# Underwater Sounds Produced by Neonatal Bottlenose Dolphins (*Tursiops truncatus*): I. Acoustic Characteristics

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# Abstract

Bottlenose dolphins (Tursiops truncatus) communicate using various acoustic signals, including whistles and pulsed sounds. Many studies have been conducted on dolphin whistle development over a long span, but little research has been done on sounds produced by neonatal dolphins just after birth. For this reason, we studied the acoustic characteristics of underwater sounds produced by two neonatal dolphins. Both whistles and burstpulses were identified as neonatal sounds at 1.5 h after birth. Whistles became longer by the hour. Whistle durations were highly correlated with respiration intervals. The neonate randomly produced various types of whistles, but no dominant whistles were documented. There were significant differences between neonates in the proportion of whistles to burst-pulses used, and also in the acoustic characteristics of their whistles. Acoustic characteristics that are unique to each individual neonate might help a mother dolphin to recognize her neonate.

**Key Words:** bottlenose dolphin, *Tursiops truncatus*, burst-pulses, neonates, parent-offspring recognition, development, whistles

# Introduction

Bottlenose dolphins (*Tursiops truncatus*) produce two broad categories of sounds: (1) pulsed or broadband "click" type sounds, including clicks and burstpulse sounds; and (2) whistles or frequency-modulated narrowband sounds (Evans, 1967). Whistles and burst-pulse sounds typically are classified as social sounds, whereas clicks are used in echolocation (McCowan & Reiss, 1997). Burst-pulse sounds often are described as squawks, yelps, barks, etc. (Caldwell & Caldwell, 1967), and may be used in communication (see Herman & Tavolga, 1980).

Whistles also are used in communication (see Herman & Tavolga, 1980). Whistles have been studied more often than burst-pulse sounds because

the fundamental frequency range of whistles is generally within the dynamic range of most recording devices, as well as within human hearing capabilities. Several studies have revealed that the bottlenose dolphin is the only mammal, other than humans and African elephants (*Loxodonta africana*), to demonstrate both vocal learning and a proclivity for vocal mimicry using whistles (Janik & Slater, 1997; McCowan & Reiss, 1995a; Poole et al., 2005; Reiss & McCowan, 1993; Richards et al., 1984).

Many researchers reported that dolphins produce stereotypic, individually distinct "signature whistles" (Caldwell & Caldwell, 1968, 1979; Caldwell et al., 1990; Janik et al., 1994; Sayigh et al., 1990), accounting for 70-95% of the whistles produced by each individual (Caldwell et al., 1990; Tyack, 1986). Signature whistles are thought to function as contact or cohesion calls in bottlenose dolphins (Caldwell et al., 1990; Janik & Slater, 1998; Tyack, 1986). Infant bottlenose dolphins use these distinctive whistles to induce cooperative responses from their mother such as approach, slowing to allow the infant to catch up, or whistling (Smolker et al., 1993). Sayigh et al. (1995) reported that there was a sex difference in the usage of signature whistles by bottlenose dolphin calves; most female calves produced whistles which have different acoustic characteristics from their mothers. whereas male calves tended to produce whistles that were similar to those of their mothers.

On the other hand, a few other researchers reported that bottlenose dolphins shared a predominant whistle type, rather than individually distinctive signature whistles in contexts of isolation from other conspecifics, even though the same approach and methods used in the studies reporting signature whistles were conducted (McCowan & Reiss, 2001). They also showed the subtle variation in the acoustic characteristics of one predominant, shared whistle type across individual dolphins; they considered that the predominant, shared whistle type contains "signature information."

Thus, there is much debate over the true function of signature whistles. Few studies have examined the existence and possible functions of other types of whistles versus signature whistles. The whistles of adult dolphins may be influenced by vocal leaning, social interactions, and many other factors. Therefore, we examined sounds produced by neonatal dolphins to investigate the functional origin and original acoustic characteristics of dolphin sounds.

Although previous studies have been conducted on vocal learning in dolphin infants (see Tyack & Sayigh, 1997; also see McCowan & Reiss, 1997), few of these studies have investigated the ontogeny of neonate sounds, especially their whistles (Caldwell & Caldwell, 1979; Killebrew et al., 2001; McBride & Kritzler, 1951; McCowan & Reiss, 1995a; Reiss, 1988). McBride & Kritzler (1951) first reported that neonatal bottlenose dolphins produce whistles from the moment of birth. Several studies of neonatal whistles in bottlenose dolphins revealed the following facts: the whistle is present at birth; it is not confined to a single sex; there is no indication of seasonality; and multi-looped whistles are not common from neonates (see review by Caldwell & Caldwell, 1979). Caldwell & Caldwell (1979) analysed the whistles of 14 bottlenose dolphin infants at varying ages in weeks and reported that neonates produce "tremulous or quavery" whistles, which have little frequency modulation and are not stereotyped. In most cases, the stereotypic "signature" whistles developed by the end of the first year. They also observed that whistle duration increased with age through subadults.

Reiss (1988) observed the sounds of neonatal bottlenose dolphins immediately after birth and reported that whistles and whistle-squawks were emitted by the neonates and might function as contact-isolation calls. McCowan & Reiss (1995a) investigated eight captive-born bottlenose dolphin infants from birth over their first year of development. They found that infants from different social groups partly shared their whistle repertoires and that all infants produced two predominant whistle types. They also found ontogenetic changes in the structure and contextual usage of whistle types. McCowan & Reiss implied that maturation of the sound-producing organs, as well as the vocal learning process, would cause the early whistle types to be less complex and that complexity of the whistles would increase as they develop.

Killebrew et al. (2001) described the sounds produced by a neonatal bottlenose dolphin one day after birth until day five. They found burstpulse sounds and whistle-squawks, but they did not find any whistles without burst-pulse characteristics in this neonate's sounds. They argued that whistle-squawks were evidence that the neonatal dolphins must first develop their muscles and/or the muscle control for whistle production before they can fully produce whistles.

In this paper, we report on the acoustic characteristics and modifications of early sounds produced by two captive-born neonatal bottlenose dolphins. We investigated whistle characteristics and modifications to whistles from a neonate, and the sound differences between neonates.

#### **Materials and Methods**

## Subjects

Two neonatal bottlenose dolphins were the subjects of this study and were housed in an outdoor elliptical pool at the Suma Aqualife Park, Hyogo, Japan. The neonates were born from the same mother on 2 June 1999 and on 12 July 2000; and we refer to them in this paper as "neonate 99" and "neonate 00," respectively. Neonate 99 was a female, and neonate 00 was a male. Neonate 99 was housed with her mother and two other adult females for the first 3.5 h after birth, and then only with her mother from 3.5 h after her birth. Neonate 00 was housed with his mother and two other adult females. Neonate 99 died at about 50 h after birth. The cause of death could not be determined by an autopsy; however, there seemed to be no abnormality in neonate 99's facial-nasal region or sound-producing organs.

#### Data Collection

All underwater recordings were made with a fixed hydrophone (OKI ST-1020) connected to an amplifier (OKI SW-1020) through a 1 kHz high-pass filter. Sounds were recorded on a digital audiotape recorder (SONY TCD-D8). One recording session was about 60 min. The sensitivity of the entire recording system was linear up to 24 kHz. Behaviours of the dolphins were recorded simultaneously with a digital video camera (SONY DCR TRV-900) through an underwater observation window, which provided a view of the entire tank. Behavioural and acoustical data were collected using a focal animal sampling technique (Altmann, 1974).

Data from neonate 99 were obtained at 1.5-4.5, 5.5-6.5, 8-9, 14-15, 17-18, 20-21, 23-24, and 26-27 h after birth. We excluded the data obtained between 28-50 h after birth to avoid possible confounding factors from the neonate's death. The data from neonate 00 were obtained at 1.5-4.5, 5-7, 10-11, 14-15, 18-19, 22-23, 24-25, 27-28, 33-34, 44-45, 47-48, 50-51, 56-57, 68-69, 74-75, 92-93, 122-123, 172-173, 291-292, 337-338, 602-603, and 770-771 h after birth. Neonate sounds were determined by the bubble stream emission from the neonate because it frequently occurs simultaneously with sound production, especially in infants (McCowan & Reiss, 1995a).

## Sound Analysis

All acoustical data were analysed using *Avisoft-SASLab Pro*, *Version 4.0*, for Windows (Avisoft Inc., Berlin, Germany, 2001). Spectrograms of whistles were generated with a sampling rate of 48 kHz, a high-

pass filter of 1 kHz, FFT length of 512, frame size of 100%, and a Hamming windowing function, which resulted in an analysis frequency resolution of 93 Hz, and a time resolution of 5.3 ms. Sounds with good signal-to-noise ratio were used for entire analyses. We categorised sounds as either burst-pulses (Figure 1a) or whistles (Figure 1b) because clicks were not produced until one week after birth in the previous study (Reiss, 1988). A few whistle-squawks (see Killebrew et al., 2001) were produced by the two neonates, which had characteristics of both frequency-modulated whistles and burst-pulse sounds. We treated whistle-squawks as the whistles only when we were able to analyse the whistle component separately in the whistle-squawks. If we were not able to clearly separate them, we discarded the sounds.

#### Whistle Analysis

Measurements of acoustic characteristics of whistles were made on spectrograms. To analyse whistles statistically, we measured six parameters for each whistle traditionally used for the quantitative whistle analysis (e.g., Steiner, 1981; Wang, 1993): (1) beginning frequency (BF), (2) end frequency (EF), (3) minimum frequency (Min), (4) maximum frequency (Max), (5) duration (D), and (6) number of inflection (NoI; change in the slope of the whistle contour from negative to positive or vice versa). We

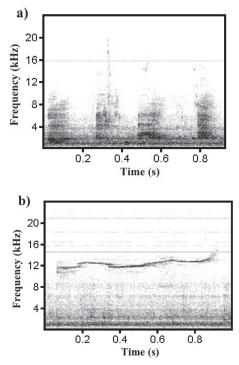


Figure 1. Examples of neonatal bottlenose dolphin sounds at Suma Aqualife Park: (a) burst-pulses and (b) whistles

then calculated frequency range (FR as Max - Min). We compared all of the whistles produced by three adult dolphins living with the neonates to the whistles produced by each neonatal dolphin.

## Whistle Repertoire

Categorisation of a dolphin's whistle repertoire traditionally has been conducted by human observers (Janik et al., 1994; Tyack, 1986); recently, however, computer processing of whistle parameters into categories has begun to take the place of the more traditional methods (McCowan, 1995; McCowan & Reiss, 1995b). Janik (1999) reported that both methods include potential pitfalls. Here, we classify the whistles by visual inspection and by statistical analysis to investigate the repertoire of the neonatal whistles accurately.

One of the authors (TM) categorised whistle types by visual inspection, with the resulting set of whistle types termed the "visual repertoire." A quantitative classification method on these same whistles was also conducted. Whistles were categorised by six parameters with UPGMA (Unweighted Pair Group Method using arithmetic Average) clustering (Sokal & Michener, 1958). The cluster number from the computer quantitative method was set to the same number from the visual repertoire. The resulting set of whistle types from computer analysis was termed the "quantitative repertoire."

## **Respiration Interval**

To investigate the physiological indicator which might influence whistles, we measured the respiration intervals. These data were derived from the first 10 min of each 1-h recording, and the average of these data was considered as a representative of respiration intervals for the h.

## Statistical Analysis

StatView, Version 5.0 (SAS Institute Inc., Cary, North Carolina, USA, 1998); JMP, Version 5.0 (SAS Institute Inc., Cary, North Carolina, USA, 2002); and VisualStat for Windows, Version 4.3J $\beta$  (VisualStat Computing Inc., Smyrna, Georgia, USA, 1993) were used for statistical analyses. A simple linear regression model was used for assessing the changes of whistle durations and number of inflections; the changes of respiration intervals; the relationship between average durations of whistles and the average of the respiration intervals at each 1-h recording; and the relationship between the number of whistle types and the number of whistles per recording in neonate 99. Five frequency parameters (beginning, end, minimum, and maximum frequency, and frequency range) tended to show remarkable change at the early period after birth but to show little change in the later period after birth. Instead of a simple linear regression model, we fitted the two

linear regression line models (broken stick regression or breakpoint regression) on these parameters to minimise the total of residual sum-of-squares (RSS) using a VBA (Visual Basic for Application) programme written by Shigenobu Aoki (Faculty of Social & Information Studies, Gunma University, Japan, 2003). A Fisher exact test was conducted to compare the proportions of whistles to burst-pulses between the two neonates. One-way analysis of variance (ANOVA) with Tukey-Kramer honestly significant difference (HSD) post-hoc test was done to compare each parameter of the whistles among neonate 99, neonate 00, and all adults. We also used discriminant analysis to compare whistle difference among neonate 99, neonate 00, and all adults.

#### Results

We analysed 603 min of videotape and DAT data from 1.5 h to 27 h after the neonate's birth and identified 483 sounds from neonate 99. We used 351 whistles with a high signal-to-noise ratio for statistical analysis and for quantitative repertoire analysis, and 444 whistles for visual repertoire analysis. Few sounds were not correlated with bubble stream productions. Six whistles from 26 h after birth were excluded in the analyses of the quantitative repertoire because of a small sample size. To compare visual repertoires with quantitative repertoires accurately, we excluded 12 whistles from 26 h after birth in the analysis of the visual repertoire.

We analysed 1,637 min of videotape and DAT data from 1.5 h to 1 month after birth and identified 651 sounds from neonate 00. Many of these sounds were discarded because it was determined that many of the whistles were produced by at least one of the three adult female dolphins and, thus, the signal-to-noise ratio decreased significantly. Because only nine whistles and 16 burst-pulses were identified from 1.5 h to 27 h after birth, we could not use data from neonate 00 for our study of whistle modulation within an individual; we were able to use these data for the comparisons between individuals, however. Eleven whistles were identified as produced with adults' whistles, and included one whistle from the mother and 10 whistles from the other adults.

#### Within Individual (Neonate 99)

Whistle Parameter Change—Each neonate produced whistles and burst pulses by 1.5 h after birth; however, whistle acoustic characteristics changed throughout the day. Four frequency parameters—beginning, end, minimum, and maximum frequencie—were best fitted when we applied the different regression models in the data of 1.5 to 8 h and in those of 14 to 26 h after birth (total of residual sum of squares [RSS]: 778.9 [BF], 2,095.4 [EF], 597.9 [Min], 1,712.3 [Max]). Beginning

frequencies became higher by the hour until 8 h (y =8.39 + 0.36x,  $F_{1,166} = 60.3$ ; p < 0.0001), and became slightly lower from 14 h after birth (y = 12.8 - 0.08x,  $F_{1,181} = 4.14$ ; p = 0.04; Figure 2a). End frequencies also became higher by the hour until 8 h (y = 10.9 +0.47x,  $F_{1,166} = 24.9$ ; p < 0.0001), and became slightly lower from 14 h after birth (y = 18.3 - 0.22x, F<sub>1,181</sub> = 19.0; p < 0.0001; Figure 2b). Minimum frequencies became higher by the hour until 8 h (y = 8.18+ 0.33x,  $F_{1,166} = 59.5$ ; p < 0.0001), and did not show significant change from 14 h after birth (y = 11.6-0.05x,  $F_{1,181} = 2.15$ ; p = 0.14; Figure 2c). Maximum frequencies became higher by the hour until 8 h (y =11.2 + 0.47x,  $F_{1,166} = 30.3$ ; p < 0.0001), and became slightly lower from 14 h after birth (y = 18.3 - 0.19x,  $F_{1,181} = 16.8; p < 0.0001;$  Figure 2d).

On the other hand, frequency range was best fitted when we changed the model between 1.5 to 14 h and 17 to 26 h after birth (RSS: 1,649.7). It became higher by the hour until 14 h after birth (y = 2.99 + 0.14x,  $F_{1.205} = 16.3$ , p < 0.0001), and did not show significant change from 17 h after birth (y = 5.48 - 0.08x,  $F_{1.142} = 1.88$ ; p = 0.17; Figure 2e).

Whistle durations became longer by the hour (F<sub>1,349</sub> = 163.2; p < 0.0001, R<sup>2</sup> = 0.32; Figure 3). Number of inflections became slightly longer by the hour (y = 1.49 + 0.06x, F<sub>1,349</sub> = 28.5; p < 0.0001, R<sup>2</sup> = 0.07). Respiration intervals became slightly longer by the hour (F<sub>1,296</sub> = 10.3; p = 0.002, R<sup>2</sup> = 0.03). We found a strong correlation between the average whistle durations and the average of the respiration intervals for each 1-h recording (F<sub>1,9</sub> = 14.5; p = 0.005, R<sup>2</sup> = 0.64; Figure 4).

Whistle Repertoire—The repertoire composition of whistles varied with age. The total number of whistle types in the visual repertoire was 38. Only one type (Rise; see Tyack, 1986) was found throughout the whole time; it was also the most often documented among whistle types (17.1% of all whistles). Other types also appeared as often as the Rise (e.g., 11.8%: Rise with end modulation; 7.4%: long Flat; Table 1). Each whistle type in the visual repertoire has a different temporal pattern. Some types (e.g., Rise or long Flat) were found throughout the whole time, whereas the other (Wave) was only produced at a later stage (14 to 23 h).

We categorised "quantitative repertoire" whistles into 38 clusters by UPGMA clustering methods. Two types (6 and 24) were recorded during the study period. Type 27 appeared the most often of all whistle types (16.5% of all whistles). Other types also appeared with similar frequency to Type 27 (e.g., Type 24: 11.9%; Type 6: 11.6%; Type 37: 10.1%; Table 2). Each whistle type in the quantitative repertoire also has a different temporal pattern. Type 27 was mainly produced during an early stage (1.5 to 3.5 h), whereas types 37 and 28, for example, were only produced at a later stage (14 to 23 h).

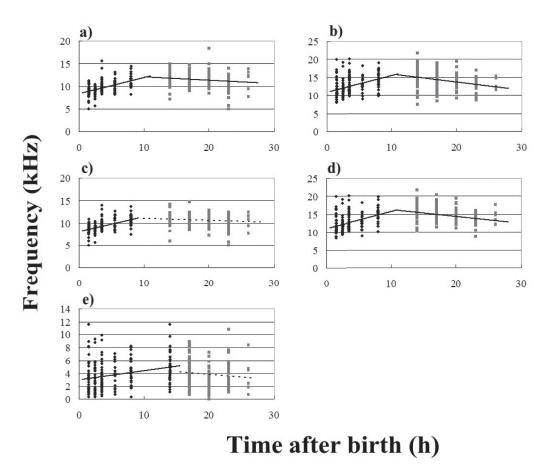


Figure 2. Changes in whistle frequency parameters by time after birth of neonatal bottlenose dolphins at Suma Aqualife Park: (a) beginning frequency, (b) end frequency, (c) minimum frequency, (d) maximum frequency, and (e) frequency range; the x-axis shows the time after birth (h) and the y-axis shows frequency (kHz). Solid and dashed lines indicate significant and nonsignificant trend effects (p < 0.05), respectively, of the time after birth on whistle frequency.

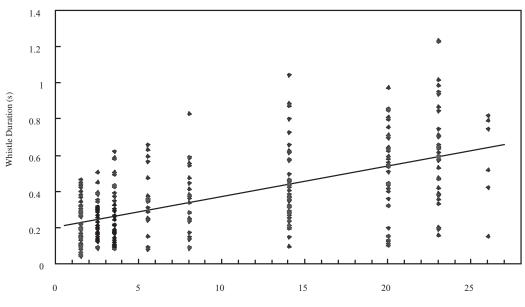
Tables 1 and 2 present the number of whistles used for the analysis and the number of whistle types from both quantitative and visual repertoire analyses across times from birth. The number of whistle types in the visual repertoire was strongly correlated with the number of whistles per 1-h recording ( $F_{1.8} = 22.9$ ; p = 0.002,  $R^2 = 0.77$ ; Figure 5). The number of whistle types in the quantitative repertoire was also correlated with the number of whistles per 1-h recording ( $F_{1.8} = 6.31$ ; p = 0.04,  $R^2 = 0.47$ ; Figure 5).

#### Between Individuals

Recorded sounds varied between neonates. The ratio of whistles to burst-pulses showed significant differences between neonates (Fisher exact test:  $X^2$ = 763.5, p < 0.0001). Neonate 99 produced many whistles (458, including 103 whistle-squawks) but few burstpulses (25), while neonate 00 produced many burstpulses (573) but few whistles (78, including 6 whistle-squawks). Neonate 00 produced 16 burst-pulses and nine whistles from 1.5- to 28-h recordings, or the same period of time after birth as neonate 99, which also differed significantly from the ratio of whistles to burst-pulses that were produced by neonate 99 (Fisher exact test:  $X^2 = 110.9$ , p < 0.0001).

Whistle characteristics also varied between neonates and between each neonate and the adults. All whistle parameters, except frequency range, were different between neonate 99 and neonate 00 (oneway ANOVA with Tukey-Kramer HSD test [ $\alpha$  = 0.05]; Table 3). All whistle parameters were different between the adult dolphins and both neonate 99 and neonate 00 (one-way ANOVA with Tukey-Kramer HSD test [ $\alpha$  = 0.05]: F<sub>2,426</sub> = 149.6, *p* < 0.0001 [BF]; F<sub>2,426</sub> = 193.9, *p* < 0.0001 [EF]; F<sub>2,426</sub> = 814.6, *p* < 0.0001 [Min]; F<sub>2,426</sub> = 822.3, *p* < 0.0001 [Max]; F<sub>2,426</sub> = 189.6, *p* < 0.0001 [FR]; F<sub>2,426</sub> = 55.4, *p* < 0.0001 [D]; F<sub>2,426</sub> = 13.3, *p* < 0.0001 [NoI]; Table 3).

We also conducted discriminant analysis and detected the significant difference among six



Time After Birth (h)

**Figure 3.** Changes in whistle durations by time after birth for a neonatal bottlenose dolphin at Suma Aqualife Park; the x-axis shows the time after birth (h) and the y-axis shows whistle durations (s). The regression line is shown.

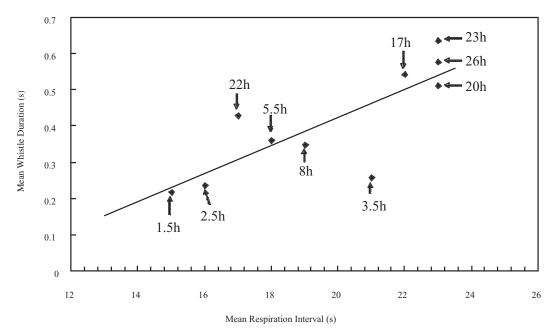


Figure 4. Relationship between mean respiration intervals (s) and mean whistle durations (s) per 1-h recording; the regression line is shown. The numbers (1.5h, 2.5h, etc.) in the graph indicate the time after birth.

whistle parameters (BF, EF, Min, Max, D, and NoI) by adult dolphins, neonate 99, and neonate 00 ( $F_{12,842}$  = 73.8, *p* < 0.0001; percent correct classification score was 95.6%). Whistle parameters by neonate

99 and neonate 00 were classified more exactly than those by adults, which indicated that neonates' whistles were more different from each other than they were from adults' whistles (percent correct

Whistle type \ Time from birth (h)	1.5	2.5	3.5	5.5	8	14	17	20	23	Sum	Percent
Rise	11	2	11	6	4	9	11	8	12	74	17.1
Rise with end modulation	9	7	5	5	7	10	7	1	0	51	11.8
long Flat	7	3	8	1	0	2	3	5	3	32	7.4
Short Almost Flat	0	11	11	4	0	0	0	3	0	29	6.7
Break Mountain	0	2	1	0	0	6	8	8	3	28	6.5
Wave	0	0	0	0	0	8	12	5	3	28	6.5
Short	8	3	0	0	2	4	4	3	1	25	5.8
Flat with one Break	5	5	0	1	3	1	3	4	3	25	5.8
Remainder	15	21	16	5	14	20	23	13	13	140	32.4
Number of whistles	55	54	52	22	30	60	71	50	38	432	100
Number of whistle types	13	15	12	9	12	17	18	15	13	38	

 Table 1. Visual repertoire of whistles; the number of whistles and the number of whistle types for each recording hour are also shown.

 Table 2. Quantitative repertoire of whistles; the number of whistles used for the analysis and the number of whistle types at each recording hour are shown.

Whistle type \ Time from birth (h)	1.5	2.5	3.5	5.5	8	14	17	20	23	Sum	Percent
Type 27	18	15	15	4	2	2	0	1	0	57	16.5
Type 24	1	3	4	4	2	2	12	9	4	41	11.9
Туре 6	7	4	7	3	6	5	5	1	2	40	11.6
Туре 37	0	0	0	0	0	4	18	7	6	35	10.1
Type 28	0	0	0	0	1	4	6	2	3	16	4.6
Remainder	17	16	17	8	14	22	29	16	17	156	45.2
Number of whistles used for quantitative analysis	43	38	43	19	25	39	70	36	32	345	100
Number of whistle types	11	10	14	9	12	16	19	16	15	38	

classification score: 98.3% for neonate 99; 86.6% for neonate 00; 63.6% for adults).

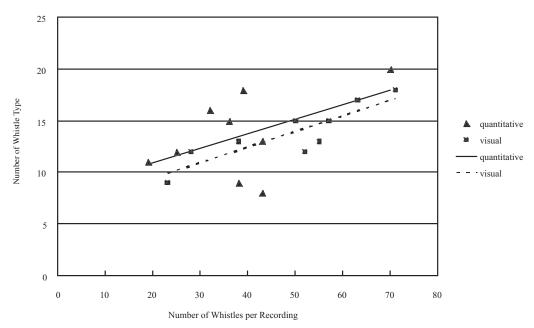
# Discussion

Two neonatal bottlenose dolphins produced various sounds, including whistles and burst-pulses. The whistles changed throughout the day of birth, and each neonate produced various types. Acoustic characteristics of these neonate sounds were significantly different between neonate 99 and neonate 00.

#### Within Individual (Neonate 99)

Whistle Parameter Change—The neonates produced many sounds, including whistles and burstpulses, just 1.5 h after their births. The whistle characteristics changed throughout the day. All frequency parameters of the whistles (beginning, end, minimum, and maximum frequency, and frequency range) became higher by the hour during the early stage in our study period but became slightly lower or did not change by the hour during the late stage. Frequency range and maximum frequency of adults' whistles were significantly higher than those of each neonate, which indicated that the changes of neonates' whistle characteristics, especially these parameters, might not completely stop after the early stage in our study period. Thus, frequency parameters of neonatal whistles may change drastically at the very early stage in their life, and may change slowly after the early stage. The drastic changes in their very early stage of life may result from their physical development such as muscle development. The muscles of neonatal dolphins are different from those of adults in their aerobic capacity, which affects locomotion ability (Dearolf et al., 2000).

The number of inflections continuously became slightly longer by the h during our study period, which may also result from muscle development, and to some extent, from the whistle durations. It may be more difficult for neonates to produce whistles that have many inflections than those with little inflections; in other words, it may be more difficult for neonates to tense and loosen the muscles of their sound-producing organs alternately than to just tense or loosen their muscles. Thus, at the early stage of development, the



**Figure 5.** Relationships between number of whistles and number of whistle types in quantitative and visual repertoires per 1-h recording; the solid line is the regression line for quantitative repertoires and the dashed line is for visual repertoires.

**Table 3.** Mean  $\pm$  standard deviations (SD) of seven whistle parameters produced by neonate 99, neonate 00, and adults; different letters (a, b, c) indicate statistical differences of each parameter with one-way ANOVA with Tukey-Kramer HSD test ( $\alpha = 0.05$ ).

	Neonate 99 ( <i>n</i> = 351)	Neonate $00 (n = 67)$	Adults $(n = 11)$
BF (kHz)	10.61 ± 1.82 a	6.32 ± 2.03 b	8.22 ± 2.98 c
EF (kHz)	13.44 ± 2.71 a	6.29 ± 2.77 b	9.84 ± 3.76 c
Min (kHz)	10.11 ± 1.57 a	4.83 ± 1.64 b	6.92 ± 1.36 c
Max (kHz)	13.92 ± 2.56 a	8.74 ± 3.15 b	16.69 ± 2.88 c
FR (kHz)	3.81 ± 2.23 a	3.92 ± 2.88 a	9.77 ± 2.06 b
D (s)	$0.41 \pm 0.25$ a	$0.60 \pm 0.70 \text{ b}$	1.57 ± 0.84 c
NoI	$2.21 \pm 1.83$ a	$1.60 \pm 2.12$ b	4.73 ± 2.33 c

neonatal dolphins cannot move their muscles—for example, in the nasal regions—quickly, or cannot control their nervous system, which is involved in whistle production (see Killebrew et al., 2001).

Whistle durations became longer by the hour, and the duration was strongly correlated with respiration intervals. The neonates have a lower aerobic capacity in their muscles than adults do, so they are limited in their diving ability (Dearolf et al., 2000). Thus, neonates have to use their respiration efficiently in one dive. Respiration interval may strongly correlate with the maximum volume of air during a dive. Neonatal dolphins can produce longer whistles as they become better able to hold air in their lungs for longer periods of time. Number of inflections also can be affected by the whistle durations, that is, whistle durations become longer, number of inflections become greater and vice versa. The whistles produced by the neonates thus continued to change throughout the day. These changes may be caused by the development of the muscles or the nervous systems involved in respiration that are responsible for sound production abilities.

Whistle Repertoire—Neonate 99 produced various types of whistles, and no dominant type of whistle was produced repeatedly throughout the day. The whistle type that was produced most often was about 17.1% and the second type was more than 11% of all whistle types in the visual repertoire. Each whistle type has a different temporal pattern. From these results, we did not find a "signature whistle" from neonate 99 as reviewed by Caldwell et al. (1990). A follow-up recording is needed to reveal whether or not neonate 99 produced signature whistles.

One type of whistle (Rise) was produced throughout the day. This type of whistle resembles

Whistle Type 2, which was predominantly shared by all infants across all social groups and by almost all adults and in which may contain signature information according to McCowan & Reiss (1995a, 2001). We can easily imagine that adult bottlenose dolphins use this whistle type in various contexts for example, in contexts of separation—because neonates can produce it in such an early stage of development. Rise often is produced by infants during contexts of separation from other dolphins (McCowan & Reiss, 1995a; but see Smolker et al., 1993). Rise may be a basic and important whistle for bottlenose dolphins in social situations.

The number of whistle types in the quantitative repertoire showed the same tendencies as those in the visual repertoire, which positively correlated with the number of whistles. Each whistle type in both repertoires has a different temporal pattern. These results indicated that neonate 99 produced various whistle types at random except for a few types such as Rise. Birds that exhibit song-learning practice their songs to match their own song template in the motor phase (their early stage of development) (see Catchpole & Slater, 1995). Bottlenose dolphins also have exhibited "vocal learning" in the production of their whistles (Tyack & Sayigh, 1997). Our results indicated that neonates may practice producing whistles in these early periods to be able to produce stable whistles.

# Between Individuals

Two neonates from the same mother produced obviously different sounds. The sound characteristics of their whistles showed significant differences between adults and each neonate. This indicates that body size or age may not affect beginning, end, and minimum frequency but only the maximum frequency and frequency range of whistles. Frequency range can be a better indicator of age or developmental stage.

Sound categories and characteristics of whistles showed a significant difference between neonates, and whistles could be discriminated easily by discriminant analysis. These results might imply that the mother dolphin uses sound cues to recognise her neonates. Some animals-for example, many species of penguins, such as King penguins (Aptenodytes patagonicus) (Jouventin, 1982), or Subantarctic fur seal (Arctocephalus tropicalis) (Charrier et al., 2002)-recognise their young by vocal cues. Mammals in the air often recognise their offspring by odour to prevent any allo-suckling attempts (see Chalmers, 1983). Cetaceans, however, must recognize their offspring under water, where olfactory cues are of no use. Moreover, cetaceans completely lack the olfactory class I receptor genes and have class II genes, which exist as pseudogenes (Freitag et al., 1998). Thus, they have to use other cues to

recognize or know their calves. Our results suggest that the neonatal sounds—not only the whistle characteristics, but also the ratio of sound categories (whistles versus burst-pulses)—may be used by mother dolphins for recognising their offspring.

The difference between the two neonates might be explained by the sexual difference in neonatal whistles, such as in Amazonian manatees (*Trichechus inunguis*), which may be revealed by further studies on the acoustic characteristics of whistles produced by neonatal dolphins (Sousa-Lima et al., 2002).

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#### Literature Cited

- Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour*, 49, 227-265.
- Caldwell, M. C., & Caldwell, D. K. (1967). Intraspecific transfer of information via the pulsed sound in captive odontocete cetaceans. In R-G. Busnel (Ed.), *Animal sonar* systems: Biology and bionics, Vol. II (pp. 879-937). Jouyen-Josas, France: Laboratoire de Physiologie Acoustique.
- Caldwell, M. C., & Caldwell, D. K. (1968). Vocalization of naïve captive dolphins in small groups. *Science*, 159, 1121-1123.
- Caldwell, M. C., & Caldwell, D. K. (1979). The whistle of the Atlantic bottlenosed dolphin (*Tursiops truncatus*): Ontogeny. In H. E. Winn & B. L. Olla (Eds.), *Behavior of marine animals: Current perspectives in research. Volume 3: Cetaceans* (pp. 369-401). New York: Plenum Press.
- Caldwell, M. C., Caldwell, D. K., & Tyack, P. L. (1990).
  Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 199-233). San Diego: Academic Press.
- Catchpole, C. K., & Slater, P. J. B. (1995). *Bird song*. Cambridge: Cambridge University Press.

- Chalmers, N. (1983). The development of social relationships. In T. R. Halliday & P. J. B. Slater (Eds.), Animal behaviour. Volume 3. Genes, development and learning (pp. 114-148). London: Blackwell Scientific Publications.
- Charrier, I., Mathevon, N., & Jouventin, P. (2002). How does a fur seal mother recognize the voice of her pup? An experimental study of Arctocephalus tropicalis. Journal of Experimental Biology, 205, 603-612.
- Dearolf, J. L., McLellan, W. A., Dillaman, R. M., Frierson, D., Jr., & Pabst, D. A. (2000). Precocial development of axial locomotor muscle in bottlenose dolphins (*Tursiops truncatus*). *Journal of Morphology*, 244, 203-215.
- Evans, W. E. (1967). Vocalization among marine mammals. In W. N. Tavolga (Ed.), *Marine bio-acoustics, Vol. II* (pp. 159-186). New York: Pergamon.
- Freitag, J., Ludwig, G., Andreini, I., Rössler, P., & Breer, H. (1998). Olfactory receptors in aquatic and terrestrial vertebrates. *Journal of Comparative Physiology*, A, 183, 635-650.
- Herman, L. M., & Tavolga, W. N. (1980). The communication system of cetaceans. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 149-209). New York: Wiley-Interscience.
- Janik, V. M. (1999). Pitfalls in the categorization of behaviour: A comparison of dolphin whistle classification methods. *Animal Behaviour*, 57, 133-143.
- Janik, V. M., & Slater, P. J. B. (1997). Vocal learning in mammals. Advances in the Study of Behavior, 26, 59-99.
- Janik, V. M., & Slater, P. J. B. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, 56, 829-838.
- Janik, V. M., Dehnhardt, G., & Todt, D. (1994). Signature whistle variations in a bottlenosed dolphin, *Tursiops* truncatus. Behavioral Ecology and Sociobiology, 35, 243-248.
- Jouventin, P. (1982). Visual and vocal signals in penguins, their evolution and adaptive characters. Berlin and Hamburg, Germany: Verlag Paul Parey.
- Killebrew, D. A., Mercado III, E., Herman, L. M., & Pack, A. A. (2001). Sound production of a neonate bottlenose dolphin. *Aquatic Mammals*, 27, 34-44.
- McBride, A. F., & Kritzler, H. (1951). Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. *Journal of Mammalogy*, 32, 251-266.
- McCowan, B. (1995). A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins (Delphinidae, *Tursiops truncatus*). *Ethology*, 100, 177-193.
- McCowan, B., & Reiss, D. (1995a). Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): Role of learning. *Journal of Comparative Psychology*, 109, 242-260.
- McCowan, B., & Reiss, D. (1995b). Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae, *Tursiops truncatus*): A re-evaluation of the signature whistle hypothesis. *Ethology*, *100*, 194-209.
- McCowan, B., & Reiss, D. (1997). Vocal learning in captive bottlenose dolphins: A comparison with humans and

nonhuman animals. In C. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 178-207). Cambridge: Cambridge University Press.

- McCowan, B., & Reiss, D. (2001). The fallacy of "signature whistles" in bottlenose dolphins: A comparative perspective of "signature information" in animal vocalizations. *Animal Behaviour*, 62, 1151-1162.
- Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. *Nature*, 434, 455-456.
- Reiss, D. (1988). Observations on the development of echolocation in young bottlenose dolphins. In P. E. Nachtigall & P. W. B. Moore (Eds.), *Animal sonar: Processes and performance* (pp. 121-127). New York: Plenum Press.
- Reiss, D., & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): Evidence for vocal learning. *Journal of Comparative Psychology*, 107, 301-312.
- Richards, D. G., Woltz, J. P., & Herman, L. M. (1984). Vocal mimicry of computer-generated sounds and labelling of objects by a bottlenose dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology*, 98, 10-28.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins, *Tursiops truncatus*: Stability and mother-offspring comparisons. *Behavioral Ecology and Sociobiology*, 26, 247-260.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Scott, M. D., & Irvine, A. B. (1995). Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus. Behavioral Ecology and Sociobiology*, 36, 171-177.
- Smolker, R. A., Mann J., & Smuts, B. B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioral Ecology and Sociobiology*, 33, 393-402.
- Sokal, R., & Michener, C. D. (1958). A statistical method for evaluating systematic relationships. University of Kansas Scientific Bulletin, 38, 1409-1438.
- Sousa-Lima, R. S., Paglia, A. P., & Da Fonceca, G. A. B. (2002). Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). *Animal Behaviour*, 63, 301-310.
- Steiner, W. W. (1981). Species-specific differences in pure tonal whistle vocalizations of five western north Atlantic dolphin species. *Behavioral Ecology and Sociobiology*, 9, 241-246.
- Tyack, P. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: Mimicry of signature whistles? *Behavioral Ecology and Sociobiology*, 18, 251-257.
- Tyack, P. L., & Sayigh, L. S. (1997). Vocal learning in cetaceans. In C. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 178-207). Cambridge: Cambridge University Press.
- Wang, D. (1993). Dolphin whistles: Comparisons between populations and species. Ph.D. dissertation, Institute of Hydrobiology, the Chinese Academy of Sciences, Wuhan, PR China.