



The Development of Echolocation in Bottlenose Dolphins (*Tursiops truncatus*)

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This study aimed to expand on previous efforts to evaluate the ontogeny of echolocation in Atlantic bottlenose dolphin calves (*Tursiops truncatus*). Data consisted of echolocation recordings and concurrent behavioral observations collected from six calves housed at the U.S. Naval facility in San Diego, CA between 2000 and 2002. A total of 361 echolocation click train samples, ranging in duration from 0.14 to 7.48 sec and 12 to 506 clicks per train, were isolated from weekly recording sessions collected over the first 6 months of life for each calf. The first echolocation click train attributed to a calf was recorded at 22 days postpartum, and the number of echolocation click trains from calves increased steadily with age. The duration and number of clicks per calf echolocation train increased with age while click train density (clicks/sec) and interclick interval values remained fairly consistent across the first 6 months. The most click trains were collected between 5 and 6 months of age, especially when swimming independently of their mothers and when multiple calves were present in the social grouping. When considering these results in the context of possible maturation of a calf's melon physiology, it seems very likely that the first two months of life are critical for the development of some parameters of echolocation and correlated behaviors. While the first click train recorded for two different calves in this study was approximately 3 weeks of age, it is possible that dolphin calves may innately produce functional sonar clicks immediately after birth, which were not captured in the current study. Future research will need to investigate this possibility using more controlled conditions and a better understanding of the anatomy and physiology of the sonar system of neonates.

Despite an impressive and growing body of work, echolocation in bottlenose dolphins (*Tursiops truncatus*) is not fully understood. How dolphins use such a system to interpret their environment remains enigmatic. For some odontocetes, echolocation may be used as a communicative device (e.g., Hector's dolphin, *Cephalorhynchus hectori*, Dawson, 1991; harbour porpoise, *Phocoena phocoena*, Clausen, Wahlberg, Beedholm, Deruiter, & Madsen, 2011). Bottlenose dolphins (*Tursiops* sp.) appear to use echolocation more as a sensory tool to navigate about an environment (reviewed by Herzing & dos Santos, 2004; Wisniewska, Johnson, Nachtigall, & Madsen, 2014) or hunt for prey (reviewed by Herzing & dos Santos, 2004) while gaining information from a returning sonar echo produced originally by the animal (Au, 1993; Madsen, & Surlykke, 2013; Tyack & Miller, 2002) or by another animal (i.e., eavesdropping, Gregg, Dudzinski, & Smith, 2007; Madsen & Surlykke, 2013; Xitco & Roitblat, 1996). Although this system appears to have very constrained characteristics, echolocation signals are modifiable with exposure to various factors. For example, bottlenose dolphins produced lower intensity clicks in tanks than in open water, demonstrating an ability to modify their echolocation clicks (Au, 1993; Rasmussen & Miller, 2002). Different odontocetes can adjust the intensity with which clicks are produced dependent upon distance to the object of echolocation (reviewed by Tyack, 2015; Au, 1993; Au & Benoit-Bird, 2003; Rasmussen & Miller, 2002; Supin & Nachtigall, 2012; Wisniewska et al., 2015). Additionally, operant conditioning can be used to shift the peak frequency of echolocation clicks as demonstrated by a single bottlenose dolphin (Moore &

Pawloski, 1990). When taken together, these studies support the interpretation that dolphins may have partial control of their echolocation.

Relevant Characteristics of Echolocation Signals

Several similar but distinct definitions of *clicks* and *click trains* (i.e., trains) appear in the extant literature. Au (1997) descriptively classified echolocation clicks by dolphins as short duration (50-80 microseconds, μsec), high intensity (pressure ratio in decibels, $\text{dB} = 20 \log (\text{pressure}_1/\text{pressure}_2)$), broadband (3-dB, or half power, bandwidths of 20-60 kHz), exponentially decaying pulses with peak frequencies between 30 and 130 kHz. Alternatively, Purves and Pilleri (1983) defined clicks more subjectively as “signals which can be broken up into a series of single pulses” (p. 99), and Houser, Helweg, and Moore (1999) chose “trains or sequences of impulsive sounds” (p. 1579). A number of parameters are used to characterize echolocation signals, including frequency range, train duration, number of clicks per train, interclick interval, click frequency range, click intensity level, and the click train envelope (reviewed by Herzing & dos Santos, 2004). In free-swimming animals, recording clicks that are on-axis, a signal that is emitted directly perpendicular to an object of interest to maximize all parameters, is a very difficult measurement to attain and thus limits the parameters that can be measured reliably for direct and absolute comparison purposes. Two parameters that can be recorded with greater ease in a free-swimming environment are train duration and clicks per train (e.g., wild Australian Irrawaddy dolphin, *Orcaella brevirostris*, Van Parijs, Parra, & Corkeron, 2000). For bottlenose dolphins, individual clicks range from 4 to 600 μsec (Au, 1993), and typically last less than 100 μsec (e.g., Au, 1997). Duration can describe the length of a single click or the length of a train (clicks emitted in discrete sets or series). Click repetition rate can be measured using train density (i.e., number of clicks emitted in a second within a train) and interclick interval (ICI, or the length of the interval (time span) between successive click peak pressures). ICI depends on a variety of factors including distance to target, how difficult it is to detect the target, the presence or absence of the target of interest, and whether or not the animal has an expectation of finding the specified target (Au, 1993).

The Ontogeny of Echolocation

Only five studies, with a total of six calves between them, previously evaluated the neonatal production of echolocation signals. Carder and Ridgway (1983) observed the production of high-frequency sounds from a 60-day old calf, although burst-pulse sounds and whistles were heard soon after birth. The authors recorded seven click trains from the calf, reporting peak frequencies from 33-120 kHz with 3-dB bandwidths of 28-81 kHz, although it is unclear whether the clicks were recorded on the maximum response axis of the echolocation beam. At approximately two weeks postpartum, Reiss (1988) found that two dolphins emitted shorter duration (1 ms) click-like signals and began to exhibit head scanning motions in conjunction with sound production. By 35-38 days postpartum, the recorded signals of both animals were reported as indistinguishable from adult clicks. Lindhard (1988) noted that a dolphin calf appeared to dramatically decrease the ICI between clicks occurring at the end of a click train, even at 2 weeks of age, possibly demonstrating a convergence towards a portion of the click train known as the *terminal buzz*. Other observations of individual calves suggest that the echolocation signal characteristics and echolocation behavior (i.e., head scans) of dolphin calves approaches that of adults over a period of months, including changes in the frequency content and increased interest in exploring their environment (Favaro, Gnone, & Passani, 2013; Ricciardi, Azzali, & Manoukian, 2003).

All of these previous studies had methodological issues and small sample sizes, which clearly limits their generalizability. Several studies were limited in the frequency range over which they could characterize the echolocation signals, and all had issues of unequivocally determining whether recorded signals were on the main response axis of the echolocation beam. Additionally, because calves were with their mothers, the issue of localizing echolocation click trains to one source presented a challenge to resolving the ambiguity of whether mother or calf was clicking. Finally, some studies indicated that calves engaged in some behavior such as open mouth posturing, bubble streams, and head scans while presumably emitting echolocation clicks or trains (Favaro et al., 2013; Reiss, 1988; Ricciardi et al., 2003).

Physiological Maturation

Important to this study are developmental changes that occur in odontocete sensory systems. The odontocete melon is comprised of lipids composed largely of isovaleric acid, an unusual lipid that is rarely found in other fatty tissues (Varanasi & Malins, 1972). This “acoustic” fat is involved in the columnation of echolocation and is present as well inside mandibular bony tissues, which are considered the anatomical acoustic window for sound reception (Au, 1993). Gardner and Varanasi (2003) reported that concentrations of isovalerate butyl ester (iso 5:0) detected in the melon lipids of adult *Phocoena phocoena* specimens were significantly higher than concentrations from fetal *Phocoena* melons. The authors also found a significant difference in the proportion of isovalerate in adult and neonate (as determined via body length) bottlenose dolphin melons. The observed positive correlation between animal length and the proportion of isovaleric acid in the melon suggests that some anatomical features of the odontocete acoustic system are not fully developed at birth but mature physiologically over time (Frainer, Huggenberger, & Moreno, 2015).

Together, studies in which the development of echolocation has been studied appears to indicate several behavioral patterns for a calf’s initial development of echolocation abilities. The evidence from a small number of calves and a limited number of observations suggested that echolocation may appear soon (i.e., within 2 weeks) after birth and likely changes over time in terms of the length of time between emitted clicks within a train, signal frequency (if clicks are on-axis), and train duration. The present study expanded on previous research by examining specific aspects of the development of echolocation in Atlantic bottlenose dolphin calves during free-swim scenarios in which a hydrophone was present from birth to six months, postpartum. The purpose of the current study was to determine if any components of echolocation (i.e., click train duration, clicks per train, train density, ICI, and behavioral correlates) were fully developed at birth or if any component appeared or changed with age. Frequency information was not measured for this study. The preliminary predictions tested by the current study include:

1. The duration of recorded echolocation click train samples was expected to change over time as the calves experimented with emitting clicks (e.g., Carder & Ridgway, 1983; Favaro et al., 2013; Reiss, 1988).
2. The number of clicks per train was expected to change with age (e.g., Favaro et al., 2013).
3. Because train density is dependent on both clicks per train and train duration, train density was expected to change with age (e.g., Favaro et al., 2013; Lindhard, 1988).
4. The ICI may change with age, with a decrease in ICI suggesting an increased proficiency in echolocation emission (e.g., Lindhard, 1988).
5. Dolphin calves were expected to initially display and then reduce open mouth posturing as they matured. Additionally, echolocation was expected to be indicated by the appearance of and an

increase in the frequency of head motions oriented toward the hydrophone (e.g., Carder & Ridgway, 1983; Favaro et al., 2013; Reiss, 1988; Ricciardi et al., 2003).

Method

Subjects

Six calves and their mothers housed at the U.S. Naval Marine Mammal Program Facility (MMP), located at the Space and Naval Warfare Systems Center in San Diego, CA, represented the subjects for this study (Table 1). These mother-calf pairs represent all the live births at the facility between 2000 and 2002. All calves were healthy at birth and were born into open-bay pens, which were separated by nets and net gates. The MMP facility featured 10 m x 10 m and 10 m x 20 m enclosures that were surrounded by floating wooden docks. As a study on the ontology of echolocation, only the echolocation click trains recorded from the calves were examined.

Table 1
Demographics of Study Subjects

Calf	Date of Birth	Calf Sex	# Echolocation Click Trains	# Trains for ICI Measures
BLY	04/30/00	F	79	--
CHM	05/31/02	M	42	11
HRT	06/07/02	F	109	59
LBU	06/10/02*	F	7	2
CST	06/16/02	F	65	33
IND	06/18/02	M	59	25

Note. Sample size is presented for the number of echolocation click trains used for analyses and the number of trains used to measure interclick intervals (ICI). *LBU died on 09/7/02 due to complications from pneumonia.

Materials

A single Bruel & Kjaer (B&K) 8103 omni-directional hydrophone (sensitivity ± 2 dB over the frequency range re: 1 V/ μ Pa) was used to collect echolocation click data. The hydrophone was placed into a 2 m PVC pipe positioned at a 90-degree angle from the dock into the water. The hydrophone extended below the end of the pipe by approximately 7.6 cm to facilitate recording while also minimizing the amount of cable visible to the animals in the water. This hydrophone collected underwater sounds and transmitted them via cables through a B&K charge amplifier (transducer sensitivity 0.97 dB), a Stanford Research Systems Model SR560 low noise amplifier (band passed between 30 – 300 kHz with a 6 dB/octave rolloff, Gain x2) and an Optimus power amplifier (Figure 1). Signals were transmitted into a poolside computer with a National Instruments PCI6110E 4-channel DAQ board sampling at 1 M (buffer size 5 M). Data were acquired as 12-bit binary signals and saved in a 16-bit format on CD-ROMs. To maximize the chance of recording calf echolocation clicks at the earliest possible age, two different channels were used during recording sessions. The first channel, a *mother* channel designed to allow capture of the full range of adult clicks, had a + /-10 V range. The second channel had a much smaller range (+/- 0.5 V) with the intent to capture smaller amplitude clicks that may be associated with neonatal and juvenile animals or different behavioral activities.

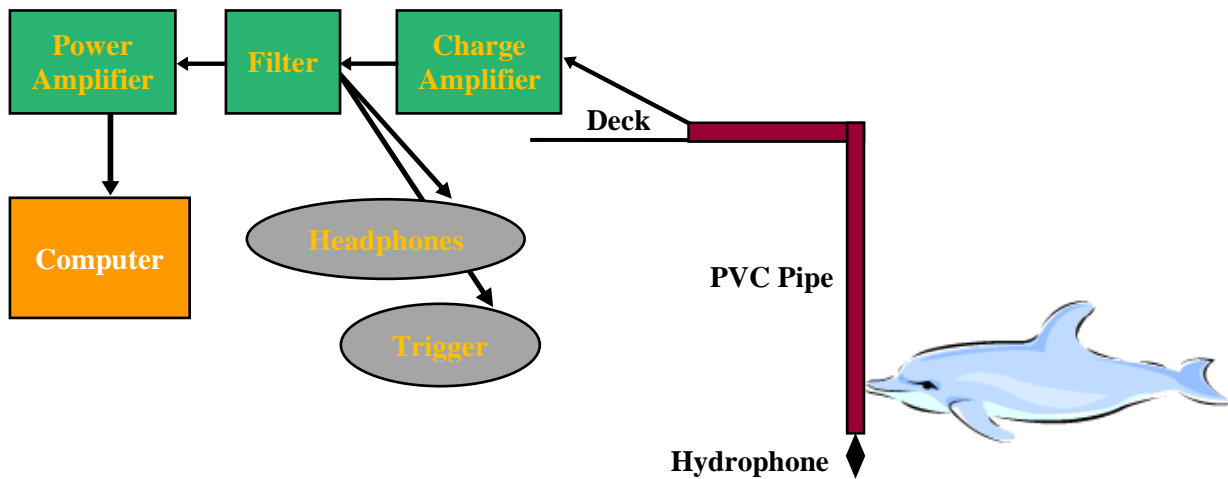


Figure 1. Schematic of experimental set up.

Definitions

Click measures. A number of parameters were examined to assess the characteristics of echolocation clicks presumably emitted by dolphin calves during their first few months, postpartum. A click train was defined as a series of clicks that were emitted close together in time and visually defined by a characteristic envelope. Click train duration was defined as the span of time between the visually determined onset of the first click in a train to the termination of the last click in a train. Clicks-per-train was operationally defined as the number of individual positive click peaks within an identified train. Train density represented the clicks per train divided by the train duration (clicks/sec). ICI (ms) is measured as the time span between the peaks of successive pressure spikes (clicks) in a click train.

Behavioral measures. Several behavioral correlates were examined in association with echolocation click production. These behaviors included swim position, head motions directed at the hydrophone, open mouths, presence of “other” vocalizations, presence of bubble emissions from animal presumed to target on the hydrophone, physical interactions with hydrophone (e.g., biting or hitting hydrophone), and social interactions (e.g., rubbing, calf discipline). Table 2 summarizes these behaviors and their definitions.

Data Collection – Observations and Recordings

During recording sessions, two to three researchers positioned themselves on the docks surrounding the pool(s) containing animals of interest, which provided them an unobstructed view of the animals’ interaction with the research hydrophone and its protective pipe. Placement of the hydrophone was selected to ensure that the pens directly behind the recording apparatus contained no dolphins in order to minimize inadvertently audio sampling non-focal animal(s). During recording sessions, the researchers did not solicit interactions with the animals but did not prohibit trainers from any animal interactions. These interactions proved to be beneficial at times, keeping adult females occupied in training sessions while allowing calves more freedom to explore their environment and interact more freely with the hydrophone. Recording sessions (1-4 hours/day) were repeatedly attempted five days a week from the date of birth until calves reached 6 months of age. Although the frequency of recordings per animal depended largely on uncontrollable factors (e.g., individual interest in the recording apparatus, weather, permissiveness of the mother, etc.), each animal present in the pen, especially each calf, was sampled at least once in a given week, if not every day.

Recordings began and ended using a trigger operated by the primary researcher. As the focal animal entered a swim pattern likely to bring it near the hydrophone, the researcher depressed the trigger, started the recording, and continued to record until the animal was well past the hydrophone to prevent cutting off the beginning or ending of a train. This trigger allowed for targeted recordings of echolocation from animals within 1-4 m of the hydrophone. This researcher also narrated all behaviors exhibited preceding and following the targeted echolocation, which were recorded onto a third channel of the same DAQ board for simultaneous behavioral analysis. In addition to the narration, a second research assistant took hand-written notes of ongoing activities of the focal animal and other animals from an independent position that was out of hearing distance of the primary

researcher. These additional notes were later compared to the recorded narration. Using tape marks placed on the dock (1 m to each side of the hydrophone), the second research assistant recorded the approximate distance (e.g., < 0.5 m) each time an animal was within inside of the 1 m tape mark of the hydrophone, the number of animals present during the recording, the direction of travel relative to hydrophone placement, and body position of the target animal (i.e., ventral or dorsal surface facing up).

Table 2
Behavioral Correlates and Operational Definitions

Behavior	Operational Definition
Swim Positions	
Solo	Target animal passes by the hydrophone alone with no other animals within 1 m of itself.
Echelon	Calf close to the mother, roughly parallel, and often touching the mother's flank above the midline (Mann & Smuts, 1999). Calf could be in an "inside" position toward the center of the pen from the adult or an "outside" position toward the pen perimeter from the adult. The position was reserved for mother/calf pairs only.
Infant	Calf below the female with the head aligned roughly with the female's mammary slits (Mann & Smuts, 1999). The position was reserved for mother/calf pairs only.
Ahead of	Target animal precedes another by 1 m past the hydrophone.
Behind	Target animal trails another by 1 m past the hydrophone.
Next to	Target animal beside another in any position other than echelon.
Below	Target animal under another in any position other than infant.
Group	More than one additional animal passing the hydrophone within 1 m of and in the same direction as the target animal.
Head Motions	
Head scan	Observationally wide or narrow lateral, repetitive sweeps of the head as the animal approaches the hydrophone (Dudzinski, personal communication).
Head cock	Target animal maintains rostral orientation on the hydrophone resulting in an apparent turning or cocking of the head toward the hydrophone as the animal passes.
Head turn	Head rotates side to side around a longitudinal axis through the rostrum.
Head spin	Rostrum spins in circles as the neck articulates around a longitudinal axis through head.
Other Behaviors	
Open mouth	Target animal orients head with the mouth open at the hydrophone.
Vocalizations	Any whistle or burst pulse sound or raspberry produced by the target animal.
Bubbles	Target animal releases small to medium trail of air bubbles from blow hole.

Isolating click trains. Due to limitations of recording with a single hydrophone, several steps were taken to increase confidence in determining the identity of the vocalizer. First, a vocalizing animal was identified based on its proximity to the hydrophone, any observed orientations toward the hydrophone, and relative positions while passing the hydrophone. Second, trains that could not be attributed to a single animal were eliminated. Third, as mentioned above, calves were considered focal animals and therefore emphasis was placed on collecting recordings when calves were close to the hydrophone, especially when the adult females were otherwise engaged with trainers or other activities. Finally, trains analyzed for ICI were further winnowed so that only trains from a single, identified calf, without overlapping trains or excessive background noise were included in this sub-set of data.

Several steps were taken to isolate a train. Each train's start point (visually determined onset of the first click), end point (visually determined termination of the last click), and duration (span of time between the start and end points) were then determined within the binary stream and marked with visible cursors. The number of clicks per identified train was counted manually. The number of clicks per extracted train was divided by the train duration to yield train density. Lastly, the start and end points of the train were used to excise the time waveforms for the individual click trains from the original binary recording using the audio editing software, Sound Forge™. The beginning and ending points of the train were entered in the sound file and saved to a working data

file; the rest of the recording from which the train was isolated was discarded. The resulting isolated train was transferred as a binary file again to CD-ROM, preserving the original digitization. To analyze for ICI, each train from the above isolation procedure was visually inspected. Once trains were isolated, MatLab 6.5® routines were created and used to automatically identify individual clicks and calculate the intervals between each click in a train. The computer program was designed to identify pressure spikes above a specified sound pressure level (SPL). Peak SPL ($SPL = 10 \log_{10}(Z^2 / Z_{ref}^2)$) is the maximum absolute value of the instantaneous sound pressure during a specified time interval (ANSI, 1994). As a note of caution, some structural factors of clicks and click trains (e.g., ICI, peak frequency, SPL) are critically dependent on factors such as distance to the hydrophone and angle of orientation that cannot be held constant with free-swimming animals (reviewed by Herzing & dos Santos, 2004). To accommodate this variability, this threshold was manually reset with every train until the number of computer-counted clicks roughly approximated the number of clicks observed and counted by hand. Each click was extracted from the train as 256 points of data, 31 points before the peak and 225 points after the peak, and stored to a data structure assigned to each click train, thus maintaining the order and spacing of clicks in the train. ICI was then calculated as the time between pressure peaks of successive echolocation clicks (i.e., a peak-to-peak interval). Once a data structure was created for a train, that train was evaluated manually for quality assurance. That is, signals isolated by the computer as *clicks* were visually examined to determine if their waveforms meet criteria for a click, a reflection, noise, or snapping shrimp, a common source of biological noise in the San Diego bay with a distinct waveform (Au, Lammers, & Banks, 1998). Clicks determined to be a reflection, noise, or a snapping shrimp were discarded. An initial interval threshold between clicks in a train was set at 500 ms. Interval thresholds between clicks in a train exceeding 500 ms were automatically eliminated. However, intervals above this duration threshold at the end of a train were considered as indicative of the termination of one train and the onset of a new train. Finally, to further account for artifact intervals between clicks, intervals were eliminated as outliers if they met the additional criteria:

1) Using a scatterplot of ICIs over time, the intervals were assessed for visual deviations from the pattern created by adjacent points in the scatterplot (i.e., a point representing an interval that deviated from the typical pattern of surrounding points).

2) An analysis of the original intact train from the Sound Forge series revealed that the interval in question was an artifact from the removal of a signal rather than a true interval from the train (i.e., was not present in the original train).

All data values (train start time, train end time, duration, clicks per train, density, mean train ICI, maximum ICI within the train, minimum ICI within the train, train ICI standard deviation, and train ICI variance) obtained via the procedures detailed above were then entered into a computer spreadsheet (SPSS®) for statistical analysis. All train structure variables were recorded continuously to avoid artificial polytomization.

Habituation Testing. The hydrophone did not change between each successive pass by the animals or from one session to another. As a relatively simple and possibly uninteresting stimulus, it is possible that the calves could have hypothetically lost interest in the hydrophone as it lost its novelty in a session or across sessions as indicated by less intense scanning or fewer trains. If habituation occurred, the results of the measured parameters may have been limited. Analyses were conducted for all echolocation variables measured in this study (i.e., duration, click count, density, and ICI) to assess within-session habituation. The first train per animal in each multi-train recording session was compared to the values collected from the last train per animal recorded in that session, using a Sign Test. If the values of the first train exceeded the values of the last train significantly more often than the values of the last train exceeded the values of the first, habituation was suspected. If the animal did not habituate to the hydrophone's presence, we expected a value of 0.5, which would demonstrate that the first train values exceeded the last train values equally as often as the last exceeded the first. There was no evidence of within-session habituation for any of the parameters examined.

Results

During the first 6 months of life, 369 total click trains were recorded from all study calves. Of these 369 trains, 8 were determined to be squeals¹ and the remaining 361 trains were analyzed collectively for duration, density, and clicks per train. Male calves ($n = 2$) emitted 101 trains (28%) and females ($n = 4$) produced 260 trains (72%) of this sample. After removing LBU from the females for this analysis, as her sample size was likely artificially lowered by her illness and early death, male calves (IND and CHM) produced the two lowest numbers of trains ($n = 59$ and $n = 42$, respectively). HRT was the most prolifically

¹ Squeals differ visually from echolocation clicks in that they have sweeping peak frequencies and more variable time courses (e.g., Ridgway, Dibble, Van Alstyne, & Price, 2015).

vocal calf, providing 109 (30%) of the total calf trains. Samples from calves were obtained in 21 of the 24 study weeks, beginning with week 4. The earliest train was recorded from HRT 22 days after birth, followed shortly thereafter by LBU who was recorded echolocating 24 days after birth. CST and IND were first recorded in month 2 but CHM was not successfully recorded until month 3. BAI was not successfully recorded until month 5. From 1 to 5 months, the number of echolocation samples obtained from calves increased steadily before decreasing slightly in month 6. The majority (76.6%, $n = 276$) of trains were recorded when calves were observed 1 m or less from the hydrophone. The calf approached the hydrophone alone in 66.7% ($n = 241$) of click trains used for analyses. Finally, follow-up analyses were performed at the individual calf level for each parameter to determine if the individual variability affected the collective results.

Train duration. Echolocation trains had a mean duration of 2.04 sec ($SD = 1.14$). Recorded trains ranged in duration from 0.14 to 7.48 sec. The majority (82%) of trains were shorter than 3 sec. Six trains exceeded 5 sec. Results from a one-way ANOVA revealed significant differences in calf mean train duration by month postpartum, $F(5, 360) = 2.92, p < 0.05$. A Tukey α post-hoc analysis found that calf click trains in the third month had significantly shorter durations than trains in the fifth month (Table 3). Although trains in month 1 and 2 were even shorter, on average, than month 3, the low sample size in those months likely impacted the results (Table 3). The mean train duration increased steadily from the first through the fifth months and then declined slightly during the sixth postpartum month (Figure 2a).

Table 3
Descriptive Statistics ($M \pm SE$) for Calf Acoustic Parameters

Month		Click train duration (s)	Clicks per train (f)	Train density (f/ms)	ICI (ms)
1	$M \pm SE$	1.25 ± 0.52	73.75 ± 28.83	94.55 ± 40.55	21.72 ± 4.83
	n	4	4	4	3
2	$M \pm SE$	1.37 ± 0.31	61.20 ± 25.93	35.54 ± 5.11	45.14 ± 7.09
	n	10	10	10	2
3	$M \pm SE$	1.74 ± 0.12	95.54 ± 8.09	67.37 ± 10.04	24.11 ± 1.71
	n	57	57	57	28
4	$M \pm SE$	1.99 ± 0.12	125.17 ± 10.76	66.01 ± 4.82	26.94 ± 2.30
	n	69	69	69	29
5	$M \pm SE$	2.27 ± 0.11	124.11 ± 8.84	53.93 ± 2.18	24.77 ± 1.58
	n	123	123	123	43
6	$M \pm SE$	2.05 ± 0.12	112.27 ± 7.62	58.00 ± 3.52	24.59 ± 1.64
	n	98	98	98	25

Note. Click train duration, clicks per train, and train density used a dataset containing 361 click trains. ICI was measured using a sub-set ($n = 130$) of the full dataset. See method for selection criteria.

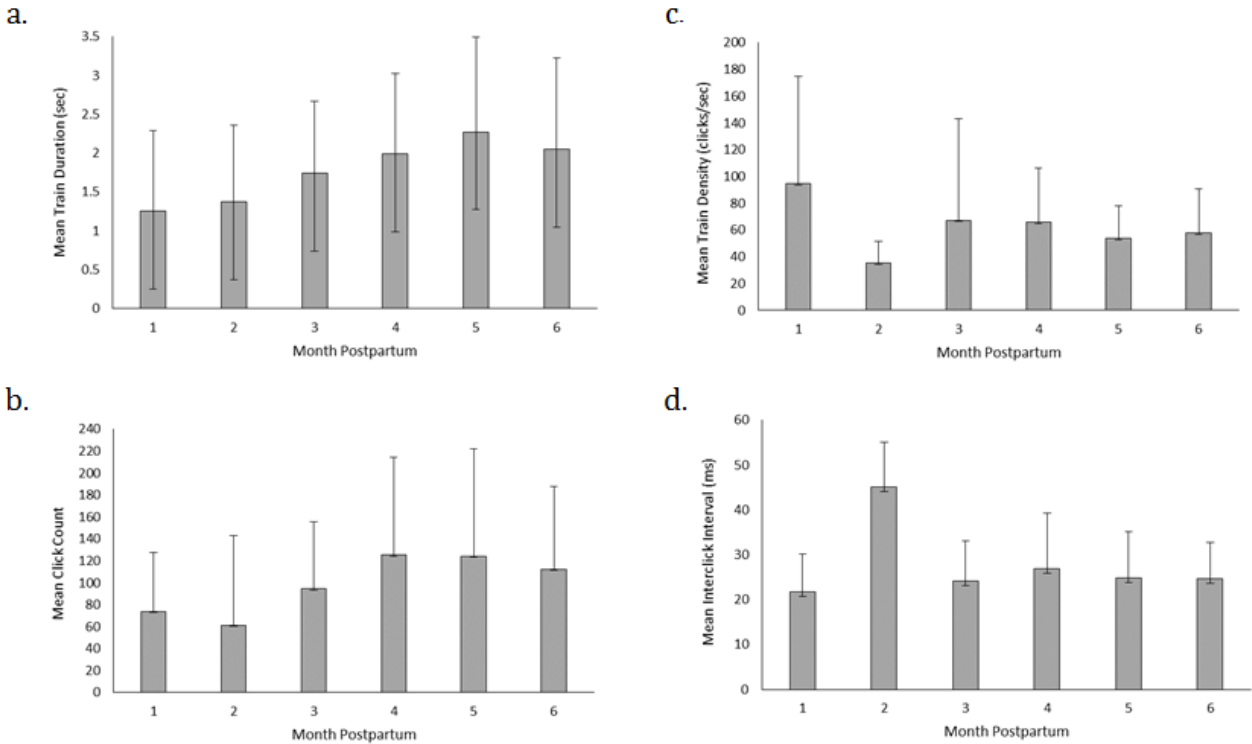


Figure 2. Descriptives per month postpartum with standard error bars. (a) Mean click train duration, (b) Mean click count per train, (c) Mean train density, and (d) Mean ICI per train.

Clicks per train. Echolocation trains had an overall mean click count of 114.13 clicks per train ($SD = 85.37$). These trains had a large range, containing from a minimum of 12 clicks to a maximum of 506. Only 16 trains (4%) exceeded a click count of 300, and 311 (86%) trains contained less than 200 clicks. There was a significant negative correlation between distance to the hydrophone and click count, $r = -0.13$, $p < 0.05$. Calves observed closer to the hydrophone predictably produced trains with a larger number of clicks. A significant positive correlation was also seen between calf train duration and click count, $r = 0.68$, $p < 0.05$, such that longer duration trains were correlated with a greater number of clicks. Results from a one-way ANOVA revealed no significant differences in mean clicks per train by month postpartum for calves. The overall average click counts for calves remained relatively consistent over the first two months then increased steadily until 5 months postpartum (Table 3). However, only four trains were recorded in the first month making the true trend for calves likely an increase in clicks per train over time. Like the mean train duration, a decrease in click count was seen in the sixth month (Figure 2b).

Train density. Echolocation trains had an overall mean density of 59.41 clicks/sec ($SD = 42.47$). These trains fluctuated from a minimum of 16.81 to a maximum of 443.48 clicks/sec. The majority (92%) of recorded densities were below 100 clicks/sec with only six trains exceeding 200 clicks/sec. There was no significant correlation between distance to the hydrophone and train density. Results from a one-way ANOVA revealed a significant effect in calf train density by month postpartum, $F(5, 360) = 2.39$, $p < 0.05$. A Tukey α post-hoc analysis, however, found no specific pair-wise month comparisons where density differences were significant (Table 3). The overall train density for calves fluctuated noticeably during the

initial period following birth, peaking early during the first postpartum month and showing a minimum density immediately thereafter in month 2 (Figure 2c). In the remaining months, calf click train density hovered around the overall mean and remained between 50 and 70 clicks/sec.

Interclick interval (ICI). Out of the 361 echolocation trains, 130 trains were selected for an analysis of interclick interval (ICI) based on the selection criteria presented in the method section. Calf trains had an overall mean ICI of 25.32 ms ($SD = 10.35$). The mean ICI per train ranged from a minimum of 5.95 ms to a maximum of 61.93 ms. The majority (76%) of mean ICIs were below 30 ms and 91% of trains fell below 40 ms. There was no significant correlation between distance to the hydrophone and ICI, $r = 0.104$, $p > 0.05$. Results from a one-way ANOVA did not produce a significant effect for month in overall calf mean train ICI. The overall mean train ICI by month postpartum for calves predictably remained consistent throughout the study period, only showing some fluctuation in the second month when just two trains were analyzed (Table 3, Figure 2d).

Concurrent behaviors. In total, head cocks were the most frequently observed head motions produced by calves, representing 67.4% of observations. Head scanning motions were observed less frequently (wide scan: $n = 22$; narrow scan: $n = 14$) than head cocks ($n = 190$), $\chi^2(3, N = 282) = 284.18$, $p < 0.001$. However, head scans were displayed more often as the dolphin calves aged (Figure 3). Only four instances of open-mouth posturing were observed. All instances occurred between 3 and 5 months postpartum. Only five instances of concurrent bubbles at the time of an echolocation train were observed. Three of those instances also occurred in conjunction with whistles.

Positions relative to other animals were noted during each echolocation recording. The calves approached the hydrophone alone more frequently as they aged before decreasing or leveling off in the sixth month (Figure 4). When calves approached the hydrophone with their mothers (33% of the trains), the most common positions included ahead of (10%), next to (8%), and infant under (5%) their mothers. Calves approached the hydrophone in a normal, dorsal up presentation in all cases but one when the calf approached in a ventral position.

Individual Responses

Individual variation was observed across the five calves for all measured parameters (Table 4, Figure 5a-d). Yet, no significant effect for calf emerged for all measured parameters except train density. Results from a one-way ANOVA revealed a significant effect for the mean train density between calves, $F(5, 360) = 6.58$, $p < 0.05$. A Tukey α post-hoc test revealed that LBU had a significantly higher mean train density than all other ($p < 0.05$). CHM also had a mean train density significantly higher than CST and BAI ($p < 0.05$). Despite removing LBU from the analysis, the overall mean effect for train density remained significant, $F(4, 353) = 4.15$, $p < 0.05$, and CHM retained her significantly higher mean train density than CST and BAI ($p < 0.05$).

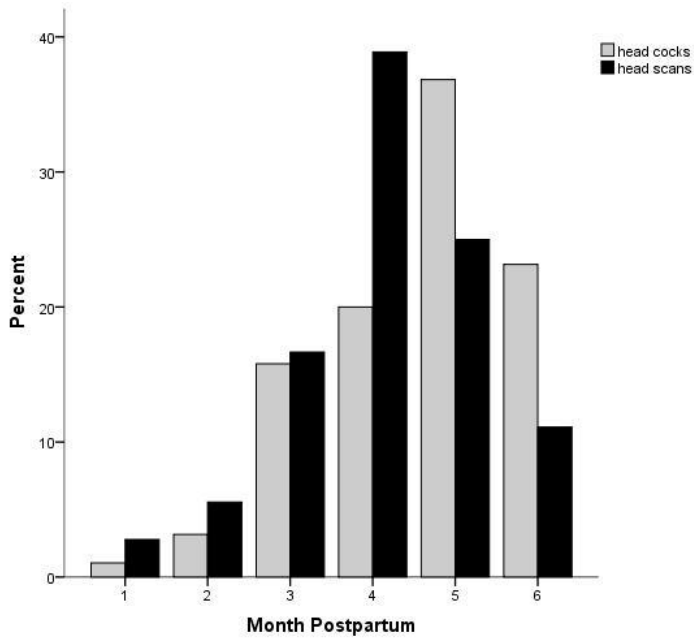


Figure 3. Percent of head cocks and head scans at hydrophone by month postpartum.

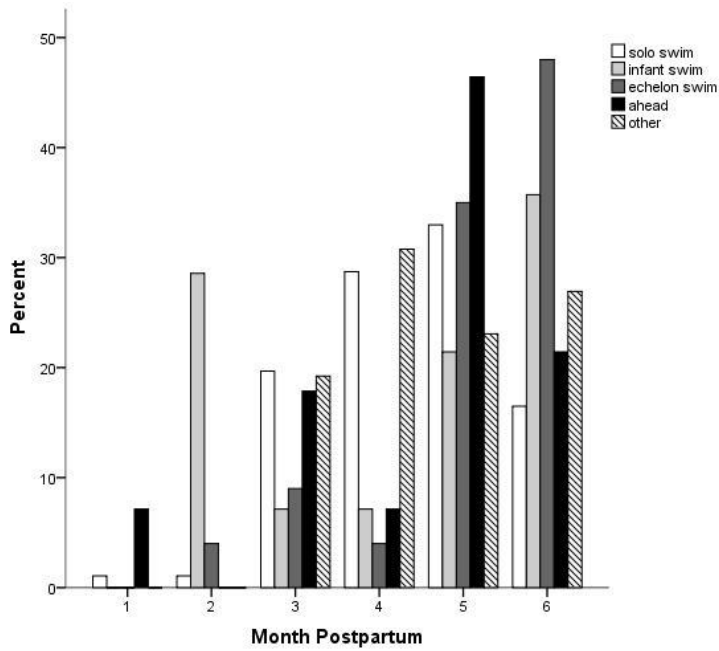


Figure 4. Percent of swims by hydrophone in different positions by month postpartum.

Table 4

Descriptive Statistics for Individual Calves on Measured Parameters

Calf		Click train duration (s)	Clicks per train (f)	Train density (f/ms)	ICI (ms)
BAI	$M \pm SE$	2.01 ± 0.11	98.57 ± 7.03	50.07 ± 2.74	--
CHM ^a	$M \pm SE$	1.92 ± 0.22	128.48 ± 14.24	76.94 ± 9.71	24.58 ± 2.57
HRT	$M \pm SE$	2.06 ± 0.11	122.53 ± 8.93	59.55 ± 2.88	25.29 ± 1.36
CST	$M \pm SE$	2.00 ± 0.13	100.32 ± 8.59	53.78 ± 4.26	26.34 ± 1.97
IND ^a	$M \pm SE$	2.20 ± 0.16	127.59 ± 13.61	57.23 ± 4.52	24.36 ± 2.00
LBU	$M \pm SE$	1.45 ± 0.59	87.57 ± 25.56	128.02 ± 58.19	25.26 ± 10.81

^aDenotes male calves.

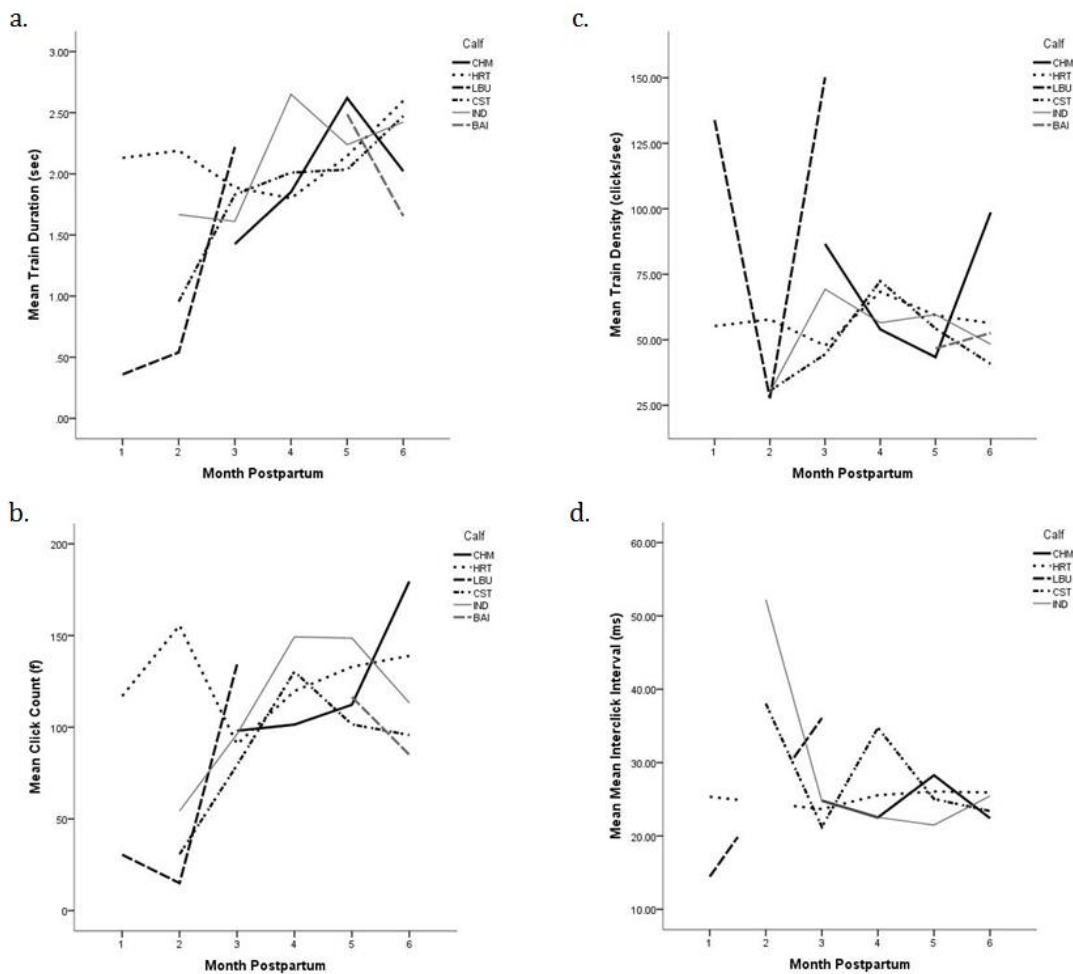


Figure 5. Individual calf responses by month postpartum per measured parameter. Note that the lines begin in the month in which the first identifiable echolocation train produced by each calf was captured. (a) Mean click train duration, (b) Mean click count per train, (c) Mean train density, and (d) Mean ICI per train.

Discussion

Echolocation click train samples were collected over the first six months postpartum from six calves housed with their mothers at the U.S. Navy Marine Mammal Program facility in San Diego, CA. This research represents the most comprehensive and extensive investigation of bottlenose dolphin echolocation ontogeny to date with a total of 361 identified calf click trains recorded and examined, a sizable improvement over previous studies in which echolocation development has been assessed in bottlenose dolphins (Carder & Ridgway, 1983; Favaro et al., 2013; Lindhard, 1988; Reiss, 1988). Earliest calf samples were recorded on day 22 and day 24, which is one week later than the first recording of a sonar-like sound captured by Favaro et al., while other studies recorded the first train at 60 days postpartum (Carder & Ridgway, 1983) and 3 months postpartum (Ricciardi et al., 2003).

Bottlenose dolphin calves appear to develop their ability to echolocate, which may depend on individual differences, in the first month to three months following parturition. Evidence of calf echolocation was not found at birth and no echolocation samples were recorded prior to 3 weeks postpartum. In contrast, Favaro et al. (2013) reported recording individual pulsed signals that had click-like qualities and co-occurred with a whistle-squawk vocalization at 14 days postpartum. However, a click train with the same characteristics as the operational definition used in the current study was not observed until approximately 21 days (Favaro et al., 2013), about the same time frame as the first click train recorded in the current study.

In the first two postpartum months, calves produced the fewest number of trains, the shortest trains (on average), and the trains with the fewest mean number of clicks. The lowest mean train ICI per month from calves also occurred in month 1 and the lowest mean train density per month occurred in month 2. All of these values are lower than previously reported adult characteristics (reviewed by Au, 1993 and Herzing & dos Santos, 2004). The results may be related to the lack of maturation in the echolocation system at birth, which is supported by evidence that fetal and neonatal dolphins have a lower concentration of acoustic fat in the acoustic tissues (Gardner & Varanasi, 2003). It seems plausible that the echolocation sensory system is not fully developed at birth and likely requires a combination of time, physiological maturation, and behavioral experience to attain full adult functionality.

Click Train Characteristics

Train duration. From birth through 5 months postpartum, the mean calf train duration increased steadily. Mean calf duration values then tapered off between the fifth and sixth months. Calves thus produced, on average, longer trains as they aged until the mean duration of those trains approximated the values seen in adults reported in previous studies (Au, 1993). All calves, except for BAI, had longer mean train durations in the last month sampled than in the first month sampled. The exception observed for BAI may have been related to a difference in her developmental timeframe as compared to the other calves. BAI may have exhibited a similar increase in train duration if recordings had continued beyond 6 months of age, which was when all recordings were terminated. Considerable variation around the mean density values per month was apparent throughout the study. Per month ranges in calf train durations, however, increased with every subsequent month possibly indicating that calves were either not in complete control of, or were experimenting with, their click trains as they matured. This increase in per month duration ranges suggests that although calves develop the ability to echolocate fairly early in life, the calves may require a slightly longer period of time to attain a more mature mastery of echolocation.

These results could indicate several different developmental patterns (i.e., maturation of anatomy, experience) in the calves' use of echolocation. The overall increase in mean train duration over time, taken in conjunction with the increase in sample size with age, indicates a development in and more extensive use of echolocation with age. Sousa-Lima, Paglia, and De Fonseca (2002) found that the length of vocalizations in Amazonian manatee (*Trichechus inunguis*) calves also increased with age and argued that longer signals may require more energy to produce. As energy sources are limited for cetacean calves at younger ages (i.e., poor thermoregulation due to a lack of fat and swimming proficiency, Noren & Edwards, 2011; Weihs, 2004), the positive correlation of duration and age may be tied to physiological maturation factors. The decrease in mean train duration after 5 months may reflect the calves' increased proficiency in swimming and thermoregulation, which when combined with a sufficient accumulation of experience with their biosonar may enable calves to use that system to gather information about their environment through a shorter, more efficient click train. The observed decrease in mean train duration could also be indicative of long-term habituation to the hydrophone.

Clicks per train. The number of clicks used by a dolphin to perform a given sonar task is a highly variable parameter, often fluctuating widely and unpredictably from trial to trial (Au, 1993). The range of clicks per train increased steadily across subsequent months before declining somewhat in month 6. As calves aged, they included more clicks in their echolocation trains, which is in accordance with data from bats that suggest a general increase in click rate with age as they develop the ability to pack clicks more closely together (Moss, Redish, Gounden & Kunz 1997; Moss, 1988). All calves except for LBU showed individual two-to-three-month periods of increases in mean clicks per train. Overall significant differences in mean clicks per train between months were not seen, but this may have been related to reduced power. Calf trains contained approximately 115 clicks on average over the study period and more than 85% of trains contained less than 200 clicks.

Overall mean clicks per train were positively correlated with overall mean train durations for the calves. This result is in contrast to some findings with bats (Moss et al., 1997; Moss, 1988) where bat trains decreased in length but increased in click counts with age. As echolocation clicks provide information to the calf about the object it is scanning, a steady increase in the number of clicks per echolocation train is therefore indicative of an increased ability for the calves to gather information about their surrounding environment. This interpretation is supported by the larger number of samples obtained from calves as they aged when sample size is used as an indication of interest in the hydrophone.

Density. Density is a measurement of clicks per second and therefore a combination of click count and train duration. Density appeared similar to ICI, limited by physical factors (e.g., the ability of the physiological system to reset itself to produce another click) and thus less likely to show maturational or developmental variation over time. The mean density values for the calves did not differ between 3 and 6 months, postpartum. More than 90% of trains in both groups fell below 100 clicks/sec, and train density decreased gradually from 3-6 months, supporting the notion that the echolocation sensory system underwent developmental changes as the calves matured. It should be noted that we are referring specifically to clicks per second within echolocation click trains and not other high-repetition-rate vocals (e.g., squawks, burst pulses). It is likely that vocal type must be developed or learned in addition to the maturation of the echolocation sensory system, however, examining other vocal types was outside the scope of this work.

Interclick interval (ICI). Overall mean per train ICI values for the calves ($M = 25.32$ ms) were consistent with the stable ICI of about 27 ms found in wild bottlenose dolphins by Goodson and Mayo (1995). The range of intervals in calves (5.95 ms to 61.93 ms) was, however, considerably smaller than the

ranges seen in wild bottlenose dolphins by Akamatsu, Want, Nakamura, and Wang (1998). Calves in the current study generally showed longer mean ICI values than the calf in the Lindhard (1988) study, a finding possibly reflective of the difference in composition of the nursery environments (i.e., open water vs. concrete habitat). At the end of the Lindhard study (38 weeks postpartum), calf recordings had a mean ICI of 16 ms, a value lower than the smallest mean ICI value per week ($M = 19.29$ ms during week 22) in this study. When compared with values found in non-cetacean animals, Moss et al. (1997) and Moss (1988) found decreases in ICI with age in bats but that finding was not duplicated here. It should be noted, however, that the developmental periods in question for bats occur across days, not months as with dolphins. Bats are considerably smaller animals than dolphins and spend far less time dependent on their mothers for survival, thus shortening the amount of time available for development of their echolocation skills, perhaps compressing trends observed in odontocetes.

Behavioral observations. The absence of echolocation in neonate calves may have an evolutionary advantage. For a time after birth, calves struggle to swim effectively. They breathe in a *head-up* fashion and are often seen in echelon position (alongside and slightly above their mothers) allowing them to slipstream in their mother's bow wave and essentially be towed through the water (Mann & Smuts, 1999; Noren, 2008; Noren & Edwards, 2011; Weihs, 2004). It may indeed take time for calves to develop proper muscle tone and coordination necessary to breathe and swim efficiently thus making neonates vulnerable to predation. If calves also require time to build up the mature fatty acid concentrations in their acoustic window tissues to allow for the proper columnation of echolocation (Gardner & Varanasi, 2003), then echolocation produced as a neonate could be poorly controlled or directed, thus potentially broadcasting the calf's presence and defenselessness to predators. As neonates do not need to forage, the observed onset of *practice foraging* (Mann & Smuts, 1999) near 1 month postpartum corresponds to the appearance of echolocation in this study. A period of echoic silence from neonates while they mature physiologically may therefore be evolutionarily beneficial.

During this period, calves need not be isolated from echolocation and may indeed be passively experiencing the echolocations of their mothers, allomaternal females, or other conspecific members of their social group. Although the outgoing echolocation beam produced by adult animals is narrow and forward-focused (Au, 1993), the reception beam is broader (Moore, 1988) and calves in the common infant or echelon positions may indeed receive echolocation transmitted by their mothers. Such echoic eavesdropping has been proposed between adult Hector's dolphins during foraging bouts (Dawson, 1991) and adult bottlenose dolphins engaged in detection tasks (Xitco & Roitblat, 1996). While maturing, therefore, the calves can procure exposure to one half of the echolocation process (receiving clicks) while mothers can potentially keep their calves safe from predators.

Calf associations and behaviors documented in this study mirror the patterns of other investigations. Calves spent increasingly more time observed apart from their mothers and increasingly less time observed in infant and echelon swim positions with age, as has been previously reported in several studies (e.g., Gubbins, McCowan, Lynn, Hooper, & Reiss, 1999; Hill, Greer, Solangi, & Kuczaj, 2007; Mann & Smuts, 1999). Similar results have been reported for other odontocetes in managed care, such as belugas (Hill, 2009; Hill & Campbell, 2014; Hill, Campbell, Dalton, & Osborn, 2013; Schneider, Schamel, & Noonan, 2003). That dolphins appear to begin to assert their independence at two months postpartum and also began to show large increases in the number of observed echolocation attempts is likely not coincidental. The acquisition of at least a rudimentary ability to echolocate would be crucial to the calf's ability to explore its environment beyond the direction of its mother. Thus, it appears that maturational and developmental components (i.e., efficient swimming ability, breathing and nursing patterns, maternal bonds, acoustic communication through

whistles, and the use of echolocation) come together by about 2 months after birth to allow the calf to begin to operate in its environment with more autonomy.

Unlike previous studies where only one calf was present (e.g., Carder & Ridgway, 1983; Favaro et al., 2013; Lindhard, 1988; Ricciardi et al., 2003), the current study had five calves of similar age with which to interact. In this study and others where calves were housed with peers (Reiss, 1988) or within a larger stable social group (Lindhard, 1988), echolocation was observed earlier (22 days, 2 weeks, and 2 weeks, respectively per previous reference) than in studies where the mother and calf were housed in isolation or where no other calves were present (Carder & Ridgway, 1983 – 2 months; Favaro et al., 2013 – 21 days; Ricciardi et al., 2003 – 3 months). Having other animals, and particularly calves, in their environment may have encouraged the calves to explore their surroundings earlier, more freely and in more detail (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006).

In terms of other behaviors observed during the ontogeny of echolocation, Gould (1975), Brown and Grinnell (1980), and Reiss (1988) noted an early appearance and then disappearance of open-mouth posturing during echolocation in odontocetes and bats. Open mouth posturing was rarely observed in this study, occurring only between the third and fifth months postpartum, well after the 6-week end of open-mouth posturing reported in odontocetes by Reiss (1988). The relatively infrequent appearance of this behavior suggests that open mouth postures are not a critical element in echolocation development. Similarly, the presence of concurrent bubbles during echolocation was almost non-existent in the current sample, similar to research conducted with other delphinid vocalizations (Fripp, 2005). Like open mouth behavior, the presence of concurrent bubbles with echolocation trains was observed rarely. Out of 361 click trains, only two trains co-occurred with bubble streams only and three trains had bubble streams plus a whistle. The rare production of bubble streams in conjunction with echolocation trains appears to disconfirm the assertion that bubble production was a reliable indicator of calf echolocation (Killebrew, Mercado, Herman, & Pack, 2001; Reiss, 1988). Although water turbidity in the bay enclosures could occlude bubble visibility, bubble streams was usually readily visible as the calves were rarely more than 2 m below the surface of the water immediately under the researcher with the hydrophone. It is likely that these bubble streams were coincidental to the echolocation click trains and may have been related to calves learning to manipulate their blow hole as well as mature in their production and use of echolocation clicks.

Conclusion

The current study provides acoustic evidence that echolocation may develop during the first few months of life in correspondence with physiological maturation. Despite intense, repeated attempts to record calf samples, echolocation trains from calves simply were not captured in any large numbers until the third month. At this time, calf echolocation samples increased over 5-fold without any changes in the recording apparatus or research protocol, indicating that time was an influential factor in the appearance of echolocation in calves. However, the results of the study could in fact be a byproduct of the low number of samples obtained from calves in these early months rather than from any true difference in their echolocation parameters. Acoustic recordings were not made 24 hours a day, and the animals had access to a very large area in which to swim during recording sessions. Several factors may have influenced the frequency of samples from an individual calf including age, health, individual interest in the hydrophone, social status of the calf's (e.g., dominant females preventing other subordinate females from approaching the hydrophone), the degree of permissiveness of the calf's mother, and the boldness of the calf for exploring its environment. Habituation to the apparatus within a session by individual calves did not appear to impact the study. Given

the targeted efforts made to record the days immediately following parturition, lack of sampling effort does not seem to be the best explanation for the small sample sizes. Future studies should examine the role of individual differences and the importance of learning in the development of echolocation. It would also be of interest to conduct a similar study in a wild population or in a population that lives in a naturalistic controlled environment similar to the facility in which the current study dolphins resided. Finally, in the current study, the frequency range or intensity of click trains were not measured due to the difficulty in ascertaining the distance at which the animal produced the click train and if the head was pointed directly at the hydrophone for an on-axis recording or if it was off-axis. While some previous studies examined these parameters, all studies faced the same limitations of a reduced frequency recording range and the difficulty in determining on-axis versus off-axis recordings (Carder & Ridgway, 1983; Favaro et al., 2013; Lindhard, 1988; Reiss, 1988). Perhaps future research should compare the parameters of juvenile or adult animals during a free-swim paradigm to a controlled, bite plate testing paradigm to determine the difference between on-axis and off-axis measurements.

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