The University of Southern Mississippi

THE ONTOGENY OF ECHOLOCATION IN THE ATLANTIC BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

by

Jennifer Leigh Hendry

Abstract of a Dissertation

Submitted to the College of Education and Psychology

of The University of Southern Mississippi

in Partial Fulfillment of the Requirements

for the Degree of Doctor of Philosophy

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ABSTRACT

THE ONTOGENY OF ECHOLOCATION IN AN ATLANTIC BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

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This study aimed to expand on previous efforts to evaluate the ontogeny of echolocation in Atlantic bottlenose dolphins (*Tursiops truncatus*). Data consisted of echolocation recordings and concurrent behavioral observations taken from one calf in 2000 and from five additional dolphin calves and their mothers in 2002 housed at the U.S. Naval facility in San Diego, CA. A total of 361 echolocation samples from calves and 187 samples from their mothers were recorded over the first 6 months of the calves' lives. The earliest calf train was recorded at 22 days postpartum and the number of echolocation attempts from calves increased steadily with age. Calf echolocation trains were found to increase in duration and the number of clicks per train with age while train density (clicks/sec) and interclick interval values remained more consistent. Results further implicate the first 2 months of life as essential for the development of echolocation and related behaviors.

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DOLPHIN (*TURSIOPS TRUNCATUS*)

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Approved:

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Director

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Dean, College of Education and Psychology

May 2004

DEDICATION

This final document and the lifetime of learning, living, and loving on which it is built is dedicated to my grandfather, David Hendry, and my grandmother, Henrietta Hendry. It stands in their honor as my response to all those voices who have ever uttered "no, you can't." Thank you, Papa & Nana, for breeding this family strong in your Scottish tenacity. I love and miss you.

ACKNOWLEDGMENTS

I would like to thank the committee chair, Dr. Stan Kuczaj, and the other committee members, Dr. Kathleen Dudzinski, Dr. Dorian Houser, Dr. Tammy Greer, and Dr. John McCoy for their advice and support throughout the duration of this project. I would especially like to thank Dr. Sam Ridgway, Dr. Jim Finneran, Dr. Don Carder, & Dr. Patrick Moore for their encouragement, patience, and, above all, expertise.

Special thanks go to the many animal care and training interns at the U.S. Navy Marine Mammal Program who assisted me in the intricate process of collecting and analyzing the data in this study, and to Erika Putman who allowed me access to their able minds and bodies during their time at the Navy. Another nod of appreciation must go to the trainers and supervisors in the breeding department at the Navy for their patience in working over and around cumbersome pieces of research apparatus, yards of cables and cords, and my perpetual requests for just “5 more minutes.”

Finally, I must profusely thank my incredible family and the most unforgettable friends to be found anywhere on earth for their boisterous and bolstering support. Without their humor, their loyalty, and their love, this research and my part in it would not have been possible.

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CHAPTER I

INTRODUCTION

The following research project aimed to expand on previous efforts to evaluate the ontogeny of echolocation in Atlantic bottlenose dolphins (*Tursiops truncatus*). Such evaluations are scant and often rely on infrequent sampling and small subject pools.

This type of study may, therefore, help to illuminate the mechanisms of sound production in these and related animal species.

Whistles

One of the most investigated facets of dolphin communication is whistles. Dolphins produce tonal (harmonic or pure tone) frequency modulated (showing changes in frequency) 'whistle' sounds. These sounds are defined as sinusoidal (bearing some resemblance to sine waves) sounds of variable length used for communication (Caldwell, Caldwell, & Tyack, 1990) (see Figure 1). Whistles occur either singularly or in a series of 2-10 repetitive elements called

'loops' (Purves & Pilleri, 1983). Dolphins demonstrate flexibility in the production of whistles both through the diversity of their natural repertoires (Sayigh, Williams, Plant, & Wells, 2001) and through more unexpected manifestations, such as vocally mimicking computer-generated tones (Richards, Wolz, & Herman, 1984). Interestingly, a controversy currently exists surrounding the production of whistles by individual identified dolphins. Some researchers (e.g. Caldwell, et al., 1990) believe that each animal produces an individually characteristic and distinctive 'signature whistle,' as first suggested by Caldwell & Caldwell (1965). These individually distinct whistles may function socially in identification among conspecifics and as contact calls between individuals such as mothers and calves (Janik, 2000; Amundin & Mello, 2001; Plesner, McGregor, & Janik, 2001; Priester, Sayigh, & Wells, 2001). Conversely, McCowan and Reiss (1995; 1997; 2001) argue against the formation of an individualized 'signature' whistle. Instead, they argue that dolphins produce a large variety of whistles that change depending on several factors, including social context, and that adult dolphins share predominant whistle types across social groups. In this interpretation, individual dolphins do not produce individual whistles but rather produce individual variations of group whistle types. Individual dolphins, therefore, may use some whistle parameter(s) for identification but not the whistles' contour pattern specifically.

Despite differences in the scientific interpretation for the function of whistles, there have been documented developmental changes in a dolphin's whistle repertoire. Although whistles generally appear in the first few months of life, the development of 'signature' whistles shows considerable variability: an infant's stable 'signature' whistle

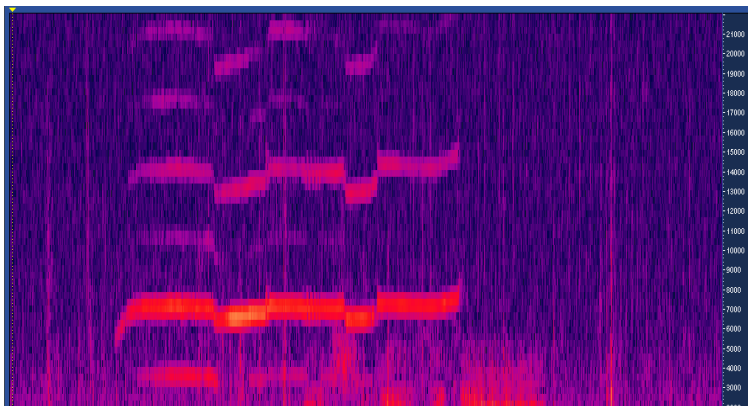

Figure 1. Cool Edit spectrograph (frequency/time) of a bottlenose dolphin whistle. The horizontal red and purple bands represent a whistle. This whistle has one primary frequency band (dark red) with several harmonics (lighter red and purple duplicates of the primary band at secondary frequencies).

may occur between 1.5 and 17 months (Caldwell & Caldwell, 1979). Caldwell & Caldwell also highlight several features of whistles that appear to increase with age including duration (also reported by Morisaka, Shinohara, & Taki, 2001), number of sound loops per whistle, and frequency sweep.

Several researchers have focused their efforts on investigating further the effects of the mother-infant interaction on 'signature' whistle development. Amundin & Mello (2001) found that during the first 15 days of life, the mother dolphin in their study whistled only her 'signature' whistle. This finding suggests that an imprinting process may play a role in the calf's association of its mother's 'signature' whistle with its mother. Other studies present evidence that vocal learning may play a large role in the development of such 'signature' whistles. Janik & Slater (1997, p.59) narrowly define vocal learning as "instances where the vocalizations themselves are modified in form as a result of experience with those of other individuals." Vocalizations generally refer to pressure disturbances, shaped through the modification of internal air spaces that often function in communication. Although influenced by genetic factors (e.g. structural physiology, maturation, etc.), vocal learning by definition reflects the environmental influences of acoustic stimuli. Calves have been reported to develop whistles similar to their mothers, other animals in their social group (Fripp, Owen, Quintana, Buckstaff,

Jankowski, Shapiro, & Tyack, 2001; Tyack, 1997), or even routine non-biological noises (i.e. bridging whistles from trainers) typical to their nursery environments (Miksis, Tyack, & Buck, 2001).

Fripp et al. (2001) found that three of the six calves in their study produced whistles that strongly resembled the whistles of their mothers and three calves produced whistles resembling the whistles of unrelated dolphins. Miksis et al. (2001) determined that the whistles of captive dolphins were significantly shorter and less frequency modulated than whistles recorded from wild dolphins. This finding might suggest that exposure to trainer's whistles, which are far less modulated in frequency than typical dolphin whistles, may influence the course of the captive dolphin's whistle development. In another series of studies, Sayigh and colleagues (Sayigh, Tyack, Wells, Scott, & Irvine, 1995; Sayigh, Tyack, Wells, & Scott, 1990) studied the developing whistles of free-ranging dolphin calves in Sarasota Bay, FL. They found that whistles of male calves more frequently resembled the whistles of their mothers while female calves tended to produce whistles that differed markedly from their mothers. The process of vocal learning during development could account for both findings given the social structure of dolphin adulthood. Males tend to leave the maternal pod and join bachelor groups, making differentiation from their mother less important on a daily basis and identification with the mother crucial on a reproductive basis to prevent inbreeding. Conversely, female calves often remain with their matrilineal pod for extended periods of time making differentiation of high importance. It is important to note, however, that these findings are controversial. Levin, Mello, Blomqvist, & Amundin (2003) found no significant differences based on gender in the signature whistles of male and female calves. Disconfirming evidence also exists from fostering studies that illuminate the potential role of vocal learning in bottlenose dolphin whistle ontogeny. Tyack

(1997) provided an example of a stranded 1-2 month old dolphin calf ("April") foster-raised by a captive female ("Cindy"). Early recordings of April's 'signature' whistles differed markedly from recordings taken at 6-7 months of age where her whistle now closely resembled Cindy's. Experience hearing her foster mother's whistles apparently changed the course of April's own 'signature' whistle development. Thus, even though it is believed that dolphin calves produce whistles from birth (Mello & Amundin, 2001; Caldwell, et al., 1990), the structure of whistles in adulthood may be linked to social factors. However, conclusions regarding the role of vocal learning in whistle ontogeny must be guarded as more evidence is required to elucidate the impacts of genetics, gender and physiological maturation on vocal learning. Regardless, such evidence clearly encouraged a further exploration of changes in other segments of the dolphin's sound production system.

Recently, Killebrew, Mercado, Herman, & Pack (2001) reported on acoustic features of burst-pulse sounds observed in a newborn Atlantic bottlenose dolphin calf. The authors recorded sounds from the calf beginning on the second day postpartum and ending on the fifth day (the calf died the next day). On day 2, the recorded calf sounds consisted entirely of broadband burst-pulses with spectral energies between 0.45 and 9.5 kilohertz (kHz), peaking at 1.7 kHz. Beginning on day 5, the calf's pulses included whistle-like components near the end of the vocalization. The authors found no evidence of echolocation clicks from the calf during the five days of its life. The fact that the calf was unhealthy makes it impossible to determine if the sounds from the calf were normal for a calf that age or a reflection of the calf's illness.

Vocal learning

Vocal learning may play a role in the ontogeny of echolocation as well as the ontogeny of whistles in cetaceans. Current research suggests a communicative role for echolocation in

several, if not all, species (e.g., Dudzinski, Lepper, & Newborough, in preparation; Tyack, 2000; Xitco & Roitblat, 1996; Dawson, 1991; Backus & Schevill, 1966). The data suggest that the acoustic nature of echolocation signals is indeed modifiable with exposure to auditory stimuli. In fact, Caldwell & Caldwell (1972) initially believed that mimicry was possible only in the echoic system, not the whistle system, due to the relative ease with which dolphins could be behaviorally conditioned to mimic phrases such as "happy birthday" and sounds resembling human laughter or singing using click trains.

As discussed previously, vocal learning is only possible if the animal can modify the sound in question in response to auditory signals. Au (1993) reported that bottlenose dolphins produce lower intensity clicks in tanks than in open waters, demonstrating an ability to modify their echoes. Additional support for such modifications comes from reported differences in the echolocation signals from dolphins housed in a biologically noisy environment (Kaneohe Bay, Hawaii) compared to dolphins housed in a relatively quiet biological environment (e.g., San Diego Bay, California) (Au, 1980). Dolphins in Hawaii exposed to higher levels of ambient noise produced higher frequency whistles than did animals in lower ambient noise levels, a response termed the "Lombard effect" (Adret, 1993). Au, Carder, Penner, & Scronce (1985) also demonstrated echolocation shifts in the emissions from beluga whales (*Delphinapterus leucas*) housed in both settings. Beluga peak click frequencies in Kaneohe Bay measured between 100 and 120 kHz while frequencies in San Diego Bay peaked between 40 and 60 kHz. Beluga signal intensities in the same study were up to 18 decibels higher in Hawaii than in California. In another example, Moore & Pawloski (1990) used operant conditioning to induce peak frequency shifts in a bottlenose dolphin, again indicating conscious control of their

echolocation and an ability to modify their echolocation at will. Backus & Schevill (1966) reported echolocation clicks from sperm whales (*Physeter macrocephalus*) that, over time, approximated the ping rate of an echo sounder. Of particular note is the asynchrony of clicks with the sounder when the clicks were first recorded: the click rate became synchronous with the sounder following repeated exposure. More recently, Dudzinski et al. (in preparation) reported that dolphins can voluntarily shift the energy content of their click trains between two frequency bands centered on 70 and 120 kHz. Voluntary variations in click rate in both frequency bands were also noted. Taken on the whole, these findings suggest adaptive control of echolocation in cetacean species in response to changes in auditory conditions and stimuli, providing one requisite component of vocal learning.

Echolocation

Echolocation, also called *biosonar*, is a dolphin's (and other cetacean and non-cetacean species) ability to interpret information in the returning echoes of ultrasonic transmissions the animals produced themselves. Biosonar, first suggested in dolphins by McBride (1956), utilizes a series of pressure waves emitted through the dolphin's melon. Those waves then reflect off of objects in the animal's environment and the resulting echoes are received through fat bodies which transmit sound from the characteristically thin pan bones in the lower jaw to the tympanoperiotic bone (Brill, Sevenich, Sullivan, Sustman, & Witt, 1988; Brill, Moore, & Dankiewicz, 2001). Finally, the information in these echoes is transmitted through the inner ear to the brain where it is neurologically processed and used by the animal to identify, locate, and categorize environmental objects such as food items, obstacles, conspecifics, et cetera. However, despite an impressive and growing body of work, echolocation is not fully

understood. How the animals use such a system to interpret their environment remains enigmatic. The current research project was designed to more carefully investigate the ontogeny of echolocation in bottlenose dolphin calves by recording echolocation samples when animals voluntarily oriented at a research hydrophone[1]. Specifically, this project longitudinally investigated the development of echolocation, focusing on an evaluation of the sample variables (click train duration, number of clicks per train, interclick interval (ICI), and density in clicks/sec) produced when the dolphin calves echolocate.

Several similar but distinct definitions of 'clicks' and 'click trains' (i.e. trains) appear in the scientific vernacular, described somewhat differently by individual researchers rather than universally by the scientific community (sample clicks shown in Figure 2). For example, Au (1997) descriptively classified echolocation clicks as short duration (50-80 microseconds, μsec), high intensity (pressure ratio in decibels, $dB = 20 \log (pressure_1/pressure_2)$), broadband (3-dB, or half power, bandwidths of 20-60 kHz), exponentially decaying pulses with peak frequencies between 30 and 130 kHz. Alternatively, Purves & Pilleri (1983) defined clicks more subjectively as "signals which can be broken up into a series of single pulses" (p. 99) and Houser, Helweg, & Moore (1999) chose "trains or sequences of impulsive sounds" (p. 1579). Various other definitions appear in Table 1.

Without a unifying definition, this study faced the immediate problem of interpreting current data against the data of other studies. For example, while I would have liked to

[1] Because animals in this study were free-swimming, I was not able to positively state whether the entirety of each echolocation train was captured on the recordings. Animals changed both body positions and head positions in a dynamic and fluid way, introducing the possibility that their echolocations had begun prior to their orientations or continued when the orientation was complete. Recorded echolocation bouts may thus have been artificially delimited by the period of orientation. Referring to samples as "trains," therefore, may be inaccurate. Although I acknowledge this possible discrepancy, for the sake of comprehension and brevity, the term "train" will be used here to describe animal orientations.

investigate how the waveforms of the clicks themselves may change over time, the variety of click definitions made it somewhat difficult to determine if clicks that appeared different were due to the age of the animal, the acoustics of their nursery environment, or some aspect of the recording procedure. Underwater acoustical properties rather than age-related variables may also account for any observed variability in recorded clicks (e.g. Au, 1993). For example, distortions frequently result from the free-swimming animals not being 'on-axis' with the static hydrophone. Such misaligned beam axes sometimes occur when an animal cocks their head as they pass the hydrophone. Clicks recorded in these situations may appear elongated and/or may decrease in amplitude (Au, 1993). An off-axis orientation with respect to the hydrophone also prevents the calculation of the 'source level' (the sound pressure 1 m from the source recorded on the acoustic axis re @ 1 μPa) of the clicks (Rasmussen, Miller, & Au, 2002). The likelihood that some clicks recorded from free-swimming animals are on-axis can be increased by deploying multiple-hydrophone arrays (e.g. Rasmussen, et al., 2002). Financial constraints prevented the use of such an array in this study.

The first two echolocation parameters of interest in this study were train duration and clicks per train. These two structure variables have been analyzed in previous studies of click trains collected from free-swimming cetaceans such as the 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). This extremely short duration allows the signal to maintain its integrity from emission to target with a reduced risk of reflection off of acoustic boundaries (i.e. the surface or the bottom). The short signal duration leaves the receiver open to echoes, eliminating the danger of beginning to receive an echo while still transmitting the signal. 'Duration' can describe the

length of a single click or, as it is used in this document, the length of a train (clicks emitted in discrete sets or series). The number of clicks used by a dolphin to perform a given sonar task varies widely, often fluctuating unpredictably from trial to trial (Au, 1993). No cause for this fluctuation has been ascertained and more research is called for. An evaluation of the ontogeny of clicks per train will thus add to the body of knowledge surrounding this parameter.

The two evaluations of the click repetition rate of interest to this study were train density and ICI. Train density was defined as the number of clicks emitted in a second within a train. ICI was defined as 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). These intervals often change from click to click, especially if the animal is moving as the train is being emitted (Au, Floyd, Penner, & Murchison, 1974). The authors argued that the amount of movement in the dolphins, however, was too small to account for the variability in successive click intervals, indicating that dolphins optimize their click intervals to match the acoustic task at hand. Studies of free-swimming dolphins indicate that dolphins generally do not emit a new click before the previous click has returned from its target (e.g. Johnson, 1967; Morozov, Akapiam, Burdin, Zaitseva, & Solovykh, 1972; Evans & Powell, 1967; Au, Floyd, Penner, & Murchison, 1974). Dolphins thus emit clicks slower than the two-way transit time required for a click to leave the animal, encounter a target, and return to the animal (Au, 1993). Continual modification in the ICI as the animal moves in on a target while still exceeding the two-way transit time indicates that dolphins have a certain amount of control over their ICI in adulthood. ICI was also evaluated (via a single hydrophone) in free-ranging baiji (*Lipotes vexillifer*), finless porpoise (*Neophocaena*

phocaenoides), and bottlenose dolphins (Akamatsu, Wang, Nakamura, & Wang, 1998). In an open ocean environment, click intervals from bottlenose dolphins were observed up to 200 ms but successive intervals were often under 20 ms. In concrete tanks, intervals were noticeably shorter (e.g. 4-6 ms), again indicating adaptability in ICI.

The dolphin brain is specialized for the rapid processing of auditory stimuli and the midbrain in particular is specialized for processing ultrasonic, very short, closely spaced sounds like echolocation (Ridgway, 1990). Arguably, "much of the hypertrophy of the dolphin auditory system—and perhaps of the entire cerebrum—results from the animal's need for great precision and speed in processing sound" (Ridgway, 1990, p. 92). Several studies of ICI support the notion of a processing lag time, defined as the time difference between the ICI and the two-way transit time (Au, 1993). In this view, dolphins would neurologically process the incoming click prior to emitting the next click, thus accounting for ICI values that exceed the two-way transit time to target. Au (1993) reports a suggested processing time between 19 and 45 ms for distant (>0.4 m) targets and 2.5 ms for very close (<0.4 m) targets (Evans & Powell, 1967). A critical interval, defined as the time frame where two acoustic events become perceived as one, has been identified in dolphins (Moore, Hall, Friedl, & Nachtigall, 1984). In a backward masking task, the dolphin's ability to detect an object echoically dropped below a 70% detection threshold at 265 μsec and to chance levels when the masking delay reached 100 μsec. As the minimum two-way transit time for a click to be emitted, travel to the end of the rostrum, and return is approximately 500 μsec, the dolphin's ability to discriminate clicks at shorter intervals likely functions in the analysis of within-echo factors rather than in determining the distance to a target (Moore et al., 1984). The continual interest in evaluations of ICI under various circumstances prompted the inclusion of the variable in this investigation.

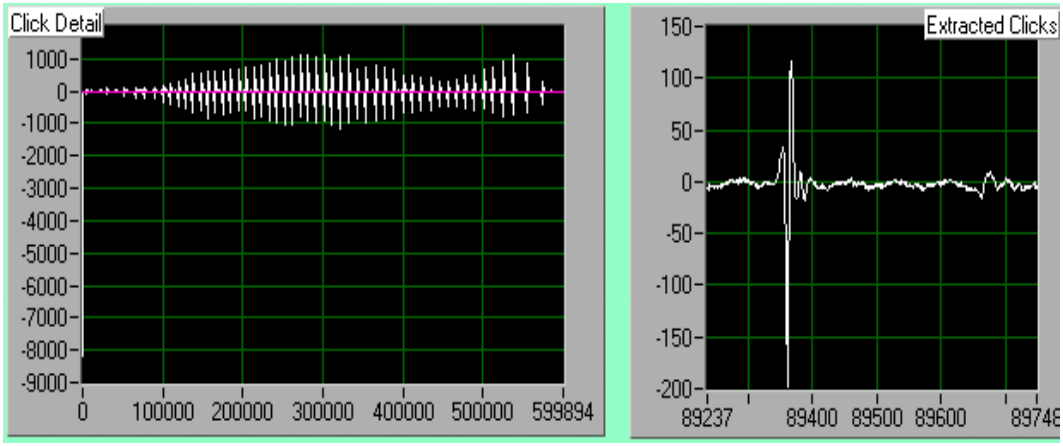

Figure 2. Computerized image (relative amplitude/relative time in computer sample points) of an echolocation click train (left) and the first isolated click from that train (right), recorded September 11, 2000.

Echolocation ontogeny

Although more work exists covering the development and function of other sounds in a dolphin's repertoire, minimal research exists on the ontogeny of echolocation. A comprehensive understanding of echolocation can be enhanced through an examination of how echolocation develops. Only four previous studies, representing a total of five calves between them, have previously evaluated the neonatal appearance of echolocation. In the first study of its kind, Carder & Ridgway (1983) observed the apparent production

Table 1. Click and click train definitions

Definition	*Source*
Clicks	
A broad frequency sound of short duration	Berta & Sumich, 1999
Short, broad spectrum burst-pulses	Harrison & Bryden (Eds.), 1988
Very short sonar pulses	Cahill, 2000
Directional, forward-projecting, brief, pulsed sounds of high intensity and frequency	Richardson, Greene, Malme, & Thomson, 1995, p. 181
Series of broadband pulses	Andrè & Kamminga, 2000, p. 163
Click trains	
A rapid series of three of more pulsed noises, each of which resembles a single-frequency chirp, or "tsk, tsk, tsk."	Adler, 1996
Click trains are short pulsed vocalizations of high and wide-band frequency that are used to	Cahill, 2000

investigate objects or search for fish

of high-frequency sounds from a 60-day old calf in conjunction with the head scanning motions noted both in Reiss' (1988) study and in the behaviors of echolocating adult dolphins. Although burst-pulse sounds and whistles were heard soon after birth, clicks were not noticed until the calf was 2 months old. The authors only recorded seven click trains from the calf, reporting peak frequencies from 33-120 kHz with 3-dB bandwidths of 28-81 kHz. The authors make no mention of attempts to determine whether clicks were recorded on the maximum response axis.

Reiss (1988) also attempted to document the ontogeny of echolocation through the systematic observation and recording of both non-vocal and vocal behaviors in two captive male bottlenose dolphins. Between 6 and 9 days after birth, both animals produced a variety of burst-pulse sounds while holding their mouths open, a characteristic that disappeared by the sixth week postpartum. Unfortunately, Reiss provided no information describing how often this open-mouth posture occurred during this time period. This omission makes it impossible to evaluate the specific dynamics of this postural change with age (e.g. if the open mouth behavior was constant or intermittent at younger ages, etc.). The sounds produced by the calves contained click-like components but exhibited a longer duration (20-40 ms) and remained lower in frequency than typical adult clicks.

At approximately two weeks postpartum, both animals emitted shorter duration (1 ms) but consistently low frequency clicks. The calves also began to exhibit head scanning motions in conjunction with echolocation sounds. Finally, by days 35-38 postpartum, the recorded

signals of both animals were reported as indistinguishable from adult clicks. It must be noted, however, that Reiss' had technical and study design limitations. The equipment used in the study only differentiated the peak frequencies of sounds below 16 kHz. Above this threshold, sounds could only be categorized as "above 16 kHz." As noted earlier, adult echolocation clicks show peak frequencies between 30-130 kHz, well outside the recorded range of Reiss (1988). As a result, Reiss' study is limited to these relatively low frequency clicks. Secondly, researchers experienced some difficulty determining which animal emitted a given signal. Reiss reportedly identified the echolocating animal partly by which individual produced air bubbles. Unfortunately, although this practice is still used in some free-swimming acoustic sampling studies (e.g. Killebrew, et al., 2001), air bubble production is not a requisite behavior for click production and thus does not represent a viable echolocation indicator. Finally, clicks were recorded from free-swimming animals, making it difficult to determine if clicks were on-axis with the hydrophone. As discussed previously, off-axis clicks show distortions that affect variables such as amplitude and duration. Therefore, results concerning click durations reported in Reiss may be of limited use in identifying developmental stages of click production.

Lindhard (1988) recorded echolocations from a captive bottlenose dolphin calf, "Venus," at 2, 7, and 38 weeks of age. During Venus' first recorded train (at 2 weeks) the click interval varied between 10 and 70 ms through the first 80 clicks, decreasing to roughly 2ms for the last 200-300 clicks. At 7 weeks postpartum, Venus emitted a train with click intervals varying from 6 ms to nearly 1 sec. Finally, at 38 weeks postpartum, recordings of Venus' click trains had a mean ICI of 16 ms. The observed variation in click interval indicates modification of the echolocation emissions over time but does not identify the source of that modification. Lindhard

could not determine if the observed variation in click interval stemmed from maturational factors (i.e. physiological development), instrumentation issues (observed variability may have been due to the recording system or apparatus rather than biological factors), or environmental conditions such as enclosure type or the complexity of available stimuli. For example, an environment with more physically complex enrichment devices such as toys, rock outcroppings, or other animals, might induce more complex echolocations than a simple round concrete tank with no such objects. Furthermore, Lindhard acknowledged difficulty in identifying the animals in the recordings due to the housing arrangement. The calf was housed with its mother and five other dolphins and the shape of the enclosure did not allow for the separation of individual animals. Lindhard could not completely discount the other animals as the source of some of his recordings. Animals in this study were free-swimming, preventing assurances of on-axis click recordings and potentially altering the accurateness of the study's findings concerning ICI. Finally, Lindhard made these observations 16 years ago which allowed for possible instrumentation limitations including recording quality, recording media (i.e. reel to reel tape vs. compact disc) and frequency range limitations.

Finally, and most recently, Ricciardi, Azzali, & Manoukian (2003) presented a poster at the 2003 European Cetacean Society (ECS) conference discussing the development of sonar signals in a calf housed in Verona, Italy. The calf and its mother were isolated from other animals during the 6 month study. The data consists of one hour ethogram observations 2 days a week and 2 hours of acoustic recordings 3 days a month. Authors report clicks from the calf approximately 3 months postpartum but did not see bi-modal clicks in the calf until 5 months of age. Some behavioral correlates such as increased interest in exploring its environment were also reported.

These four studies suggest some possible behavioral patterns in a calf's initial development of echolocation abilities. There is evidence for echolocation shortly (i.e. within 2 weeks) after birth, some indications of changes in the length of time between emitted clicks within a train as the animal ages (note caveats above), and changes in other components such as signal frequency (if clicks are indeed on-axis) and train duration. Behaviors such as head scanning motions, open-mouth postures, and an increased frequency of environmental exploration were also noted. However, these findings are based on a small number of calves and a limited number of observations. The present study, therefore, sought to expand on these findings and provide additional information concerning the development of echolocation in young dolphins.

Echolocation Ontogeny in Other Species

Other Cetaceans

The ontogeny of echolocation in other cetacean species has also been studied. Watkins, Moore, Clark & Dalheim (1988) offered a preliminary investigation of the development of click sounds in sperm whales. They made recordings of four stranded calves (animals who washed or ran themselves ashore and were held in captivity for short periods prior to death or release) and compared the recordings to those made of larger calves free-swimming in natural settings. Sperm whales make a variety of click-type sounds including 'usual clicks' (series of click sounds with relatively stable inter click intervals of .5-2.0 sec made during foraging bouts), 'slow clicks' (clicks with an extended inter click interval made only by males), and 'codas' (a precise rhythm found in group-specific, repeated click series lasting .5-1.5 sec) (Tyack, 2000). Though animals

of all sizes in the Watkins et al. study made "typical" sperm whale sounds, the smaller calves appeared to produce sounds with noisy, tonal components resulting in improperly formed clicks. Furthermore, the appearance of patterns in the click sequences appeared to increase as a function of calf size (and, accordingly, with calf age). However, the results of this study must be interpreted with caution. The signals of the four stranded animals were obtained under extraordinarily stressful conditions (i.e. strandings). Animals that strand usually are injured or ill and can experience disorientation as a result of their injury or illness (Klinowska, 1994). Thus, these signals may not serve as a valid comparison against the free-swimming, non-stressed sample animals. This investigation of sperm whales again faces the off-axis recording problems inherent in the analysis of free-swimming animals, calling into question the conclusions of improperly formed clicks.

Madsen, Carder, Mohl, & Ridgway (2003) also discuss neonate sound production in two sperm whale calves. One male calf stranded in Texas in 1989 and the second female whale stranded in Hawaii in 2001. The female subsequently died while undergoing rehabilitation and no disposition was given for the male calf. Again, differences from general adult norms were observed. The clicks of the neonates were low in directionality, of long duration (2-12 ms), and of low frequency (centroid frequency 300-1700 Hz). Directionality was determined when sound pressure levels registered 4-8 dB higher directly in front of the animal then when placed laterally to the eye for both calves. Calves echolocated in short trains but did not show the stereotyped, repetitive click patterns reported for adult codas. The authors further hypothesize that although the low frequency and long duration of the clicks make them poor candidates for echolocation, these features would be more suited to interspecific communication and may serve to convey information between calf and mother or calf and an allomaternal female. Madsen et al. drew

parallels to the Watkins et al. (1988) study by finding similar click properties in the recordings from the calves in both studies. Frequency and duration findings also parallel findings in the Reiss (1988) investigations with Atlantic bottlenose dolphins. Madsen et al. correctly notes, however, that these results should be taken cautiously given that the animals were recorded in less than ideal acoustic surroundings and likely were in poor health.

Another investigation of sound production ontogeny in a toothed whale species is Bowles, Young, and Asper's (1988) discussion of stereotyped calls and echolocation in a killer whale (*Orcinus orca*) calf. Recordings were made over 3-day periods at each of three ages: 12, 255, and 396 days old. During the first recording session, the calf repeatedly passed the hydrophone in isolation (i.e. not with the mother) but showed no evidence of interest in the object. The calf did not orient at or approach the hydrophone. Echolocation clicks were not detected until the second recording session (beginning at 255 days postpartum) and accompanied the animal's heightened interest in the hydrophone when compared to the first recording session. Peak frequencies of clicks at this stage ranged from 10 to 17 kHz. The authors described the clicks as resembling the pulses of adult animals. Similar to bottlenose dolphin calves, the killer whale calf employed a head scanning motion while investigating the hydrophone. Unfortunately, the time span between the first and second recordings diminishes the strength of any conclusions concerning the development of echolocation in this species given that we cannot determine how early this calf began to echolocate. This study also contends with off-axis click concerns.

Most recently, Vergara & Barrett-Lennard (2003) reported on the vocal development of a beluga whale calf born at the Vancouver Aquarium Marine Science Centre. Unlike reports of

dolphin calves, the beluga calf emitted low-frequency click trains within 12 hours of birth but did not begin emitting whistles until 4 weeks postpartum. The structures of the calf's click trains were observed to change with age as peak intensity increased and ICI decreased.

Non-Cetacean Species

Cetaceans do not represent the only extant order known to use biosonar to interpret their environment. Au (1993) estimates that as many as three or four times as many scientists study the echolocation abilities of bats as those of dolphins. A larger body of work exists, therefore, regarding the ontogeny of echolocation in bat species than in cetaceans. Griffin (1958) hypothesized that scientists could follow the development of adult bats' characteristic frequency-modulated (FM) pulses from the disorderly, harmonic-rich signals emitted by young animals. Bat infants vocalize on the day of their birth. Laboratory research demonstrates that the ability to do so is not only innate but resistant to interference factors such as juvenile isolation from adult calls and exposure to adults with surgically altered vocal folds (Gould, 1975). Several species, including big brown bats (*Eptesicus fuscus*) and little brown bats (*Myotis lucifugus*) produce lower frequency echolocation sounds as juveniles than they do as mature adults (Masters, Raver, & Kazial, 1995; Moss, Redish, Gounden, & Kunz, 1997). Other species (e.g. greater horseshoe bats, *Rhinolophus ferrumeguinum*) show a curvilinear relationship between age and tonal frequency (Jones & Ransome, 1993). These bats emit low frequency calls in their first year, reach their highest frequencies in the third year, and then decrease again as animals age past their tenth year. While the observed changes in both species of brown bats could be due to maturation, changes in the greater horseshoe bat provide the strongest evidence for vocal learning. As young horseshoe bats begin to hunt, both males and

females produce echolocation signals with a frequency that is strongly correlated with the echolocation frequency of their mother. Young with mothers over five years of age produce echolocation clicks lower in frequency than those born to females under five years of age, suggesting that exposure to maternal echolocation affects the frequency of the young's echolocation signals.

In general, bats increase their click repetition rate and decrease their click train duration with age (Moss et al, 1997; Moss, 1988). Duration decreased dramatically during the first post-natal week (from a mean of 10 ms in the first few days to 4 ms by 4-6 days), and then decreased to roughly 2 ms by 9 days. The click repetition rate increased with age primarily due to decreases in the inter click interval, allowing the bats to pack their clicks more closely together. However, one study found no detectable relationship of age to differences in echolocation signals in microchiropteran bats (*Pipistrellus pipistrellus*) (Jones, Hughes, & Rayner, 1991). Therefore, in all but one studied species, developmental changes were detected in the production of echolocation signals in bats. Although adult bats emit their sonar signals through their nasal passages, neonates apparently show a tendency to begin emitting signals through their mouths and shift to the nasal pathway with age. Gould (1975), for example, found that although adult phyllostomatid bats emit low intensity nasal sounds, neonatal phyllostomatid bats emitted relatively high intensity oral signals. Brown & Grinnell (1980) further noted reports of an intermittent combination of both nasal and oral pathways during the same pulse for bats under one week old. This shift results from a physiological closing of the laryngo-nasal junction as these bats mature, thus allowing airflow either through the nose or mouth but not both simultaneously (Matsumura, 1979).

Physiological maturation

Some evidence indicates that cetacean sensory systems undergo developmental modifications. 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 fat is nicknamed acoustic fat and is also present inside mandibular bony tissues which are anatomically considered the acoustic window for sound reception (Au, 1993). Gardner & Varanasi (2003) report 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 the cetacean acoustic system is not fully developed at birth but rather matures physiologically over time. In another example of sensory and anatomical maturation, Pryor (1990) pointed out that although newborn dolphin calves possess taste buds on their tongues, these buds disappear in the first few months of life. Pryor (1990) and Mann & Smuts (1999) also note that vibrissae, or mechanoreceptive sensory hairs, often found on neonatal cetaceans vanish shortly (i.e. within 3-4 days) after birth. Such changes could be due to modifications of the sensory system during development or could simply be physical manifestations of evolutionary relics useful to the organism in the past but that are no longer adaptively relevant. Finally, changes in dolphin hearing have been noted with advanced age, most notably in males. Brill et al. (2001) report high frequency hearing losses (reduced sensitivity above 55 kHz in both ears) in a 33 year old male captive dolphin. Although the

source of the loss could not be conclusively proven, one explanation is a form of age-related hearing analogous to presbycusis in humans. Again, these indications of maturational changes in sensory systems prompted my inquiry into the development of the echolocation system.

The Current Study

The current study sought to identify any components of echolocation that are fully developed at the beginning of the study period and those that appeared or changed as the age of the study animals increased. Studies of bottlenose dolphin calves have demonstrated that activities like respiration and swimming technique improve as newborn calves mature (Mann & Smuts, 1999). For several reasons, I suspected that the same findings will be true for echolocation. First, echolocating animals such as bats appear to modify both their behaviors during signal emission and the signals themselves as they age, although Brown & Grinnell (1980) noted that research has yet to assess the role of learning versus maturation in such ontogenic changes. Second, although such reports remain primarily anecdotal, there seems to be a reduction in open mouth postures during echolocation both in bats and odontocetes as individuals of each order age (Reiss, 1988; Brown & Grinnell, 1980).

The current study aimed to investigate the ontogeny of certain features of click trains produced by bottlenose dolphins. I specifically analyzed echolocation samples from calves and their mothers for train duration, clicks per train, train density, and ICI. I did not have specific *a priori* predictions for the study variables due primarily to the exploratory nature of the project. Several hypotheses pertaining to each variable, however, were considered possibilities:

1) Click train duration (sec): Train duration was defined as the span of time between the visually determined onset of the first click in a train and the termination of the last

click in a train. The length of recorded echolocation samples may increase over time as the calves experiment with emitting signals and begin to explore their environment in more echoic detail. Alternately, train duration may decrease as the animal acquires a greater degree of skill with click production and interpretation of the returning echoes or as animals habituate to the stimulus.

2) Clicks per train: Clicks per train was operationally defined as the number of individual positive click peaks within an identified train. The number of clicks per train could also justifiably increase or decrease with age. An increase might signify the calves' intensified interest in scanning the object for fine detail. A decrease in the number of clicks per train, however, would again support the hypothesis that the animal is attaining a competence with echolocation that allows it to gain sufficient information with fewer clicks. Habituation could again account for an observed decrease in click count with age.
3) Train density (clicks/sec): Train density represented the clicks per train divided by the train duration (clicks/sec). Because train density is dependent on both clicks per train and train duration, it could increase or decrease systematically over time with any of the hypothesized fluctuations in either of those variables.
4) ICI (ms): ICI is measured as the time span between the peaks of successive pressure spikes (clicks) in a click train. Modification with age could result in a decreased ICI (as animals venture closer to the object) or an increased ICI (as animals habituate to the object and scan it from farther distances). With maturation, a decreased ICI with age could indicate developing echolocation proficiency. Animals may become able to produce clicks more closely together, thus decreasing the interval. Conversely, the

animal could come to comprehend more information from fewer clicks, thus producing fewer clicks per train and perhaps increasing the interval between them.

5) Behavioral correlates: The interest in other behaviors surrounding the ontogeny of echolocation represents a preliminary investigation. I held few specific hypotheses concerning how behaviors would change with the animals' age. If dolphin calves develop like young bats, I would expect to see an appearance and subsequent diminishing of open mouth posturing accompanied by an appearance and subsequent increase in the frequency of head motions toward the hydrophone. Hypothetically, as discussed above, animals could increase their proximity to the hydrophone with repeated exposures or choose to avoid the hydrophone possibly due to fear or a lack of interest. Head motions toward the hydrophone should increase with age as should independence from the calf's mother.

Developmental changes in the early months could result from a variety of factors including physiological maturation, observational learning, or vocal learning. Later in life, echolocation is likely to come under more conscious control and so vary as a function of the task at hand. However, failing to detect significant developmental differences in a study variable is also open to a variety of interpretations. For instance, developmental changes may have occurred but not been observed due to sampling variables or may be innate at parturition. One pertinent influence on our study variables is the psychological process of habituation.

Habituation

Some of the observed trends in the variables for this study could potentially be due to habituation, a widespread form of learning revealed by a change in behavior due to experience, not fatigue (Flaherty, 1985). More specifically, habituation is defined as "the relatively

persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Ramirez, 1999, pg. 542) or "a progressive decrease in the vigor of an elicited response that may occur with repeated presentations of the eliciting stimulus" (Domjan, 2000). Habituation is common in prenatal, newborn and young children (e.g. Rubenstein, Kalakanis, & Langlois, 1999; Adamson, 1995; Hunter & Ames, 1988), and generally indicates a diminished sensory interest in stimuli as those stimuli become familiar. Furthermore, habituation is currently recognized as an important component of adaptation that allows an animal to function in its environment by properly metering its attention (Hurley & Holmes, 1998). In order to survive, animals must learn what stimuli warrant their attention and what stimuli can be safely ignored (Flaherty, 1985). Habituation has also been used extensively in animal research to test sensory development and discrimination in audition (e.g. Masataka, 1985; Kerr, Ostapoff, & Rubel, 1979), vision (e.g. Swartz, 1983), taste (e.g. Domjan, 1976), and smell (e.g. Swaisgood, Lindburg, & Zhou, 1999). These studies often make use of the orienting response, an organism's natural tendency to turn toward and orient on a novel stimulus like a sound, photograph, or object. In this study, I exposed subjects repeatedly to an identical stimulus, the recording hydrophone. An observed waning of the orienting response due to habituation would reduce the number, duration, and/or intensity of scans a dolphin would make of the hydrophone. Furthermore, habituation is specific to a particular stimulus, in our case the hydrophone, that the subject is not reinforced for investigating but which it finds at least initially interesting. Absent changes in the stimulus (e.g. location, visual properties, echoic properties, etc.) the initial interest may diminish overtime. In this case, I could not change the properties of the stimulus because that could change how the animal perceives that stimulus thus altering its echolocation. Such a confound would impair our ability to determine if changes observed over time were due to

developmental influences or stimulus changes. Tests for habituation were therefore applied throughout this study.

CHAPTER II

METHODS

Subjects

Many of the factors involved in housing captive bottlenose dolphins greatly reduce their availability for scientific research. Dolphins are resource intensive to maintain, require large aquatic enclosures and multiple-animal social groups, and enjoy a great deal of protection via the Marine Mammal Protection Act (1972) and other legislative directives (see Appendix A for IACUC research project approval). These factors often lead to unusually small sample sizes (e.g. Houser, et al., 1999; Au, Penner, & Turl, 1988; Richards, et al., 1984). This study expanded on data taken from one calf and her mother in 2000 (Hendry, 2002) by analyzing data from five additional dolphin calves and their mothers housed at the U.S. Naval facility in San Diego, CA (see Table 2). These mother/calf pairs represent all of the live births at the Navy in their given years.

Table 2. Study subjects

Calf Name	Date of Birth	Calf Gender	Maternal Name	Paternal Name
Bailey	4/30/00	Female	Snapper	Unknown
Little Opai	5/31/02	Male	Opai	Jake
Little Shasta	6/07/02	Female	Shasta	Nihoa
Little Blue	6/10/02*	Female	Blue	Makai

Little Kolohe	6/16/02	Female	Kolohe	Nihoa
Little April	6/18/02	Male	April	Nihoa

*Little Blue died on 9/7/02 due to complications from pneumonia.

The NMMP facility features 30'x30' and 30'x60' open-ocean pens separated by nets and net gates strung below floating wooden docks. During recording sessions, researchers positioned themselves on the docks surrounding the pool(s) containing animals of interest, giving them an unobscured view of the animals' interaction with the research apparatus. I chose the recording location to insure that pens directly behind the recording apparatus should be free of other animals to minimize the chance of inadvertently sampling the wrong animal. During recording sessions, 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 recording apparatus. Recording sessions (1-4 hours/day) were repeatedly attempted 5-days a week from the date of birth until the 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 adult female, etc.), I endeavored to obtain samples from each animal, and most certainly each calf, in every given week.

Data Collection

Echolocation

A single Bruel & Kjaer (B&K) 8103 hydrophone (sensitivity ±2 dB over the frequency range *re:* 1 V/μPa) was used to collect samples of the animals' echolocation clicks. The hydrophone was fed down a 6' PVC pipe at a 90-degree angle from the dock into the water, protruding below the end of the pipe by approximately 3". 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 and 300 kHz with a 6 dB/octave rolloff, Gain x2), and an Optimus power amplifier (see Figure 3). 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 was acquired as 12-bit binary signals and saved in a 16-bit format on CD-ROMs. To maximize the chance of recording calf echolocation attempts at the earliest possible age, echolocation was recorded on two different channels. The first channel, a "mother" channel designed to allow the capture of the full range of adult clicks, had a +/- 10V range. The second channel had a much smaller range (+/- 0.5V) to allow the capture of smaller amplitude clicks that may be associated with neonatal and juvenile animals. The addition of this second "calf" channel sought to help identify echolocation attempts from calves at significantly younger ages than in the previous pilot study.

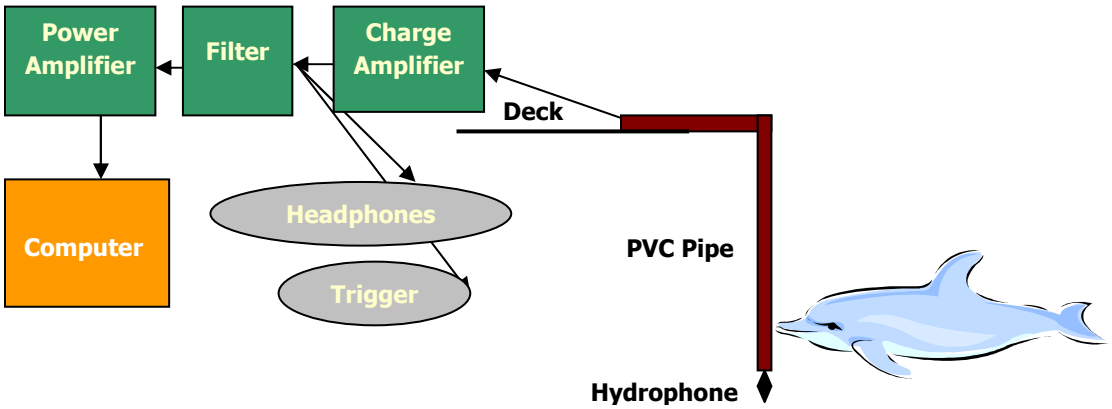

Figure 3. Recording apparatus schematic

Recordings began and ended on a trigger-cue from the on-scene researcher. As the target 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 the capture of specific instances of echolocation and avoided extensive recordings containing no

echolocation clicks. Specifically, the use of trigger recordings increased the likelihood that the researcher captured trains only from targeted animals observed proximally (within 1-4 m) to the hydrophone rather than indiscriminately collecting trains from any animal present in the enclosure[2]. While collecting the underwater recordings, the on-scene researcher wore a microphone headset also connected to the computer to allow for the narration of events surrounding the recording. This narration was simultaneously sampled on another channel on the same DAQ board as the hydrophone recordings.

Concurrent Behaviors

A final improvement over the original pilot study was the addition of concurrent behavioral analysis. While the primary researcher was focused on collecting the echolocation samples and providing the vocal narration, an assisting observer recorded concurrent behavioral data on an Echolocation Recording Behavioral Observations (ERBO) sheet as both a supplement to and a written record of the vocal narration of each echolocation event (see Appendix B for sample ERBO form). The ERBO sheet was used to document the environment surrounding the recording session. The location of the hydrophone was noted (both which floating pen the hydrophone was placed in and what side of that pen the hydrophone was on). Animals both in the pen with the hydrophone and in any proximal pens were also noted. Behaviors were specifically documented during each triggered recording, not continually during the recording session. Each triggered recording, therefore, contained both an echolocation recording and an instantaneous sampling of three different facets of the target animal's behavior.

First, the assisting observer documented how the animal passed the hydrophone. Tape marks were placed on the dock 1 m on either side of the hydrophone and the observer used those

[2] Unfortunately, early recordings of Bailey did not utilize a trigger. The trigger was introduced on July 1, 2000 but not used exclusively until after August 24, 2000. Therefore, on recordings without a trigger, we attempted to isolate trains from longer continuous recordings.

marks to estimate a radius of 1 m around the hydrophone. The observer could then document the closest point to the hydrophone that the animal passed, recorded as the approximate distance to the hydrophone. Direction of travel relative to approximate compass headings (i.e. North, South, East, and West) were included and often depended greatly on the placement of the hydrophone. Finally, the observer also documented the body position of the target animal (i.e. ventral or dorsal surface facing up) and whether the target animal passed the hydrophone by themselves or in conjunction with other animals. Within this observation were details concerning the relative positioning of the animals. These positions were operationally defined as:

- Solo: target animal passes by the hydrophone alone (i.e. with no other animals within 1 m of itself)
- Echelon position: 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 position: 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

The second facet of concurrent behavior documented by the assisting observer was head motions. These head motions were operationally defined as:

- 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

The final facet of concurrent behavior documented on the ERBO sheet was ancillary behaviors. Observers were instructed to document any other behaviors of note occurring in conjunction with the trigger recording not encompassed by one of the above categories. These behaviors included whether whistles were heard, if bubbles were seen from the target animal, any open mouth posturing, any physical interaction with the hydrophone (e.g. biting or hitting the hydrophone), and social interactions (e.g. rubbing, calf discipline, etc).

Data Analysis

Echolocation

Several task-specific computer programs were used for analyzing the echolocation recordings. First, a series of programs written with LabView® (National Instruments) were used to strip one hydrophone channel (either the “calf” or “mother” channel, depending on which

animal is of interest at the time) from the original file, leaving a 2 channel binary signal. These binary signals were converted to .wav files and fed into Cool Edit 2000® (Syntrillium) to visually display the spectrograph (a frequency versus time visual representation of target sounds) and acoustically play the recording from the underwater hydrophone simultaneously with the recorded vocal narration (see Figure 4). Spectrographs enabled the identification of the general location of the targeted echolocation event within the larger recording envelope. Approximate starting times, ending times, and rough train durations found using Cool Edit then allowed researchers to locate target trains within the recording file when using other programs (e.g. Sound Forge 6.0® (Sonic Foundry), etc.) for subsequent analyses.

Time frames, intensity, and other sounds such as whistles, squeals (very intense bursts of clicks emitted in extremely rapid succession), static, bubble-noise, other animals, and snapping shrimp (*Synalpheus parneomeris*) (see Figure 5) were identified or determined through Cool Edit and other LabView programs. Snapping shrimp represent a major source of biological noise in certain areas of the ocean, including the Naval facility in San Diego (Au & Banks, 1998; Au, Lammers, & Banks, 1998). The waveform signatures, however, differ from echolocation signals. Thus, we identified and subsequently accounted for snapping shrimp and other interfering noise occurrences.

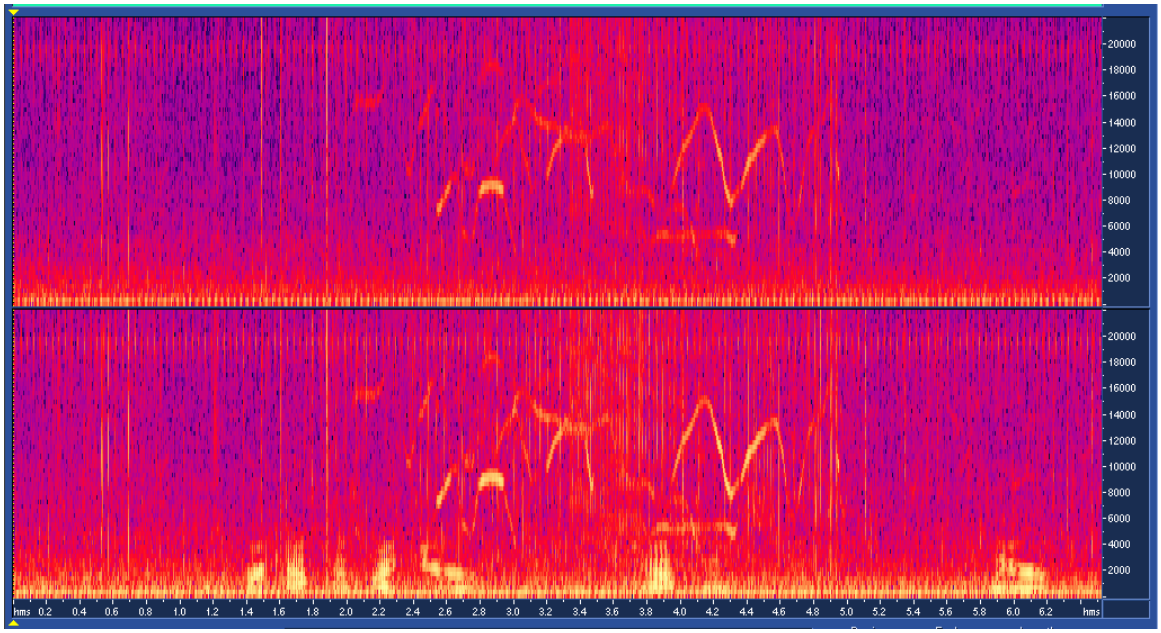

Figure 4. Cool Edit representation (frequency/time) of a click train (red vertical bands) and whistles (yellow/red upsweeping bands). Color denotes relative intensity with dark red and yellow bars on bottom spectrograph representing the spoken narration.

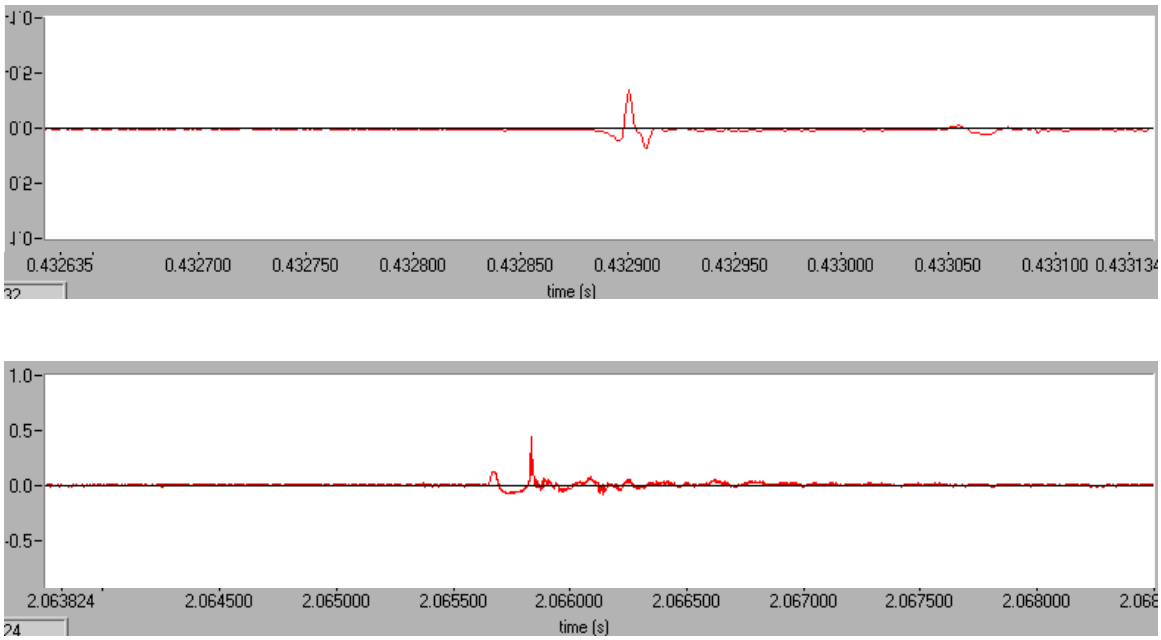

Figure 5. Bottlenose dolphin (top*)* vs. snapping shrimp (bottom) clicks (relative amplitude/time). Note that y-axis values for all Data Viewer figures denote relative amplitude only. X-axis values also represent relative time with each axis second denoting 2 seconds of real-time sound.

Once click trains were identified, I relied heavily upon the vocal narration and ERBO sheets to determine which animal emitted the observed train. Animals were identified based on their proximity to the hydrophone, any observed orientations toward the hydrophone, and relative positions as they passed the hydrophone. Trains I could not comfortably attribute to a single animal were eliminated. Once I identified the animal, the voiceover was stripped from the recording leaving only the single channel binary signal. 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. Excised waveforms were printed for archival purposes and visual analysis. The number of clicks per extracted train was counted by hand using a magnifying glass. The number of clicks per extracted train was divided by the train duration to yield the 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 Sound Forge. The beginning and ending points of the train were entered in the sound file and the rest of the recording was eliminated. 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. If the train was from a single identified dolphin, without overlapping trains or excessive background noise, we selected the train for further analysis. 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 the train. The computer program was designed to identify pressure spikes above a specified sound pressure level (SPL). Peak SPL ($SPL=10\log_{10}(P^2/P^2_{ref})$) 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 etc.) are critically dependent on factors such as distance to the hydrophone and angle of orientation that could not be held constant with free-swimming animals. Because these factors could not be controlled, 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. Signals isolated by the computer as "clicks" which in fact could visually be identified as reflections, noise, or snapping shrimp were discarded (see Figures 6 and 7). An initial interval threshold was set at 500 ms and intervals in excess of 500 ms were automatically eliminated. If legitimate, intervals above this magnitude were considered to indicate that the animal had terminated one train and begun another. Because we had already determined we were working with single trains, intervals of this length more likely represented areas where individual signals were eliminated during the above procedure and were thus not representative of the original train sequence. To further account for artifact intervals, intervals were eliminated as outliers if they met the following criteria;

1) The interval visually deviated (i.e. was markedly longer or shorter than surrounding intervals in a manner not reflected in the printed waveforms of the original

train) from the pattern created by other intervals in the train on a scatterplot of ICIs over time.

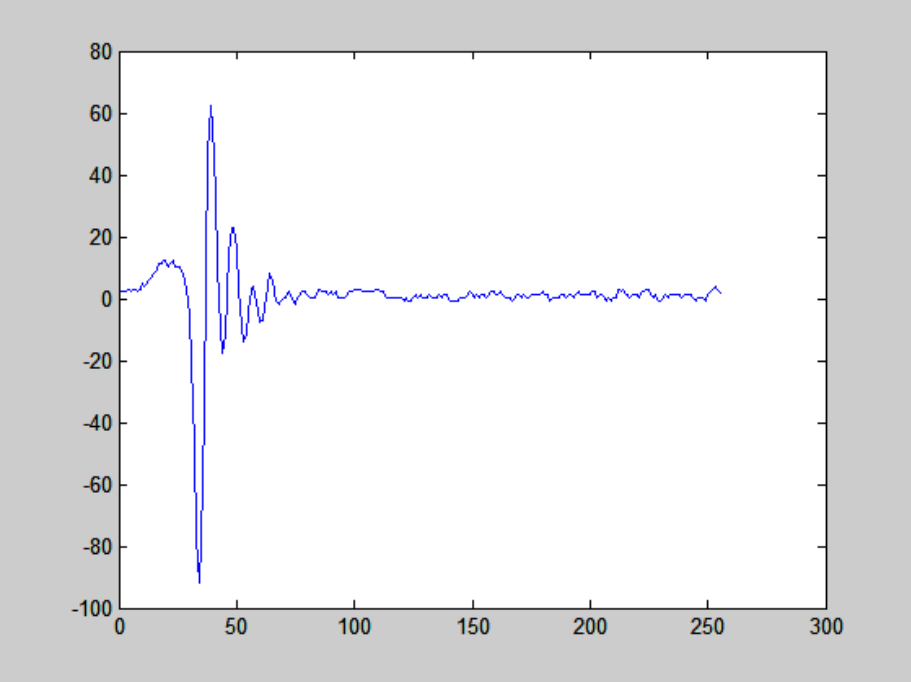

Figure 6. Example of an acceptable click (number of samples/time)

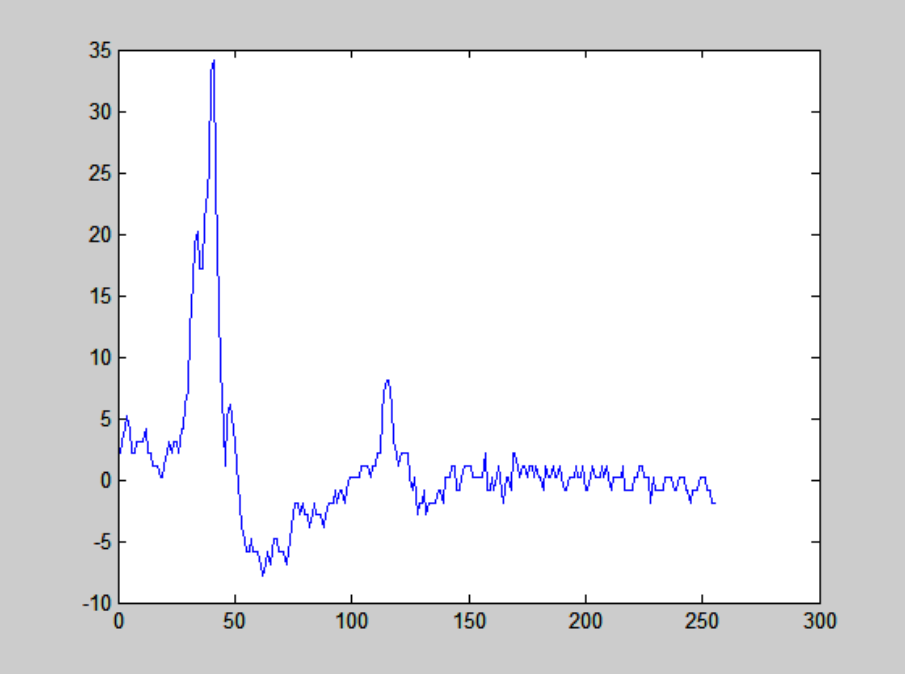

Figure 7. Example of a signal eliminated during the analysis procedure (number of samples/time)

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 (see results). All train structure variables were recorded continuously to avoid artificial polytomization.

Within Session Habituation Effects.

During a given recording session, the hydrophone was lowered into the water and remains in place until the last recording for that session was obtained. Because the hydrophone did not change between each successive pass by the animals, the target animals could hypothetically passively lose interest in the object as it loses its novelty, scanning it less intensely with each pass. Essentially, the animals may habituate to the hydrophone's presence within sessions, thus potentially altering the study variables due to their diminished interest in exploring the object. To test this hypothesis, the values on each primary echolocation variable (duration, click count, density, and ICI) for the first train per animal in each multi-train recording session was compared to the value for the last train per animal recorded in that session. The results were then analyzed using the Sign Test to determine 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. If the animal did not habituate to the hydrophone's presence, we would expect to see a π=0.5, demonstrating that the first train values exceeded the last train values equally as often as the last exceeded the first. However, if these proportions were not equal, that is if the first train

values exceeded the last train values significantly more often than the inverse, that result would indicate the possible effects of within-session habituation.

Concurrent Behaviors

Data from the ERBO sheet for each train were also entered into the SPSS database. Time was recorded continuously (using exact military time). The day, week, and month postpartum of each train was documented. Values for adult females were recorded by the day, week, and month postpartum of their calf. The remaining behavioral variables were categorical in nature and were recorded polytomously or dichotomously as the case may be.

CHAPTER III

RESULTS

Signal samples were collected over 0-6 months postpartum from 6 calves and their mothers housed at the U.S. Navy Marine Mammal Program facility, the Space and Naval Warfare Systems Center, in San Diego, CA. Data from 1 mother/calf pair (calf born in 2000) were analyzed in 2002 as the pilot project for this study. Data from the remaining 5 mother/calf pairs, born during the summer of 2002, were used to bolster and further expand the investigations begun with the first mother/calf pair from 2000.

Adult Females

During the 6-month postpartum period, 190 total trains were collected from 6 adult females following the birth of each calf. Samples of echolocation trains were successfully obtained during 22 of the 24 weeks of the study. Of the 190 trains, 187 trains were analyzed for duration, clicks per train, and density. The remaining three samples were burst-pulse sounds or "squeals," broadband sounds of short duration and high density thought to function in communication rather than in sensory perception (Popper & Edds-Walton, 1997). Because of this potential functional discrepancy, these trains were separated from the analysis of regular click trains.

Click Train Duration.

Overall Results.

Trains recorded from adult females had a mean duration of M=2.08 sec (N=187, SD=1.01) (see Figure 8). Trains ranged in duration from 0.5 to 5.50 sec. The majority (84%) of trains were shorter than 3 sec. Most (54.4%) trains were recorded when animals were 1 m or less from the hydrophone. There was no significant correlation between train duration and observed distance to the hydrophone (r=-0.024).

A Univariate General Linear Model (GLM) revealed an overall significant difference in mean train duration by month postpartum for adult females ($F_{(5,186)}$=2.50, α<0.05). A Tukey a post-hoc analysis revealed that adult mean train duration was significantly lower in month 4 (M=1.56 sec, n=14) than in month 6 (M=2.67 sec, n=16). During the study period, mean train duration for adult females by week postpartum fluctuated from a low of M=1.34 sec during week 18 to a high of M=3.06 sec during week 24

(see Figure 9). Mean train duration declined steadily from the first through the fourth month and then increased steadily between 4 and 6 months postpartum for adult females (see Figure 10).

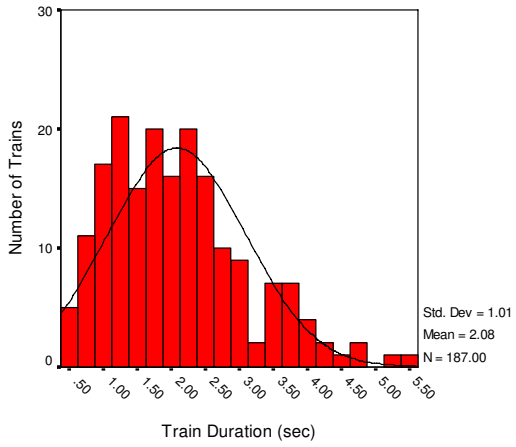

Figure 8. Frequency histogram of adult female train duration (in seconds).

Individual Adult Females.

A Univariate GLM revealed no significant differences in the mean train duration between adult females ($F_{(5,186)}$=0.90). Overall, the number of echolocation samples collected from individual adult females were not equal, reducing the power to detect significant differences (see Table 3). Because of a research protocol designed to maximize the number of trains collected from the first calf in the study for example, only five trains were collected from Snapper.

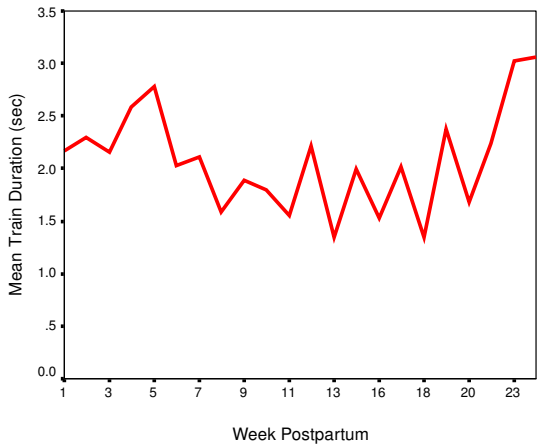

Figure 9. Mean adult female train duration (in seconds) by week postpartum

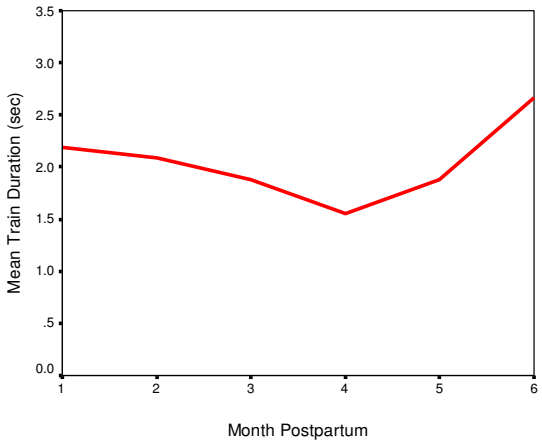

Figure 10. Mean adult female train duration by month postpartum

Excluding Snapper, the overall differences between adult mean train durations remained non-significant ($F_{(4,181)}$=0.706). Blue spent a great deal of energy and attention caring for her ailing calf and subsequently showed a waning interest in the hydrophone as the calf's illness progressed. Despite a similar observation effort being given to each mother and calf, for Blue's 22 trains, only 3 were recorded after the second month. Excluding both Snapper and Blue, the results remained non-significant ($F_{(3,159)}$=0.323). A general sampling trend was observed over time indicating a decreased interest in the hydrophone. Of the 187 trains analyzed, 109 trains were recorded in the first 2 months and only 37 trains in the last 2 months. Possible causes of this trend will be discussed later in this report. Evidence of within session habituation, however, was not found for any adult female. Within recording sessions, last trains were longer than first trains statistically as often as first trains were longer than last trains (π=0.5).

Table 3. Train duration descriptive statistics per adult female

Animal Name	N	Minimum	Maximum	Mean	Std. Deviation
Opai	50	.56	4.84	2.1100	1.1144
Shasta	43	.64	5.50	2.2507	.9689

Blue	22	.52	4.12	1.8209	.9037
Kolohe	40	.50	5.18	2.1225	1.0310
April	27	.56	4.00	2.0096	.9808
Snapper	5	.68	2.54	1.5040	.7415

Individual adult trends generally reflected the overall average adult trends (see Figure 11). Although trends in train duration variance were indistinct (see Figure 12), the mean duration of each adult's samples generally decreased over the first 4 months of the study. At that time, Blue's data ended due to the death of her calf. The remaining 4 adults from the 2002 collection period all showed increases in train duration between 4 and 6 months postpartum. The only available data from Snapper occurred during months 5 (*n*=4) and 6 (*n*=1). This sampling bias greatly reduces the strength of any arguments regarding her trends over time. Further, it should be noted that a different number of samples were captured from each animal in each given month. Some averages were based on 10 or 13 trains while other months have only one train representing that animal. This data pattern most likely influenced the observed results.

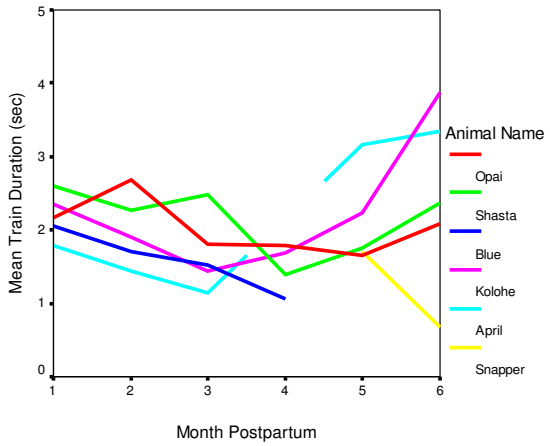

Figure 11. Mean train duration per adult female by month postpartum

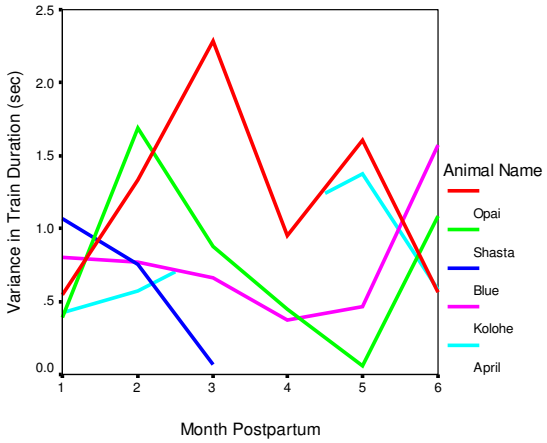

Figure 12. Train duration variance per adult female by month postpartum

Clicks per Train

Overall Results.

Trains recorded from adult females had an overall mean click count of M=116.6 clicks per train (N=187, SD=65.63). These trains showed a large range from a minimum of 17 to a maximum of 409 clicks (see Figure 13). Only three trains, however, exceeded a click count of 300 while 89% of trains contained less than 200 clicks. There was no significant correlation between mean clicks per train and distance to the hydrophone (r=-0.14) but there was a significant positive correlation between mean clicks per train and mean train density (r=0.66, $\alpha<0.01$).

A Univariate GLM revealed no significant differences in mean train click count by month postpartum ($F_{(5,186)}$=1.12). Over the 6-month study period, mean clicks per train for adult females by week postpartum fluctuated from a low of M=80 clicks during week 8 to a high of M=210.83 during week 24 (see Figure 14). The longest trains were also recorded during week 24. The overall average click counts for adult animals remained relatively constant through the first 3 months then decreased but held steady between the fourth and fifth months postpartum. Like the mean train duration, a sharp increase in click count was seen in the sixth month (see Figure 15).

Individual Adult Females.

A Univariate GLM revealed no statistically significant differences in the mean clicks per train between adult females ($F_{(5,186)}$=1.64). Excluding Snapper's data ($F_{(4,181)}$=1.26) and then Snapper's and Blue's data ($F_{(3,159)}$=1.32), the results were still non-significant. However, the bias in sample sizes per animal and its impact on the power to detect meaningful differences should be noted (see Table 4).

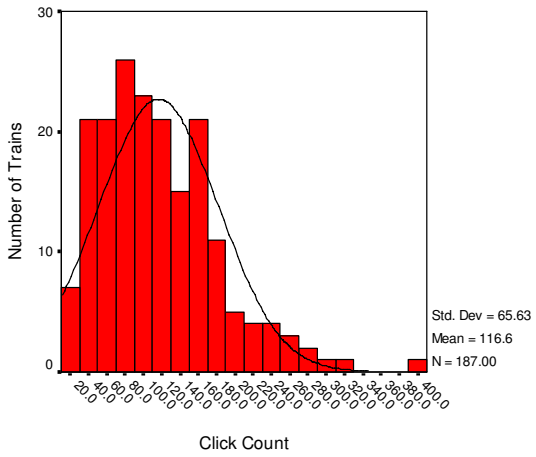

Figure 13. Adult female click count per train.

Evidence of within session habituation was not found for any adult female. Within recording sessions, last trains contained more clicks than first trains statistically as often as first trains contained more clicks than last trains (π=0.5).

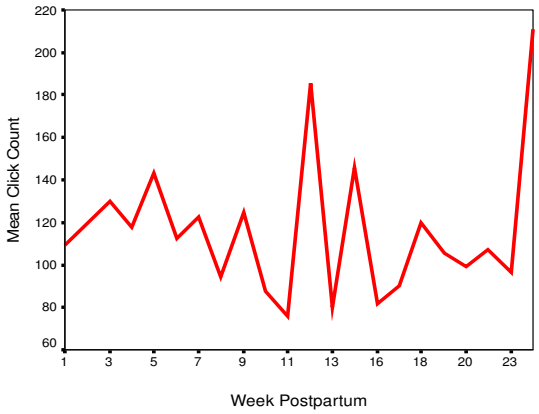

Figure 14. Mean adult female click count per week postpartum

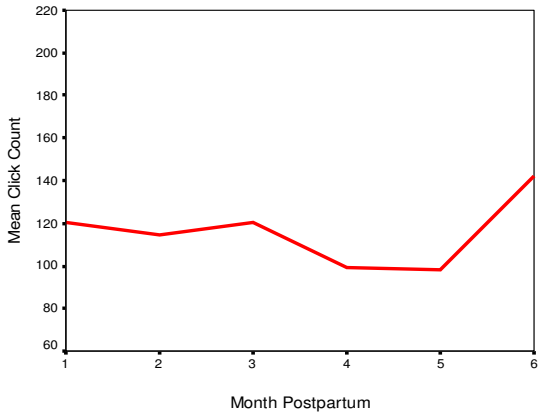

Figure 15. Mean adult female click count per month postpartum

Table 4. Train click count descriptive statistics per adult female

Animal Name	N	Minimum	Maximum	Mean	Std. Deviation

Opai	50	27	268	110.94	60.60
Shasta	43	31	313	133.02	64.04
Blue	22	23	273	131.45	64.79
Kolohe	40	28	301	110.72	65.46
April	27	17	409	106.63	77.89
Snapper	5	52	98	66.40	18.06

Individual adult trends in mean click count appeared more discrepant from one another than those seen between train durations (see Figure 16). Each animal showed individual variability in their trends but some general tendencies can be noticed. Variance remained relatively consistent across dolphins until the sixth month (see Figure 17). Of the 5 dolphins who supplied echolocation samples during the first 2 months, 4 animals displayed a decrease in mean clicks per train from months 1 to 2. Trend patterns generally split 3-to-2 for the remaining months. For example, from months 3 to 4, Blue, Kolohe, and April all increased their mean clicks per train while Opai and Shasta decreased in their mean click counts. Some months of the study had only one train recorded for a given dolphin (e.g., Blue for month 4). The differences in the number of trains recorded per individual perhaps biased the graphical representation.

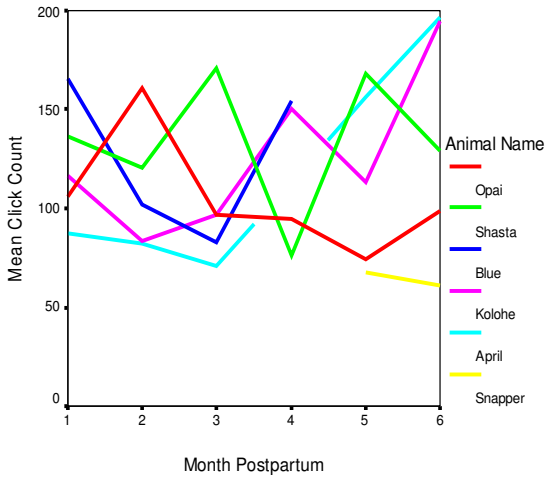

Figure 16. Mean click count per adult female by month postpartum

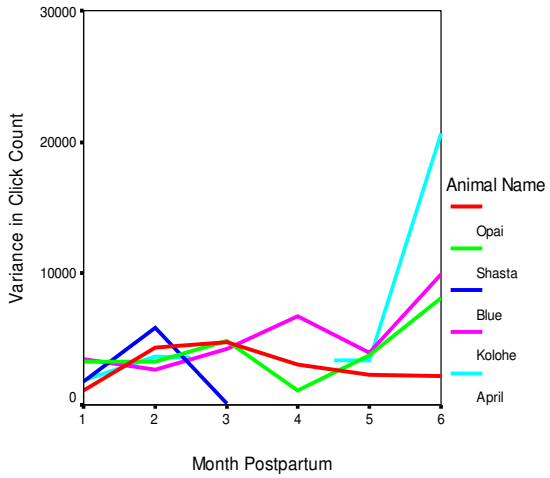

Figure 17. Variance in click count per adult female by month postpartum

Train Density

Overall Results.

Trains recorded from adult females had an overall mean density of *M*=59.5 clicks/sec (*N*=187, *SD*=32.14). These trains had a large range from a minimum of 20.24 to a maximum of 261.36 clicks/sec (see Figure 18). The majority (95%) of densities fell below 100 clicks/sec with only 10 trains exceeding this number. A significant negative correlation was also found between train density and distance to the hydrophone (r=-0.166, α<0.05). As distance to the hydrophone decreased, mean train density for adults increased.

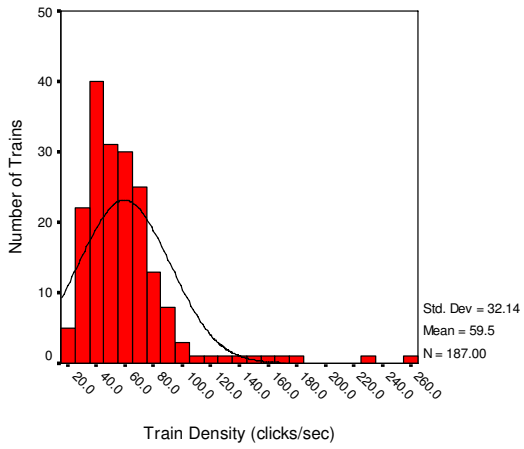

Figure 18. Adult female train density (clicks/sec).

A Univariate GLM revealed no statistically significant differences in adult mean click train density by month postpartum ($F_{(5,186)}$=0.97). Over the 6-month study period, mean train density for adult females by week postpartum fluctuated from a low of *M*=45.46 clicks/sec during week 11 to a high of *M*=89.55 clicks/sec during week 18 (see Figure 19). Note that the highest click densities were recorded during a week when only one adult train was collected, negating any ability to account for individual variation. A high of *M*=83.58 during week 12 (*n*=5) was thus more representative. The overall train density for adult dolphins remained relatively constant throughout the study period, peaking at *M*=70.58 clicks/sec at about 3 months postpartum (see Figure 20). Because train density is a product of the clicks per train and the train duration, and also in part due to physiological factors expressed as the dolphin maintains a click rate slower than the two-way transit time to and from their target, the minimal overall fluctuation in the train densities of adult females is not unexpected.

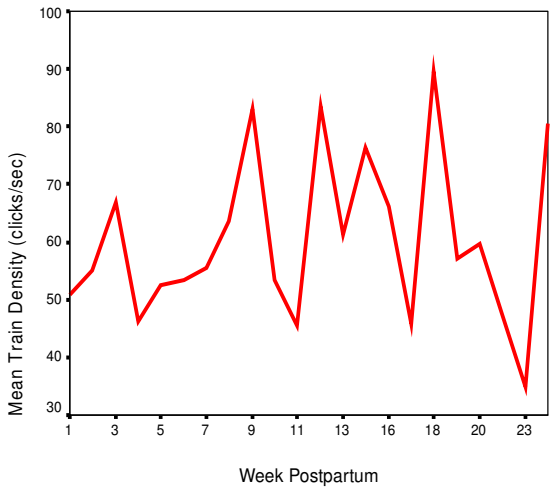

Figure 19. Mean adult train density (clicks/sec) by week postpartum

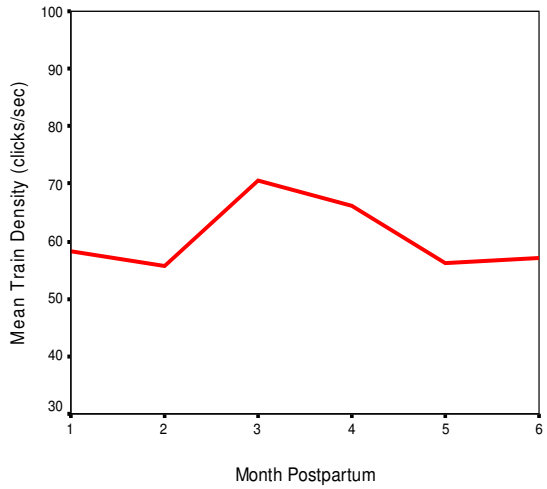

Figure 20. Mean adult train density (clicks/sec) by month postpartum

Individual Adult Females.

A Univariate GLM revealed no significant differences in the mean train density among adult females sampled ($F_{(5,186)}$=1.98). Excluding Snapper because of her exceptionally low sample size, the differences in mean densities between adult females remained non-significant ($F_{(4,181)}$=2.36). Also excluding Blue because of the death of her calf did not alter the significance ($F_{(3,159)}$=0.357). The bias in sample sizes, however, impacts the power to detect differences that may occur (see Table 5). Evidence of within session habituation was not found for any adult female. Within recording sessions, last trains were denser than first trains statistically as often as first trains were denser than last trains (π=0.5). In Opai's case, the last trains in a session were denser significantly more often than first trains (p=0.039).

Table 5. Train density descriptive statistics per adult female

Animal Name	N	Minimum	Maximum	Mean	Std. Deviation
Opai	50	28.01	168.87	55.4348	24.3909
Shasta	43	25.33	155.92	61.1177	23.7816
Blue	22	24.19	226.92	78.3164	43.8827

Kolohe	40	21.88	261.36	56.5108	39.4594
April	27	20.24	182.59	55.0696	31.5706
Snapper	5	31.12	89.71	51.2480	23.2545

Adult female trends in mean train density differed noticeably between dolphins (see Figure 21). For example, while Opai and April remained relatively constant over the study period, Shasta and Kolohe both showed considerable variability in their mean click density values. Although the spike in month 4 from Blue appears noteworthy, only one train was recorded from her during that month and thus this value may not be representative of her click behavior. The same is possible for Snapper during the sixth month when a spike is seen but only one train was recorded. Obvious spikes were also seen in the variance in train density by month postpartum (see Figure 22).

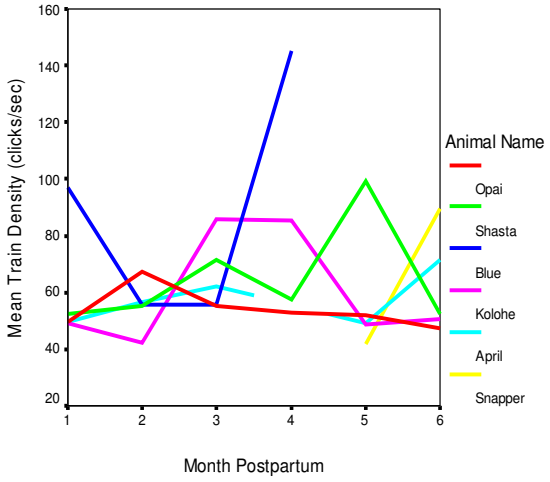

Figure 21. Mean densities (clicks/sec) per adult female by month postpartum.

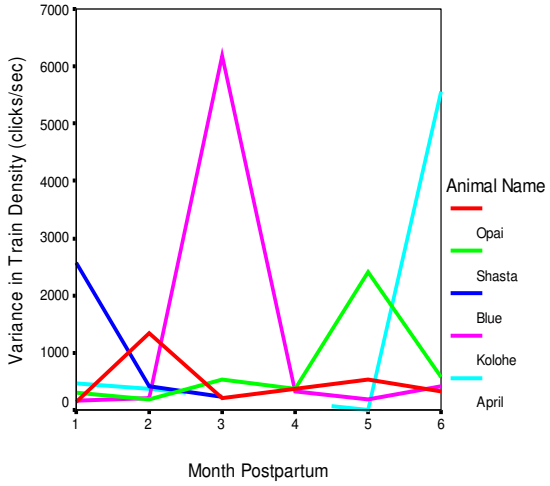

Figure 22. Variance in train density per adult female by month postpartum.

Interclick Interval (ICI)

Overall Results.

In the 2002 calving season, 94 click trains were selected from the five adult females as suitable for an analysis of interclick interval (ICI) based on selection criteria outlined in the methods. Trains

recorded from adult females had an overall mean ICI of *M*=21.94 ms (*N*=94, *SD*=8.45). The mean ICI per train ranged from a minimum of 6.43 ms to a maximum of 49.98 ms (see Figure 23). The majority (84.4%) of mean ICIs were below 30 ms with only 15 trains exceeding this value. There was no significant correlation between mean train ICI and distance to the hydrophone (*r*=0.008).

A Univariate GLM revealed statistically significant overall differences in adult mean train ICI by month postpartum ($F_{(5,93)}$=2.33, p<0.05). A Tukey *a* Post-hoc analysis showed the mean train ICI to be significantly higher in month 6 than in month 3. Mean train ICI values were lower in month 4 than month 3 but the low sample size (*n*=5) may have been too low to detect meaningful differences. In general, sample sizes were far larger in the first 3 months than in the last 3 months of the study.

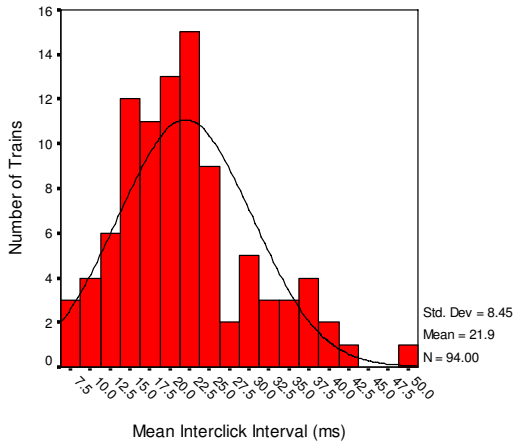

Figure 23. Adult female mean interclick interval per train (ms).

Over the 6-month study period, mean per train ICI for adult females by week postpartum fluctuated from a low of *M*=11.00 ms during week 18 to a high of *M*=39.59 ms during week 24 (see Figure 24). Both the lowest and highest mean ICI per week were during weeks where only one train was analyzed. A low *M*=13.84 ms (n=2) during week 12 and high *M*=29.38 ms (n=3) during week 23 may be

somewhat more representative. The overall mean train ICI by month postpartum for adult dolphins predictably remained fairly constant throughout the study period, peaking at *M*=29.18 ms at 6 months postpartum (see Figure 25).

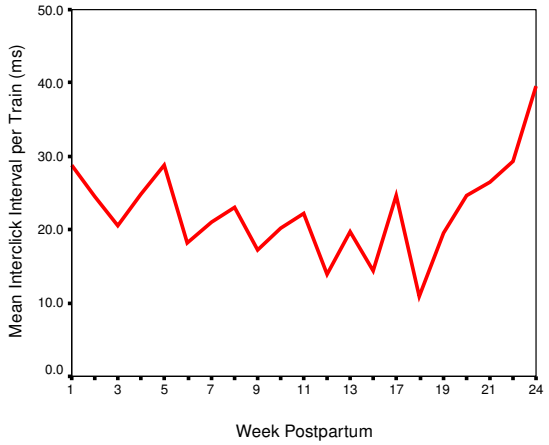

Figure 24. Mean adult ICI (ms) per train by week postpartum

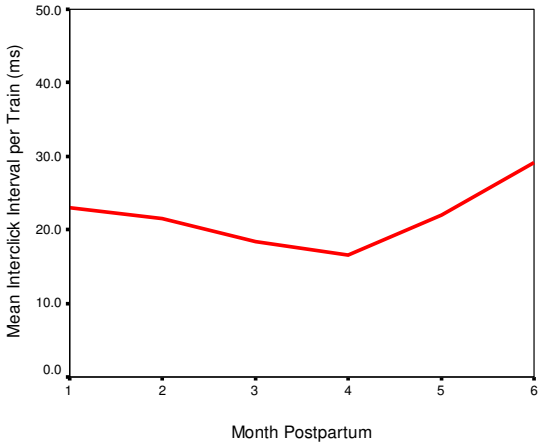

Figure 25. Mean adult ICI (ms) per train by month postpartum

Individual Adult Females.

A Univariate GLM revealed statistically significant differences in the mean train ICI between sampled adult females ($F_{4.93)}$=3.16, α<0.05). Specifically, Blue's mean per train ICI (*M*=16.67 ms) was significantly lower than April's (*M*=26.52 ms) (Tukey α, α<0.05). The bias in sample sizes per animal, though not large, may have impacted the significance of these results (see Table 6). Evidence of within session habituation was not found for any adult female. Within recording sessions, last trains had longer mean ICI values than first trains statistically as often as first trains had longer mean ICI values than last trains (π=0.5).

Table 6. Train ICI descriptive statistics per adult female

Animal Name	N	Minimum	Maximum	Mean	Std. Deviation
Opai	17	11.0050	34.3628	21.445141	6.315186

Shasta	25	13.2979	37.9970	21.175632	6.365452
Blue	15	6.4330	40.2896	16.673993	8.862454
Kolohe	21	10.6268	39.5941	23.539814	8.336197
April	16	11.4651	49.9843	26.520806	10.682980

Trends in mean train ICI per adult closely reflected the previously discussed overall trends and did not differ markedly between dolphins (see Figure 26). Opai and Shasta remained nearly constant over all 6 months while Kolohe and April varied more noticeably both early and late in the study period. More obvious between-dolphin trend discrepancies and spikes were seen in the mean variance per train by month postpartum (see Figure 27).

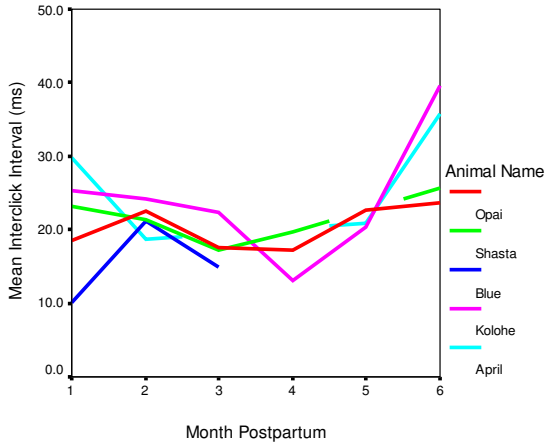

Figure 26. Mean per train ICI (ms) by month postpartum per adult female

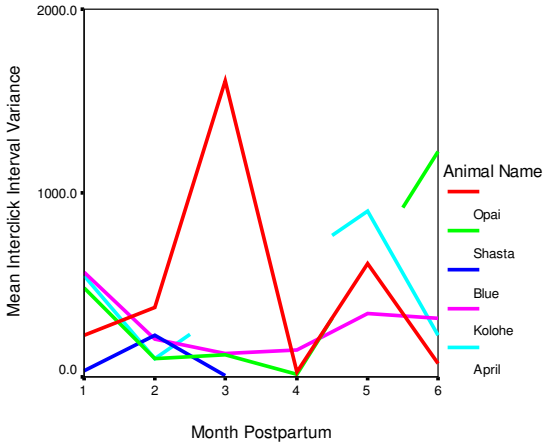

Figure 27. Mean per train ICI variance by month postpartum per adult female

Concurrent Behaviors

Adult females dolphins displayed head motions typically ascribed to dolphins during echolocations (e.g., Dudzinski, 1996; Dudzinski et al., in prep.). Adults were frequently (58.8% of recordings) observed cocking their heads toward the hydrophone as they passed it. Over time,

the frequency of observed head cocks appeared to decrease for all females except Opai who showed more variation in head movement (see Figure 28). Nearly as common was no discernable (to the observer) head motion (38.5%). Head scanning motions were infrequently observed (total *n*=1 for wide and *n*=4 for narrow).

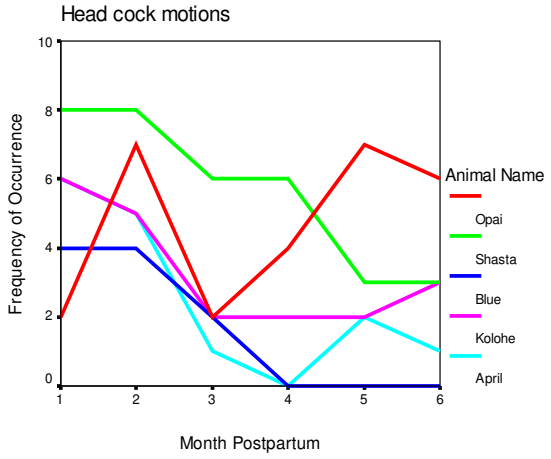

Figure 28. Adult female head cock motions per month postpartum

The breadth of observed ancillary behaviors was small. Instances were restricted to concurrent whistles (*n*=20), bubble production (*n*=2), hitting the hydrophone (*n*=2), and calf discipline (*n*=2), cumulatively representing only 14.4% of the behavioral observations. Kolohe exhibited the majority of these behaviors. She produced 11 whistles, both cases of calf discipline observed during the recording of an adult train (see calf results for other instances), and one occurrence of hitting the hydrophone. During the discipline incidents, Kolohe was observed chasing her calf at an accelerated rate of speed and occasionally assume an open mouth posture toward the calf. Kolohe was also the only adult dolphin to echolocate on the hydrophone with an open mouth (*n*=1). During the majority (85.6%) of adult click trains, however, no concurrent ancillary behaviors were observed.

Positions of calves relative to their mothers were recorded for each observation. Of the 187 adult trains recorded, calves were observed in an echelon swim position 63.3% of the time. Predictably, instances of echelon swimming were very common during early recordings of adults but tapered off as the calves attained more physiological maturity and behavioral independence (see Figures 29 and 30). Echelon swims occurred in 89.6% of adult recordings during the first month but dropped to 62.7% of recordings in month two and represented less than 40% of recordings from the fourth to the sixth months. Instances of calves swimming in an infant position were comparatively rare and only represented 15.9% (*n*=29) of all recordings. Even less frequent (*n*=7, 3.8%) were solo passes of the hydrophone by adult females.

Squeals

All three recorded adult burst-pulse "squeals" came from Kolohe, an adult female Pacific bottlenose dolphin. These three squeals were recorded during the same session on the second day after her calf was born. These burst-pulse emissions had a mean duration *M*=0.067 sec, mean pulse count *M*=55, and mean density *M*=825.00 pulses/sec. Kolohe's calf was swimming in an inside echelon position during all three squeals. Kolohe made no overt motions toward the hydrophone with her head and maintained a closed mouth posture.

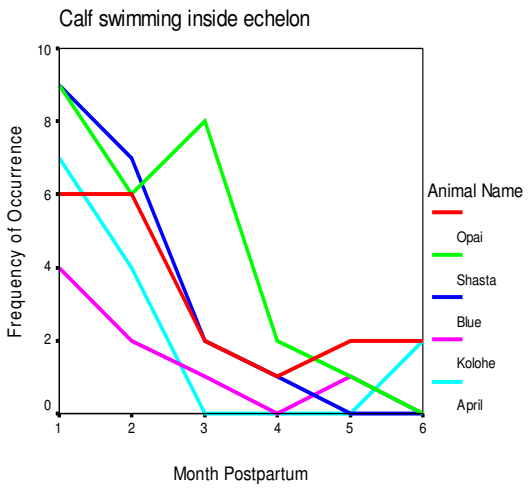

Figure 29. Frequency of calves swimming inside echelon relative to their mothers during recordings by month postpartum

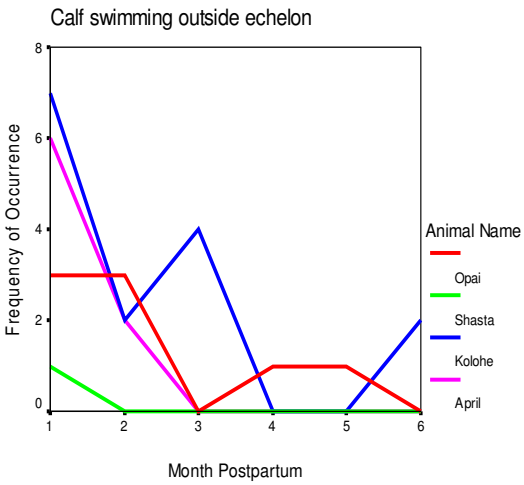

Figure 30. Frequency of calves swimming outside echelon relative to their mothers during recordings by month postpartum

Calves

During the first 6 months of life, I recorded 369 total click trains from the sampled calves. Of these 369 trains, 8 were determined to be squeals and the remaining 361 trains were analyzed together for duration, density, and clicks per train. Male calves (n = 2) emitted 101 trains (28%) that were collected and 260 trains (72%) were recorded from the females (n=4). Excluding Little Blue whose sample size was likely artificially lowered by her illness and early death, male calves (Little April and Little Opai) produced the two lowest numbers of trains (n=59 and n=42, respectively). Little Shasta was the most prolifically vocal calf, providing 109 (30%) of the total calf trains. Samples from calves were obtained in 21 of the 24 weeks of the study, beginning with week 4. The earliest train was recorded from Little Shasta 22 days after her birth, followed shortly thereafter by Little Blue who was recorded echolocating 24 days after her birth. 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%) of trains were recorded from dolphins observed 1 m or less from the hydrophone.

Train Duration

Overall Results.

Trains recorded from calves had a mean duration of *M*=2.04 sec (*N*=361, *SD*=1.14) (see Figure 31). 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 and only two trains exceeded 6 sec. There was no significant correlation between calf gender (*r*=-0.03) or distance to the hydrophone (*r*=-0.10) and train duration.

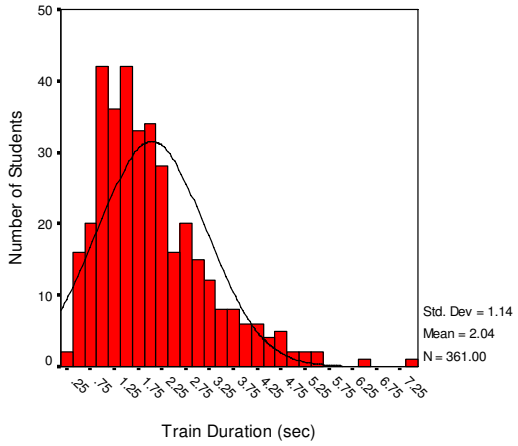

Figure 31. Calf click train duration (in seconds).

A Univariate GLM revealed statistically significant differences in calf mean train duration by month postpartum ($F_{(5,360)}$=2.92, α<0.05). A Tukey a post-hoc analysis found that calf click trains in the third month had significantly shorter durations (*M*=1.74 sec) than trains in the fifth month (*M*=2.27 sec). Although trains in month 1 and 2 were on average even shorter than month 3, the low sample size in those months likely impacted the power to detect significant differences. Over the course of the study period, mean train duration for calves by week

postpartum fluctuated from a low of *M*=0.74 sec during week 5 to a high of *M*=3.01 sec during week 8 (see Figure 32). However, these means were calculated during weeks with only one and two trains, respectively. A low of *M*=0.92 sec during week 6 (*n*=3) and a high of *M*=2.60 sec during week 19 (*n*=31) were more representative and more able to account for individual variation. The mean train duration increased steadily from the first through the fifth months and then declined slightly during the sixth postpartum month (see Figure 33).

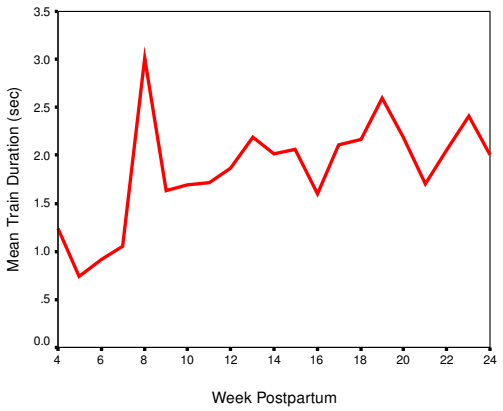

Figure 32. Mean calf train duration by week postpartum

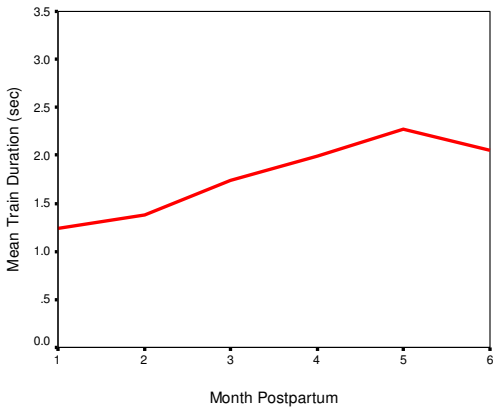

Figure 33. Mean calf train duration by month postpartum

Individual Calves.

A Univariate GLM revealed no significant differences in the mean train duration between calves ($F_{(5,360)}$=0.74). However, the large discrepancy in the number of echolocation samples collected from individual calves contributed to the low observed power to detect significant differences (see Table 7). Due in part to her death at 4 months and likely due to the preceding illness, for example, only seven trains were collected from Little Blue from the first 3 months. When her data was excluded, the results were still non-significant ($F_{(4,353)}$=0.45). In contrast to the adult females, a general sampling trend indicating an increased interest in the

hydrophone was observed over time. Of the 361 trains analyzed, 221 trains (61%) were recorded in the last 2 months and only 14 trains (4%) in the first 2 months. Evidence of within session habituation was likewise not found for any calf. Within recording sessions, last trains were longer than first trains statistically as often as first trains were longer than last trains (π=0.5). Possible causes of this trend will be discussed later in this report.

Table 7. Descriptive train duration statistics per calf

Animal Name	N	Range	Minimum	Maximum	Mean	Std. Deviation
Little Opai	42	7.30	.18	7.48	1.9229	1.4157
Little Shasta	109	5.92	.46	6.38	2.0644	1.1164
Little Blue	7	3.64	.14	3.78	1.4486	1.5546
Little Kolohe	65	4.06	.40	4.46	2.0046	1.0746
Little April	59	5.00	.60	5.60	2.2038	1.2216
Bailey	79	4.50	.40	4.90	2.0134	.9642

Individual calf trends in train duration generally reflected the overall averaged trends by increasing as the calves aged (see Figure 34). Although trends in train duration variance were somewhat more variable (see Figure 35), the mean duration of each calf's samples generally increased over the course of the study. Four of the 5 calves sampled in 2002 showed an increase in train duration from the first month they were successfully recorded to the second month they were recorded. The remaining calf, Little April, maintained her mean train duration between the two months. Three of the 5 calves sampled in the last 2 months of the study

showed increases in duration from month 5 to month 6. Four of the 5 surviving calves showed a sixth month mean train duration that was longer than the train duration during the first month they were recorded[3]. Much like the adult females, the opportunistic sampling method employed led to the capture of a different number of trains for each calf in a given month. Some averages were based on upwards of 30 or 40 trains while other months have only one train representing that dolphin. This protocol may have influenced the results.

[3] The only available data from Bailey occurred during months 5 and 6 (34 trains in month 5 and 45 train in month 6). This sampling bias diminishes the strength of arguments regarding her trends over time.

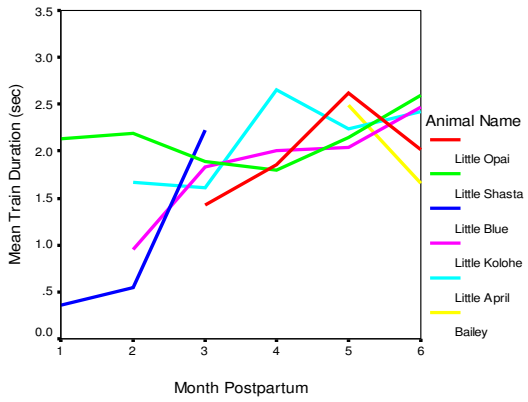

Figure 34. Mean train durations per calf by month postpartum

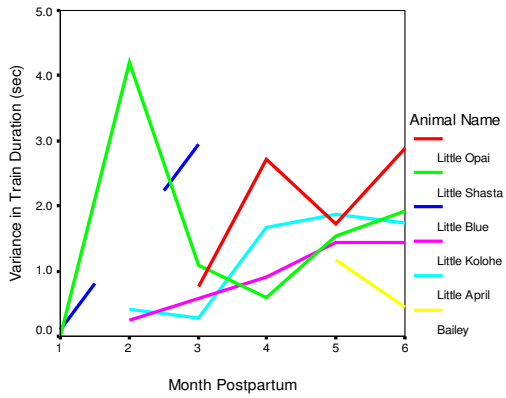

Figure 35. Train duration variance per calf by month postpartum

Clicks per Train

Overall Results.

Trains recorded from calves had an overall mean click count of *M*=114.13 clicks per train (*N*=361, *SD*=85.37). These trains had a larger range than that of the adult animals, containing from a minimum of 12 clicks to a maximum of 506 (see Figure 36). Only 16 trains (4%) exceeded a click count of 300, and 311 (86%) of trains contained less than 200 clicks. There was no significant correlation between calf gender and train click count (*r*=-0.10) but there was a significant negative correlation between distance to the hydrophone and click count (*r*=-0.13, α<.05). Calves observed closer to the hydrophone predictably trains with a larger number of clicks, likely in part as a function of the decrease two-way transit time for click emission and reception as the distance to the hydrophone decreased. A significant positive correlation was also seen between calf train duration and click count (*r*=0.68, α<0.01).

A Univariate GLM revealed no significant differences in mean clicks per train by month postpartum for calves ($F_{(5,360)}$=2.16). Over the 6-month study period, mean clicks per train for calves by

week postpartum fluctuated from a low of *M*=25 clicks during week six to a high of *M*=191 during week eight (see Figure 37). Again week 8 only contained two trains making a high *M*=148 during week 19 more representative. Recall that some of the shortest trains were also recorded during the sixth week and the longest trains were recorded during the eighth and nineteenth weeks. The overall average click counts for calves remained relatively consistent over the first 2 months then increased steadily until 5 months postpartum. 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 (see Figure 38).

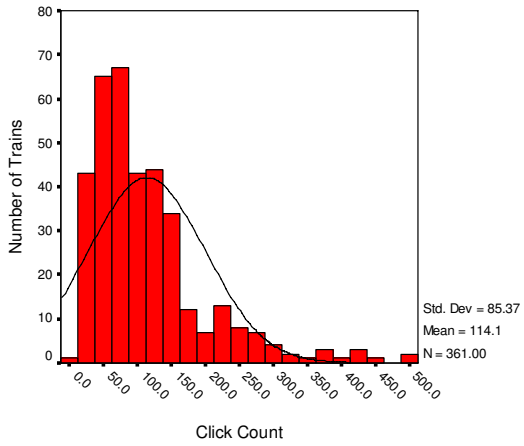

Figure 36. Calf click count per train.

Individual Calves.

A Univariate GLM revealed no significant differences in the mean clicks per train between calves ($F_{(5,360)}$=1.76). Excluding Little Blue's data, the results were still non-significant ($F_{(4,353)}$=2.01). However, the discrepancy in sample sizes per dolphin calf impacts the power to detect significant differences (see Table 8). Evidence of within session habituation was not found for any calf. Within recording sessions,

last trains contained more clicks than first trains statistically as often as first trains contained more clicks than last trains (π=0.5).

Individual calf trends generally mirrored the overall trends of increasing in click count as dolphins aged (see Figure 39). Although variance for clicks per train was large at times and each animal showed individual variability in their trends, some general tendencies were noticed (see Figure 40). Four of the 5 animals that were sampled early in the 6-month period (i.e., excluding Bailey) all had an initial increasing trend in the number of clicks per train. Only Little Blue showed a decline from month 1 to 2 but spiked noticeably in month 3 just prior to her death.

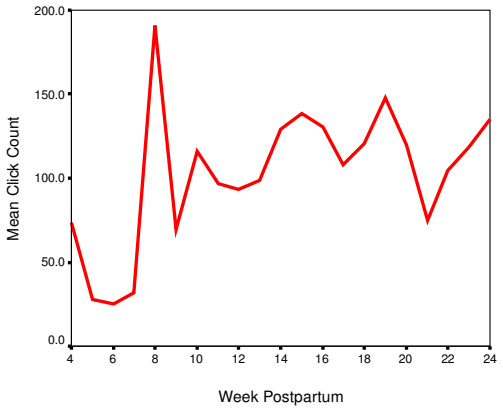

Figure 37. Mean calf click count per week postpartum

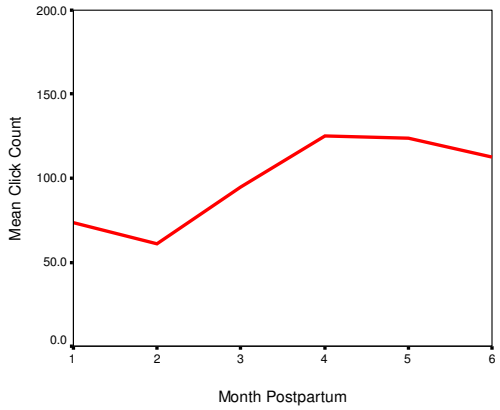

Figure 38. Mean calf click count per month postpartum

Table 8. Descriptive statistics for train click count per calf

Animal Name	N	Range	Minimum	Maximum	Mean	Std. Deviation
Little Opai	42	350	21	371	128.48	92.25
Little Shasta	109	488	18	506	122.53	93.27
Little Blue	7	189	15	204	87.57	67.63

Little Kolohe	65	406	12	418	100.32	69.26
Little April	59	470	18	488	127.59	104.51
Bailey	79	300	13	313	98.57	62.44

However, Little Blue only provided two trains in month 1, one train in month 2, and four trains in month 3, and thus the significance of her trends over time is questioned. Four calves (i.e., Little Shasta, Little April, Little Opai, and Little Kolohe) showed steadily increasing trends over various 2 to 3-month periods supporting the notion of a stable trend toward increasing clicks per train with age. Finally, 3 of the 5 surviving animals showed a decrease in clicks per train between months 5 and 6. Little Shasta and Little Opai both showed an increase during this period and Little Opai subsequently attained her highest mean click count per month of the testing period. Little Shasta had the greatest range in click count (range=488 clicks) while Little Blue's range was, understandably, smallest (range=189 clicks). Some months were represented by a very small number of trains per individual (e.g., two trains each in months 1 and 2 for Little Shasta), making those months difficult to compare to months with a larger sample size.

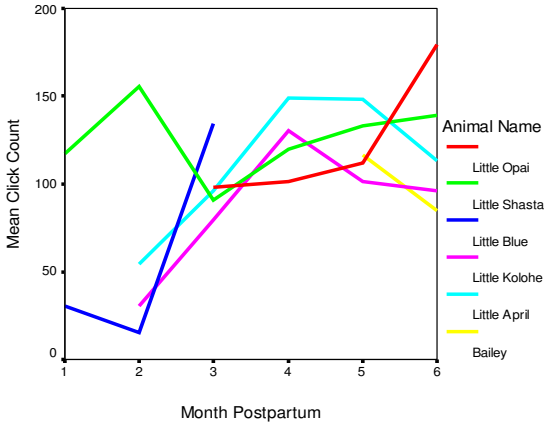

Figure 39. Mean click counts per calf by month postpartum

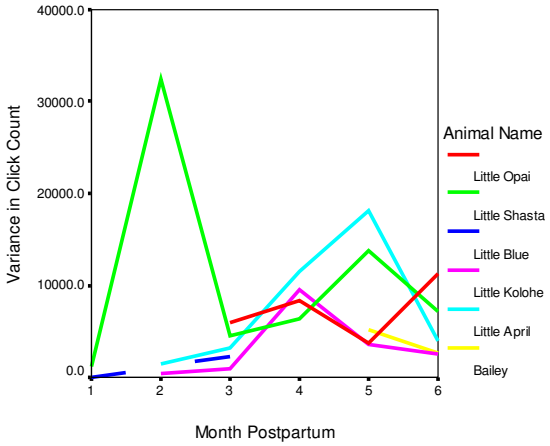

Figure 40. Variance in clicks per train per calf by month postpartum

Train Density

Overall Results.

Trains recorded from calves had an overall mean density of *M*=59.41 clicks/sec (*N*=361, *SD*=42.47). These trains showed nearly twice the range of those from adult females, fluctuating from a minimum of 16.81 to a maximum of 443.48 clicks/sec (see Figure 41). The majority (92%) of densities were below 100 clicks/sec with only six trains exceeding 200 clicks/sec. There was no significant correlation between calf gender (*r*=-0.09) or distance to the hydrophone (*r*=0.01) and train density.

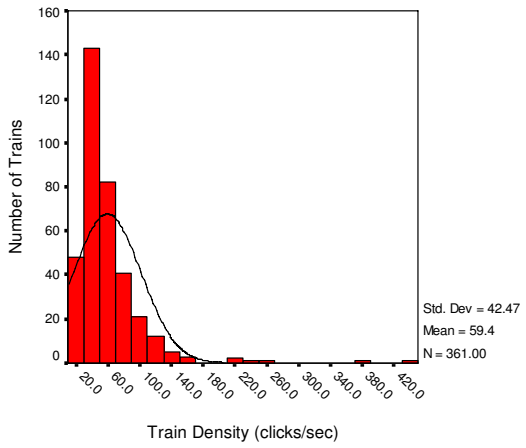

Figure 41. Calf train density (clicks/sec).

A Univariate GLM revealed overall significant differences in calf train density by month postpartum ($F_{(5,360)}$=2.390, p<0.05). A Tukey *a* post-hoc analysis, however, found no specific pair-wise month comparisons where density differences were significant. Over the 6-month study period, mean train density for calves by week postpartum fluctuated from a low of *M*=27.00 clicks/sec during week 6 to a high of *M*=94.55 clicks/sec during week 4 (see Figure 42). These weeks contained three and four trains, respectively, thus containing a substantially lower

sample size than other weeks. The overall train density for calves fluctuated noticeably early in the testing period, peaking early at *M*=94.55 clicks/sec during the first postpartum month and showing a minimum density immediately thereafter at *M*=35.54 clicks/sec in month 2 (see Figure 43). In the remaining months, calf density hovered around the overall mean and remained between 50 and 70 clicks/sec. Possible causes of this fluctuation and subsequent leveling of the density trend will be discussed later in this report.

Individual Calves.

A Univariate GLM revealed significant overall differences in the mean train density between calves ($F_{(5, 360)}$=6.58, p<.05). A Tukey α post-hoc test revealed that Little Blue had a significantly higher mean train density than all other (α<0.05). Little Opai also had a mean train density significantly higher than Little Kolohe and Bailey (α<0.05). Removing Little Blue from the analysis, the overall mean differences in calf train density remained significant ($F_{(4,353)}$=4.15, α<0.05) and Little Opai retained her significantly higher mean train density than Little Kolohe and Bailey (α<0.05). Per the Central Limit Theorem, Little Opai (n=42) and Little Blue (n=7) had the two lowest overall sample sizes, possibly affecting how representative these differences were (see Table 9). Evidence of within session habituation was not found for any calf. Within recording sessions, last trains were denser than first trains statistically as often as first trains were denser than last trains (π=0.5).

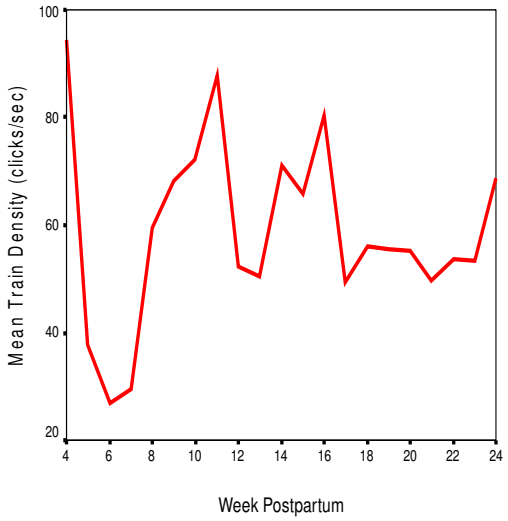

Figure 42. Mean calf train density per week postpartum

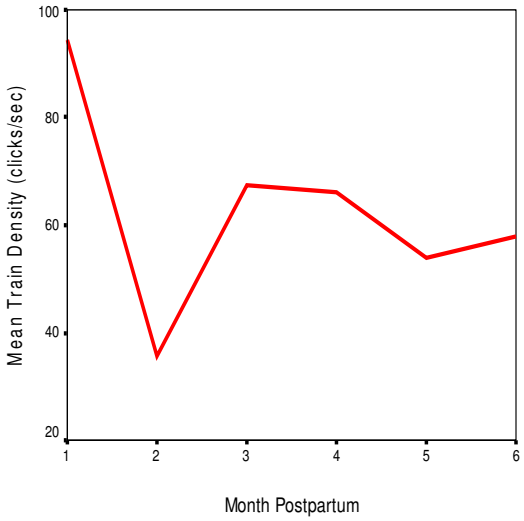

Figure 43. Mean calf train density per month postpartum

Calf trends in train density again differed noticeably between animals (see Figure 44). For example, while Little Opai decreased over the first 3 months she was sampled and then rose markedly from month 5 to month 6, Little Shasta, Little April, and Little Kolohe all increased in train density originally then leveled off for the remainder of the study period. Bailey's data appears to come after the stabilization seen in the other dolphins had already occurred and therefore shows little fluctuation. In general, variance in train density per calf increased over time while showing some by-month fluctuations (see Figure 45).

Table 9. Descriptive statistics in train density per calf.

Animal Name	N	Range	Minimum	Maximum	Mean	Std. Deviation
Little Opai	42	360.43	28.46	388.89	76.9367	62.9552
Little Shasta	109	137.89	22.00	159.89	59.5528	30.1152
Little Blue	7	415.71	27.77	443.48	128.0186	153.9729
Little Kolohe	65	210.00	22.22	232.22	53.7809	34.3522
Little April	59	244.05	17.31	261.36	57.2312	34.7249

Bailey	79	128.92	16.81	145.73	50.0658	24.3290

Although Little Blue's trend appears in stark contrast to the others, her low sample size and an illness that may have affected her developmental progress may account for the large range of values.

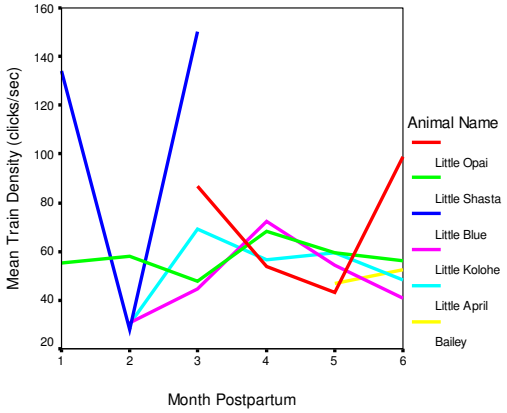

Figure 44. Mean train densities (clicks/sec) per calf per month postpartum.

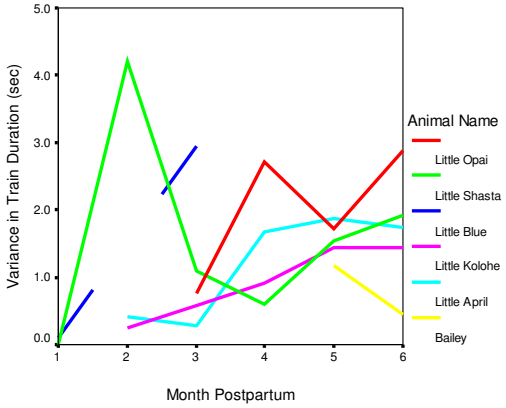

Figure 45. Variance in train density (clicks/sec) per calf by month postpartum.

Interclick Interval (ICI)

Overall Results.

From the 5 calves in the 2002 calving season, 130 trains were selected as suitable for an analysis of interclick interval (ICI) based on the selection criteria detailed in the methods. Calf trains had an overall mean ICI of *M*=25.32 ms (*N*=130, *SD*=10.35). The mean ICI per train ranged from a minimum of 5.95 ms to a maximum of 61.93ms (see Figure 46). The majority (76%) of mean ICIs were below 30 ms and 91% of trains fell below 40 ms. There was no significant correlation between calf gender (*r*=-0.22) or observed distance to the hydrophone (*r*=.104) and ICI.

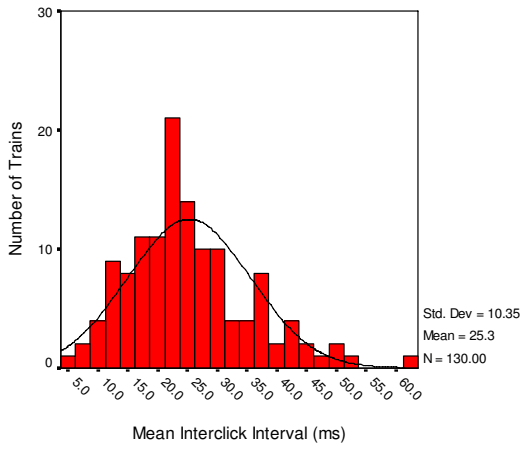

Figure 46. Calf mean ICI per train (ms).

A Univariate GLM did not find significant differences in overall calf mean train ICI by month postpartum ($F_{(5,129)}$=1.87). Per month sample sizes were inconsistent, potentially reducing the power to detect differences as they occurred. Over the 6-month study period, mean per train ICI for calves by week postpartum fluctuated from a low of *M*=19.29 ms during week 22 to a high of *M*=52.23 ms during week 6 (see Figure 47). The highest mean ICI per week was achieved during a week where only one train was recorded. A high *M*=35.71 ms (*n*=8) during week 17 is thus more representative. The overall mean train ICI by month postpartum for calves predictably remained fairly constant throughout the study period, only showing apparent fluctuation in the second month when just two trains were analyzed (see Figure 48).

Individual Calves.

A Univariate GLM revealed no significant differences between calves in mean train ICI ($F_{(4,129)}$=0.145). Excluding Little Blue due to her low sample size, the differences in mean train ICIs remained non-significant ($F_{(3,127)}$=0.195). The difference in sample sizes likely reduces the ability to detect significant differences (see Table 10). Evidence of within session habituation

was not found for any calf. Within recording sessions, last trains had longer mean ICI values than first trains statistically as often as first trains had longer mean ICI values than last trains (π=0.5).

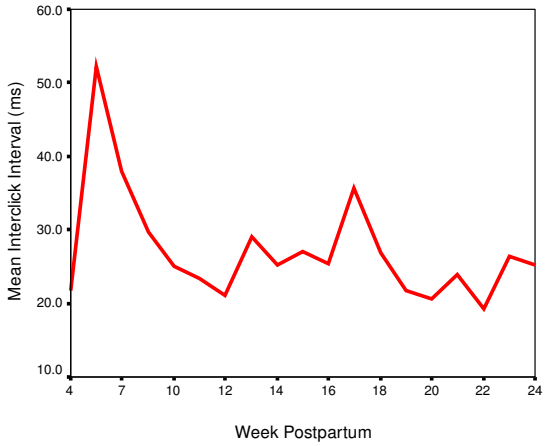

Figure 47. Mean calf ICI per train (ms) by week postpartum

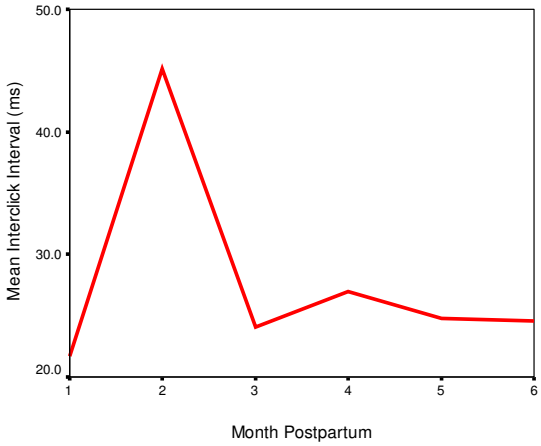

Figure 48. Mean calf ICI per train (ms) by month postpartum

Table 10. Descriptive statistics for each calf's ICI (ms).

Animal Name	N	Minimum	Maximum	Mean	Std. Deviation
Little Opai	11	15.6206	45.6462	24.575209	8.507655
Little Shasta	59	5.9513	50.8351	25.294363	10.445465
Little Blue	2	14.4587	36.0707	25.264700	15.281992
Little Kolohe	33	8.3195	61.9269	26.340518	11.288448
Little April	25	8.3772	52.2261	24.356756	9.991969

Per calf trends in mean train ICI were predictably erratic in the first 2 months (*n*=5) before attaining a level of conformity across animals in the later 4 months of the study (see Figure 49). Little Shasta and Little Opai showed little variability in mean per train ICIs throughout the study period. Little Kolohe showed somewhat more variability. Although Little Kolohe showed an initial spike during a month where she was represented by only one train, her

smaller spike in month 4 is represented by six trains. Spikes in mean per train ICI for Little April and Little Blue were in months when only one train was available for analysis from each calf. The remaining months from those animals were remarkably consistent. More obvious between-animal discrepancies were seen in the mean variance per train by month postpartum (see Figure 50).

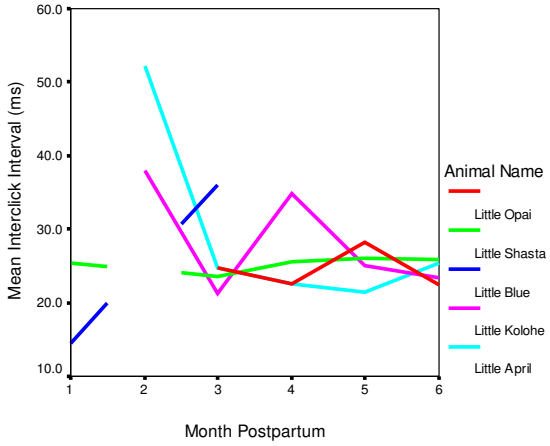

Figure 49. Mean per train ICI (ms) by month postpartum per calf

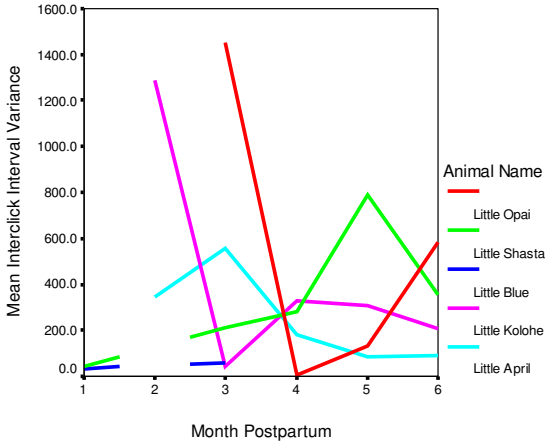

Figure 50. Mean per train ICI variance by month postpartum per calf

Concurrent Behaviors

Calves displayed a variety of behaviors during the recording sessions[4]. Previous authors (Carder & Ridgway, 1983; Bowles, Young, and Asper, 1988; Reiss, 1988) noted an increase in the observation of head motions as echolocation attempts became more prevalent. Calves here were observed cocking their heads as they passed the hydrophone more frequently as they aged in all cases except for Little Blue who maintained an equal number of head cocks across her observation period (see Figure 51). In total, head cocks were the most frequently observed

[4] During recordings of Bailey, concurrent behavioral observations were not recorded. This omission was noted and behavioral observations were added for the other calves.

head motions from the calves, representing 67.4% of observations. Head scanning motions were far less frequently observed (*n*=22 for wide and *n*=14 for narrow) than head cocks (*n*=190) but also appeared to generally increase in frequency as the dolphins aged.

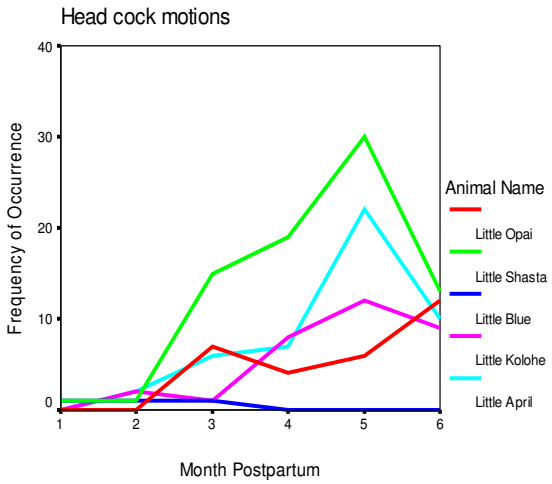

Figure 51. Head cock frequencies for calves by month postpartum.

Positions relative to other animals were noted during each echolocation recording. Unlike adults, the majority (66.7%) of recordings were attained when the calves approached the hydrophone alone. The frequency of solo hydrophone approaches increased for all calves over time before decreasing or leveling off in the sixth month (see Figure 52). The next most common positions included ahead of (9.9%), next to (7.8%), and infant to (5.0%) their mothers. In all but one case from Little Shasta, calves approached the hydrophone in a normal, dorsal up presentation.

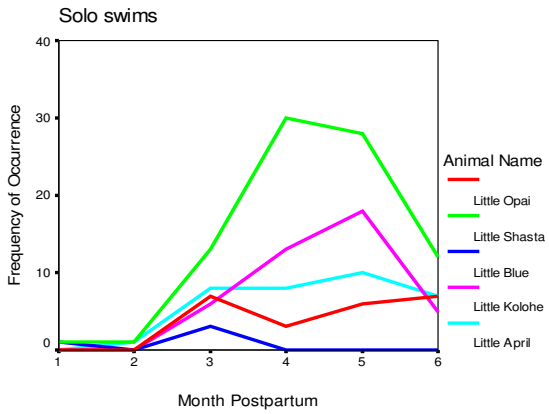

Figure 52. Calf solo swims by month postpartum

Finally, calves displayed a variety of other opportunistic behaviors during the study period (see Table 11). For example, Little Shasta (*n*=3), Little Kolohe (*n*=3), and Little April (*n*=1) were observed orienting on objects (e.g., sea birds, fingers, etc.) in the area of the hydrophone during the echolocation recordings. Instances of calf discipline (*n*=2) were seen with Little Shasta and Little Kolohe and involved the adult female chasing her calf. Twenty-five different occurrences of whistles were recorded during the echolocation recordings although the identity of the whistler could not be convincingly identified.

Squeals

Eight squeals were recorded from calves, four from Little Shasta and four from Little April. Squeals from Little Shasta were recorded in the third (*n*=3) and fourth (*n*=1) month postpartum and all squeals from Little April (*n*=4) were recorded during month 6. These squeals were very short and very dense (see Table 12). Both calves were solo swimming in a typical, dorsal up posture with their mouths closed when the squeals were emitted. Little Shasta showed no head motions toward the hydrophone but Little April head cocked toward the hydrophone during each of her four squeals.

Table 11. Other behaviors associated with calf echolocation click trains.

Animal Name			Frequency	Percent	Cumulative Percent
Little Opai	Valid	None	39	92.9	92.9
		Whistles	2	4.8	97.6
		Bubbles	1	2.4	100.0
		Total	42	100.0	
Little Shasta	Valid	None	96	85.0	85.0
		Whistles	5	4.4	89.4
		Whistles with bubbles	3	2.7	92.0
		Hit hydrophone	1	.9	92.9
		Orient at Object (e.g., seagull, kelp, fingers, etc.)	3	2.7	95.6
		Discipline	1	.9	96.5
		Squeal	4	3.5	100.0
		Total	113	100.0	
Little Blue	Valid	None	7	100.0	100.0
Little Kolohe	Valid	None	54	83.1	83.1
		Whistles	6	9.2	92.3
		Whistles with bubbles	1	1.5	93.8
		Orient at Object (e.g., seagull, kelp, fingers, etc.)	3	4.6	98.5
		Discipline	1	1.5	100.0
		Total	65	100.0	
Little April	Valid	None	50	79.4	79.4

		Whistles	8	12.7	92.1
		Orient at Object (e.g., seagull, kelp, fingers, etc.)	1	1.6	93.7
		Squeal	4	6.3	100.0
		Total	63	100.0	

Table 12. Calf squeal descriptive statistics

Animal Name		N	Minimum	Maximum	Mean	Std. Deviation
Little Shasta	Train Duration (sec)	4	.18	.64	.3550	.2009
	Click Count	4	105	593	277.50	215.67
	Train Density (clicks/sec)	4	583.33	926.56	727.7000	166.5869
Little April	Train Duration (sec)	4	.04	.08	6.000E-02	1.633E-02
	Click Count	4	72	97	88.25	11.35
	Train Density (clicks/sec)	4	1212.50	1800.00	1519.7900	243.7974

Adults vs. Calves

A total of 187 trains were collected from adult females over the 6-month study while 361 trains were collected from calves. Highly prolific adult females tended to have highly prolific calves, and mothers who produced fewer samples of recorded click trains also had offspring with smaller sample sizes. Shasta, for example, provided the second highest number of adult samples (*n*=43) and her calf produced the most click trains per calf of the group (*n*=109). Excluding the Blue pair due to Little Blue's death and the Snapper pair due to the calf-focused research design, April provided the fewest adult samples (*n*=27) and Little April provided the second fewest calf samples (*n*=59). Kolohe provided the third most adult trains (*n*=40) and Little Kolohe provided the third most calf trains (*n*=65). The exception to this finding is the Opai pair.

Opai provided the most overall adult trains (*n*=50) but Little Opai provided the fewest trains (*n*=42) of all calves except Little Blue. Excepting, then, the Opai pair and then the Snapper pair due to a sampling bias against adult trains in that study design, the Spearman's rank correlation between adult and calf sample size rank is perfect (r_s=1.00, α<0.01).

No significant differences were found between adult animals in mean train duration, clicks per train, or train density. Significant differences were similarly absent between calves for mean train duration, clicks per train, or per train ICI. Thus for three of the four train variables, both groups of animals showed similar results within their group. The values for individuals in these groups could thus be combined, creating overall calf and adult models to be used in further comparisons.

Train Duration

Overall Comparisons.

A Univariate GLM revealed no significant differences in the overall mean train duration for adults (*M*=2.08 sec) and calves (*M*=2.04 sec) ($F_{(1,547)}$=0.193). When results were separated by months postpartum, calves and adults showed the most discrepancy in mean train duration in the first 2 months although significant differences between adults and calves per month were found in month 1 ($F_{(1,61)}$=4.85, α<0.05, see Figure 53) and month 6 ($F_{(1,114)}$=3.96, α<0.05). During the first 2 months, adult mean train durations were 0.95 sec and 0.71 sec longer, respectively, than the mean train duration of calf trains. Adults, however, were represented by far more trains than calves were in these first 2 months (*n*=58 vs. 4 in month 1; *n*=51 vs. 10 in month 2). As calf sample size per month increased, mean values began to more closely approximate the higher-sample size adult per month values. Similarly, the fourth month contained the lowest mean adult train duration (*M*=1.56 sec) and was also the month with the smallest adult train

sample size (*n*=14). Adult mean train duration and sample size per month declined steadily over the first 4 months while calf mean train duration and sample size per month rose steadily resulting in a low duration discrepancy of 0.14 sec during the third month. At that time, a shift is apparent where calf trains became longer than adult trains during month 4 and 5. Adult trains were significantly longer than calf trains in the sixth month despite calves being represented by nearly six times as many trains that month as adults.

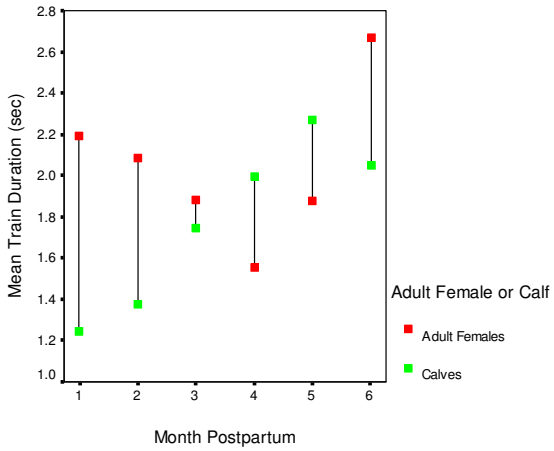

Figure 53. Adult female vs. calf mean train duration (sec) by month postpartum

Individual Mother/Calf Pairs.

Overall mean train durations between individual mother/calf pairs were not statistically significantly different (Univariate GLM, $F_{(5,540)}$=0.50). Excluding the Blue pair due to their low sample size, results remain non-significant ($F_{(4,514)}$=0.343). Apart from the Snapper and Blue pairs because they were not sampled over the entire study period, April and Little April had the longest combined mean train duration (*M*=2.14 sec, *n*=86). The shortest combined mean train duration was found with Opai and Little Opai (*M*=2.02, *n*=92). For all six mother/calf pairs, the overall standard deviation for the calf exceeded the overall standard deviation for the adult

female indicating a greater variability of recorded train durations for calves than adults (see Figures 54-59).

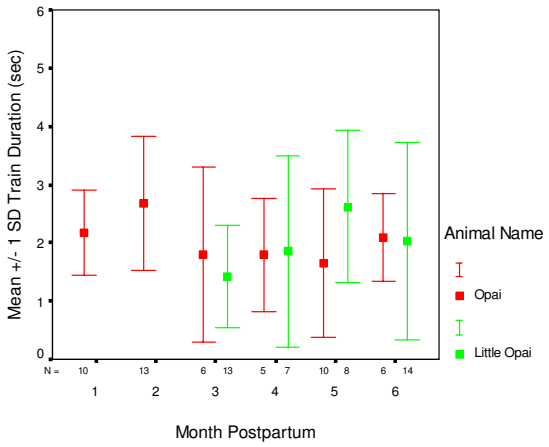

Figure 54. Opai & Little Opai train duration error plot by month postpartum

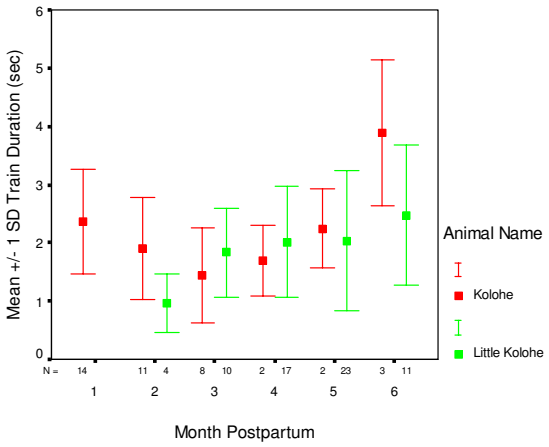

Figure 55. Kolohe & Little Kolohe train duration error plot by month postpartum

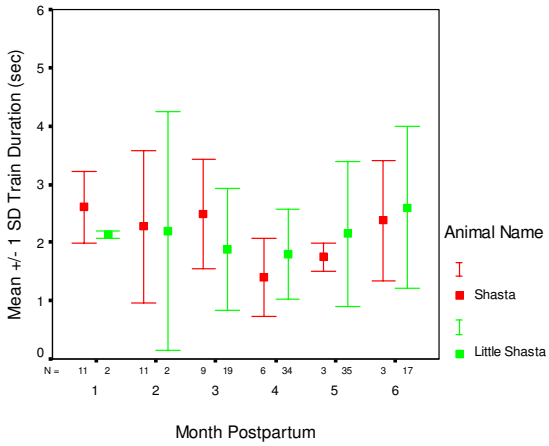

Figure 56. Shasta & Little Shasta train duration error plot by month postpartum

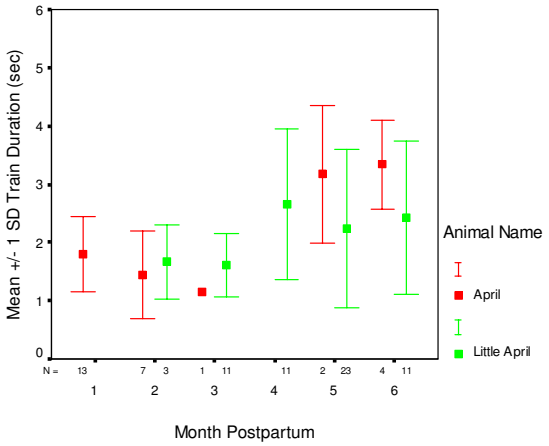

Figure 57. April & Little April train duration error plot by month postpartum

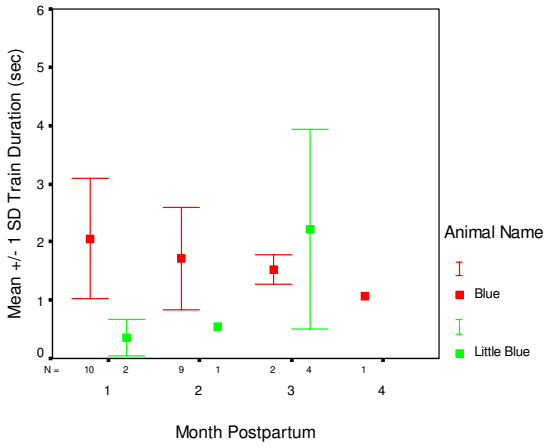

Figure 58. Blue & Little Blue train duration error plot by month postpartum

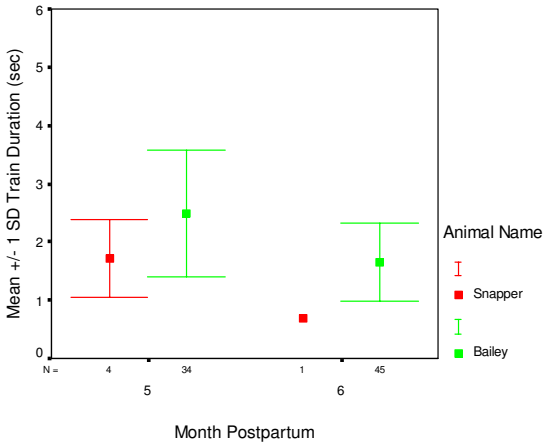

Figure 59. Snapper & Bailey train duration error plot by month postpartum

Clicks per Train

Overall Comparisons.

Overall mean clicks per train for adults (*M*=116.6 clicks) and calves (*M*=114.1 clicks) did not differ significantly (Univariate GLM, $F_{(1,547)}$ =0.117). Significant differences were found, however, showing fewer clicks per train from calves than adults in the second postpartum month ($F_{(1,60)}$=4.82, α<0.05). Differences in the average number of clicks per train between adult females and calves were, like train duration, most visually prominent in the first 2 months (see Figure 60). During these months, adult trains contained, on average, 46 and 53 more clicks, respectively, than calf trains. Adult mean train click count remained steady over the first 3 months while calf mean clicks per train dropped from month 1 to month 2 and then rose sharply to month 3 as the sample size for calves rose nearly six-fold. Calf trains contained more clicks than adult trains during month 4 and 5 as calf sample sizes rose and adult sample sizes decreased. Similar to findings with train duration, adult trains exceeded the mean calf train click count in the sixth month.

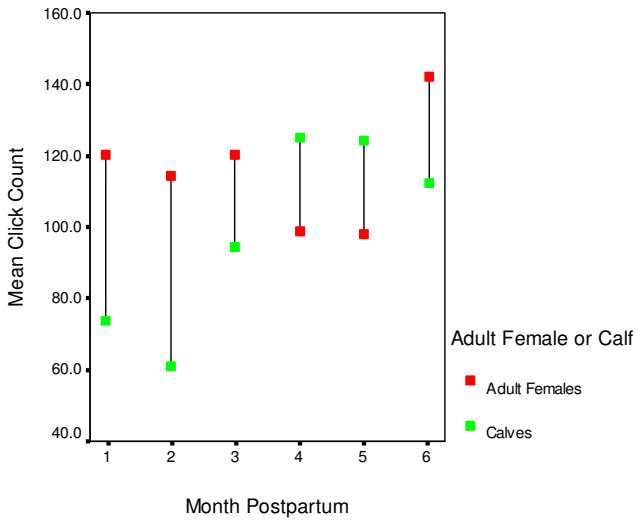

Figure 60. Adult vs. calf mean click count by month postpartum

Individual Mother/Calf Pairs.

Overall mean clicks per train did not differ significantly between mother/calf pairs ($F_{(5,540)}$=2.17). When the Blue pair was excluded due to low sample size, however, overall significant differences between pairs were found ($F_{(4,518)}$=2.44, α<0.05). A Tukey's *a* post-hoc analysis revealed no specific per-pair significant differences. Apart from the Blue and Snapper pairs, Shasta and Little Shasta had the largest combined mean clicks per train (*M*=125.50 clicks, *n*=152). The fewest combined mean train click count belonged to Kolohe and Little Kolohe (*M*=104.29, *n*=105). For all six mother/calf pairs, the overall standard deviation for the calf was greater than the overall standard deviation for the adult female indicating a greater variability of clicks per train for calves than adults (see Figures 61-66).

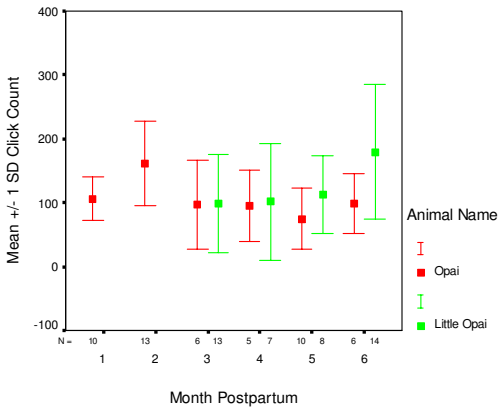

Figure 61. Opai & Little Opai train click count error plot by month postpartum

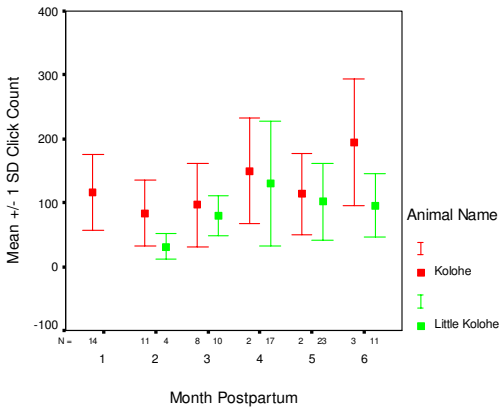

Figure 62. Kolohe & Little Kolohe train click count error plot by month postpartum

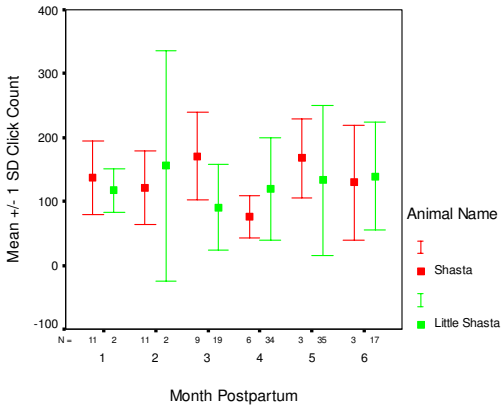

Figure 63. Shasta & Little Shasta train click count error plot by month postpartum

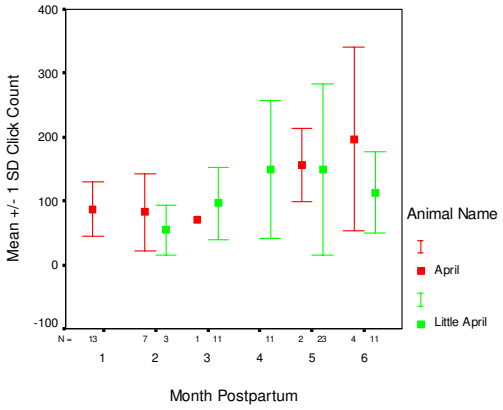

Figure 64. April & Little April train click count error plot by month postpartum

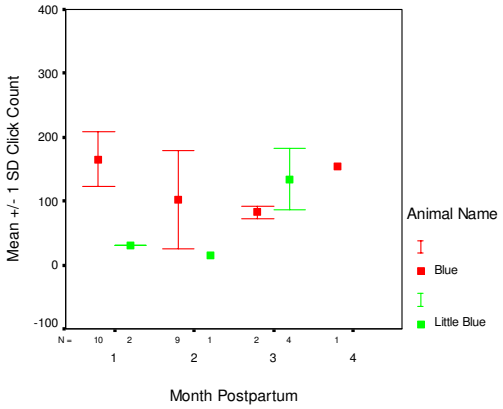

Figure 65. Blue & Little Blue train click count error plot by month postpartum

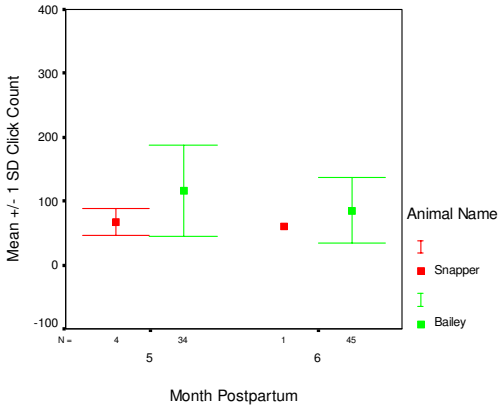

Figure 66. Snapper & Bailey train click count error plot by month postpartum

Train Density

Overall Comparisons.

Overall mean train density for adults (*M*=59.50 clicks/sec) and calves (*M*=59.41 clicks/sec) were virtually identical (Univariate GLM, $F_{(1,547)}$ =0.001). Differences in the average number of clicks per train between adult females and calves were, like train duration, most visually prominent in the first 2 months (see Figure 67). During month 1, adult trains were significantly less dense than calf trains by, on average, 36.36 clicks/sec ($F_{(1,61)}$=4.085, α<0.05). During month 2, calf trains were significantly less dense than adult trains by, on average, 20.18 clicks/sec ($F_{(1,60)}$=6.30, α<0.05). Adult mean train densities remained relatively constant over the 6-month study period while calf mean train densities dropped from month 1 to month 2 before leveling off for the remaining 4 months of the study. For months 3-6, calf and adult mean train densities were virtually indistinguishable.

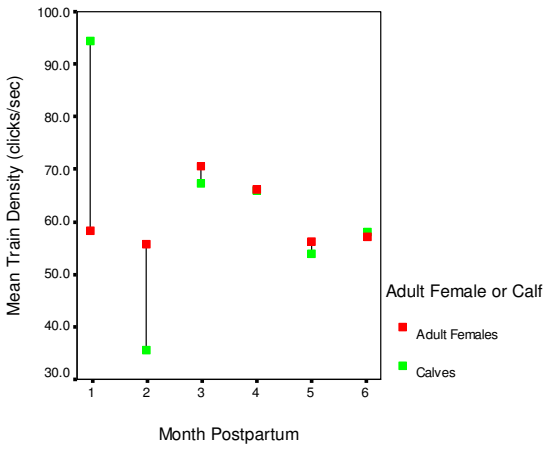

Figure 67. Adult vs. calf mean train density by month postpartum

Individual Mother/calf Pairs.

Overall mean train density differed significantly between mother/calf pairs ($F_{(5,540)}$=.3.45, α<0.05). When the Blue pair was excluded due to low sample size, overall significant differences remained ($F_{(4,518)}$=2.51, α<0.05). A Tukey's *a* post-hoc analysis found the Opai pair to have significantly more dense trains than the Snapper Pair (α<0.05). Apart from the Blue and Snapper pairs, Shasta and Little Shasta had the lowest combined train density (*M*=28.40 clicks/sec, *n*=152). The highest combined mean train click count belonged to Opai and Little Opai (*M*=47.14 clicks/sec, *n*=92). For all mother/calf pairs except the Kolohe pair, the overall standard deviation for the calf was greater than the overall standard deviation for the adult female indicating a greater variability in train density for calves than adults (see Figures 68-73).

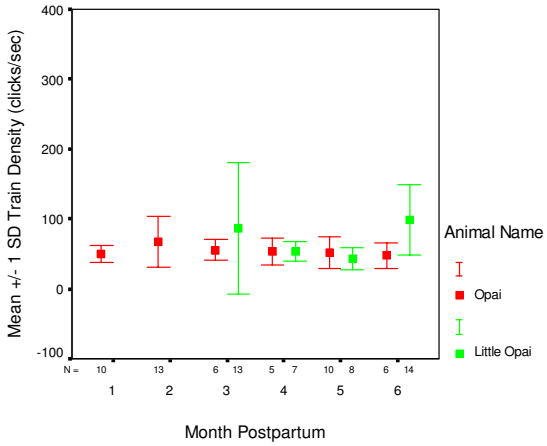

Figure 68. Opai & Little Opai train density error plot by month postpartum

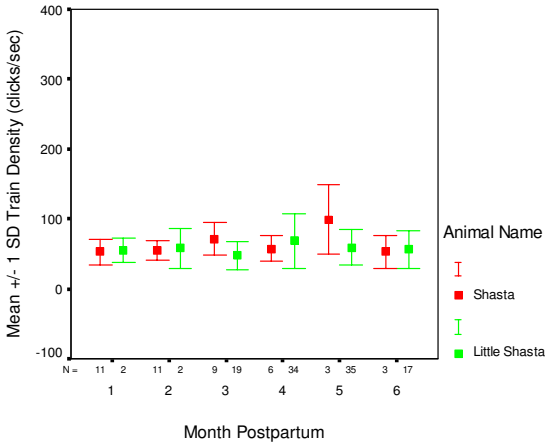

Figure 70. Shasta & Little Shasta train density error plot by month postpartum

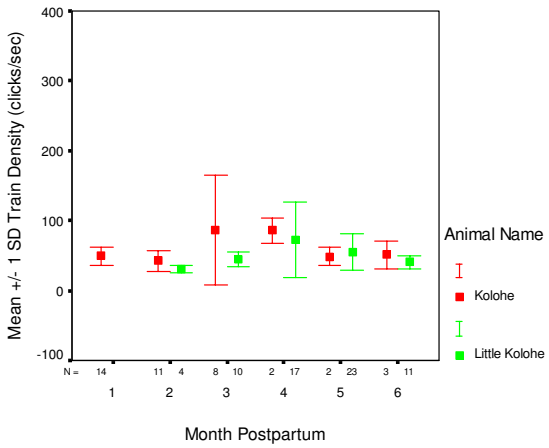

Figure 69. Kolohe & Little Kolohe train density error plot by month postpartum

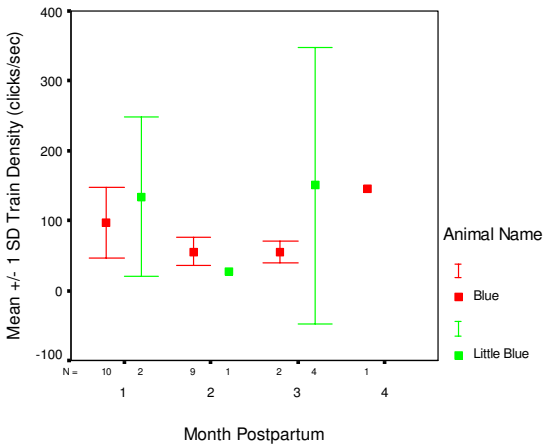

Figure 72. Blue & Little Blue train density error plot by month postpartum

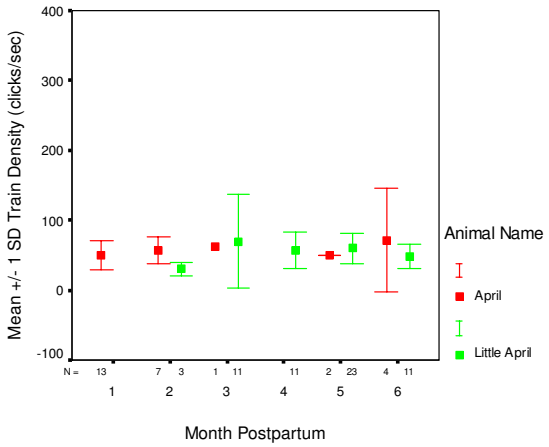

Figure 71. April & Little April train density error plot by month postpartum

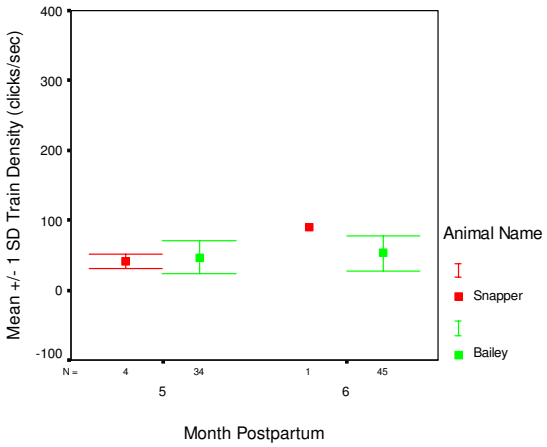

Figure 73. Snapper & Bailey train density error plot by month postpartum

Interclick Interval (ICI)

Overall Comparisons.

Overall mean train ICI for adults (*M*=21.95 ms) was significantly lower than for calves (*M*=25.32 ms, Univariate GLM, $F_{(1,547)}$ =6.74, α<0.05). Differences in the mean train ICI between adult females and calves were most visually evident in the second month (see Figure 74). Mean adult train ICI were significantly lower than calf train ICIs in month 2 ($F_{(1,29)}$=16.98, α<0.05) and

month 3 ($F_{(1,29)}$=4.60, α<0.05). Although the differences in month 4 are visually prominent, insufficient power existed to detect significant statistical differences. Adult mean train ICIs declined until month 4 then rose again through month 6. In contrast, calf mean train ICI's fluctuated from month 1 to month 2 before leveling off for the remaining 4 months of the study as the per month sample size grew.

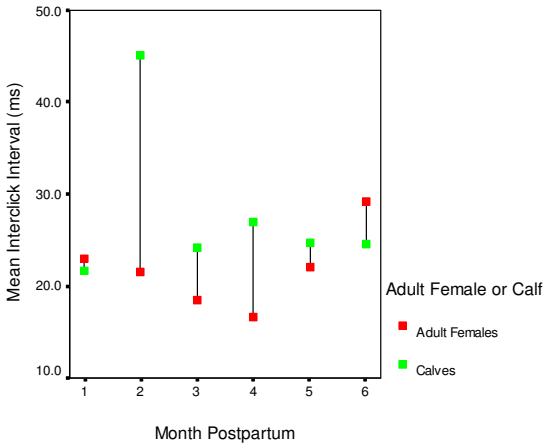

Figure 74. Adult vs. calf mean train ICI by month postpartum

Individual Mother/Calf Pairs.

Overall mean train ICI did not differ significantly between mother/calf pairs ($F_{(4,223)}$=2.35). When the Blue pair was excluded due to low sample size, overall differences remained non-significant ($F_{(3,206)}$=0.57). Excepting the Blue pair, Kolohe and Little Kolohe had the longest mean train ICI (*M*=25.25 ms, *n*=54). The shortest combined mean train click count belonged to Opai and Little Opai (*M*=22.67, *n*=28). For all mother/calf pairs except April and Little April, the overall standard deviation for the calf was greater than the overall standard deviation for the adult female indicating a greater variability of train ICI for calves than adults (see Figures 75-79).

Concurrent Behaviors

Head Motions.

Both adults and calves displayed a variety of head motions during their passes by the hydrophone (see Figure 80). In both adults and calves, head cock motions were the most prevalent (58.8% and 67.4%, respectively, of observations). Head scanning motions, both wide and narrow, were more common in calves than in adults.

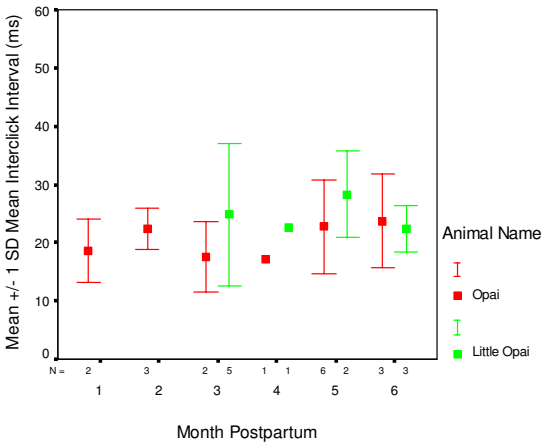

Figure 75. Opai & Little Opai mean train ICI error plot by month postpartum

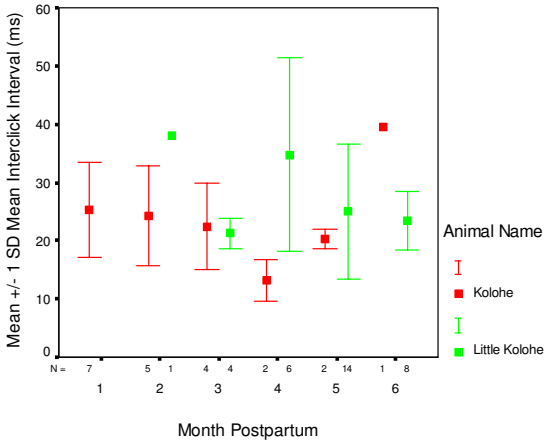

Figure 79. Kolohe & Little Kolohe mean train ICI error plot by month postpartum

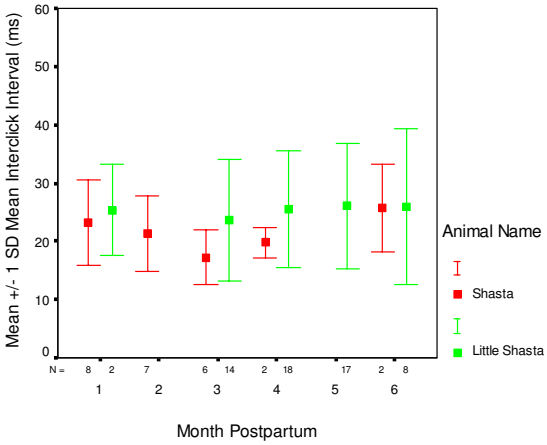

Figure 77. Shasta & Little Shasta mean train ICI error plot by month postpartum

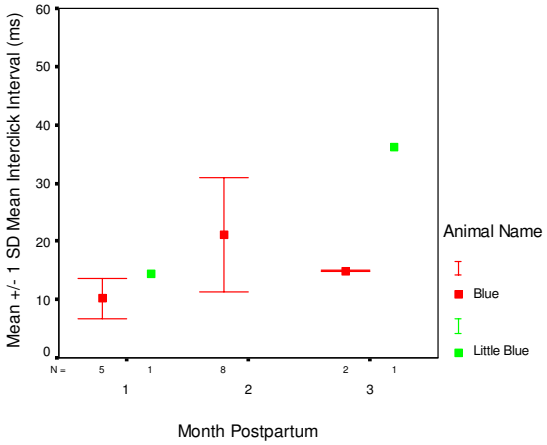

Figure 76. Blue & Little Blue mean train ICI error plot by month postpartum

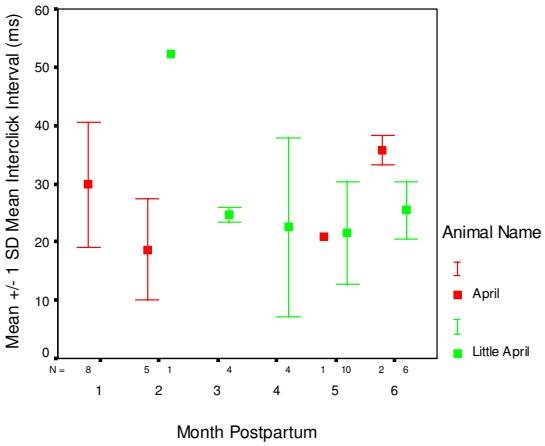

Figure 78. April & Little April mean train ICI error plot by month postpartum

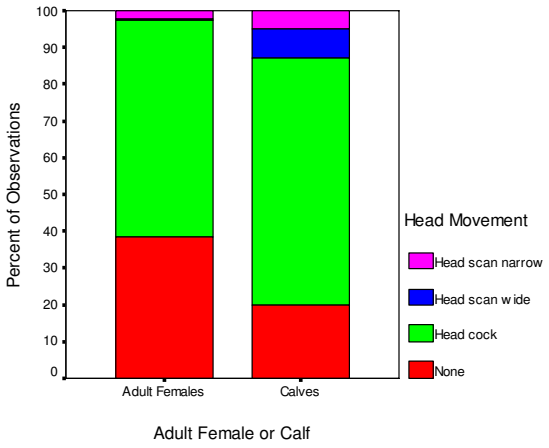

Figure 80. Head motion observation percentages for adult females vs. calves

Relative Approach Positions.

Calves were recorded while passing the hydrophone alone (66.7% of observations) more often than adults (3.8%). Many adult recordings were obtained early in the study period while accompanied by the calf. As the calves aged and exercised more independence, their sampling rate increased in conjunction with the increased amount of time they spent swimming away from their mothers. In general, recordings of calves made while they were with adult females were rare but recordings of adults in the company of their calves were more common (see Figure 81).

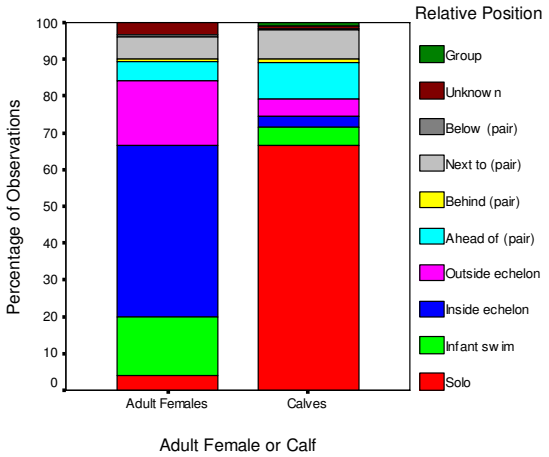

Figure 81. Percentage of the Calf relative-swim position from observations for adult females vs. calves

Opportunistic Behaviors

The breadth of opportunistic behaviors seen in calves was larger than seen for adults. Both categories of dolphins were observed producing bubbles during their hydrophone passes and whistles were heard during recordings for each group. However, the majority of adult and calf recordings contained no observed concurrent ancillary behaviors (see Figure 82).

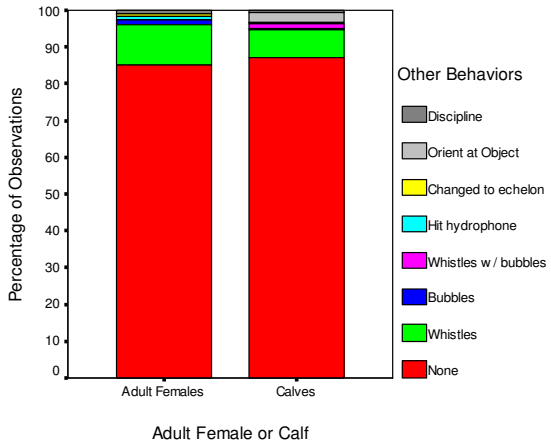

Figure 82. Other behavior observation percentages for adult females vs. calves

Squeals

Eight burst-pulse emissions were recorded from 2 calves and 3 burst-pulses were recorded from a single adult female. The mean squeal duration was somewhat longer for Little Shasta (*M*=0.355 sec, *n*=4) than for either Little April (*M*=0.06 sec, *n*=4) or Kolohe (*M*=0.067 sec, *n*=3). Accordingly, Little Shasta's squeals contained, on average, more clicks (*M*=278) than Little April (*M*=88) or Kolohe (*M*=55).

Density of burst-pulses was inconsistent between animals with Little April emitting far more dense squeals (*M*=1519.79 clicks/sec) than either Little Shasta (*M*=727.70 clicks/sec) or Kolohe (*M*=825.00 clicks/sec).

CHAPTER IV

DISCUSSION

General Discussion

This research project represents the most comprehensive and extensive investigation of bottlenose dolphin echolocation ontogeny to date. A total of 275 trains were collected over the first 6 months of life from 5 calves in 2002, a nearly 3-fold increase over the 94 calf trains collected from the first calf in the pilot study (Hendry, 2002). Taken together, these 369 calf trains represent a sizable improvement over the 7 trains recorded by Carder & Ridgway (1983) or the 3 trains recorded by Lindhard (1988) (number of recorded trains was not provided by Reiss, 1988). Successful recording sessions occurred far more frequently in this evolution than in the pilot study. Calf samples were recorded on 88 days in 2002 compared with 24 days in 2000. Calf samples were also recorded far earlier in life (on day 22) in this investigation than in the pilot study, where the first calf train was recorded on

day 117, the Carder & Ridgway (1983) investigation, where the first train was seen 60 days postpartum, or the Ricciardi, et al. (2003) study, where the first train was not recorded until 3 months postpartum. Finally, unlike any of the five previous investigations of calf echolocation (Ricciardi, et al., 2003; Hendry, 2002; Lindhard, 1988; Reiss, 1988; Carder & Ridgway, 1983), this investigation included a substantial number of echolocation samples provided by adult females. This deliberate concurrent investigation of the calves' mothers allowed for more direct adult to calf comparisons.

Bottlenose dolphin calves appear to develop their ability to echolocate in the first few months following parturition. Evidence of calf echolocation was not found at birth and no echolocation samples were recorded prior to 3 weeks postpartum. In the first 2 postpartum months, calves produced the fewest number of trains, the shortest trains (on average), and the trains with the fewest mean number of clicks of the study period. 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 the average adult values as sampled across the study period. Taken in conjunction with the Gardner & Varanasi (2003) report of a lower concentration of acoustic fat in the acoustic tissues of fetal and neonate dolphins, these findings indicate that the echolocation sensory system is not in mature use at birth and likely requires a combination of time, physiological maturation, and behavioral development to attain full adult-like functionality.

For the last 4 months of the study, calf values and adult values were significantly divergent on only two occasions; calf click trains were significantly shorter, on average, in the sixth month than adult click trains, and adult mean train ICI was significantly lower than calf mean train ICI in month 3. Although sample size incongruities again impact the ability to detect significant differences that may have occurred (e.g., the visually apparent but statistically non-significant differences between adult and calf mean ICI per train in month 4), the similarities between adult and calf mean values from month 3 to

month 6 and the overall lack of significant differences in train duration, click count, or density between adults and calves when averaged across the entire study period indicates that calf echolocation samples, on average, approximated mean adult values by roughly 3 months postpartum. Fluctuations in individual variables around these mean values will be covered later in this discussion.

These results must be viewed with caution, however. Two distinct possibilities are evident. First, calves could be born without the ability to properly echolocate, developing those abilities over the first few months of life. The observed data, therefore, would be reflective of this developmental period. A strong piece of evidence for this conclusion is the small sample size from calves in early months. Despite intense, repeated attempts to record calf samples, echolocation trains from calves simply were not captured in any large amounts 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.

Second, the observed values in the study variables 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. Variability is generally higher in smaller samples than in larger samples. Had a larger number of samples been obtained during these months, values might have more closely approximated the calf values seen later in the study period and the adult values recorded on average. Months of low sample sizes from calves also contained high sample sizes from adults, and vice versa, further biasing the comparisons and possibly altering the meaningfulness of the results. Several factors may have influenced the frequency of samples from an individual adult including personal interest in the hydrophone, social status (e.g. dominant females preventing other subordinate females from approaching the hydrophone, etc.), and the health and tendencies of their calf. Factors that may have influenced the frequency of samples from an individual calf included age, health, personal interest in the

hydrophone, the degree of permissiveness of the calf's mother, and the boldness of the calf for exploring its environment. Although this study focused deliberately on capturing early echolocation samples from calves, and in fact did so 4 months earlier than in the pilot study, an even stronger attempt to capture more very early echolocation attempts could elucidate the role of sample size in the observed echolocation variable changes.

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, replicating results reported for Bailey in the pilot study (Hendry, 2002). Calves thus produced, on average, longer trains as they aged until the mean duration of those trains approximated the values seen in adults (on the order of 2 seconds). For both adults and calves, more than 80% of recorded trains lasted less than 3 seconds, and all calves except for Bailey had longer mean train durations in the last month they were sampled than in the first month they were sampled. Considerable variation around the mean density values per month was apparent throughout the study. Although an analysis of standard deviations shows a fairly wide range of per month values for both calves and adults, standard deviations are impacted by sample sizes and must thus be interpreted in light of the sample size inequalities in this 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 experimenting with their click trains as they aged. Calves emitted more very long trains than did adults (7 trains vs. 2 trains, respectively, exceeded 5 sec) and more very short trains (8 trains below 0.5 sec for calves, no trains below 0.5 sec for adults). As this increase in per month duration ranges was not mirrored in the adult values, these findings support the idea that although calves develop the ability to echolocate fairly early in their lives, they may require a slightly longer period of time to attain a more mature mastery of their echolocation.

These results could indicate developmental patterns 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, & 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 is limited in both dolphin and manatee calves at younger ages, the expanding length of acoustic signals in these species with age may be tied to physiological maturation factors. The decrease in mean train duration after 5 months may therefore represent the calves' sufficient accumulation of experience with their biosonar to enable them 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). Consequently, standard deviations for click counts in biosonar studies tend to be high. The standard deviation of calf values in this study was larger than the standard deviation of adult values for all 6 mother/calf pairs, and calves displayed a larger range of clicks per train than adults over the course of the study. As with duration, the range of clicks per train increased steadily across subsequent months before declining somewhat in month 6. This trend was not mirrored in the adults, again potentially indicating that calves were still developing their echolocation abilities across the study period. As calves aged, they included more clicks in their echolocation trains in accordance with data from bats which suggests a general increase in click rate with age as they develop the ability to pack clicks more closely together (Moss et al., 1997; Moss, 1988). All calves except for Little Blue showed individual 2 to 3-month periods of

increases in mean clicks per train. The most apparent differences occurred between the first 2 months and results from later in the study. Due perhaps to the reduced power to detect differences, however, overall significant differences in mean clicks per train between months were not seen. For both adults and calves, trains contained approximately 115 clicks on average over the study period and more than 85% of trains contained less than 200 clicks. Differences between mean click counts for adults and calves were smaller in months 3-6 than they were in the first 2 months of the study, again illuminating those early months as notable in the ontogeny of echolocation.

Individual differences in the number of clicks used in a given detection task has been reported previously (Au & Penner, 1981; Au & Turl, 1983). Little Shasta and Little Opai did not show a decrease in mean clicks per train between months 5 and 6, trends possibly explained by anecdotal observations of the calves' demeanors. Little Shasta was a very independent calf, providing substantial numbers of echolocation samples and investigating the hydrophone frequently from an early age. A steady and continual increase in the degree to which she investigated her world is not unexpected. Little Opai, on the other hand, was infrequently seen away from his mother and only began to show a noticeable degree of independence and curiosity about his environment later in the study period. An increase in his values between month 5 and 6 may thus be reflective of a developmental delay in his case.

Overall mean clicks per train were positively correlated with overall mean train durations for both adults and calves. This finding 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 and possibly indicative of an increase in curiosity. This

interpretation is bolstered 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 is likely similar to ICI, limited by physical factors and thus less likely to show maturational or developmental variation over time. As such, mean density values for adults and calves were nearly indistinguishable between 3 and 6 months postpartum and when taken overall. More than 90% of trains in both groups fell below 100 clicks/sec and, for both calves and adults, train density decreased gradually from 3-6 months. Differences between the two groups were only apparent, as with train duration and click count, in the first 2 months postpartum further implicating these early months as significant in the development of the echolocation sensory system.

Interclick Interval (ICI)

Overall mean per train ICI values for both adults (*M*=21.95 ms) and calves (*M*=25.32 ms) was on par with the stable ICI of around 27 ms found in wild bottlenose dolphins by Goodson & Mayo (1995). The range of intervals in calves (5.95 ms to 61.93ms) and adults (6.43 ms to 49.98 ms) was, however, considerably smaller than the ranges seen in wild bottlenose dolphins by Akamatsu et al. (1998) who also employed a single hydrophone in their data collection. 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 the composition of the nursery environments (i.e. open water vs. concrete habitat). At the end of the Lindhard (1988) 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. Bats are considerably smaller animals than dolphins and spend far less time dependent on their mothers for their survival, thus shortening the amount of time available for the development of their echolocation skills and perhaps compressing trends observed in cetaceans species.

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 'heads-up' fashion and are often seen in echelon positions with their mothers, allowing them to slipstream in their mother's bow wave and be essentially towed through the water (Mann & Smuts, 1999). It may indeed take some time for calves to develop the proper muscle tone and coordination necessary to breathe and swim commandingly thus making neonate calves vulnerable to predation. If calves also require time to build up the mature fatty acid concentrations in their acoustic window tissues for the proper production and reception of echolocation, then echolocations produced as a neonate could be ill formed, ineffective, and un-controlled, potentially broadcasting the calf's presence and defenselessness to predators. As calves do not need to forage as neonates, 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 neonate calves while they mature physiologically may therefore be evolutionarily beneficial.

During this period, calves need not be isolated from echolocation and may indeed be gathering passive experience hearing 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 be able to receive echolocations transmitted by their mothers. Such echoic eavesdropping has been proposed between adult Hector's dolphins (*Cephalorhynchus hectori*) during foraging bouts (Dawson, 1991) and adult bottlenose dolphins engaged in detection tasks (Xitco & Roitblat, 1996). While their acoustic tissues are maturing, therefore, they can procure exposure to one half of the echolocation process (receiving clicks) without betraying their presence to alert foes within acoustic range. Behavioral patterns seen in this study may support this notion as adults provided far more echolocation samples in the presence of their calves then they did alone, perhaps as part of a process evolutionarily designed to increase their calves' exposure to echolocation. The stimulus in this study, essentially a simple PVC pipe, was likely not terribly interesting echoically to an adult animal with years of exposure to open-ocean fine detection tasks. That adults chose to echolocate on the object at all, and did so without showing within session habituation effects, indicates that either they saw the object as threatening and continued to be vigilant of its presence and/or they continued to acknowledge the object in the presence of their calves perhaps as a means of exposing the calves to echolocation. Their decreased interest in echolocating on the hydrophone in later months would thus be indicative of their habituation to the hydrophone as a non-threatening object in their environment or an acknowledgement that the calves were capable of echolocating on the hydrophone by themselves and thus did not require their continued assistance. Taken loosely, these findings may be indicative of a preliminary form of teaching in bottlenose dolphins, although much more research and evidence is required before any conclusive claims can be made.

Behavioral patterns of calf associations seen in this study mirror the results of other investigations. Calves spent increasingly larger amounts of time observed apart from their mothers and increasingly smaller amounts of time observed in infant and echelon swim positions with age as has been previously reported in several studies (e.g., Mann & Smuts, 1999; Davis, Kuczaj, Hendry, Powell, & Solangi, 2004). Results from Davis et al. again point to the first 2 months postpartum as significant in

the development of dolphin calves as the calf in that study only began to decrease the amount of time spent in one-on-one contact with his mother after the second month. Similar results were reported by Schneider, Schamel, & Noonan (2003) in their evaluation of behavioral landmarks in beluga whale calves. Calves did not spend considerable amounts of time more than 5 m from their mothers until the second postpartum month. Although the 2 calves in their study shared the same enclosure, they were not observed to make direct contact with one another until 7 weeks of age. That dolphins appear to begin to assert their independence at 2 months postpartum and also being 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. adequate swimming ability, grasp of breathing and nursing patterns, maternal bonds possibly via whistle communication, and the use of echolocation) come sufficiently together by roughly 2 months after birth to allow the calf to begin to operate in its environment with more autonomy. Interactions with other calves also increased around the 2 month mark both in this study and in Davis et al. (2003). Early periods in a calf's life may thus be focused energetically on physiological maturation while somewhat later periods allow for a reallocation of energy to social and psychological development.

Behavioral findings in this study support the notion of calves producing more echolocation trains as they attain higher levels of independence from their mothers. Unlike previous studies where only 1 calf was present (e.g. Carder & Ridgway, 1983; Lindhard, 1988; Hendry, 2002; Ricciardi et al., 2003), the 5 calves in this study had extensive interactions with one another. In this study and others where calves were housed with other calves (Reiss, 1988) or within a larger stable social group (Lindhard, 1988), echolocation was observed earlier (22 days, 2 weeks, and 2 weeks, respectively) than in studies where the mother and calf were housed in isolation or where no other calves were present (Carder & Ridgway, 1983, 2 months; Hendry, 2002, 117 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. Studies on play in dolphins in controlled settings have shown that juvenile peers are more important than adult animals for facilitating novel play (Kuczaj, Trone, Paulos, Ramos, & MacMorris, 2002). Dolphin calves in that study also displayed an increase in play complexity with age. Kuczaj (1998) argued that young animals might be most likely to play with behaviors they are in the process of acquiring and with moderately discrepant events. These events occur when an organism is faced with something, for example an object, which is both familiar and novel to some extent (Piaget, 1936). They hydrophone stimulus in this case was seen repetitively over the course of the calves first 6 months of life (i.e. was familiar) but came and went frequently, making it novel on some level with every new recording session.

Young animals can also experiment with objects in the context of play, thus producing their own moderately discrepant events. Head motions appear to be common during echolocation in adult animals and became more prevalent in calves with age. By adjusting the position of its head, a dolphin can change the angle at which their clicks impact the object and thus change the parameters of that click when it returns to them for reception. Head motions, therefore, change the echoic 'picture' that a dolphin receives of its target. An increase in the use of head motions in calves with age could be interpreted as an increase in the calves' experimentation with their own echolocation. Piaget (1936) identified similar actions in young children (12-18 months) that he called tertiary circular reactions. In these reactions, children experiment with different actions to observe the different outcomes, introducing behavioral variation and monitoring the changing results. For instance, children may bang softly or vigorously on a table to hear the different sounds, or they may adjust the orientation of their hand under a running water spigot to observe the changes in the water spray. Even beyond human children, a series of studies have found tentative, preliminary evidence for Piagetian tertiary circular reactions in other mammalian species including stump-tailed macaques (*Macaca arctoides*), gorillas

(*Gorilla gorilla gorilla)*, chimpanzees (*Pan troglodytes*), and wolves (*Canis lupus lycaon*) (for a review, see Dorè & Dumas, 1987). Finally, Piaget believed that cognitive development, and subsequent knowledge, stem from an organism's continued, varied interactions with the environment. He argued that children engage in tertiary circular reaction solely out of an intrinsic curiosity about the world, not due to the influence of a teacher or parent. Similarly, the calves may have been experimenting with the informational results of varying their echolocations out of an intrinsic curiosity about their environment. Varied head or body positions could hypothetically provide a calf with entirely different sets of information about the object in question. Such an experimentation process would expose the calves to numerous different ways to analyze their own environments, a trait likely to be evolutionarily favored as it would contribute positively to the animal's survival.

Finally, Gould (1975), Brown & Grinnell (1980), and Reiss (1988) noted an early appearance and then disappearance of open-mouth posturing during echolocation in cetaceans and bats. We did not find supporting evidence for this behavioral trend. Only four instances of open-mouth posturing were noted and all occurred between the third and fifth months postpartum, well after the 6-week end of open-mouth posturing reported in cetaceans by Reiss (1988). Finally, only five instances of concurrent bubbles were observed and three of those instances also involved whistles, further disconfirming the assertion (Killebrew, et al., 2001; Reiss, 1988) that bubble production is a reliable indication of calf echolocation.

Limitations

Habituation

Habituation was identified as a concern in the pilot study (Hendry, 2002). In that case, decreases in many of the study variables were seen over time and short-term habituation for train duration was found within sessions. However, those data only evaluated trains taken in the fifth and

sixth months postpartum, a sampling error corrected in this study. Increases seen here over time until 5 months postpartum for train duration and clicks per train argue against long term habituation for calves. Conversely, adult females did show a waning long term interest in the hydrophone. As stated previously, the hydrophone was not an exceptionally interesting object acoustically in light of the adult animals' professional histories making long term habituation a predictable explanation for their diminished sample sizes over time. No evidence of within session habituation was seen for calves or adults. The decreases seen in duration and click count for calves in month 6 could be attributed to long term habituation but the evidence at hand in inconclusive.

The paucity of evidence of habituation in calves in this study may be a factor of study design. Because more calves were available to sample, each calf was exposed to the hydrophone less frequently and for shorter periods of time than they would have been had they been the sole study subject. The opportunity to habituate to the apparatus was thus diminished.

Recording Apparatus

Future investigations of the ontogeny of echolocation in delphinids should employ a multi-hydrophone array or other suitable systems designed to more exactly identification animal location and distance to the hydrophone during echolocation bouts. The single hydrophone in this study did not allow us to triangulate exact animal position thus limiting the types of analyses we could run. Simultaneous video recordings of the sessions should also be employed to better investigate behavioral postures and movements during echolocation emissions.

Study design

Although every attempt was made to record as many early echolocation samples as possible from calves, any innovations that could increase this effort should be investigated. Comparisons

between adults and calves should continue again with equal effort given to recording both classes of dolphins. Every effort should be made to record mothers and calves in normal social settings without isolation as these situations proved to be far more fruitful than when the mother/calf pair was removed from other animals. The presence of other calves in particular appears to encourage environmental exploration and these tendencies should be used to the researcher's advantage. Finally, replications of this study should be done in different housing situations (e.g. in concrete or other reverberation-rich enclosures), in wild settings, with future generations of offspring from these adults, and with calves of other cetacean species if possible to expand the external validity of the findings and to more broadly explore the ontogeny of echolocation in cetaceans.

APPENDIX A

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL

APPENDIX B

ECHOLOCATION RECORDING BEHAVIORAL OBSERVATION SHEET

ECHOLOCATION RECORDING BEHAVIORAL OBSERVATIONS

DATE: _____ START TIME: _____

ANIMAL(S): _____ _____

_____ _____

_____ _____

ANIMAL LOCATION: _____ HYDROPHONE LOCATION: _____

TRIGGER#	TIME	SOLO?	POSITION	HEAD SCAN, ETC.?	OTHER

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