for many animal species. In cetaceans, this is partly due to difficulties in studying wild cetacean calves for long periods of time. However, when a species like the beluga can be well managed in captive care, it is of upmost importance to learn as much as we can about

these animals in a controlled environment in order to aid understanding of the species' wild counterparts. It was the primary objective of this study to increase our knowledge of the beluga species through exploration of beluga vocal ontogeny.

APPENDIX A – IACUC Approval Letter



INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE

118 College Drive #5116 | Hattiesburg, MS 39406-0001 Phone: 601.266.6791 | Fax: 601.266.4377 | iacuc@usm.edu | www.usm.edu/iacuc

NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:16041402PROJECT TITLE:Beluga (DelphinaptePROPOSED PROJECT DATES:04/2016 - 09/2018PROJECT TYPE:NewPRINCIPAL INVESTIGATOR(S):Stan KuczajDEPARTMENT:PsychologyFUNDING AGENCY/SPONSOR:N/AIACUC COMMITTEE ACTION:Full Committee AppPROTOCOL EXPIRATON DATE:September 30, 2018

16041402 Beluga (Delphinapterus leucas) Vocal Ontogeny 04/2016 – 09/2018 New Stan Kuczaj Psychology N/A Full Committee Approval

Date

6.2M0000

Frank Moore, PhD IACUC Chair 4/14/2016

APPENDIX B - Animal Care & Welfare Committee Approval Lett



Valeria Vergara Vancouver Aquarium Marine Science Centre 845 Avison Way, Vancouver, BC V6G 3E2, Canada

Valeria.vergara@vanaqua.org

9th November 2016

DECISION OF ANIMAL CARE & WELFARE COMMITTEE RELATING TO APPLICATION FOR USE OF ANIMALS AT OCEANOGRÁFIC – BIOLOGICAL SAMPLE

Project Title: Beluga vocal development Project reference: OCE-9-16

Dear Valeria,

We have carefully evaluated the above-named project.

I am pleased to inform you that your Application to use Animals for Research was Approved as a Biological Sample Request

The conditions under which sampling may proceed are as follows:

- The Applicant will allow Oceanogràfic to review a draft of any project report based on analysis of the specimens or data originating from the Oceanogràfic. Any communication made public or open access is considered a report.
- (ii) The Applicant will acknowledge Oceanogràfic in any publication arising from the Project, and provide Oceanogràfic with a copy of any printed publication.
- (iii) The applicant will not use the samples for any other purpose that the ones specified in the original request.
- (iv) The applicant will not use the samples for commercial purposes.

Please sign a copy of this letter at the bottom of the page to confirm your agreement of the conditions and return to Ms. Silvia Tecles at <u>stecles@oceanografic.org</u>. Silvia will be the initial point of contact for providing information, addressing concerns and for ensuring all aspects of the research activities follow Oceanogràfic policies.

We look forward to working with you on this important project.

Sincerely,

Andreas Fahlman, Director of Research Fundación Oceanogràfic Administration

I accept the terms and conditions detailed above:

Name: Valeria Vergara

Date:

Viling Constant-Signature:

Fundación Oceanogràfic de la Comunitat Valenciana Address: C/. Eduardo Primo Yúfera (Científic), nº 1B 46013 Valencia España Fiscal Address: Gran Vía Marqués del Turia 19. 46005 Valencia España Tlf: (+34) 961 975 500 Fax(+34) 96 1975511 web:www.avanqua.org

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