Pre- and Postpartum Acoustic Activity in Captive Pacific White-Sided Dolphin (Lagenorhynchus obliquidens) Mothers

Authors: Mishima, Yuka, Matsumoto, Teruyo, Morisaka, Tadamichi, and Nakahara, Fumio

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Yuka Mishima[1],*, Teruyo Matsumoto[2], Tadamichi Morisaka[3] and Fumio Nakahara[4]

[1] *Department of Marine Resources and Energy, Tokyo University of Marine Science and Technology, 4-5-7, Konan, Minato-ku, Tokyo 108-8477, Japan*
[2] *Niigata City Aquarium, Marinepia Nihonkai (Sea of Japan), 5932-445 Nishifunami-cho, Chuo-ku, Niigata 951-8555, Japan*
[3] *Cetacean Research Center, Graduate School of Bioresources, Mie University, 1577, Kurimamachiya-cho, Tsu-shi, Mie 514-8507, Japan*
[4] *Faculty of Human Sciences, Tokiwa University, 1-430-1, Miwa, Mito-shi, Ibaraki 310-8585, Japan*

Abstract.   Active acoustic emission from a mother to a calf after parturition is one strategy used to enhance recognition of mothers by calves and develop, then maintain, a mother–calf bond from an early stage. This study predicted that a high-calling postpartum period exists in a social delphinid, the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). This species produces pulsed call sequences for vocal exchange with conspecifics, and these sequences appear to be an important signal between mothers and calves. Sounds were recorded from three pregnant females at the Niigata City Aquarium, Marinepia Nihonkai, Japan, before and after each birth in 2019, 2020, and 2021 to investigate the rate of their pulsed call sequences. Continuous data from prior to four days to five days following parturition, opportunistic data within the last pre-parturition month, and data from the postpartum period were obtained from the females. The pulsed call sequence gradually increased during the last gestational month. A high-rate sequence was repeated daily for four days pre-parturition and faded within several hours postpartum, and few sequences were produced from the day after parturition. Contrary to our prediction, the many pre-parturition sequences and fewer postpartum sequences suggest a low efficiency of postpartum imprinting in this species.

Key words: birth, contact call, imprinting, mother–calf, parturition.

Changes in the call production of mothers related to parturition have been reported in some mammalian species such as pinnipeds, ungulates, and toothed whales. The calling activity of Galápagos fur seal (*Arctocephalus galapagoensis*) and sea lion (*Zalophus californianus wollebaeki*) mothers was high during the initial days of a pup's life (Trillmich 1981). Red deer (*Cervus elaphus*) mothers produced postpartum calls more often than pre-parturition (Vaňková and Málek 1997), and a higher calling rate during the first two weeks after birth than subsequent postpartum experimental periods was documented in the pampas deer (*Ozotoceros bezoarticus*) (Olazábal et al. 2013). Domestic goats (*Capra hircus*) produced frequent calls from the hour preceding parturition to 4–6 h postpartum (Lickliter 1985). Similarly, high-rate bleats were observed in sheep (*Ovis aries*) during labor and the early postpartum period (Dwyer et al. 1998; Sèbe et al. 2007); mothers increased bleats in the last 3 h before parturition, and a peak of bleats was observed during the first 3 h following parturition, consequently, the number decreased until 12 h postpartum, and subsequently remained low (Sèbe et al. 2007).

In odontocetes, the acoustic activity of mothers before and after parturition has been investigated in common bottlenose dolphins (*Tursiops truncatus*) and belugas (*Delphinapterus leucas*). Common bottlenose dolphins use individually distinct "signature whistles" (Caldwell and Caldwell 1965; Caldwell et al. 1990) to maintain contact with conspecifics (Janik and Slater 1998) in their extensive social networks (Connor et al. 2000). Signature whistles are also used to facilitate mother–calf reunions after separation (Sayigh et al. 1990; Smolker et al. 1993;

To whom correspondence should be addressed. E-mail: ymishi0@kaiyodai.ac.jp

Tyack and Sayigh 1997; Mello and Amundin 2005; King et al. 2013). Some studies have shown the use of signature whistles by mothers before and after parturition; during a calf's first week following birth, the occurrence of signature whistles produced by a mother interacting with her calf increased (Fripp and Tyack 2008; Ames et al. 2019), and thereafter declined and remained low (Ames et al. 2019). However, special cases of calf theft (Fripp and Tyack 2008) and calf switching (King et al. 2016) may affect the duration of high-acoustic activity in mothers. The signature whistle production of a mother whose calf was stolen by another mother immediately after birth and was returned to the sixth day increased for two weeks postpartum (Fripp and Tyack 2008). The signature whistle rate of mothers who switched calves in the third week after birth remained high at four weeks postpartum (King et al. 2016).

Belugas produce various calls. One type of pulsed call that sounds like a creaking door is thought to be used as a contact call to maintain group cohesion in their fission–fusion society (Michaud 2005; Colbeck et al. 2013; O'Corry-Crowe et al. 2020) because it is commonly produced in the context of separation (Mishima et al. 2015), is used in vocal exchanges (Morisaka et al. 2013; Mishima et al. 2018), and contains individuality (Morisaka et al. 2013; Mishima et al. 2015, 2018; Vergara and Mikus 2019). Like common bottlenose dolphins, beluga mother–calf pairs use contact calls to maintain their bond (Vergara and Barrett-Lennard 2008; Vergara et al. 2010; Ames and Vergara 2020). The highest rate of contact calls produced by mothers occurred during a recording period of 2 h following birth, compared to other recording sessions, such as separation, re-introduction, and normal behavior (Vergara et al. 2010). A mother was silent during the last five days prior to parturition, while one of her three call subtypes was more frequently produced during the 2 h following birth, and another subtype comprised most of her sounds from day three post-birth to three months later (Vergara and Barrett-Lennard 2008; Vergara et al. 2010). Alternatively, another mother, who had two subtypes of her individually distinctive call type, produced both subtypes regularly for two months pre-parturition. She used one subtype for one month postpartum and, thereafter, hardly produced either subtype for two years postpartum (Ames and Vergara 2020). Therefore, several postpartum emissions of certain calls by mothers seem to be related to birth in belugas as well as in common bottlenose dolphins.

Researchers have discussed various physiological and functional factors, such as stress, restlessness, arousal, hormones (e.g., estrogen and cortisol), and imprinting, which are not mutually exclusive and could cause high acoustic activity in pre- and postpartum mothers (e.g., Dwyer et al. 1998; Mello and Amundin 2005; Sèbe et al. 2007; Ames et al. 2019). Imprinting is known to enhance the recognition of mothers' calls by calves and allows mother–calf dyads to develop and maintain their bonds at an early age. According to playback experiments, ten-day-old Galapagos fur seal and sea lion pups could recognize their mother's call (Trillmich 1981). Recognition of mothers' calls by pups could be established within two to five days postpartum in subantarctic fur seals (*A. tropicalis*) (Charrier et al. 2001) and between ten days and two months of age in Australian sea lions (*Neophoca cinerea*) (Pitcher et al. 2009). In ungulates, sheep calves at 48 h after birth and goat calves at least one week after birth can recognize their mother's calls (Sèbe et al. 2007; Briefer and McElligott 2011).

Mann and Smuts (1998) hypothesized that imprinting for mother–calf recognition may occur during the first few days of life in Indo-Pacific bottlenose dolphin (*T. aduncus*) calves. The period when mother–calf recognition is established is usually associated with the age of the first mother–calf separation (e.g., as the subantarctic fur seal: Charrier et al. 2001). In Shark Bay, Australia, calves begin to separate from their mothers in the second week after birth (Mann and Smuts 1998, 1999). The mothers prevented calves from straying to other dolphins during the initial few days but began to allow them by the second week (Mann and Smuts 1998). Given the period when mothers allow their calves to separate socially, imprinting may be completed within approximately the first week with this species (Mann and Smuts 1998). Subsequent studies of common bottlenose dolphins found a high whistling rate in mothers about one week after parturition, which supported the imprinting hypothesis (Fripp and Tyack 2008; King et al. 2016; Ames et al. 2019).

The current study predicted a similar pattern of acoustic activity for mothers in another delphinid species, the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). Although Black (1994) suggested this species exhibits fission–fusion dynamics and forms long-term associations with certain individuals, information about the details of their social structure is scarce. Pacific white-sided dolphins produce a unique and rhythmic call named "pulsed call sequences" that are successions of three or more pulsed calls with inter-call intervals of less

than 325 ms and that have a repeated structure composed of several types of pulsed calls (Mishima et al. 2019). Pulsed call sequences are clearly divided into types, and each dolphin preferentially uses a specific type of sequence, although sharing of sequence types has also been observed (Mishima et al. 2019). Pacific white-sided dolphins produce the pulsed call sequences particularly in mixed contexts of foraging and milling, or traveling (Henderson et al. 2011) as well as in the context of separation (Mishima et al. 2019). Therefore, these call sequences are likely to promote group cohesion and coordination during search behavior, a transition to another behavior, and separation (Henderson et al. 2011; Mishima et al. 2019). Similar to the signature whistles of common bottlenose dolphins and the pulsed calls of belugas, pulsed call sequences appear to be an important signal for the mother–calf bond in Pacific white-sided dolphins.

In captive Pacific white-sided dolphins, calves begin to associate with conspecifics within an average of six days (range of four to seven days; Smith 2019), which is comparable to bottlenose dolphins (Mann and Smuts 1998, 1999; Gubbins et al. 1999). Therefore, we hypothesize that many call emissions from mothers to their calves may occur for approximately one-week postpartum to facilitate the early recognition of mothers by calves. In this study, we recorded sounds from three mothers at an aquarium for pre- and postpartum days and months. Pulsed call sequences were extracted from recordings and classified into types. Changes in the number of sequences in mothers per minute were investigated before and after parturition to elucidate the possibility of imprinting in this species.

Additionally, the calling of mothers is expected to correlate with their physiology. A decline in body temperature before parturition has been observed in many cetaceans such as common bottlenose dolphins (Terasawa et al. 1999), killer whales (*Orcinus orca*) (Katsumata et al. 2006b), harbor porpoises (*Phocoena phocoena*) (Blanchet et al. 2008), and spotted dolphins (*Stenella attenuata*) (Ikeshima et al. 2021). The relationship between the production rates of pulsed call sequences for mothers and their body temperature, which is an indirect physiological indicator controlled by hormones, was also analyzed in parallel during the pre-parturition period to investigate the possibility that hormones cause the acoustic activity in mothers. For example, body temperature changes during the estrous cycle are positively correlated with progesterone levels in a female beluga (Katsumata et al. 2006a) and a female killer whale (Kusuda et al. 2011). The acrophases of diurnal rhythms in body temperature and cortisol levels were observed at approximately the same time in male Indo-Pacific bottlenose dolphins (Funasaka et al. 2011). Cortisol levels have been used as a stress indicator, as they increased during stressful situations in common bottlenose dolphins (Noda et al. 2007) and their whistle rate also increased under stress, such as brief capture–release events (Esch et al. 2009) and vessel approaches (Buckstaff 2004; Guerra et al. 2014). Therefore, if the production rates of pulsed call sequences for mothers are significantly correlated with their body temperature during the pre-parturition period, we hypothesize the possibility of hormonal effect occurring on the acoustic activity of mothers.

Materials and methods

Facility and subjects

This study was conducted in the Niigata City Aquarium, Marinepia Nihonkai, Niigata, Japan. The social group included one adult male and three adult female Pacific white-sided dolphins, along with three adult common bottlenose dolphins, were kept in a dolphin pool at the start of the study in July 2019. The study subjects were three adult female Pacific white-sided dolphins, #F1, #F2, and #F3 (daughter of #F1). All females were rescued from the coastal waters of the Noto Peninsula in Ishikawa, Japan. The number of years they came to the aquarium was 2007 for #F2, and 2015 for #F1 and #F3 (Table 1). In this species, conception typically occurs from June to October (Ferrero et al. 1993; Heise 1997; Robeck et al. 2009), and they have a gestation period of approximately 12 months (Heise 1997; Robeck et al. 2009). #F1 gave birth to a male calf on 29 July 2019, #F2 gave birth to a male calf on 4 August 2020, and #F3 gave birth to a female calf on 13 July 2021 (Table 1). All mothers and calves were healthy. A main show pool and three other pools were interconnected, and recordings were taken at the indoor pool with a maximum depth of 3 m (Fig. 1). Recording system A was used for #F1 and #F3, and recording system B was used for all mothers. The present study was conducted according to the guidelines of the Animal Experiment Committee of the Tokyo University of Marine Science and Technology (Approval No.: R2-5). This observational study did not involve handling of animals and did not affect the welfare of dolphins.

Table 1. Information on the subjects and recording details

	#F1	#F2	#F3 (daughter of #F1)
Body length in the year of parturition	207 cm	202 cm	211 cm
The date they came to the aquarium	15 February 2015	17 April 2007	15 February 2015
Parturition date	29 July 2019	4 August 2020	13 July 2021
Sex of the calf	Male	Male	Female
The day that body temperature began to fall	4 days before parturition	2 days before parturition	4 days before parturition
The day that temporary introduction of the conspecifics began	52 days after parturition	12 days after parturition*	11 days after parturition** (A training*** began at 5 days after parturition)
Recording system A (*autonomous sound recorder*)			
Recording periods	Continuous recordings from –18 to 21 days after parturition	None	Continuous recordings from –33 to 24 days after parturition
			Continuous recordings for approx. 20 days in each month of the 3–6 months after parturition
Analyzed data			
Data recordings were analyzed only when it was confirmed that the mother was isolated (with her calf) in the indoor pool.	Continuous data from –4 to 5 days and 24-h data on 10, 15, and 20 days after parturition	None	Temporary data (50–90 min recordings) between 1130–1430 h on days 25, 24, 23, 17, 8, 7, and 6 before parturition
			Continuous data from –4 to 4 days and 24-h data for 2, 4, 2 and 8 days in the 3rd, 4th, 5th, and 6th months after parturition, respectively
Recording system B (*two hydrophones*)			
Recording sessions for approximately 1 h	Five sessions on birthday at 0, 1, 2, 7, and 8 h after parturition	Six sessions on birthday at 1 h before and 0, 1, 2, 10, and 11 h after parturition	Five sessions on birthday at 8, 7, and 2 h before and at 0 and 21 h after parturition
		Three sessions on the eighth day after parturition	
		Three sessions on the twenty-fourth day after parturition	

* In one instance, #F1 was introduced into the indoor pool for only 1 h on the day after #F2 parturition.
** In this instance, #F1 was introduced into the indoor pool for only 2 h on the day following #F3 parturition.
*** The training for #F3 calf to move between the indoor pool and adjacent pool with #F3 began before the temporary introduction of conspecifics.
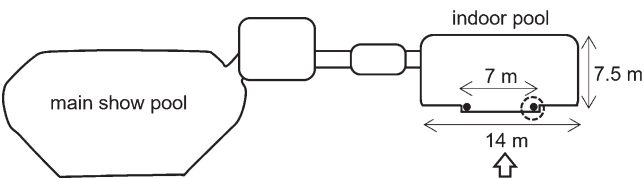

Fig. 1. Schematic of the dolphin pool. An autonomous sound recorder for recording system A was placed at the dashed circle in the indoor pool, and the two dots represent the hydrophones for recording system B. Observation with a video camera was conducted from the wide outside arrow.

Recording system A for #F1 and #F3

An automatic underwater sound monitoring system, the AUSOMS-mini Stereo (AquaSound, Kobe, Japan), was used around the parturition days of #F1 and #F3 only (recording system A). The system recorded sounds from 100 Hz to 23 kHz with a dynamic range between 70 and 160 dB re 1 µPa. The gain was set to 47 dB, resulting in the sensitivity of the system to be approximately –160 dB re 1 V/µPa. Compressed Windows Media Audio (WMA) format, with a bit rate of 128 kbps, allowed continuous recording for a maximum of 23 days but limited

the effective frequency band to 19 kHz. Although it did not cover the frequency band of the pulsed call sequences, which were suggested to have energies up to approximately 150 kHz (Mishima et al. 2019), the pulsed call sequences could be identified and their types could also be discriminated. The autonomous sound recorder was submerged in the indoor pool to a depth of 1.1 m (Fig. 1).

Continuous recordings were conducted from 18 days before to 21 days after #F1 parturition and from 33 days before to 24 days after #F3 parturition with some replacements of the batteries and storage cards of the autonomous sound recorder (Table 1). Additional recordings were made for #F3 only, during the third to sixth month postpartum for a duration of approximately 20 days. The limited data that were recorded only when the target female was isolated (with her calf after parturition) in the indoor pool were used for analysis.

Isolation periods of mothers and calves

Individual pregnant females were isolated in the indoor pool, and continuous isolation began when their body temperature started dropping (four days, two days, and four days before parturition of #F1, #F2, and #F3, respectively) (Table 1). After parturition, the females remained isolated in the pool with their newborns until temporary introduction of other dolphins began on calf day 52 for #F1, day 12 for #F2, and day 11 for #F3. However, training for the #F3 calf to move between the indoor pool and the adjacent pool with #F3 began on the calf's fifth day before the temporary introduction of conspecifics, therefore, their continuous isolation in the indoor pool was completed on the calf's fourth day. Data obtained from recording system A during continuous isolation were used for analysis.

Before continuous isolation began, pregnant females were temporarily isolated. Similarly, after continuous isolation was completed, mother–calf pairs were temporarily isolated. Opportunistic and temporary isolation with a uniform time zone was recorded only for #F3; for 50–90 min between 1130 and 1430 h on several days during the one month prior to its parturition, and two to eight approximately 24-h isolations per month with her calf during the third to sixth months postpartum (Table 1). Data from recording system A obtained during temporary isolations were additionally analyzed for #F3. During isolation, the lattice between the indoor pool and the adjacent pool was closed, preventing visits between pools but still enabling acoustical and visual communication through the lattice (Fig. 1).

Recording system B for all mothers

Discrete short-term broadband recordings were made with recording system B. The recording system was composed of two AQH-200 hydrophones (AquaSound, Kobe, Japan), which exhibited a flat frequency response from 20 Hz to 200 kHz (over –220 dB re 1 V/μPa); an Aquafeeler III preamplifier (AquaSound, Kobe, Japan), which had an analog bandpass filter between 1 and 200 kHz and amplified by 50 dB; and an EZ7510 data recorder (NF, Yokohama, Japan), with 500-kHz and 16-bit sampling. This recording equipment covered the frequency band of the pulsed call sequences (Mishima et al. 2019). The hydrophones were submerged at a depth of 0.8 m and separated by 7.0 m (Fig. 1). Video recordings were also performed using an HDR-CX485 video camera (Sony, Tokyo, Japan) to obtain the position of the female. The time synchronization between the recorder and video was conducted by taking a video of the recorder's clock.

#F1 and #F3 data obtained with recording system B were used to verify the accuracy of caller identification in recording system A data (details are described below). Data of five discrete recording sessions of approximately 1 h each at 0, 1, 2, 7, and 8 h after parturition were used for #F1. Similarly, data of five 1-h sessions at 8, 7, and 2 h before and 0 and 21 h after parturition were used for #F3 (Table 1).

Recording sessions were also performed with #F2. The discrete short-term data obtained with recording system B from parturition day to one month after parturition were used for pre- and postpartum analyses of #F2 because recording system A included no data for #F2. Six 1-h sessions were conducted 1 h before and 0, 1, 2, 10, and 11 h following parturition, and three 1-h sessions were performed on days eight and 24 after #F2 parturition (Table 1). All data were obtained during the isolation of the mothers (including with their calves after parturition).

Identification of pulsed call sequences

Pulsed call sequences were extracted by the first author for both recording systems using Audacity version 2.4.2. (Audacity Team 2000) based on the definition of a succession of three or more pulsed calls with inter-call intervals of less than 325 ms (Mishima et al. 2019). The "pulsed call" is a succession of pulses with inter-pulse intervals of less than 10 ms (Lammers et al. 2004). Pulsed call sequences were acoustically and visually classified into types on a spectrogram.

Identification of callers

It was impossible to identify callers using only the autonomous sound recorder of recording system A, if two or more dolphins were present in the indoor pool. However, when the pregnant females were isolated in the indoor pool before parturition, their pulsed call sequences could be relatively identified because sounds in the indoor pool were less attenuated at the location of recording system A than sounds from the other pools (Fig. 1). When the target mother and calf were isolated in the indoor pool after parturition, the mother's sequences could also be identified, because her calf did not produce stereotyped sequences during the recording period (unpublished data). However, the caller identification method that is based only on a relative comparison of the sequence amplitude is less reliable.

Meanwhile, caller identification in recording system B could be based on a commonly used method using the time-of-arrival difference. When the position estimated by the time-of-arrival difference of a sequence between the hydrophones corresponded to the position of the mother in the video data, the sequence could be identified as being produced by the mother. In addition, sequences can be produced by conspecifics in other pools. However, when the mother produced a sequence on the left side of the left hydrophone in the indoor pool (Fig. 1), the time-of-arrival difference at the location of the hydrophones could not be used to determine whether the sequence was produced by the mother or the conspecifics in other pools. Only in such cases, we used relative amplitude and frequency characteristics, as the sequences of the conspecifics in other pools were attenuated, especially the high-frequency component. However, the sequences of the mother could be clearly recorded in broadband for both hydrophones and easily identified. If a conspecific was housed in the adjacent pool, remained near the lattice between the pools, and directed its head towards the indoor pool, and if the mother also swam on the left side of the hydrophone, we would not be able to use time-of-arrival difference, relative amplitude, and frequency characteristics, and we would not be able to identify which individual produced the sequence. However, no such ambiguous data were obtained in the present study.

The first author performed all caller identification. For the #F1 and #F3 data, the number of each of the mother's sequences and the number of the sequences of the conspecifics were compared between recording systems A and B to verify the caller identifications made in record-

ing system A. The data from recording systems A and B were synchronized using a clock to find the corresponding sequences. The number of pulsed call sequences produced by the mother and conspecifics identified in each session of recording system B was compared with those in recording system A during the corresponding time window. If the values were similar, calculation of the mothers' sequences using recording system A was used for further analysis of #F1 and #F3.

Analysis of mothers' pulsed call sequences

The sequence type used by each mother was first investigated using recording system B with high acoustic quality. When we verified that the calculation of the sequences of mothers using recording system A was usable, continuous long-term data were used to analyze the production rates of #F1 and #F3 before and after parturition in the following three time periods. First, the number of pulsed call sequences by #F3 per minute during 50–90 min on each of the 11 days in the last month of gestation was investigated. Second, the hourly production rates (number of pulsed call sequences per minute for each hour) from 95 h prior to parturition to 48 h postpartum were investigated for #F1, and from 98 h prior to parturition to 48 h postpartum for #F3. As pulsed call sequences were often exchanged within 1 s (Mishima et al. 2019), such adjacent sequences exchanged before and after the mother's sequence with conspecifics in other pools were considered vocal exchanges, and the number of exchanged sequences per minute was also calculated for each hour. Third, daily production rates (calculated by averaging hourly rates for 24 h) were investigated from four days pre-parturition to five days postpartum, and on days ten, 15, and 20 postpartum for #F1, and from four days pre-parturition to four days postpartum and in each of the third to sixth months postpartum for #F3.

Only the data from recording system B were collected from #F2; therefore, discrete short-term data were used for the analysis of #F2 and the number of pulsed call sequences per minute was calculated per session.

Body temperature

Voluntary rectal temperatures were obtained from the pregnant females to predict the onset of parturition and the interrelationship between body temperature and acoustic activity. A thermometer (Terumo Finer CTM-303; Terumo, Tokyo, Japan) was inserted into the rectum at a depth of 30 cm. Temperatures were taken by aquar-
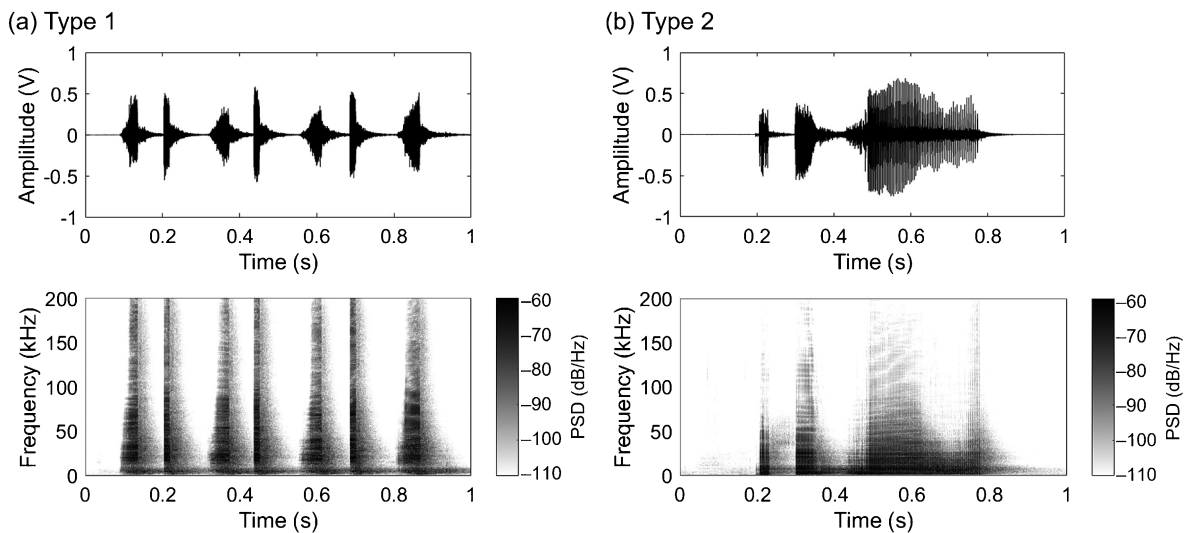
Fig. 2. Type-1 (a) and Type-2 (b) pulsed call sequences. Type 1 comprised two elements of pulsed calls with several repetitions. Type 2 was composed of three successive elements of pulsed calls. Spectrograms were generated by short-time Fourier transform (STFT) with a fast Fourier transform (FFT) size of 1024 points, Hanning window, and 50% overlap.

ium staff twice per day until a decrease was noted, and then three to ten times per day thereafter.

Statistical analysis

Differences in the number of pulsed call sequences identified between recording systems A and B for #F1 and #F3 were tested using the Wilcoxon signed-rank test. The relationship between the days in the last pre-parturition month and the mother's production rate was analyzed by Spearman's rank correlation. The coefficient of variation (CV) was used to examine the variability in acoustic activity within and between days. The CV was calculated according to the following formula: $CV = (SD/mean) \times 100$, where SD is the standard deviation. The ratio of within-day CV (CVw) to between-day CV (CVb) was used to show the relative within-day variability. CVw was calculated for each day from the mean and standard deviation of the hourly production rates within a day, and $meanCVw$ was the mean of the CVw. CVb was estimated from the grand mean and standard deviation based on mean values of each day. A $meanCVw/CVb$ ratio of > 1 indicated that the production rate of mothers was relatively more variable within days (Gasser et al. 2009). Spearman's rank correlation test was performed to test the correlation between body temperature and hourly production rates. The statistical analyses in this study were performed using MATLAB version 2021b (The MathWorks, Inc., USA).

Results

Types of pulsed call sequences

The pulsed call sequences of this captive population were primarily divided into two types: Type 1 and Type 2 (Fig. 2). Type 1 comprised two elements of pulsed calls with several repetitions, whereas Type 2 was composed of three successive elements of pulsed calls. #F1 exclusively produced Type 1 and never produced Type 2 throughout the data of recording system B. Similarly, #F2 produced only Type 2. #F3 produced only four Type-2 sequences out of the total ($n = 213$) in recording system B, and the remaining 209 sequences were of Type 1. Consequently, the rarely produced Type 2 of #F3 was excluded from further analysis, and only Type-1 sequences for #F1 and #F3 were counted in the long-term data of recording system A.

Difference of the identified number of pulsed call sequences between recording systems A and B

The number of hourly sequences recorded by recording system B was compared to the number of sequences recorded during the same time period by recording system A (Supplementary Fig. S1). In #F1 recordings, the number of Type-1 sequences produced by #F1 in recording system A was marginally lower (mean: –0.8, range: –3.0 – 0.0%) than the number of Type-1 sequences produced by #F1 in recording system B. The number of sequences produced by conspecifics in the adjacent

pools was higher (mean: 6.8, range: 0.0 – 17.1%) in recording system A than in recording system B. Similarly, in #F3 recordings, the number of Type-1 sequences produced by #F3 in recording system A was lower (mean: –4.3, range: –18.8 – 0.0%) than that in recording system B. The mean number of sequences produced by conspecifics was higher (mean: 5.0, range: –13.6 – 25.0%) in recording system A than that in recording system B. Although there was a tendency toward lower estimation of recording system A than of system B for the target mothers and higher estimation of recording system A than of system B for the conspecifics, the values calculated in recording system A did not significantly differ from recording system B values (Wilcoxon signed-rank test, $Z = 30.5$, $P = 0.52$) and were usable for further analysis.

Production rate of pulsed call sequences produced by the mothers

The pulsed call sequence production rate was calculated using #F3 data collected during temporary isolation in the last month of gestation (Fig. 3). Our results indicated a positive linear relationship between the negative period from parturition and the number of sequences per minute (Spearman's rank correlation, $r_s = 0.86$, $P < 0.005$).

The hourly production rates of mothers' pulsed call sequences spanning the 95 h before #F1 parturition and spanning the 98 h before #F3 parturition showed that there were daily rhythms and higher acoustic activity was found from evening to night (Fig. 4). The *meanCVw* of the pre-parturition days for #F1 and #F3 were calculated as 72.8 (67.2–82.6) and 74.1 (67.7–78.9), respectively. The *CVb* of pre-parturition days for #F1 and #F3 were calculated as 14.0 and 14.6, respectively. The *meanCVw/ CVb* ratios were thus estimated to be 5.2 for #F1 and 5.1 for #F3; both were greater than 1. This result suggested that, in the period of a few days before parturition, the within-day variability was relatively higher than the between-day variability. There were mothers' sequences that occurred in the vocal exchange with conspecifics, but they occupied only 14.5 ± 18.1% (mean ± *SD*) and 37.3 ± 21.2% of sequence production in #F1 and #F3 before parturition, respectively, and mothers often produced sequences solitarily, particularly at night. The body temperature decreased as parturition approached, and daily rhythms also occurred, but there was no correlation between body temperature and the mothers' production rate (Spearman's rank correlation, $r_s = 0.40$, $P = 0.09$ for #F1 and $r_s = -0.07$, $P = 0.73$ for #F3).
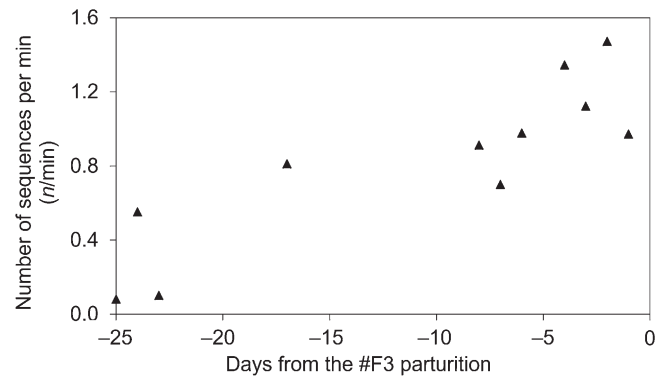

Fig. 3. Production rates of pulsed call sequences for 25 days before parturition. The number of sequences per minute was calculated using the #F3 data collected for 50–90 min between 1130–1400 h.

The first production sequences after parturition were determined to be 30 s for #F1, and 2 min 53 s for #F3. #F1 produced sequences repeatedly with a rate of 5.65 sequence/min during the first hour postpartum. The production rate decreased to 3.17 and 1.08 sequence/min during the second and third hour postpartum, respectively, and #F1 rarely produced sequences thereafter (Fig. 4). The production rate of #F3 was 1.25 sequence/ min during the first hour postpartum but dropped thereafter, approximately 0.20 sequence/min during the second and third hour postpartum. Both mothers produced sequences again at a rate of approximately 1.00 sequence/ min during the daytime of their calves' second day, but they hardly produced sequences during the following night, and the production rate of sequences remained low during the daytime of the third day.

The daily production rates of pulsed call sequences are shown in Fig. 5. In both #F1 and #F3, the high calling rate suddenly reduced after the parturition day and then were almost silent for over one month. The mean sequence rate in the third, fourth, fifth, and sixth months after #F3 parturition was 0.00 ± 0.001, 0.02 ± 0.01, 0.02 ± 0.005, and 0.01 ± 0.005 sequences/min, respectively.

From the data recorded for #F2 using recording system B, the first production sequence after parturition was determined to be 31 s. The #F2 sequence rates along the 1 h before parturition and 0, 1, 2, 10, and 11 h following parturition were calculated as 0.07, 7.42, 5.42, 2.00, 3.52, and 2.08 sequence/min, respectively. The three 1-h recordings on the eighth day after parturition showed mean rates of 0.00 ± 0.00 sequences/min. Similarly, the three 1-h recordings on twenty-fourth day after parturition showed mean rates of 0.03 ± 0.05 sequences/min.
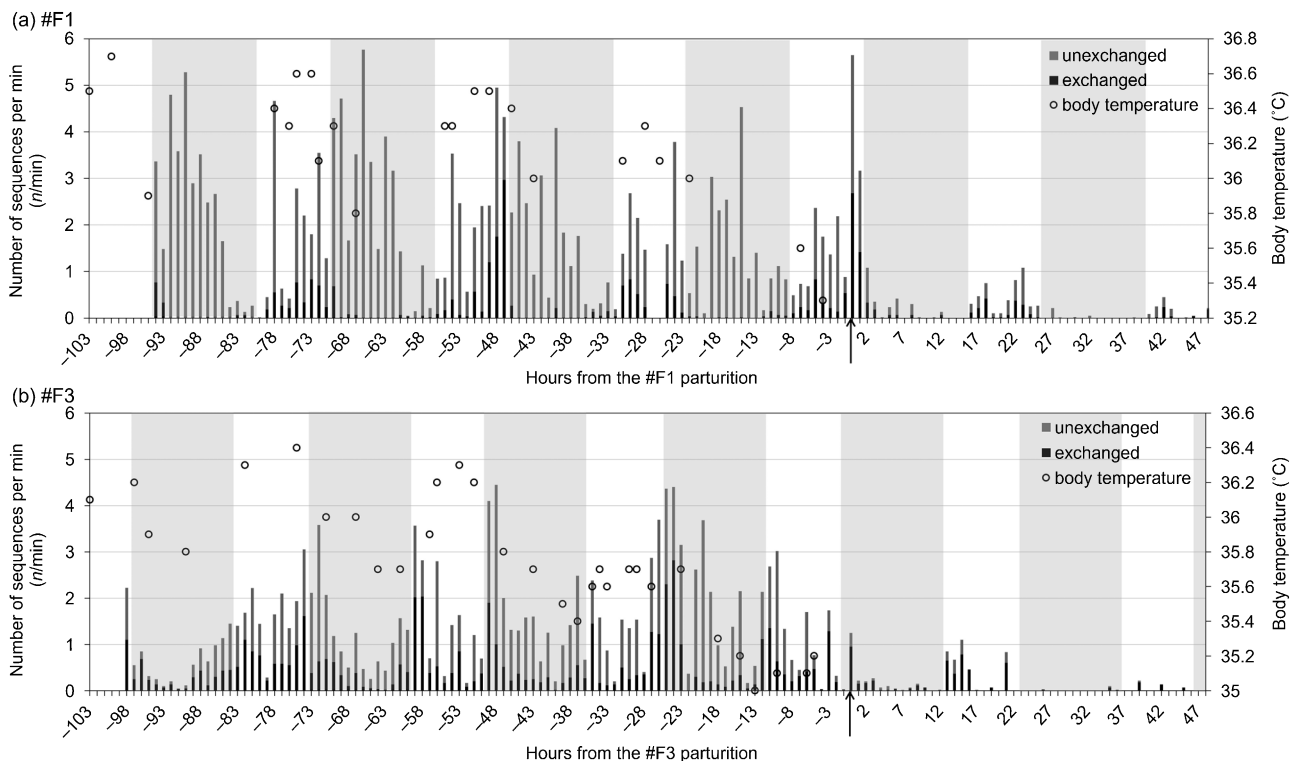
Fig. 4. Hourly production rates of pulsed call sequences before and after the parturition of #F1 (a) and #F3 (b). The number of sequences per minute was calculated each hour. The black bars show the rate of mothers' sequences used for exchanges with conspecifics, and the grey bars show the rate of mothers' sequences produced solitarily. The circles are body temperatures. The light-off periods from evening to early morning are shown as light grey shadows. The parturition occurred at the arrows. There was a lack of data during –26 and –27 h from #F1 parturition.
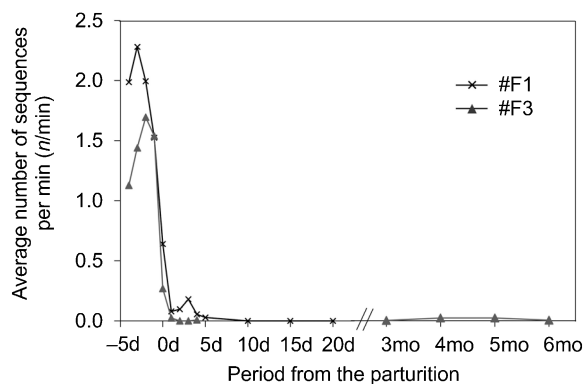

Fig. 5. Daily production rates of mothers' pulsed call sequences before and after parturition. The number of sequences per minute was calculated by averaging the hourly rate each day and each month. The black line with cross markers and the gray line with triangle markers show the results from #F1 and #F3, respectively.

Discussion

Contrary to our prediction, Pacific white-sided dolphin mothers produced a relatively higher number of pulsed call sequences during pre-parturition days than during postpartum days, and they hardly produced sequences after several hours postpartum. Pacific white-sided dolphin mothers gradually increased the production rate of pulsed call sequences during the last month of pregnancy (Fig. 3). Pregnant common bottlenose dolphin females also tended to increase the number of signature whistles for seven months pre-parturition, and this trend was still observed during the month preceding parturition, with acceleration to a peak occurring in the last few days (Mello and Amundin 2005). In addition, our hourly analysis for #F1 and #F3 showed that intense acoustic activity was repeated on a daily basis for four days before parturition, and the production rate remained above 1.00 sequence/min for several hours after parturition with individual differences (#F1: 3 h; #F2: > 11 h; #F3: 1 h) but ceased thereafter (Fig. 4). The postpartum period of active calling in Pacific white-sided dolphins was too short to compare with the period of approximately one week for common bottlenose dolphins (Fripp and Tyack 2008; King et al. 2016; Ames et al. 2019). The period was short, even considering that the calves of Pacific white-sided dolphins began to separate from their

mothers 4–7 days after birth (Smith 2019). Additionally, Pacific white-sided dolphins produced a relatively higher number of pulsed call sequences during pre-parturition days than during postpartum days (Fig. 5), which is contrary to the results in deer (Vaňková and Málek 1997), sheep (Sèbe et al. 2007), belugas (Vergara and Barrett-Lennard 2008; Vergara et al. 2010), and common bottlenose dolphins (Fripp and Tyack 2008; King et al. 2016; Ames et al. 2019). Thus, it is more likely that the postpartum mothers' sequences have weak or no imprinting function, although the possibility that this species may imprint in a short period is not excluded. The reason for the short period of postpartum active calling should be considered with the following long-term silence of mothers, which is described later.

In the pre-parturition days, a high production rate occurred, and most of the sequences were not accompanied by calls and responses of other dolphins (Fig. 4). Hence, the frequent acoustic activity of mothers was unlikely to be elicited by vocal interactions with conspecifics. This result is comparable to the behavior of common bottlenose dolphins, in that the signature whistle rate of non-mothers was unchanged before and after parturition (Fripp and Tyack 2008; King et al. 2016; Ames et al. 2019).

Because body temperature was not correlated with the sequence production rate in this study, the possibility of a hormonal effect on the acoustic activity of mothers could not be inferred. Moore and Ridgway (1996) reported no significant correlation between progesterone levels and whistle production in both female common bottlenose dolphins and common dolphins (*Delphinus delphis*). However, before and after parturition, there are hormonal changes that cannot be measured using body temperature. The cortisol concentrations in pregnant common bottlenose dolphins and killer whales peak during the last gestational month (Steinman et al. 2016; Robeck et al. 2017). Notably, cortisol increased rapidly during the period of less than ten days before parturition and declined after parturition in both species (Biancani et al. 2017; Robeck et al. 2017). Similarly, sheep and horses showed increased cortisol levels for a few days before parturition (Drost et al. 1973; Nagel et al. 2012). Therefore, it could not be ruled out that the high acoustic activity of Pacific white-sided dolphin mothers during the pre-parturition period and immediately after parturition may be related to the cortisol concentration and perhaps be an acoustic response to stress. The direct measurement of hormones may indicate hormonal effects on the calling

of mothers. Furthermore, not only the short-term effects in the present study but also the long-term effects of hormones can be related to the acoustic activity of the mother.

Consequently, a high calling rate in mothers may provide an opportunity for an auditory experience for the fetus. Internal sounds generated by ewes can be discerned by a hydrophone inside the amniotic sac, and external sounds can be picked up with lower attenuation of approximately 16–37 dB (Armitage et al. 1980). Additionally, prosodic information such as the intonation and rhythm of language is preserved and available to the human fetus (Fifer and Moon 1988). In guinea pigs (*Cavia porcellus*) and sheep, a neonate group that experienced prenatal stimulation of alien calls showed a lower heart rate response to the same sounds than the control group after birth (Vince 1979; Vince et al. 1982). Newborn humans younger than three days of age prefer their mother's voice with limited postnatal maternal contact (DeCasper and Fifer 1980). When human mothers recited a particular story to their fetus during the last six weeks of gestation, the story became a more effective reinforcer for their postnatal neonates (DeCasper and Spence 1986). Likewise, exposure of human fetuses to music during the last trimester led to a strong brain response to the melody, both at birth and at the age of four months (Partanen et al. 2013). Hence, it may be possible for dolphin fetuses to learn and habituate their mothers' calls during the last prenatal stage. A beluga mother who had two subtypes of her individually distinctive type of call regularly produced both subtypes during the pre-parturition period, but used one of the subtypes for the first month postpartum, and thereafter, rarely produced both subtypes (Ames and Vergara 2020). Nevertheless, her calf produced calls similar to the subtype that his mother rarely produced after parturition. This implies that the calf may have heard the subtype during the prenatal period (Ames and Vergara 2020). Pacific white-sided dolphin calves may also hear and learn their mother's sequences during the last prenatal stage, in addition to the relatively short postpartum period.

The scarce call production of mothers after parturition is a pronounced characteristic of the captive population in the present study. The production rates in #F1 and #F3 decreased several hours postpartum and they remained almost silent for at least one month (Fig. 5). Although the data for #F2 were limited, a similar trend was observed. From the occasional 24-h recordings in the third, fourth, fifth, and sixth month after #F3 parturition,

the production rate slightly increased again after the fourth month (Fig. 5). One possible reason for the silent period could be the avoidance of predation risk by diminishing calling. Acoustic crypsis has been observed in several cetaceans. Some small odontocete species use only high-frequency calls above 100 kHz to avoid detection by a predator, the killer whale (Morisaka and Connor 2007), which is most sensitive to the frequency range of 18–42 kHz and cannot hear high frequencies above 100 kHz (Szymanski et al. 1999). In addition, Blainville's beaked whales (*Mesoplodon densirostris*) remain silent at depths above 170 m (Aguilar de Soto et al. 2012). Tropical dolphins produce fewer calls when in the proximity of killer whales (Rankin et al. 2013). The mother–calf pairs of humpback whales (*Megaptera novaeangliae*) and southern right whales (*Eubalaena australis*) infrequently produce calls during diving associated with nursing (Videsen et al. 2017; Nielsen et al. 2019). Mother–calf pairs also use low-amplitude calls to restrict their acoustic active space (Videsen et al. 2017; Nielsen et al. 2019; Parks et al. 2019), even if they increase the call rate during more frequent separation (Indeck et al. 2022). The dominant energy of pulsed call sequences produced by Pacific white-sided dolphins is below 100 kHz and can be easily detected by killer whales, which are one of their predators (Black 2018). The cessation of mothers' sequences for several months after parturition might be an anti-predator strategy in this species to protect vulnerable neonates, and the slight increase in sequence rate after a few months may be related to the physical development of their calf.

An alternative hypothesis for the low production rate by Pacific white-sided dolphin mothers in the postpartum hours is that the animals rest by decreasing acoustic activity and conserving energy. In the mothers and calves of killer whales and common bottlenose dolphins, the typical immobile rest behavior, staying at the surface and bottom for a long time, was rarely observed for the first few months after birth and was suppressed for several months (Lyamin et al. 2005). However, the mothers and calves of common bottlenose dolphins, even one week after parturition, showed a considerable amount of swimming rest behavior (Gnone et al. 2006; Sekiguchi et al. 2006), with the animals resting by slow circle swimming along a fixed trajectory close to the bottom (Sekiguchi and Kohshima 2003). In addition, the first unilateral eye closure of the mother was recorded 11 h postpartum, and the time for which one eye was closed during swimming as rest behavior gradually increased

for one week postpartum (Sekiguchi et al. 2006). Resting may be important for postpartum mothers of Pacific white-sided dolphins. Pacific white-sided dolphins require higher energy intake than toothed whales of similar sizes and temperate habitats, and the energy requirement is the highest for lactating females, similar to other marine mammals (Rechsteiner et al. 2013). Lactation in this species lasts for at least 8–10 months (Heise 1997), and all the subject mothers were lactating during their postpartum recording periods. In addition, calves often swim in echelon position, which is characterized by calves swimming close to the mid-lateral flank of their mother; and infant position, which is when calves swim in close proximity below their mother's tailstock (Gubbins et al. 1999; Mann and Shuts 1999; Krasnova et al. 2006). These behaviors were also observed in the present study. The constant swimming positions of calves relative to their mothers also increase the energy requirements of the mother (Noren 2008, 2013). The metabolic costs of producing communication sounds, whistles, and burst-pulse squawks in common bottlenose dolphins have been debated (Noren et al. 2013; Holt et al. 2015; Noren et al. 2020; Pedersen et al. 2020a, 2020b). Studies on the energy expenditure related to pulsed call sequence production are also required to evaluate this hypothesis.

The results of this study lead to the question of whether calves can recognize their mother's pulsed call sequence when they did not hear it very often postpartum. If they can, the next question is when the calves learn their mothers' sequence, whether the learning is conducted in the prenatal period, the short period immediately after parturition, or the period after postpartum of a few months. Subsequent studies on mother–calf acoustic interaction and recognition are required to answer these questions.

Supplementary data

Supplementary data are available at *Mammal Study* online. **Supplementary Fig. S1.** Comparison of the number of pulsed call sequences between recording systems A and B.

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References

Aguilar de Soto, N., Madsen, P. T., Tyack, P., Arranz, P., Marrero, J., Fais, A., Revelli, E. and Johnson, M. 2012. No shallow talk: cryptic strategy in the vocal communication of Blainville's beaked whales. Marine Mammal Science 28: E75–E92.

Ames, A. E., Macgregor, R. P., Wielandt, S. J., Cameron, D. M., Kuczaj, S. A. and Hill, H. M. 2019. Pre- and post-partum whistle production of a bottlenose dolphin (*Tursiops truncatus*) social group. International Journal of Comparative Psychology 32: 1–22.

Ames, A. E. and Vergara, V. 2020. Trajectories of vocal repertoire development in beluga (*Delphinapterus leucas*) calves: insights from studies a decade apart. Aquatic Mammals 46: 344–366.

Armitage, S. E., Baldwin, B. A. and Vince, M. A. 1980. The fetal sound environment of sheep. Science 208: 1173–1174.

Audacity Team. 2000. Audacity. Version 2.4.2. Available at https://www.audacityteam.org/ (Accessed 25 August 2023).

Biancani, B., Dalt, L. D., Gallina, G., Capolongo, F. and Gabai, G. 2017. Fecal cortisol radioimmunoassay to monitor adrenal gland activity in the bottlenose dolphin (*Tursiops truncatus*) under human care. Marine Mammal Science 33: 1014–1034.

Black, N. A. 1994. Behavior and Ecology of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*) in Monterey Bay, California. Master's Thesis, San Francisco State University, San Francisco, 133 pp.

Black, N. A. 2018. Pacific white-sided dolphin: *Lagenorhynchus obliquidens*. In (Würsig, B., Thewissen, J. G. M. and Kovacs, K. M., eds.) Encyclopedia of Marine Mammals, Third edition, pp. 673–676. Academic Press, San Diego.

Blanchet, M., Nance, T., Ast, C., Wahlberg, M. and Acquarone, M. 2008. First case of a monitored pregnancy of a harbour porpoise (*Phocoena phocoena*) under human care. Aquatic Mammals 34: 9–20.

Briefer, E. and McElligott, A. G. 2011. Indicators of age, body size and sex in goat kid calls revealed using the source–filter theory. Applied Animal Behaviour Science 133: 175–185.

Buckstaff, K. C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. Marine Mammal Science 20: 709–725.

Caldwell, M. C. and Caldwell, D. K. 1965. Individualized whistle contours in bottle-nosed dolphins (*Tursiops truncatus*). Nature 207: 434–435.

Caldwell, M. C., Caldwell, D. K. and Tyack, P. L. 1990. Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In (Leatherwood, S. and Reeves, R. R., eds.) The Bottlenose Dolphin, pp. 199–234. Academic Press, San Diego.

Charrier, I., Mathevon, N. and Jouventin, P. 2001. Mother's voice recognition by seal pups. Nature 412: 873–873.

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

Connor, R. C., Wells, R. S., Mann, J. and Read, A. J. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. In (Mann, J., Connor, R. C., Tyack P. L. and Whitehead, H., eds.) Cetacean Societies: Field Studies of Dolphins and Whales, pp. 91–126. University of Chicago Press, Chicago.

DeCasper, A. J. and Fifer, W. P. 1980. Of human bonding: newborns prefer their mothers' voices. Science 208: 1174–1176.

DeCasper, A. J. and Spence, M. J. 1986. Prenatal maternal speech influences newborns' perception of speech sounds. Infant Behavior and Development 9: 133–150.

Drost, M., Kumagai, L. F. and Guzman, M. 1973. Sequential foetal-maternal plasma cortisol levels in sheep. Journal of Endocrinology 56: 483–492.

Dwyer, C. M., McLean, K. A., Deans, L. A., Chirnside, J., Calvert, S. K. and Lawrence, A. B. 1998. Vocalisations between mother and young in sheep: effects of breed and maternal experience. Applied Animal Behaviour Science 58: 105–119.

Esch, H. C., Sayigh, L. S., Blum, J. E. and Wells, R. S. 2009. Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). Journal of Mammalogy 90: 638–650.

Ferrero, R. C., Walker, W. A. and Gosho, M. 1993. Preliminary analysis of northern right whale dolphin (*Lissodelphis borealis*) and Pacific white-sided dolphin (*Lagenorhynchus obliquedens*) age and reproductive parameters from the Japanese squid driftnet fishery, June–November 1990. International North Pacific Fisheries Commission Bulletin 53: 297–312.

Fifer, W. P. and Moon, C. 1988. Auditory experience in the fetus. In (Smotherman, W. P. and Robinson, S. R., eds.) Behavior of the Fetus, pp. 175–188. Telford Press, Caldwell.

Fripp, D. and Tyack, P. 2008. Postpartum whistle production in bottlenose dolphins. Marine Mammal Science 24: 479–502.

Funasaka, N., Yoshioka, M., Suzuki, M., Ueda, K., Miyahara, H. and Uchida, S. 2011. Seasonal difference of diurnal variations in serum melatonin, cortisol, testosterone, and rectal temperature in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). Aquatic Mammals 37: 433–442.

Gasser, H., Amezquita, A. and Hoedl, W. 2009. Who is calling? Intraspecific call variation in the aromobatid frog *Allobates femoralis*. Ethology 115: 596–607.

Gnone, G., Moriconi, T. and Gambini, G. 2006. Activity and sleep in dolphins. Nature 441: E10–E11.

Gubbins, C., Mcowan, B., Lynn, S. K., Hooper, S. and Reiss, D. 1999. Mother-infant spatial relations in captive bottlenose dolphins, *Tursiops truncatus*. Marine Mammal Science 15: 751–765.

Guerra, M., Dawson, S. M., Brough, T. E. and Rayment, W. J. 2014. Effects of boats on the surface and acoustic behaviour of an endangered population of bottlenose dolphins. Endangered Species Research 24: 221–236.

Heise, K. 1997. Life history and population parameters of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Report of the International Whaling Commission 47: 817–825.

Henderson, E. E., Hildebrand, J. A. and Smith, M. H. 2011. Classification of behavior using vocalizations of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Journal of the Acoustical Society of America 130: 557–567.

Holt, M. M., Noren, D. P., Dunkin, R. C. and Williams, T. M. 2015. Vocal performance affects metabolic rate in dolphins: implications for animals communicating in noisy environments. Journal of Experimental Biology 218: 1647–1654.

Ikeshima, S., Higa, S., Mitani, Y., Omata, M., Kobayashi, N., Ueda, K. and Kawazu, I. 2021. First observation of pregnancy and parturition in a captive pantropical spotted dolphin (*Stenella attenuata*). Mammal Study 46: 279–284.

Indeck, K. L., Noad, M. J. and Dunlop, R. A. 2022. Humpback whale adult females and calves balance acoustic contact with vocal crypsis during periods of increased separation. Ecology and Evolution 12: e8604. DOI: 10.1002/ece3.8604.

Janik, V. M. and Slater, P. J. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56: 829–838.

Katsumata, E., Furuta, C., Katsumata, H., Watanabe, G. and Taya, K. 2006a. Basal body temperature method for detecting ovarian cycle in the captive beluga (*Delphinapterus leucas*). Journal of Reproduction and Development 52: 59–63.

Katsumata, E., Jaroenporn, S., Katsumata, H., Konno, S., Maeda, Y., Watanabe, G. and Taya, K. 2006b. Body temperature and circulating progesterone levels before and after parturition in killer whales (*Orcinus orca*). Journal of Reproduction and Development 52: 65–71.

King, S. L., Guarino, E., Donegan, K., Hecksher, J. and Jaakkola, K. 2016. Further insights into postpartum signature whistle use in bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science 32: 1458–1469.

King, S. L., Sayigh, L. S., Wells, R. S., Fellner, W. and Janik, V. M. 2013. Vocal copying of individually distinctive signature whistles in bottlenose dolphins. Proceedings of the Royal Society B: Biological Sciences 280: 20130053. DOI: 10.1098/rspb.2013.0053.

Krasnova, V. V., Bel'kovich, V. M. and Chernetsky, A. D. 2006. Mother-infant spatial relations in wild beluga (*Delphinapterus leucas*) during postnatal development under natural conditions. Biology Bulletin 33: 53–58.

Kusuda, S., Kakizoe, Y., Kanda, K., Sengoku, T., Fukumoto, Y., Adachi, I., Watanabe, Y. and Doi, O. 2011. Ovarian cycle approach by rectal temperature and fecal progesterone in a female killer whale, *Orcinus orca.* Zoo Biology 30: 285–295.

Lammers, M. O., Au, W. W. L., Aubauer, R. and Nachtigall, P. E. 2004. A comparative analysis of the pulsed emissions of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*). In (Thomas, J. A., Moss, C. F. and Vater, M., eds.) Echolocation in Bats and Dolphins, pp. 414–419. University of Chicago Press, Chicago.

Lickliter, R. E. 1985. Behavior associated with parturition in the domestic goat. Applied Animal Behaviour Science 13: 335–345.

Lyamin, O., Pryaslova, J., Lance, V. and Siegel, J. 2005. Continuous activity in cetaceans after birth. Nature 435: 1177. DOI: 10.1038/4351177a.

Mann, J. and Smuts, B. B. 1998. Natal attraction: allomaternal care and mother–infant separations in wild bottlenose dolphins. Animal Behaviour 55: 1097–1113.

Mann, J. and Smuts, B. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). Behaviour 136: 529–566.

Mello, I. and Amundin, M. 2005. Whistle production pre- and postpartum in bottlenose dolphins (*Tursiops truncatus*) in human care. Aquatic Mammals 31: 169–175.

Michaud, R. 2005. Sociality and ecology of the odontocetes. In (Ruckstuhl, K. E. and Neuhaus, P., eds.) Sexual Segregation in Vertebrates: Ecology of the Two Sexes, pp. 303–326. Cambridge University Press, Cambridge.

Mishima, Y., Morisaka, T., Ishikawa, M., Karasawa, Y. and Yoshida, Y. 2019. Pulsed call sequences as contact calls in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*). Journal of the Acoustical Society of America 146: 409–424.

Mishima, Y., Morisaka, T., Itoh, M., Matsuo, I., Sakaguchi, A. and Miyamoto, Y. 2015. Individuality embedded in the isolation calls of captive beluga whales (*Delphinapterus leucas*). Zoological Letters 1: 27. DOI: 10.1186/s40851-015-0028-x.

Mishima, Y., Morisaka, T., Mishima, Y., Sunada, T. and Miyamoto, Y. 2018. Redefinition and sexual difference of contact calls in belugas (*Delphinapterus leucas*). Aquatic Mammals 44: 538–554.

Moore, S. E. and Ridgway, S. H. 1996. Patterns of dolphin sound production and ovulation. Aquatic Mammals 22: 175–184.

Morisaka, T. and Connor, R. C. 2007. Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. Journal of Evolutionary Biology 20: 1439–1458.

Morisaka, T., Yoshida, Y., Akune, Y., Mishima, H. and Nishimoto, S. 2013. Exchange of "signature" calls in captive belugas (*Delphinapterus leucas*). Journal of Ethology 31: 141–149.

Nagel, C., Erber, R., Bergmaier, C., Wulf, M., Aurich, J., Möstl, E. and Aurich, C. 2012. Cortisol and progestin release, heart rate and heart rate variability in the pregnant and postpartum mare, fetus and newborn foal. Theriogenology 78: 759–767.

Nielsen, M. L., Bejder, L., Videsen, S. K., Christiansen, F. and Madsen, P. T. 2019. Acoustic crypsis in southern right whale mother–calf pairs: infrequent, low-output calls to avoid predation? Journal of Experimental Biology 222: jeb190728. DOI: 10.1242/jeb.190728.

Noda, K., Akiyoshi, H., Aoki, M., Shimada, T. and Ohashi, F. 2007. Relationship between transportation stress and polymorphonuclear cell functions of bottlenose dolphins, *Tursiops truncatus*. Journal of Veterinary Medical Science 69: 379–383.

Noren, S. R. 2008. Infant carrying behaviour in dolphins: costly parental care in an aquatic environment. Functional Ecology 22: 284–288.

Noren, S. R. 2013. Altered swimming gait and performance of dolphin mothers: implications for interactions with tuna purse-seine fisheries. Marine Ecology Progress Series 482: 255–263.

Noren, D. P., Holt, M. M., Dunkin, R. C. and Williams, T. M. 2013. The metabolic cost of communicative sound production in bottlenose dolphins (*Tursiops truncatus*). Journal of Experimental Biology 216: 1624–1629.

Noren, D. P., Holt, M. M., Dunkin, R. C. and Willams, T. M. 2020. The metabolic cost of whistling is low but measurable in dolphins. Journal of Experimental Biology 223: jeb224048. DOI: 10.1242/jeb.224048.

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Smith, T. G., Lydersen, C., Kovacs, K. M., Orr, J., Harwood, L., Litovka, D. and Ferrer, T. 2020. Group structure and kinship in beluga whale societies. Scientific Reports 10: 11462. DOI: 10.1038/s41598-020-67314-w.

Olazábal, D. E., Villagrán, M., González-Pensado, S. X. and Ungerfeld, R. 2013. Maternal behavior and early development of pampas deer (*Ozotoceros bezoarticus*) fawns in a semi-captive environment. Journal of Ethology 31: 323–330.

Parks, S. E., Cusano, D. A., van Parijs, S. M. and Nowacek, D. P. 2019. North Atlantic right whale (*Eubalaena glacialis*) acoustic behavior on the calving grounds. Journal of the Acoustical Society of America 146: EL15–EL21.

Partanen, E., Kujala, T., Tervaniemi, M. and Huotilainen, M. 2013. Prenatal music exposure induces long-term neural effects. PLOS ONE 8: e78946. DOI: 10.1371/journal.pone.0078946

Pedersen, M. B., Fahlman, A., Borque-Espinosa, A., Madsen, P. T. and Jensen, F. H. 2020a. Whistling is metabolically cheap for communicating bottlenose dolphins (*Tursiops truncatus*). Journal of Experimental Biology 223: jeb212498. DOI: 10.1242/jeb.212498.

Pedersen, M. B., Fahlman, A., Borque-Espinosa, A., Madsen, P. T. and Jensen, F. H. 2020b. Response to: The metabolic cost of whistling is low but measurable in dolphins. Journal of Experimental Biology 223: jeb224915. DOI: 10.1242/jeb.224915.

Pitcher, B. J., Ahonen, H., Harcourt, R. G. and Charrier, I. 2009. Delayed onset of vocal recognition in Australian sea lion pups (*Neophoca cinerea*). Naturwissenschaften 96: 901–909.

Rankin, S., Archer, F. and Barlow, J. 2013. Vocal activity of tropical dolphins is inhibited by the presence of killer whales, *Orcinus orca*. Marine Mammal Science 29: 679–690.

Rechsteiner, E. U., Rosen, D. A. and Trites, A. W. 2013. Energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as predicted by a bioenergetic model. Journal of Mammalogy 94: 820–832.

Robeck, T. R., Steinman, K. J., Greenwell, M., Ramirez, K., van Bonn, W., Yoshioka, M., Katsumata, E., Dalton, L., Osborn S. and O'Brien, J. K. 2009. Seasonality, estrous cycle characterization, estrus synchronization, semen cryopreservation, and artificial insemination in the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). Reproduction 138: 391–405.

Robeck, T. R., Steinman, K. J. and O'Brien, J. K. 2017. Characterization and longitudinal monitoring of serum androgens and glucocorticoids during normal pregnancy in the killer whale (*Orcinus orca*). General and Comparative Endocrinology 247: 116–129.

Sayigh, L. S., Tyack, P. L., Wells, R. S. and Scott, M. D. 1990. Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. Behavioral Ecology and Sociobiology 26: 247–260.

Sèbe, F., Nowak, R., Poindron, P. and Aubin, T. 2007. Establishment of vocal communication and discrimination between ewes and their lamb in the first two days after parturition. Developmental Psychobiology 49: 375–386.

Sekiguchi, Y., Arai, K. and Kohshima, S. 2006. Sleep in continuously active dolphins. Nature 441: E9–E10.

Sekiguchi, Y. and Kohshima, S. 2003. Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). Physiology and Behavior 79: 643–653.

Smith, K. 2019. First Thirty Days of Life: Examining Calf Behavioral Development in Beluga Whales (*Delphinapterus leucas*) and Pacific White-sided Dolphins (*Lagenorhyncus obliquidens*) at One Zoological Facility. Master's Thesis, University of Southern Mississippi, Hattiesburg, 84 pp.

Smolker, R. A., Mann, J. and Smuts, B. B. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. Behavioral Ecology and Sociobiology 33: 393–402.

Steinman, K. J., Robeck, T. R. and O'Brien, J. K. 2016. Characteriza- tion of estrogens, testosterone, and cortisol in normal bottlenose dolphin (*Tursiops truncatus*) pregnancy. General and Comparative Endocrinology 226: 102–112.

Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S. and Henry, K. R. 1999. Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms. Journal of the Acoustical Society of America 106: 1134–1141.

Terasawa, F., Yokoyama, Y. and Kitamura, M. 1999. Rectal tempera- tures before and after parturition in bottlenose dolphins. Zoo Biol- ogy 18: 153–156.

Trillmich, F. 1981. Mutual mother-pup recognition in Galápagos fur seals and sea lions: cues used and functional significance. Behav- iour 78: 21–42.

Tyack, P. L. and Sayigh L. S. 1997. Vocal learning in cetaceans. In (Snowdon, C. T. and Hausberger, M., eds.) Social Influences on Vocal Development, pp. 208–233. Cambridge University Press, Cambridge.

Vaňková, D. and Málek, J. 1997. Characteristics of the vocalizations of red deer *Cervus elaphus* hinds and calves. Bioacoustics 7: 281– 289.

Vergara, V. and Barrett-Lennard, L. G. 2008. Vocal development in a beluga calf (*Delphinapterus leucas*). Aquatic Mammals 34: 123– 143.

Vergara, V., Michaud, R. and Barrett-Lennard, L. 2010. What can cap- tive whales tell us about their wild counterparts? Identification, usage, and ontogeny of contact calls in belugas (*Delphinapterus leucas*). International Journal of Comparative Psychology 23: 278–309.

Vergara, V. and Mikus, M. A. 2019. Contact call diversity in natural beluga entrapments in an Arctic estuary: preliminary evidence of vocal signatures in wild belugas. Marine Mammal Science 35: 434–465.

Videsen, S. K., Bejder, L., Johnson, M. and Madsen, P. T. 2017. High suckling rates and acoustic crypsis of humpback whale neonates maximise potential for mother–calf energy transfer. Functional Ecology 31: 1561–1573.

Vince, M. A. 1979. Postnatal effects of prenatal sound stimulation in the guinea pig. Animal Behaviour 27: 908–918.

Vince, M. A., Armitage, S. E., Shillito-Walser, E. S. and Reader, M. 1982. Postnatal consequences of prenatal sound stimulation in the sheep. Behaviour 81: 128–139.