A Comparative Analysis of the Pulsed Emissions
of Free-Ranging Hawaiian Spinner Dolphins
(*Stenella longirostris*)

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Introduction

Extensive research has focused on the pulsed acoustic emissions of dolphins since the discovery of their biosonar system (Kellogg 1958). While not all dolphins whistle, they all produce click trains that vary widely in click duration, interclick intervals, and spectral composition (Popper 1980). In general, two functional categories of click trains are recognized: (1) echolocation signals used in sensory tasks (Au 1993) and (2) burst-pulse signals associated with social communication (Herman and Tavolga 1980; Herzing 1988, 1996; Blomqvist and Amundin, chapter 60, this volume). While much has been experimentally learned about echolocation clicks, comparatively little is known about the characteristics and function of burst pulses. Burst pulses are often described with such qualitative terms as "yelps," "creaks," "squawks," and "blasts" (Herman and Tavolga 1980). Signals are perceived in this manner when the interval between clicks in a train drops below 5 ms, at which point humans no longer resolve individual pulses and the signal is heard as a single continuous sound (Murray, Mercado, and Roitblat 1998). Variations in the click repetition rate are perceived by the human listener as qualitatively different signals. Such labels have resulted in most analyses of burst pulses focusing on the audible spectral components of these signals (Caldwell and Caldwell 1966; Overstom 1983; Sjare and Smith 1986b; Herzing 1988, 1996).

The relatively narrowband (<20 kHz) recording equipment generally used to collect burst-pulse data has yielded peak and center frequency estimates well below those found for echolocation click trains. However, these measures may represent artifacts of the recording equipment's bandwidth limitations and be underestimates of the actual spectral energy distribution in burst pulses. Dawson (1988), using broadband equipment to examine the "cry" burst pulse produced by free-ranging Hector's dolphins (*Cephalorhynchus hectori*), a non-whistling species, reported clicks with energy centered around 120 kHz and source levels around 150 dB re

1 μPa. Au, Penner, and Turl (1987), while studying echolocation in a captive beluga (*Delphinapterus leucas*), collected burst pulses with peak-to-peak click source levels of about 206 (±6) dB re 1 μPa. Although no peak or center frequency values were reported, those source levels are comparable to echolocation click source levels. These findings suggest that burst pulses may be spectrally more similar to echolocation click trains than previously reported for many species.

An issue that remains unresolved concerns the accurate labeling of click trains as either functional echolocation signals or socially meaningful burst pulses. In other words, what specific characteristics define these classes of signals? Most efforts to date have relied primarily on qualitative aural distinctions and/or visual inspections of narrowband (<20 kHz) sonograms to classify signals. Such methods, however, make comparisons between workers difficult and can arguably lead to biologically questionable conclusions. A more quantitative and broadband approach is therefore necessary.

Experimentally, burst pulses have received little attention from workers studying echolocation. Often, the label of "burst pulse" is simply given to signals that do not conform to the types of click trains known to have an echolocation function. Target detection experiments show that bottlenose dolphins (*Tursiops truncatus*) temporally space pulses in an echolocation click train to focus their attention at a particular distance (Penner 1988). When scanning a target, clicks are spaced to account for the two-way travel time to and from a target plus an echo processing period between 19 and 45 ms long (Au 1993). Signals that do not conform to this pattern present a puzzle for researchers and raise the question: Should trains with interclick intervals less than the minimum echo processing period be treated by default as nonecholocation, social burst pulses?

To clarify the relationship between the various kinds of click trains produced by delphinids, this study examined the pulsed acoustic emissions of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*). This is a species for which pulsed signals have previously only

been qualitatively described (Norris et al. 1994). The objectives of this work were to (1) quantitatively characterize pulsed signals during social situations when acoustic activity is at a peak (Norris et al. 1994) and (2) look for evidence of definable classes (i.e., burst pulse versus echolocation trains) in the pulsed signaling repertoire of this species. To accomplish this, the temporal, spectral, and source level parameters of click trains were used to quantitatively relate signals to one another.

Materials and Methods

DATA COLLECTION

Spinner dolphins are an abundant and accessible species in Hawaiian waters. A population of several hundred animals resides along the leeward coast of the island of Oahu, and is readily reached by small boat. Using a 5.2 m, outboard-powered Boston Whaler, groups of spinner dolphins were approached and recordings made on 28 July, 11 August, and 13 August 1998. Group sizes ranged from 10 animals on 28 July, to 80–100 on 11 August and 60–70 on 13 August. Animals were approached as they milled about in waters between 5 and 18 m deep over a mostly flat, sandy bottom substrate. Upon encounter, the boat was either anchored or left to drift with the engine off. Behavioral observations were quantified using an unpublished ethogram based on the work of Norris et al. (1994) to establish the general behavioral state of the animals. In each case, group activity was classified as moderately to highly social. Distance to the animals at any given time ranged between 5 and 100 m. All recordings were made under Beaufort Sea State 1 or less.

Based on work with a captive false killer whale (*Pseudorca crassidens*), Murray, Mercado, and Roitblat (1998) proposed that all *Pseudorca* signals are best modeled along a graded continuum, rather than categorically. Similar ideas have been suggested in the past for the tonal signals of belugas (*Delphinapterus leucas*) (Sjare and Smith 1986b), pilot whales (*Globicephala melaena*) (Taruski 1979), and common dolphins (*Delphinus delphis*) (Moore and Ridgway 1995). With this in mind, an effort was made to keep a priori assumptions about the presence of signal classes (burst pulse versus echolocation) in the data to a minimum, so as to allow for a graded pattern, if present, to emerge. By relying on visual (a flashing LED) rather than aural cues to detect the presence of a signal (see below), bias toward collecting any one type of signal over another was minimized. The signals collected, therefore, accurately represent what free-ranging Hawaiian spinner dolphins produce in a moderate to highly social behavioral state.

RECORDING EQUIPMENT

Recordings were made using a custom-built (Au, Lammers, and Aubauer 1999), laptop computer–based, digital recording system with a bandwidth of 130 kHz. A custom-built hydrophone consisting of a 20 mm diameter spherical piezoceramic element with an omnidirectional, flat frequency response (±5 dB) from 10 kHz to 160 kHz and a sensitivity of 210 dB re 1 μPa was placed 3 m below the surface. Incoming signals were detected visually on an LED meter activated by peak-to-peak sound pressure levels >134 dB re 1 μPa. Upon detection, the operator of the recording system pressed a trigger signaling the event to the computer, which in turn stored 1 s of pretrigger data and 2 s of posttrigger data. Data were stored on the computer's hard disk drive. Water depth was recorded using an Under Sea Industries handheld personal dive sonar.

DATA ANALYSIS

Interclick interval, click center frequency, and rms bandwidth were extracted from each train using a custom-written Matlab 5.1 analysis program. Spectral measurements were obtained using either a 1024 or 512-point FFT window, depending on the interval between clicks (512 points were used when a larger window size would have overlapped two clicks). Peak-to-peak source levels of clicks (fig. 58.1) were estimated by geometrically localizing phonating animals using arrival-time differences between the direct click, the 180° phase-shifted surface reflection, and the nonphase-shifted bottom reflection (Aubauer et al. 2000). Using *c* as the speed of sound in seawater, the distance of the phonating animal (*r*) was estimated using the following equation:

$$r = \frac{\left(\frac{c \cdot \tau_{1b}}{2}\right)^2 + b \cdot (a - b) - \left(\frac{c \cdot \tau_{1s}}{2}\right)^2 \cdot \left(1 - \frac{b}{a}\right)}{\frac{c \cdot \tau_{1s}}{2} \cdot \left(1 - \frac{b}{a}\right) - \frac{c \cdot \tau_{1b}}{2}}$$

The source level (SL) of a click was established using:

$$SL = SPL_R + 20 \cdot \log r + \alpha \cdot r$$

where SPL_R is the sound pressure level relative to 1 μPa of the recorded signal and α is the absorption coefficient of the water measured in dB/m. Only click trains with very distinct surface and bottom reflections were used to estimate source level. Within these click trains only the five clicks with the highest amplitude were chosen for the calculation. No information was available on the orientation of the phonating animal, so it could not be established if the signals were measured on the beam axis. Thus, the spectral and source level values reported here are only estimates for the signals produced by spinner dolphins.

Results

A total of 133 click trains were analyzed. Fig. 58.2 shows the distribution of mean interclick intervals (ICIs) for
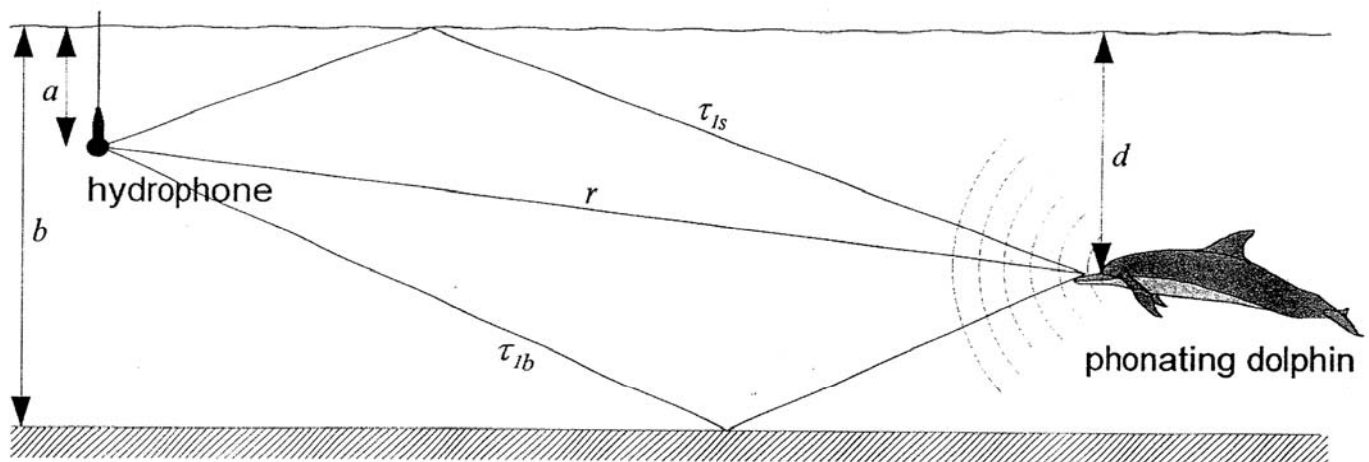
Fig. 58.1. Multipath propagation in shallow water of dolphin clicks, where a = hydrophone depth, b = water depth, r = distance of phonating animal to the hydroplane, d = depth of phonating dolphin, τ_{1b} = time delay of first order bottom reflection relative to direct click, and τ_{1s} = time delay of first order surface reflection relative to direct click.

each train. The distribution is strongly bimodal, with two peaks centered at 3.5 ms and 80.0 ms and a gap at 10 ms. To investigate how consistent ICIs remained within a train, the relationship between the first and last ICI was examined. A linear regression analysis (fig. 58.3) indicated that the two are correlated ($r = 0.87$), suggesting that within a train ICIs tended not to change drastically. Beginning ICI was a good predictor of ending ICI for trains with a mean ICI < 10 ms ($r^2 = 0.76$) and somewhat less so for trains with greater mean ICIs ($r^2 = 0.53$).

Spectrally, the mean center frequency of a train tended to increase ($r = 0.65$) with increasing mean ICI (fig. 58.4). For all trains, the mean center frequency was never below 30 kHz. The average rms bandwidth of click trains ranged between 13 and 33 kHz and did not have a strong association with mean ICI ($r = 0.4$). Thus, while trains with small ICIs generally had lower mean center
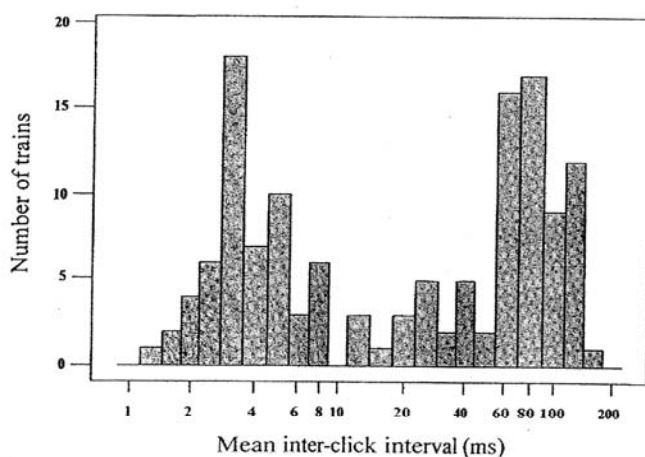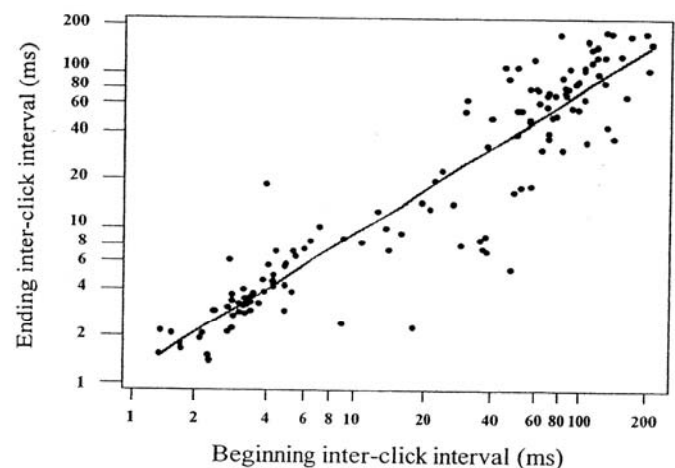

Fig. 58.3. Linear regression plot of the beginning interclick interval of a click train versus its ending interclick interval

Fig. 58.2. Histogram of number of trains by mean interclick interval plotted on a semi-logarithmic scale
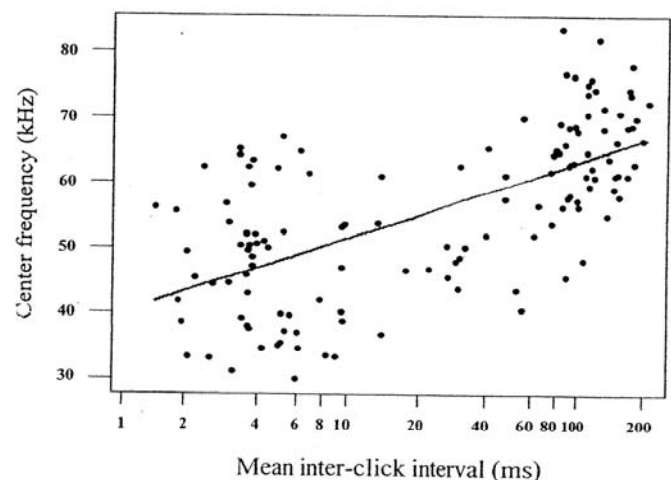

Fig. 58.4. Linear regression plot of the mean interclick interval versus the mean center frequency of each train

frequencies, their bandwidth was comparable to trains with higher ICIs.

Of the 133 trains analyzed, 33 (25%) were suitable for estimating source levels (i.e., had clear, distinguishable surface and bottom reflections). Calculated peak-to-peak source levels ranged between 191 and 216.5 dB re 1 μPa (mean = 205 dB). Linear regression revealed that ICI was a rather poor predictor of source level (r^2 = 0.2). A two sample t-test between the converted pressures (in μPa) of source level (SL) values for trains with ICIs greater than 10 ms (mean SL = 206 dB) and less than 10 ms (mean SL = 203 dB) did not reveal a significant difference between the two (p = 0.093). A somewhat better predictor of source level was the mean center frequency of the click train (r^2 = 0.46). As the mean center frequency of clicks increased, so did the source level.

Discussion

Although a distinction between burst-pulse sounds and echolocation trains has long been made in the literature, the characteristics that distinguish and unify these two classes of signals have seldom been quantified. Our results suggest that while certain features of click trains do in fact define two apparent classes of signals, other characteristics are also shared. Interpretations must be made with caution, however, in light of the fact that no positional information was available on phonating animals. It is impossible to say how much variation was introduced in the data from off-axis signals. The central assumption made in this study is that all click trains had an equal probability of being on- or off-axis and that relative comparisons are therefore justified. Defining the clear boundary of a functional distinction between burst-pulse and echolocation click trains will require further experimental study, but some provisional guidelines can be derived from the results obtained here.

Interclick Intervals

The bimodal distribution of mean click intervals reveals two general modes of click train production: trains that begin and maintain a consistently short (1.5 to approximately 10 ms, mean = 3.5 ms) ICI throughout the train (fig. 58.5A) and trains with longer, more temporally variable ICIs (fig. 58.5B). Although some signals were collected that seemed to "bridge" the two modes (as predicted by the model presented by Murray, Mercado, and Roitblat [1998]), these composed only a small part (6%) of the data set.

The conspicuously low number of trains with ICIs between 10 and 20 ms suggests that this might be a functional and/or cognitive transition point in the way spinner dolphins produce and process click trains. Schotten (1998), studying the echolocation clicks of spinner dolphins using a four-hydrophone array to localize the phonating animal, calculated a minimum echo-processing delay of about 16 ms, which supports this assertion.

In the wild, therefore, target scanning appears to takes place in the same manner as under experimental conditions. A change may occur, however, when an animal approaches a target at close range. Morozov et al. (1972) showed that shortly prior to the capture of a fish (<0.5 m away) the echo-processing delay in *Tursiops* click trains could be as low as 3 ms. These results suggest that upon final approach to a target, a change takes place in the way echoes are processed, resulting in considerably diminished ICIs. This would explain the dramatic drop in ICIs observed in the few "bridging" signals mentioned above.

It appears, therefore, that the interclick interval of a train can in some cases confound the functional distinction between burst pulses and echolocation click trains. Considerable evidence, however, suggests that the behavioral contexts in which burst pulses are usually recorded tend to be social in nature (Caldwell and Caldwell 1966; Overstrom 1983; Herzing 1988, 1996). Consequently, until further evidence about the functional occurrence of burst-pulse signals suggests otherwise, it appears reasonable to presume that, in the case of spinner dolphins, those click trains with consistent ICIs between 1.5 and approximately 10 ms represent a class of signals functionally distinct from typical echolocation trains. On the other hand, those trains characterized by variable ICIs considerably greater and less than about 10–15 ms imply a type of echolocation not yet well understood, rather than a functionally separate class of signals.

Spectrum and Source Levels

The spectral and source level results reported here are likely to be underestimates because of ambiguity with respect to the orientation of animals. Nonetheless, the values obtained are similar to results reported by Schotten (1998; also see Schotten et al., chapter 54, this volume), who measured the clicks of animals echolocating directly on the hydrophone array. His mean estimated source level of 208 dB re 1 μPa (n = 131 clicks, maximum 222 dB) is only 3 dB higher that the one obtained here, while his mean center frequency estimate of 80.4 kHz (n = 851 clicks) is approximately 17 kHz higher than what was obtained in this study for trains with mean ICIs >10 ms (presumed echolocation signals). The correlation between increasing source level and center frequency agrees well with similar results reported for *Pseudorca* (Au et al. 1995). This suggests that the spectral composition of clicks is a function of the intensity with which they are produced, regardless of the interclick interval.

All the signals collected in this study contained most of their energy well above the human hearing range. This has implications with respect to the sensory and recording equipment that must be employed to successfully study these signals. Burst pulses are not always audible and therefore could be missed with some regularity if narrowband equipment is used to record them.

Fig. 58.5. *A:* Spinner dolphin burst pulse. Mean ICI = 3.4 ms, center frequency = 63.3 kHz, rms bandwidth = 22.9 kHz, and maximum peak-to-peak source level = 215.5 dB re 1 μPa. *B:* Spinner dolphin echolocation train. Mean ICI = 32 ms, center frequency = 52.1 kHz, rms bandwidth = 18.4 kHz, and maximum peak-to-peak source level = 203.5 dB re 1 μPa.
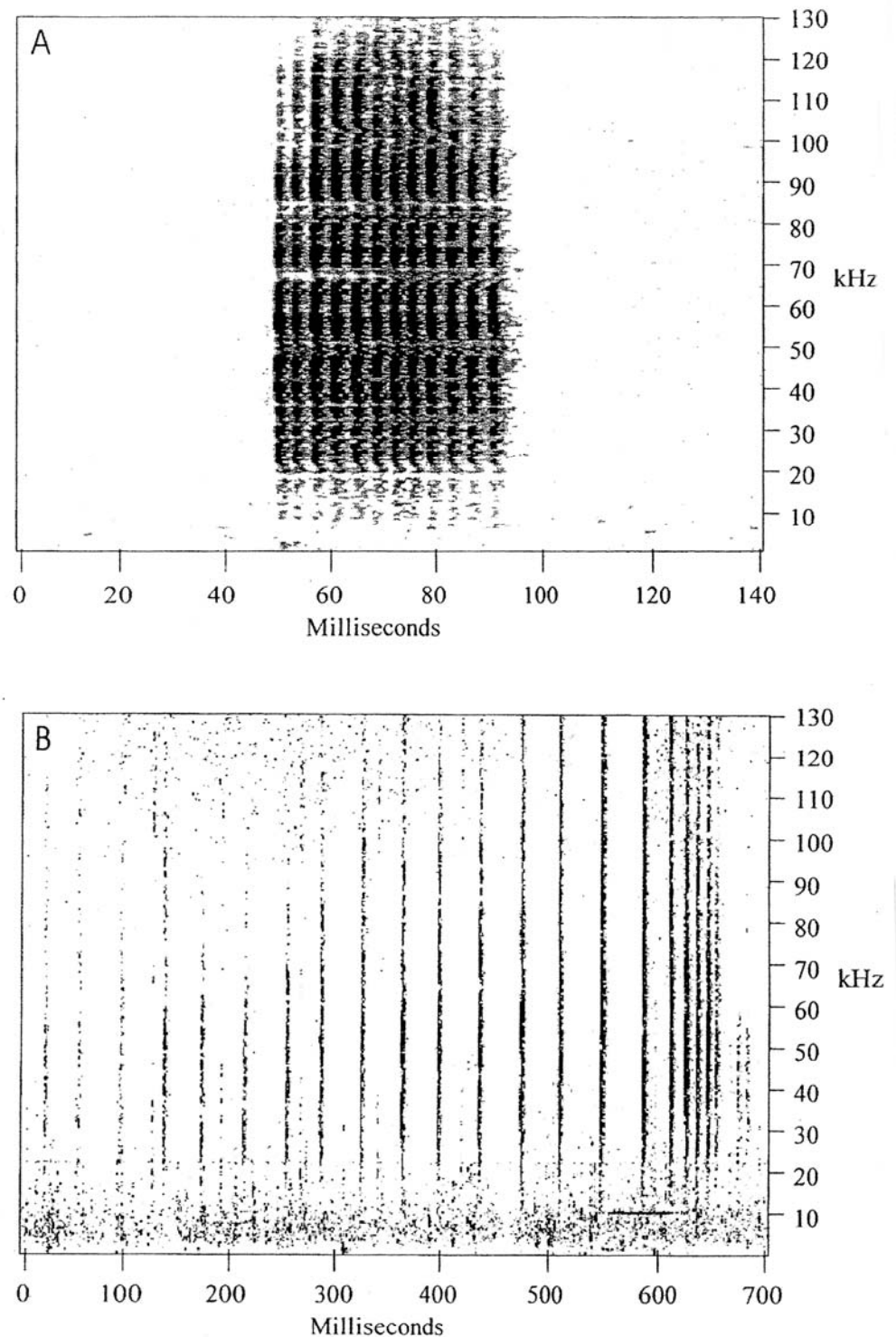
Although burst pulses tended to have lower center frequencies and slightly lower source levels, they were not as far removed from echolocation trains as reported in studies employing band-limited equipment (Caldwell and Caldwell 1966; Overstom 1983; Sjare and Smith 1986b; Herzing 1988, 1996). Diercks, Trochta, and Evans (1973) have argued that recording broadband signals with band-limited equipment results in the appearance of low-frequency artifacts not present in the original signal. Further investigation should establish whether these differences are species-specific, behaviorally related, or, in fact, undesired artifacts of methodology.

CONCLUSION

While the results presented here do not lay out a clear functional role for all the pulsed signals recorded, they

do provide a framework for further studies of the signaling system of spinner dolphins and other delphinids. It is clear that dolphins produce click trains in a variety of ways. Exactly how some of them are used, however, remains ambiguous.

Important questions persist regarding the occurrence of burst pulses. For example, while the variability found in echolocation click trains is attributable to the different sonar tasks encountered by the animals, what, if anything, does the variability in burst-pulse signal production represent? Burst pulses cannot be discounted from possibly also having an echolocation function, but little evidence exists at present to suggest this. Future efforts to clearly define functional distinctions between burst pulses and echolocation signals will need to employ a sophisticated approach to closely examine associated behavioral patterns of individuals and control for the directional and broadband nature of these signals. Advances in the technology available to researchers studying these signals will help to overcome many of the limitations in bandwidth, localization, and portability encountered in the past.

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Clicks Produced by Captive Amazon River Dolphins (*Inia geoffrensis*) in Sexual Context

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Introduction

Recorded sounds of most odontocetes are highly diversified, even at the individual level. This variation can occur in more than one acoustic parameter, such as frequency, amplitude, duration, and rate and number of pulses (W. J. Smith 1986). Evidence suggesting the occurrence of group and individual-specific calls exists for *Orcinus orca* (J. K. B. Ford 1991) and *Tursiops truncatus.* In the latter species, these calls have been considered to be used in intraspecific recognition (Caldwell and Caldwell 1965) and group cohesion (Janik and Slater 1998) functions. Establishing the function of the suit of sounds produced by a single individual is a more difficult task. In a few species, such as *Physeter macrocephalus,* a relationship has been found between sounds and observed behavior (Whitehead and Weilgart 1991). Nevertheless, knowledge about the specific function of types of sounds is generally unknown (Richardson et al. 1995). This is largely due to the high variability in sounds and their high context-dependent nature, but also to the difficulty in identifying the sender and the subsequent behavior of the receiver (W. J. Smith 1986).

Only a limited number of studies address the communication use of pulsed sounds covering the ultrasonic range (Dawson and Thorpe 1990). This seems to be a result of the limitations of readily available equipment and also from a generalized assumption, not yet grounded, that high-frequency pulses are used only in echolocation (Dawson and Thorpe 1990). In addition, there are even fewer studies of ultrasonic pulsed sounds produced during specific behaviors (Dawson 1991), such as sexual activity. In odontocetes, sexual behaviors are not restricted to mating events, occurring often in social interactions both hetero- and homosexually (Wells, Boness, and Rathbun 1999).

The Amazon River dolphin (*Inia geoffrensis*) appears to produce only pulsed sounds, as is also known to be the case in Physeteridae and Phocoenidae (W. A. Watkins and Wartzok 1985). *I. geoffrensis* belongs to Platanistidae, a primitive family of cetaceans (Layne and Caldwell 1964) and occurs in the Amazon and Orinoco rivers and their tributaries, often found in very turbid waters (Best and da Silva 1989). To our knowledge, no studies have investigated the acoustic repertoire of *I. geoffrensis* during sexual interactions in the ultrasonic

ECHOLOCATION
in Bats and Dolphins

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