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

![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).](image)
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, Florida. 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. 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 (pressure₁/pressure₂)), 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.

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.
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 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 \(\mu\)Pa) 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 (\textit{Orcaella brevirostris}) (Van Parijs, Parra, & Corkeron, 2000). For bottlenose dolphins, individual clicks range from 4 to 600 \(\mu\)sec (Au, 1993) and typically last less than 100 \(\mu\)sec (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,
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**

<table>
<thead>
<tr>
<th>Definition</th>
<th>Source</th>
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<tbody>
<tr>
<td><strong>Clicks</strong></td>
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<tr>
<td>A broad frequency sound of short duration</td>
<td>Berta &amp; Sumich, 1999</td>
</tr>
<tr>
<td>Short, broad spectrum burst-pulses</td>
<td>Harrison &amp; Bryden (Eds.), 1988</td>
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<tr>
<td>Very short sonar pulses</td>
<td>Cahill, 2000</td>
</tr>
<tr>
<td>Directional, forward-projecting, brief, pulsed sounds of high intensity and frequency</td>
<td>Richardson, Greene, Malme, &amp; Thomson, 1995, p. 181</td>
</tr>
<tr>
<td>Series of broadband pulses</td>
<td>Andrè &amp; Kamminga, 2000, p. 163</td>
</tr>
<tr>
<td><strong>Click trains</strong></td>
<td></td>
</tr>
<tr>
<td>A rapid series of three of more pulsed noises, each of which resembles a single-frequency chirp, or “tsk, tsk, tsk.”</td>
<td>Adler, 1996</td>
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<tr>
<td>Click trains are short pulsed vocalizations of high and wide-band frequency that are used to investigate objects or search for fish</td>
<td>Cahill, 2000</td>
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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 2 ms 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 ICI, 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 involved in the columnation of echolocation 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 over time. 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.