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Sound production of a neonate bottlenose dolphin

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Abstract

The development of sound production abilities in bottlenose dolphins (*Tursiops truncatus*) is poorly understood. In this paper, we describe acoustic features of early sounds produced by a newborn. Initial underwater sounds (produced 24–48 h after birth) consisted exclusively of burst-pulses. By day five, whistle-like elements were evident as components of burst-pulse sounds. These data suggest that dolphins can produce burst-pulse sounds from a very young age and that the mechanisms dolphins use to produce both whistles and burst-pulse sounds are closely related.

Key words: cetacean, communication, echolocation, vocal development, bioacoustics, vocalization

Introduction

The sounds of bottlenose dolphins (*Tursiops truncatus*) typically have been categorized into three major types: (1) narrowband whistles, (2) broadband burst-pulse sounds, and (3) broadband echolocation clicks (Popper & Edds-Walton, 1997). Although there have been extensive studies of sounds produced by adult dolphins (e.g., see Overstrom, 1983; Caldwell *et al.*, 1990; Au, 1993), only a few studies have investigated the early ontogeny of different sound types. Developmental studies have focused mainly on whistles and echolocation clicks, with little attention given to burst-pulse sounds. It is thus unclear how dolphins develop the ability to produce pulsed versus tonal sounds. The question of how sound repertoires develop in dolphins is of particular interest because the mechanisms involved in sound production are not understood well. There are several different theories describing possible mechanisms of sound production in dolphins (for recent reviews, see Morris, 1986; Au, 1993; Cranford *et al.*, 1996; Cranford, 2000), but the issue remains unresolved. Analyses of repertoire development potentially can provide clues about the mechanisms of sound production by revealing correlates with ontogenetic mechanisms (Caldwell & Caldwell, 1979; Brown & Grinnell, 1980; Moss, 1988; Au, 1993). This paper describes the earliest sounds produced by a bottlenose dolphin calf in a preliminary attempt to uncover such clues.

Caldwell & Caldwell (1979) analyzed the underwater sounds of fourteen bottlenose dolphin calves at various stages of development; of these, three were born in captivity and recorded from birth. The Caldwells concluded that whistles of newborn infants were too "tremulous and quavery" (Caldwell & Caldwell, 1979: 374) to be characterized as stereotyped "signature" whistles, as has been described for adult dolphin whistles (Caldwell & Caldwell, 1965; Caldwell *et al.*, 1990). Instead, the calf sounds were described as similar to the distorted whistles produced by adults in stressful situations, i.e., unstable, with reduced frequency modulation and with an increased number of harmonics (Caldwell & Caldwell, 1979; see also Herzing, 2000). By the end of the first year, however, all calves developed whistles with frequency modulation, and all but one developed a stereotyped whistle particular to the individual. The Caldwells concluded, therefore, that all infants were born with the ability to produce narrowband sounds.

Reiss (1988) studied the development of echolocation clicks in two captive male infant bottlenose dolphins from birth through forty days, but reported other types of sounds. Like Caldwell & Caldwell (1979), she described whistles of the neonates during the first five days as tremulous (i.e., unsteady) with little frequency modulation. The whistles at times were of high intensity, yielding many harmonics, and termed "squeals" by Reiss. In "emotional situations" (Reiss, 1988: 122), the infants often emitted "whistle-squawks" that had characteristics of both frequency-modulated and burst-pulse sounds. The squawk (burst-pulse) components of whistle-squawks had peak energy at 4 kHz, compared to the frequency-modulated (whistle) elements that had peak frequencies between 3 and 10 kHz. Both dolphins produced sounds that resembled adult echolocation clicks at the 16th to 19th day postnatal (also see Lindhard, 1988). Reiss suggested that early pulsed sounds were precursors to echolocation clicks.

McCowan & Reiss (1995) studied whistle contour development in eight captive-born bottlenose dolphins, from birth through one year old, to determine the role of learning. The observed repertoire over this time consisted of unique, highly variable and unstable sounds that either appeared inconsistently or only occurred once. The composition of each infant's repertoire changed dramatically across the year. By the end of the first year, all infants shared some whistle types, and all produced the same two predominant whistle types. However, all infants varied greatly in the number and types of whistles produced, as well as when specific whistle-types were acquired. McCowan and Reiss concluded that repertoire acquisition involves both the maturation of the sound production system and learning.

In summary, researchers agreed that: (1) initial infant sounds are unstable, lacking the refined whistle characteristics of adults and (2) calf sounds develop into relatively stereotyped whistles as the infant matures. This paper presents observations of the acoustic features of early sounds produced by a neonate dolphin, and discusses the possible relevance of these features to theories of sound production.

Materials and Methods

The subject of the present study was a single newborn male calf, housed with its mother and a second adult female, in an outdoor 15.2 m-diameter circular seawater tank at the Kewalo Basin Marine Mammal Laboratory in Honolulu, Hawaii. Underwater audio and video recordings of the calf, the first-time mother, and the companion dolphin were made in 20 min intervals throughout each 24 h period, from birth until day five*. Audio recordings also were made opportunistically when observers heard sounds. Video recordings were made with a Sony portable 8-mm recorder (Model CCD-TR101) from a deck (approximately 4 m above the water) providing a view of the entire tank. Recordings collected in previous studies (unpublished data) were also used as a source of adult sounds. Underwater recordings were made using a Labcore customized hydrophone attached to an Archer customized mini-amplifier (227-1008B). The hydrophone/amplifier system was sensitive to 12 kHz. The amplified sounds were recorded on a Marantz cassette recorder (Model PMD430) having a flat frequency response to 17 kHz (± 3 dB). Thirty-three audio tapes, each containing approximately 90 min of data were analyzed aurally for occurrences of sounds.

Identification of calf sounds were made when visible bubble stream emissions, as seen on video, were synchronized with sounds, as heard on audio. The use of bubble streams as identifiers of the individual has been implemented in several earlier studies (e.g., McCowan & Reiss, 1995; Herzing, 1996). Bubble streams are often observed during the production of whistles and do not appear to affect the quality of sound production. The physiological processes underlying repetitive release of air from the blowhole during sound production are poorly understood.

Only adult sounds attributable to a specific individual were used for comparison with the neonate phonations. Adult sounds were sampled either by isolation of the individual sound source through analyses of videotapes (e.g., by locating situations in which sounds were audible while one adult's head was out of the water), or when opportune, by recording the dolphins when they were alone. Sounds were digitally sampled at 22.05 kHz using Canary software (version 1.2) from the Cornell Laboratory of Ornithology (Bioacoustics Research Program) running on an Apple Power Macintosh computer (Model 7100/80). (Note that the frequency analysis range was constrained by the bandwidth of the recording system). Spectrograms were made of all sample sounds using a Hamming window, an analysis filter bandwidth of 175 Hz, and an FFT length of 2048. Visual and aural analyses were performed on spectrograms to subjectively assess the similarity of the calf's sounds to the narrowband frequency-modulated whistles and broadband burst-pulse sounds of the adults. Two of the authors (DAK & EM III) categorized the adult sounds, through spectrographic and aural evaluations, as whistles, clicks, or burst-pulse sounds. Very short duration (1–10 ms), broadband pulses appearing as vertical bands in spectrograms were classified as clicks. Longer duration (>200 ms on average) narrowband signals appearing as one or more horizontal bands in spectrograms were classified as whistles. Longer duration (>100 ms on average), broadband signals were classified as burst-pulse sounds (see Figs 1–3). These criteria are comparable to those used in past analyses (reviewed by Popper, 1980). Five sounds of each type were selected from both adults based on clarity of the audio signal. These sounds served as a basis for comparison with the calf sounds. The adult sounds

*An open (patent) umbilical cord and aspiration of amnionic fluid led to the death of the calf on day six. An autopsy revealed no abnormalities in the nasal and laryngeal organs and tissues of the calf.

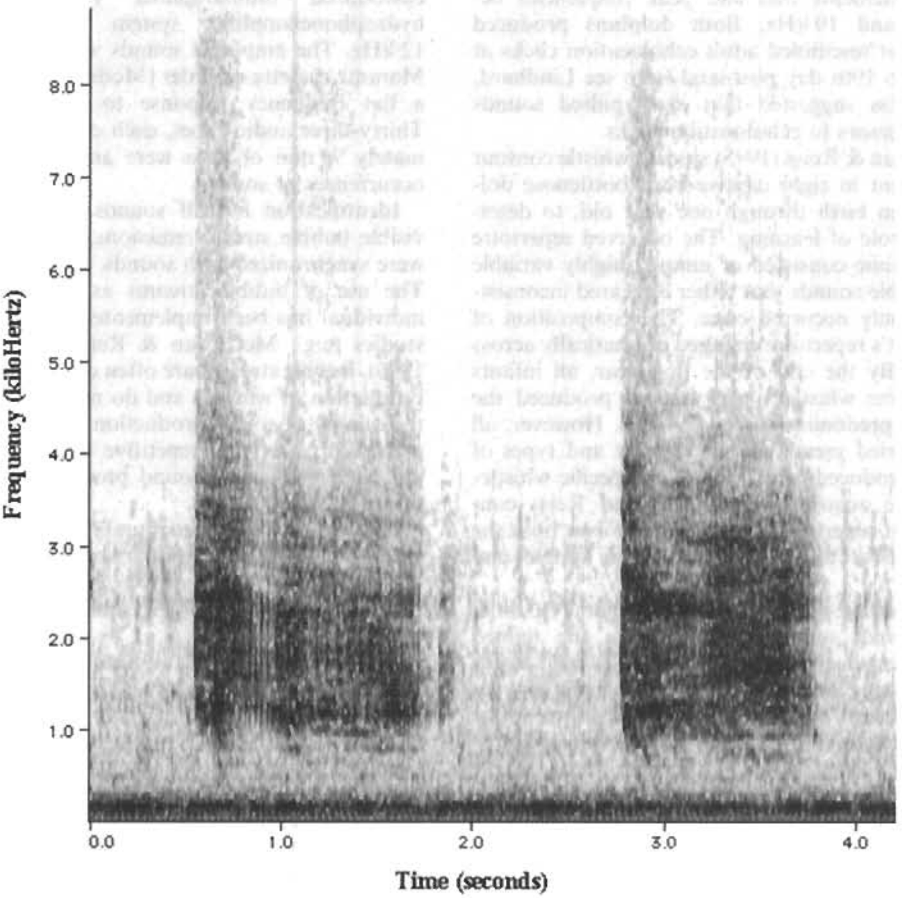

Figure 1. Typical broadband burst-pulse sounds produced underwater by the calf on the second day after birth.

we analyzed were similar to those described in numerous previous reports (reviewed by Popper, 1980, Richardson *et al.*, 1995, and Herzing, 2000) (see Table 1).

Results

Only 112 sounds on audio tapes could be correlated with videotapes of bubble streams from the calf. Of these 112, none were on day one, 56 were on day two, 17 on day three, none on day four, and 39 on day five. Sounds also occurred uncorrelated with bubble streams, but that were acoustically similar to identified calf sounds. No such sounds were heard on day one. None of the 73 sounds from day two or three contained audible narrowband components. In contrast, narrowband features were observed on day five. One of the authors (DAK) listened to all recordings containing calf sounds and chose samples for further analysis based on correlation with bubble streams and on audio recording quality (e.g., selecting signals with a high signal-to-noise ratio, no distortion, and no overlap with other signals). Fifty-three calf sounds recorded on the second day after birth, and 39 sounds recorded on the fifth day after birth were selected.

Table 2 summarizes measurements of the analyzed sounds of the calf and the two adults. Calf sounds on day two consisted exclusively of broadband burst-pulse sounds (Fig. 1); no narrowband whistles were present. These broadband sounds contained spectral energy between 0.45 and 9.5 kHz with peak energy at approximately 1.7 kHz. The sounds varied in duration from 0.35 to 1.4 s. These characteristics differed greatly from whistles recorded from the adult dolphins (see Figs 2 and 3 and Table 2). The calf sounds from the second day after birth were most similar to the burst-pulse sounds of adults (see Table 2). Development of the calf's sounds into burst-pulse sounds having

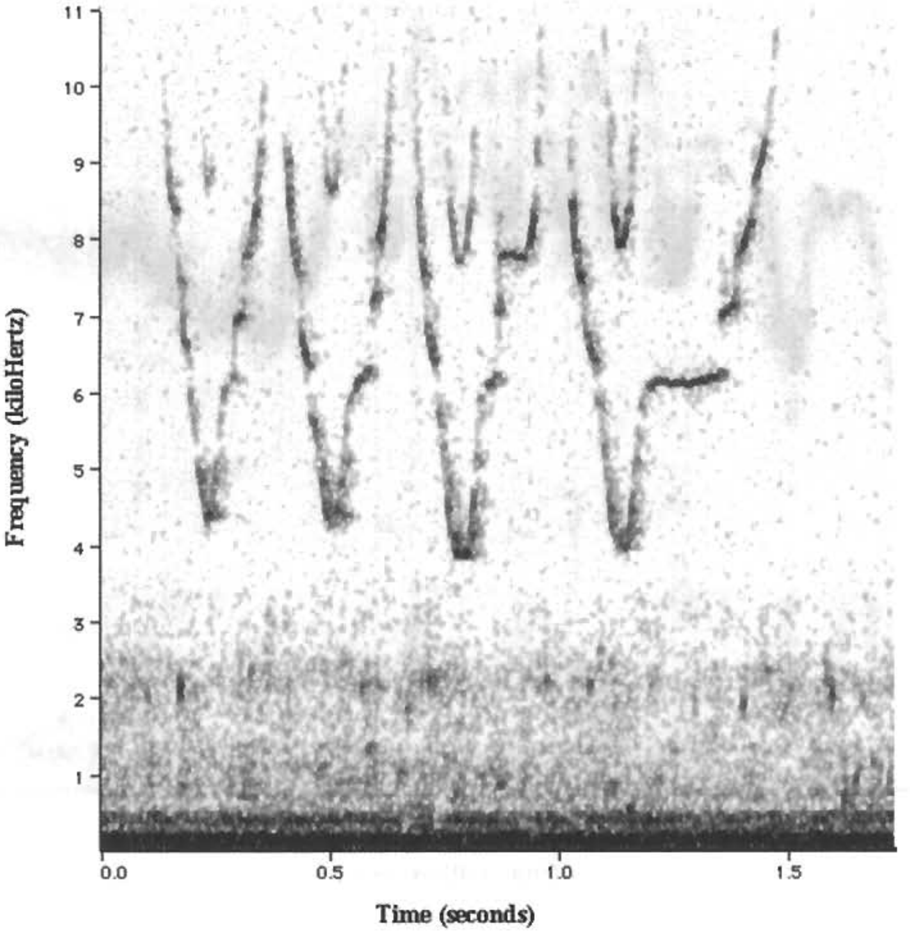

Figure 2. Typical narrowband, frequency-modulated, whistle emitted by the focal calf's mother, an adult female bottlenose dolphin.

whistle-like elements was first noted in recordings on day five after birth. Aurally, these day-five sounds appeared to start as a burst-pulse sound, from which whistle-like elements emerged. Spectrographic analysis provided additional evidence that both sound types were present (Fig. 4). These sounds appeared to be similar to the whistle-squawks described by Caldwell & Caldwell (1966) and Reiss (1988). Spectral energy was present from approximately 1.0 to 10 kHz with duration from 0.52 to 2.5 s. The whistle-elements always started within several ms after the beginning of the burst-pulse characteristics and both ended simultaneously. No whistles were found without accompanying burst-pulse characteristics. A majority of the whistles occurred within the same frequency bandwidth as the burst-pulse elements. Peak energy levels occurred at higher frequencies than those observed on day two, varying between 1.86 and 2.84 kHz, with frequency-modulated (whistle) elements that had peak amplitudes at frequencies between 3.5 and 9.7 kHz. Spectrograms of day-five sounds again were more similar to the adults' burst-pulse sounds than to other sounds of the adults. No broadband clicks attributable to the calf were found on any recordings.

Discussion

Whistle-squawks could provide clues about possible underlying sound production mechanisms. These sounds contain both burst-pulse and narrowband frequency-modulated elements, and acoustically are similar to whistles emitted by an adult dolphin in a state of excitement (Fig. 5). Caldwell & Caldwell (1979) suggested that in times of stress, muscular control could be lost momentarily, and that as a result, production quality regresses such that

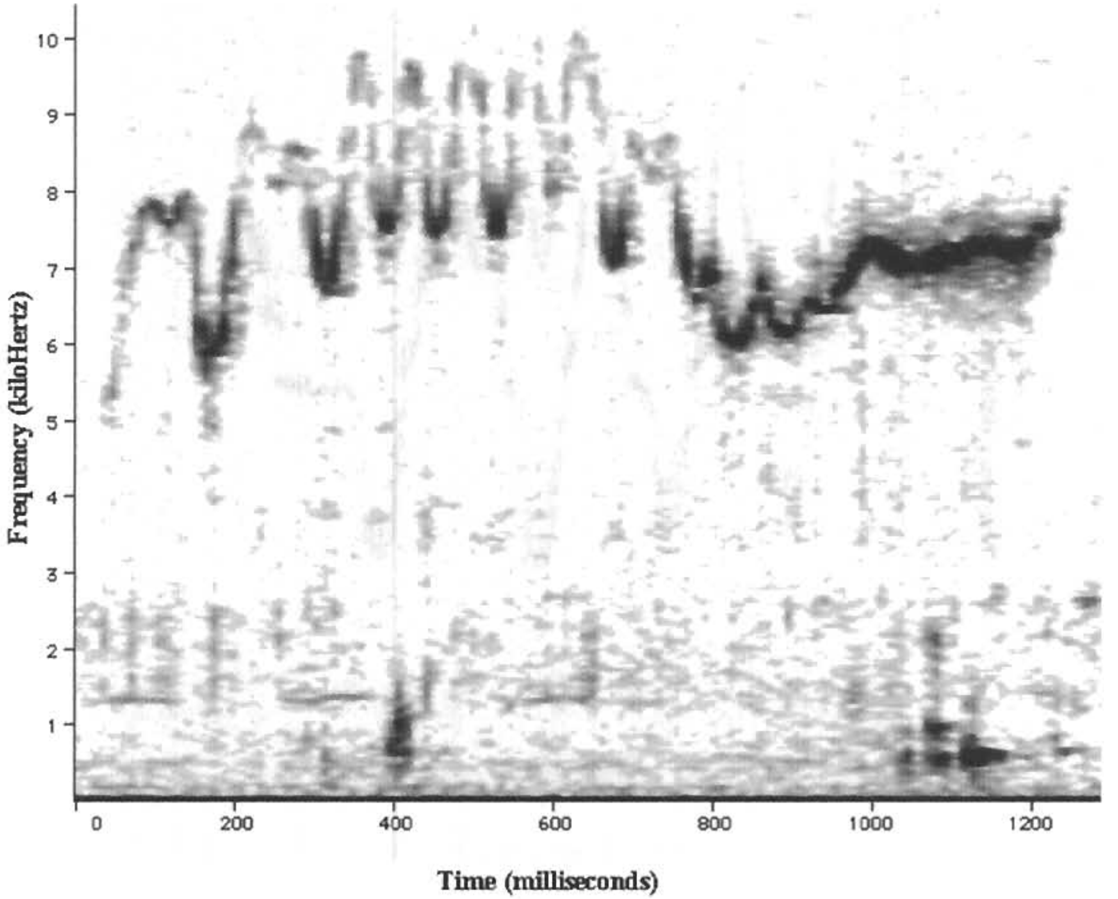

Figure 3. Typical narrowband frequency-modulated whistle emitted by a companion adult female bottlenose dolphin.

Table 1. Published measurements of frequency-modulated whistles and broadband burst-pulse sounds from bottlenose dolphins.

Type	Duration (ms)	Minimum frequency (kHz)	Maximum frequency (kHz)	Frequency at peak amplitude (kHz)	References
Whistles	—	0.8	24	3.5–14.5	Richardson *et al.*, 1995
Whistles	100–3600	4	20	—	Evans & Prescott, 1962
Whistles	800–900	2	20	—	M. Caldwell & Caldwell, 1967
Bark	100	0.2	16	—	Evans & Prescott, 1962

sounds are similar to those produced by the underdeveloped sound production system of an infant. Hence, whistle-squawks could be evidence of a developmental stage that infants pass through as they develop muscles, and/or acquire muscular control (e.g., neural activation patterns) necessary for whistle production.

Many animals generate sounds internally by controlling air pressure and air flow rate within their respiratory systems (Fletcher, 1992). When an animal develops greater muscular control, it produces sounds more precisely. Adult dolphins possess fine muscular control of sound production under normal circumstances, as evidenced by their proficiency

Table 2. Means ± standard deviation taken from spectrograms of sounds from the calf and the adults to assess similarities.

	2-day old calf	5-day old calf	Mother		Companion	
			Whistle	Burst-pulse	Whistle	Burst-pulse
N	53	39	5	5	5	5
Duration (ms)	628 (± 286)	1011 (± 286)	988 (± 225)	116 (± 25)	1143 (± 73)	114 (± 36)
Minimum frequency (kHz)	0.46 (± 0.10)	1.04 (± 0.27)	3.81 (± 0.11)	0.51 (± 0.19)	5.34 (± 0.57)	0.65 (± 0.20)
Maximum frequency (kHz)	9.48 (± 1.70)	9.97 (± 1.37)	9.86 (± 1.47)	10.67 (± 0.81)	10.27 (± 0.28)	5.71 (± 0.14)
Peak frequency (kHz)	1.72 (± 0.60)	2.38 (± 0.87)	6.36 (± 1.00)	1.91 (± 0.65)	6.61 (± 0.28)	1.48 (± 0.50)

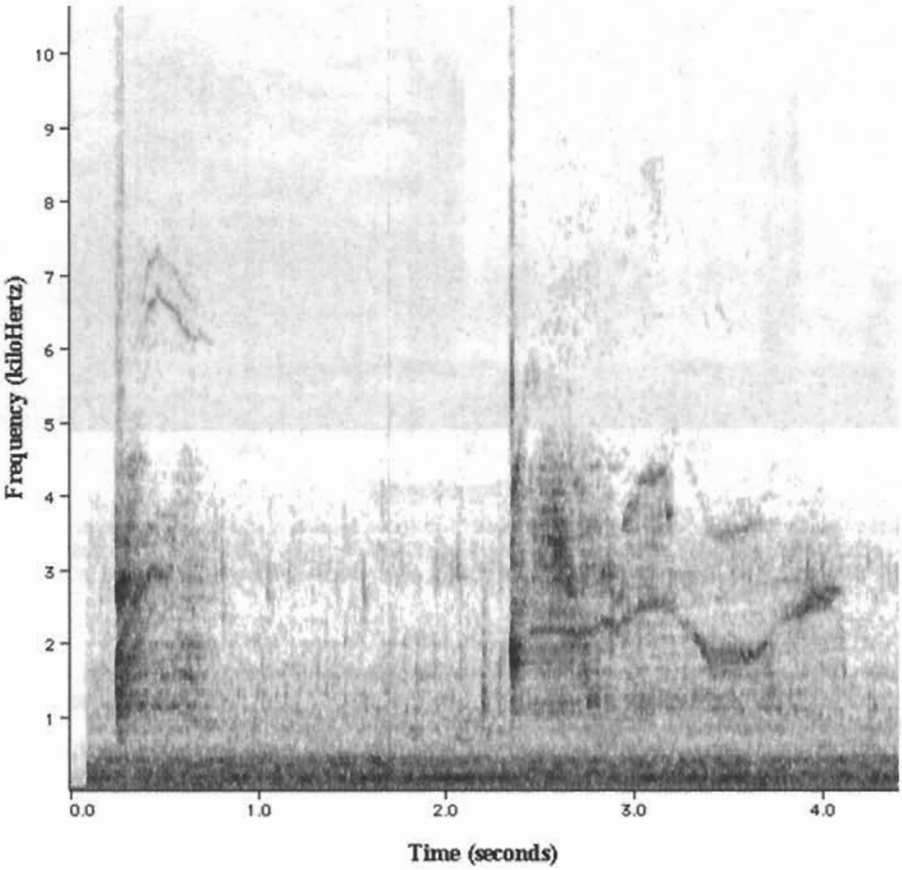

Figure 4. A whistle-squawk, commonly produced by the calf on day five with characteristics typical of both burst-pulse sounds and whistles. The frequency at peak amplitude for the two sounds was: 2.82 kHz and 1.87 kHz (respectively); and the frequency at peak amplitude for the whistle elements was: 6.59 kHz and 3.74 kHz.

at vocal mimicry (Richards *et al.*, 1984; Reiss & McCowan, 1993). When a dolphin becomes stressed or excited, however, it may not be able to retain sufficient control of the muscles involved in sound production to produce sounds with the same degree of precision.

If the variable proficiency of infants reported in the present and prior studies is the result of developing sound production mechanisms, the question remains as to which muscles or control centers might be underdeveloped. Infant bats (*Eptesicus fuscus*, *Plecotus auritus* and *Myotis lucifugus*) emit

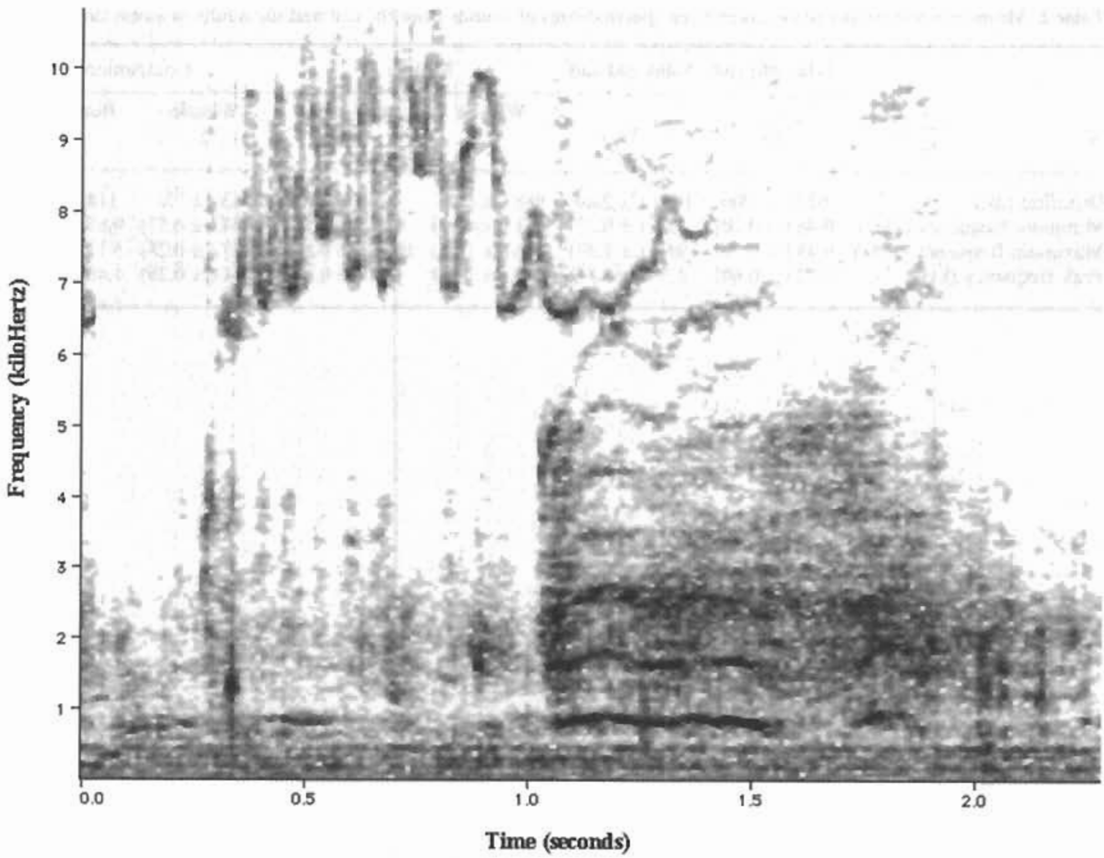

Figure 5. Sounds produced by the companion adult female bottlenose dolphin in a state of excitement. Note that the first half of the sound is frequency-modulated, whereas the second half contains burst-pulse components. The frequency-modulated elements had peak energy at 6.93 kHz, whereas the burst-pulse elements had peak energy at 860 Hz.

sounds lower in frequency and with less frequency modulation than adults (Brown & Grinnell, 1980; Moss, 1988; de Fanis & Jones, 1995; Moss *et al.*, 1997). Moss (1988) suggested that this was the result of immature muscles in an infant bat's larynx. Early vocalizations of some primates (e.g., *Saguinus oedipus*) also show reduced frequency modulation (Castro & Snowden, 2000). Anatomical studies of fetal *Tursiops* revealed midline and lateral folds around the larynx that are thinner and less developed than the same folds in adults (Reidenberg & Laitman, 1988). Agarkov *et al.* (1975) found that the nasal sac systems of several adult delphinid species have extensive musculature. Cranford *et al.* (1996) described the nasal muscles as being arranged in thin fan-like layers. Research showing that muscles in the nasal regions of infant dolphins are underdeveloped, or that infants lack full neural control of sound production systems, has yet to be conducted. Inasmuch as the site of sound generation in delphinids remains unclear, so does the specific role of several muscles in the nasal system and the larynx.

Sounds with acoustic features similar to those of whistle-squawks occasionally have been recorded from humpback whales, *Megaptera novaeangliae* (Fig. 6). Mysticetes do not have nasal sac systems comparable to odontocetes and are believed to generate sounds with their larynges (Morris, 1986). It thus seems likely that humpbacks can generate both burst-pulse sounds and narrowband sounds using a single source mechanism, the larynx. Sounds containing a mixture of tonal and pulsive components also have been described in spotted dolphins, *Stenella frontalis* (Herzing, 2000), killer whales, *Orcinus orca* (Schevill & Watkins, 1966), and in false killer whales, *Pseudorca crassidens* (Murray *et al.*, 1998). False killer whales produce sounds that modulate continuously from pulse trains to whistles, as well as sounds that rapidly

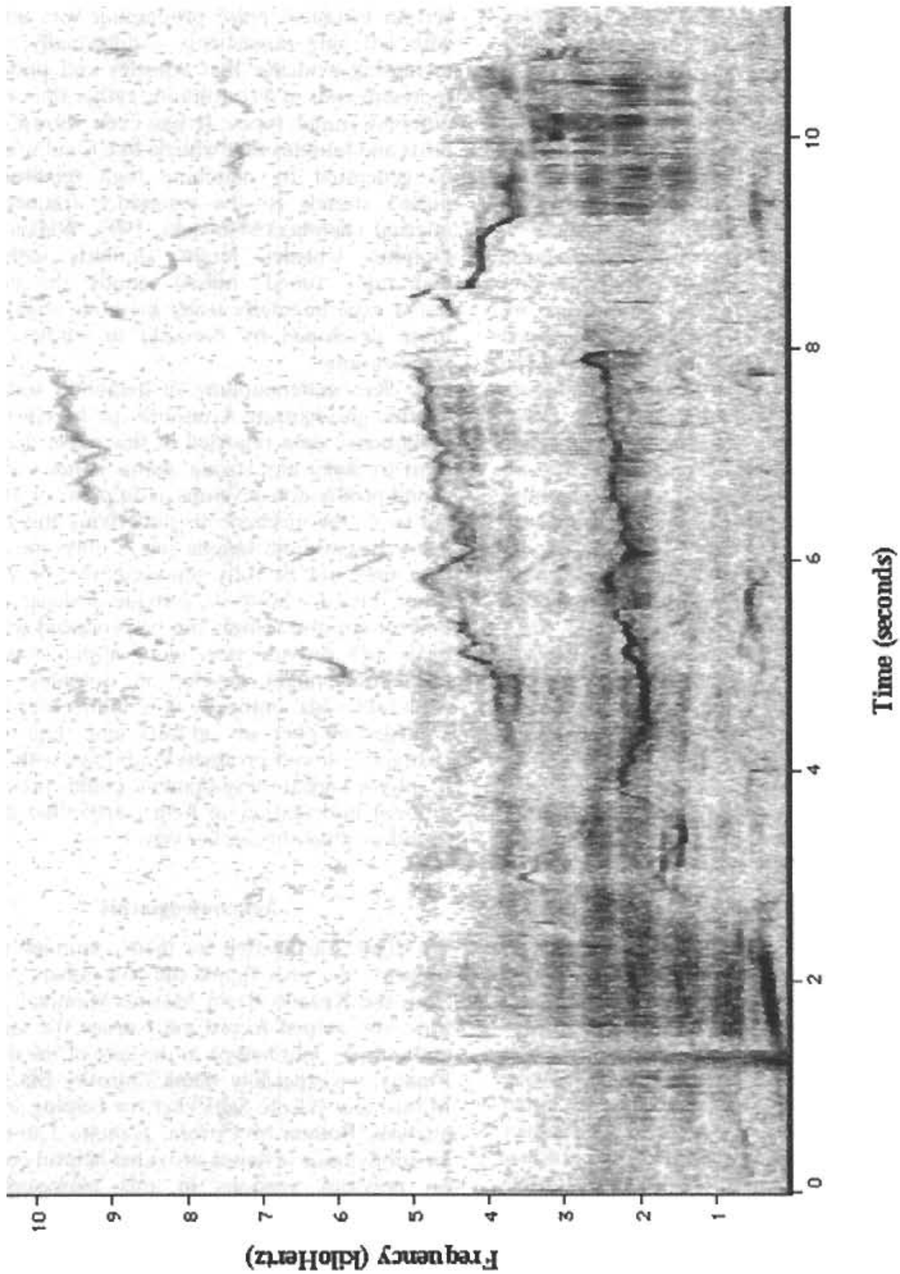

Figure 6. Sounds produced by a singing humpback whale with acoustic characteristics similar to those of the dolphin calf and of an adult dolphin in a state of excitement.

"toggle" between sound types. Interestingly, certain primates (e.g., *Cebuella pygmaea*) also appear to be able to produce such "mixed" sounds (Elowson *et al.*, 1998). This comparative evidence suggests that: (1) a single mechanism is sufficient for producing both tonal and pulsed sounds and (2) complex nasal sac systems are not required to produce either of these sound types.

Earlier studies (e.g., Caldwell & Caldwell, 1979) reported that infant dolphins produce whistles from birth. The first sounds produced by the bottlenose dolphin calf we observed, however, were burst-pulse sounds. Spectrograms of some infant sounds described as whistles by Caldwell & Caldwell (1979, Figures 1, 2, and 35) in fact display burst-pulse characteristics resembling the early sound data presented in this paper. In our later recordings, we observed that these early burst-pulses developed into sounds with whistle-like components. The ontogeny from burst-pulses to pulsed sounds containing whistle-like elements suggests that either both sound types can be produced by a single mechanism or, if multiple mechanisms are involved, that the mechanisms used to produce both burst-pulse sounds and whistles are in some way interdependent.

Other evidence, however, indicates that dolphins produce pulsed sounds and whistles using two separate mechanisms (Evans & Prescott, 1962; Bullock & Ridgway, 1972; Morris, 1986; Cranford 2000). For example, odontocetes can produce whistles and pulse trains simultaneously and independently of one another (Lilly & Miller, 1961; Murray *et al.*, 1998). Such abilities are difficult to explain without assuming that there are at least two sound production mechanisms. In adult dolphins, movement of the left nasal plug is associated with the production of whistles (Dormer, 1979), and movement of the right nasal plug is associated with the production of pulses (Mackay & Liaw, 1981), suggesting that nasal structures are specialized laterally for the production of particular sound types (also see Cranford, 2000). Finally, the youngest bottlenose dolphin reported to have produced sounds resembling adult broadband, echolocation-type clicks was 14 days old (Lindhard, 1988; Reiss, 1988). This delay in development suggests either that the structures used by dolphins to produce clicks are different from those used to produce burst-pulse and whistle sounds, or that the production of clicks requires additional muscular development and/or muscular control.

The apparent conflict between evidence suggesting that a single sound production mechanism can be used to produce both whistles and pulsed sounds, and evidence suggesting that two separate mechanisms are involved, potentially is resolvable. Assuming that dolphins have two internal mechanisms for producing sound, either one or both mechanisms could produce both whistles and pulsed sounds. Mackay & Liaw (1981) noted that although pulse production typically was associated with movements in the right side of the head, in certain instances pulse production was associated with left side movements. Additionally, there is increasing evidence that whistles and pulse trains represent ends of a continuum, rather than radically different sound types. It has been shown in both birds and humans that whistle-like tonal sounds can be generated by matching high repetition rate pulsed sounds to the resonance frequencies of internal chambers (Nowicki, 1987; Walker, 1988). Dolphin whistles might similarly consist of high rate, "tuned" pulsed sounds; this could be tested experimentally using methods analogous to those developed by Nowicki in studies of bird vocalizations.

A clear understanding of delphinid sound production mechanisms continues to be elusive. The preliminary data reported in this paper are insufficient to make any strong claims either about how sound production develops in dolphins or about the nature of the mechanisms underlying this development. Because the sample size is only one calf, the data may not be fully representative of *Tursiops*. These data do, however, provide evidence showing that burst-pulse sounds can be produced soon after birth and provide new clues about how sound production might develop in dolphins. Further studies of vocal ontogeny in dolphins that consider a larger number of subjects and that correlate changes in sound production abilities with changes in physiological development could provide additional information to help clarify the nature of sound production mechanisms.

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