The broadband social acoustic signaling behavior of spinner and spotted dolphins

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Efforts to study the social acoustic signaling behavior of delphinids have traditionally been restricted to audio-range ($<$20 kHz) analyses. To explore the occurrence of communication signals at ultrasonic frequencies, broadband recordings of whistles and burst pulses were obtained from two commonly studied species of delphinids, the Hawaiian spinner dolphin (*Stenella longirostris*) and the Atlantic spotted dolphin (*Stenella frontalis*). Signals were quantitatively analyzed to establish their full bandwidth, to identify distinguishing characteristics between each species, and to determine how often they occur beyond the range of human hearing. Fundamental whistle contours were found to extend beyond 20 kHz only rarely among spotted dolphins, but with some regularity in spinner dolphins. Harmonics were present in the majority of whistles and varied considerably in their number, occurrence, and amplitude. Many whistles had harmonics that extended past 50 kHz and some reached as high as 100 kHz. The relative amplitude of harmonics and the high hearing sensitivity of dolphins to equivalent frequencies suggest that harmonics are biologically relevant spectral features. The burst pulses of both species were found to be predominantly ultrasonic, often with little or no energy below 20 kHz. The findings presented reveal that the social signals produced by spinner and spotted dolphins span the full range of their hearing sensitivity, are spectrally quite varied, and in the case of burst pulses are probably produced more frequently than reported by audio-range analyses. © *2003 Acoustical Society of America.* [DOI: 10.1121/1.1596173]

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I. INTRODUCTION

Dolphins (family: Delphinidae) are known to produce and hear sounds well beyond the frequency limits of human hearing. Their use of short, broadband clicks with peak energies between 60 and 120 kHz is well documented in the context of echolocation behavior [see Au (1993) for a review]. In contrast, considerably less has been reported on their use of ultrasonic signaling for communicative purposes, in part because broadband recorders were until recently quite expensive and not very portable (Au *et al.*, 1999). With a few exceptions (Lilly and Miller, 1961; Brownlee, 1983; Dawson, 1991; Rasmussen and Miller, 2002), the vast majority of studies examining dolphin social signals both in captivity and in the field have been restricted in bandwidth to the human-audible range. This has left the full-band characteristics of their signals poorly described and the use of ultrasonic frequency bands for communicative purposes all but unexplored.

Most dolphin species produce two primary types of sounds thought to play a role in social interactions: tonal, frequency-modulated whistles and rapid repetition rate "burst pulse" click trains (Herman and Tavolga, 1980). A few species do not produce whistles and are believed to communicate exclusively via pulsed sounds (Dawson, 1991).

How whistles are used in communication is an ongoing topic of debate among researchers (McCowan and Reiss, 2001), but the general consensus is that they play an important role in maintaining contact between dispersed individuals (Janik, 2000a). Burst pulses have also been strongly implicated in communication (Caldwell and Caldwell, 1967; Dawson, 1991; Norris *et al.*, 1994), but their occurrence and functional significance are still only poorly understood. Some authors have suggested they play an important role in agonistic encounters (Caldwell and Caldwell, 1967; Overstrom, 1983; McCowan and Reiss, 1995), while others have proposed they represent "emotive" signals in a broader sense (Lilly and Miller, 1961; Herzing, 1988, 1996), possibly representing graded signals (Brownlee, 1983).

Dolphins produce whistles with fundamental frequencies usually in the human audible range (below 20 kHz). These whistles often also have harmonics, which occur at integer multiples of the fundamental and extend beyond the range of human hearing. Harmonics are integral components of tonal signals produced by departures of the waveform from a sinusoidal pattern. To date, no published efforts have been made to explore the occurrence and functional significance of whistle harmonics. It is not presently known how often they occur in dolphin whistles, how far in frequency they extend, how much energy they contain relative to the fundamental, or why harmonics are present in some whistles but not in others.

Little is also known about the properties of burst pulses. The spectral, temporal, and amplitude characteristics of burst

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TABLE I. The characteristics of the fundamental frequency (F_0) of spinner and spotted dolphin whistles. Values are given as mean±standard deviation unless indicated otherwise.

	N	Duration (s)[a]	Mean F_0 frequency (kHz)[a]	FM range of F_0 (kHz)	F_0 max (kHz)[a] mean±S.D. (95% C.I.)	F_0 min (kHz)[a] mean±S.D. (95% C.I.)	% energy in F_0 min, Q_1, *median*, Q_2, max	No. of harmonics
S. longirostris	167	0.66±0.36	13.8±2.3	7.3±3.9	17.4±3.0(16.9–17.9)	10.1±2.5(9.7–10.5)	65.6, 83.3, *93.1*, 95.7, 99.3	1.83±0.87
S. frontalis	220	0.44±0.30	10.9±2.0	7.4±2.9	14.5±2.5(14.1–14.9)	7.1±1.5(6.9–7.3)	47.1, 88.6, *93.5*, 96.9, 99.7	1.99±1.03

[a]$P<0.01$.

pulse click trains have been only marginally explored. Early descriptions in the literature were mostly qualitative, reflecting the subjective aural interpretations and classifications of human listeners (Busnel and Dziedzic, 1966; Caldwell and Caldwell, 1967, 1971). Later efforts were more quantitative, but as with studies of whistles, these also relied primarily on audio-range analyses (Overstrom, 1983; Herzing, 1988, 1996; McCowan and Reiss, 1995; Van Parijs and Corkeron, 2001). Presently, the only quantitative description of burst pulsing at ultrasonic frequencies is for a nonwhistling species, the Hector's dolphin (*Cephalorhynchus hectori*) (Dawson, 1991). Only anecdotal accounts exist about the occurrence of burst pulses above human-audible frequencies for whistling species (Lilly and Miller, 1961; Norris *et al.*, 1994).

In light of the acute hearing sensitivity to ultrasonic frequencies exhibited by all dolphin species tested so far (Nachtigall *et al.*, 2000), the current lack of knowledge about the broadband properties of whistles and burst pulses make it difficult to fully appreciate their design as communicative signals. In this study, we used broadband recording technology adapted for the field to examine the signaling behavior of two commonly studied species of dolphins, the Hawaiian spinner dolphin (*Stenella longirostris*) and the Atlantic spotted dolphin (*Stenella frontalis*). Our objectives here are to (1) report the full-bandwidth properties of the whistles and burst pulses of these two species, (2) present distinctions in their production, and (3) provide an estimate of the bias associated with recording dolphin social signals narrow band (0–20 kHz).

II. METHODOLOGY

A. Data collection

Recordings of dolphin whistles and burst pulses were obtained using a portable broadband data acquisition system (PBDAS), previously described in Au *et al.* (1999). The system employs a laptop computer to operate a National Instruments DAQCard-AI-16E-4 12-bit analog to digital (A/D) converter PCMCIA card. Dolphin signals were digitally sampled at a rate of 260 kHz, providing a Nyquist frequency for all recordings of 130 kHz. Prior to sampling, signals were conditioned by an analog signal processing unit consisting of a high- and low-pass filter and variable gain. The high- and low-pass filters were set at 600 Hz and 100 kHz, respectively, and the gain provided was 60 dB. Recordings were obtained using a custom-built, 2.5-cm-diam spherical hydrophone flat (±3 dB) to approximately 150 kHz with a calibrated sensitivity of −197 dB *re* 1 μPa.

The A/D card was programmed to sample a single channel continuously into a circular memory buffer in the computer's random access memory (RAM). Incoming signals were detected aurally through headphones and by monitoring a LED bar graph display that revealed the presence and amplitude of signals independent of their frequency. When signals were heard or observed on the LED, the system's operator pressed a trigger switch that initiated the transfer of data from RAM to the computer's hard disk. Usually, about 1 s of pretrigger data and 2 s of posttrigger data were automatically stored with each trigger.

Recordings were obtained from free-ranging spinner dolphins in Hawaii on 18 occasions and Atlantic spotted dolphins in the Bahamas on 17 occasions. Data were collected off the south and west shores of Oahu, Hawaii, during various periods between June 1997 and August 1998 and in the Bahamas along the western edge of the Little Bahama Bank during the month of August in 1999 and 2001. Vessels ranging from 13 to 62 ft in length were used to approach groups of dolphins in each locale. The hydrophone was typically placed 3 m below the surface, between 50 and 200 m in front of moving or milling animals. Recordings were made as groups approached and passed by the vessel. Group sizes ranged from 3 to approximately 100 individuals. The behavioral states of spinner dolphin groups included resting, traveling, and socializing. The same states were observed for spotted dolphins in addition to both daytime and nighttime foraging. Behavioral states were established using the classification method of Norris and Dohl (1980) for spinner dolphins and Herzing (1996) for spotted dolphins.

B. Data analysis

Cool Edit 96™ was used for the initial visualization of recordings. A 1024-point Hanning window was used to plot all sonograms. Subsequent quantitative analyses were carried out using custom-written Matlab™ 5.2 programs. Whistles were analyzed quantitatively if they had harmonics, if their signal to noise (S/N) ratio was sufficient to unambiguously establish their beginning and ending points, and provided they did not overlap in time and frequency with other whistles. The analysis algorithm employed a short-time Fourier transform approach to establish several parameters of interest. These included (1) the properties of the fundamental frequency contour (maximum, minimum, and mean frequencies as well as signal duration); (2) the number of harmonics present and the relative occurrence of each harmonic in the whistle (as a percent of signal duration); (3) the relationship between amplitude modulation of the fundamental (normalized to the maximum amplitude within a signal) and the

presence of a second harmonic; and (4) the amount of energy in each harmonic relative to the fundamental.

Burst pulses were quantitatively analyzed provided the S/N ratio between the peak-to-peak amplitude of clicks and the root mean square (rms) amplitude of the background noise floor was greater than 12 dB. Burst pulses were evaluated with respect to the number of clicks in a train, their interclick interval (ICI), and the peak frequency, center frequency, and rms bandwidth of individual clicks. In addition, the relative energy present above and below 20 kHz was calculated for each click.

Burst pulses were distinguished from echolocation click trains on the basis of their ICIs. Click trains were considered burst pulses if their mean ICI did not exceed 10 ms. This criterion was based on previous work by Lammers *et al.* (2003) and is discussed in more detail later.

III. RESULTS

A. Whistles

A total of 1106 and 557 whistles were collected from spinner and spotted dolphins, respectively. Visual inspection revealed that 61.4% of spinner dolphin whistles and 69.3% of spotted dolphin whistles had one or more higher harmonics. Of the 679 spinner dolphin whistles with harmonics, 167 (24.5%) were deemed appropriate for quantitative analysis. This was the case for 220 (57.0%) of the 386 spotted dolphin whistles with harmonics. Fewer spinner than spotted dolphins whistles met the criteria for quantitative analysis because spinners tended to chorus more (Brownlee, 1983), resulting in multiple overlapping whistles that did not lend themselves well to further analysis.

1. Properties of the fundamental

The contours of the fundamental frequency of spinner and spotted dolphin whistles were roughly equal in their frequency modulation (FM) range (approximately 7 kHz), but spinner dolphin whistles were significantly (two-sample *t*-test; $P < 0.01$) longer in duration and higher in their minimum, maximum and mean frequency than those of spotted dolphins (Table I). All fundamentals had most of their energy below 20 kHz. Eight (3.6%) spotted dolphin and 41 (24.5%) spinner dolphin whistles had maximum frequencies of the
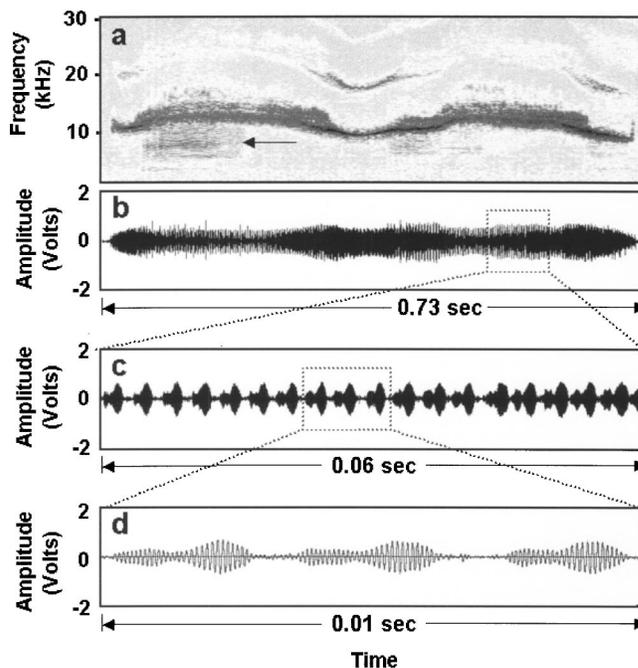

FIG. 1. Amplitude-modulated spotted dolphin whistle showing the sonogram (a), the waveform pattern (b), and a progressive magnification on the pulse-like structure of the signal [(c) and (d)]. The arrow points to a weak concurrent burst pulse.

fundamental that were above 20 kHz. The highest maximum frequency measured for a spotted dolphin whistle fundamental was 27.1 kHz. For spinner dolphins it was 24.9 kHz.

Spotted dolphins often produced whistles that were qualitatively very distinct from the whistles of spinner dolphins. To human listeners, many spotted dolphin whistles had a coarse or "raspy" aural quality that was considerably less pure-tone than those of spinner dolphins. This was because segments of the waveforms of spotted dolphin whistles frequently exhibited such a high degree of amplitude modulation (AM) that they took on pulselike properties (Fig. 1). In the spectral domain, the energy in the fundamental frequency of these kinds of whistles covered a wider band (1–5 kHz) than the more tonal whistles of spinner dolphin (<100 Hz). These rapid AM whistles often occurred either in conjunction with or immediately following burst pulses. Bouts of a specific contour type usually exhibited a very similar AM pattern on consecutive whistles, suggesting that the modula-
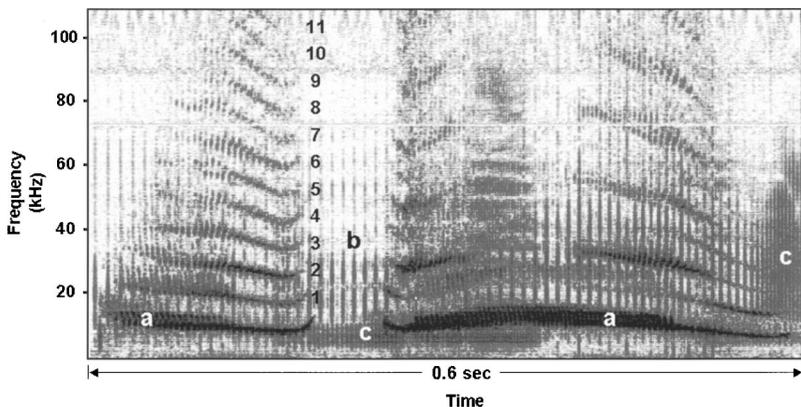

FIG. 2. A sequence of two spotted dolphin whistles (a) mixed with echolocation clicks (b) and burst pulses (c). The first whistle contains 11 harmonics (numbered).

TABLE II. The occurrence, energy content, and amplitude of the second (H_1), third (H_2), fourth (H_3), and fifth (H_4) harmonics relative to the fundamental (F_0). All values except maxima are given as mean±standard deviation.

	Harmonic	N	% of signal duration	% of total signal energy		dB less than F_0	
				Mean	Maximum	Mean	Minimum
S. longirostris	H_1	167	74.3±18.9	8.1±5.8	34.1	−11.7±3.7	−2.8
	H_2	96	56.7±27.8	2.2±2.4	13.4	−18.4±5.0	−7.7
	H_3	33	41.0±23.3	0.5±0.5	2.0	−24.6±4.9	−15.6
	H_4	9	37.1±17.5	0.2±0.3	1.0	−28.7±6.6	−19.1
S. frontalis	H_1	220	71.4±25.0	8.4±8.5	43.8	−12.3±5.0	−0.3
	H_2	133	52.1±29.5	2.2±2.6	16.0	−19.0±6.3	−5.2
	H_3	57	47.5±24.6	1.0±0.8	3.1	−20.9±5.5	−13.7
	H_4	29	43.7±22.5	0.5±0.7	3.3	−24.1±5.3	−13.5

tions observed were not simply the byproduct of surface and bottom reflections constructively and destructively interfering with the direct signal [the Lloyd mirror effect (Urick, 1983)]. Approximately 41% of spotted dolphin whistles exhibited this distinct AM pattern on at least part of the signal. Spinner dolphin whistles were also amplitude modulated to a degree, but less than 2% showed the pulsed quality exhibited by spotted dolphins.

2. Occurrence and characteristics of harmonics

The maximum number of harmonics observed was 7 for a spinner dolphin whistle and 11 for that of a spotted dolphin whistle (Fig. 2). More typically, however, the whistles of both species had between one and three harmonics. These did not usually occur throughout the duration of a whistle, but rather varied considerably in the percentage of time they were present in a signal (Table II). In some cases, one or more harmonics occurred throughout the duration of the whistle, while in others harmonics were present during only certain segments of the signal (Fig. 3).

Also variable was the amount of the signal's energy contained in higher harmonics. Although generally about 90% of a whistle's energy was found in the fundamental (F_0), the second harmonic (H_1) could contain up to 34.1% and 43.8% of the total energy of spinner and spotted dolphin signals, respectively. In terms of amplitude, in both species the second harmonic was on average approximately 12 dB lower than the fundamental. However, this difference could be as small as −0.3 dB in some spotted dolphin whistles and −2.8 dB in those of spinner dolphins. The third (H_2), fourth (H_3), and fifth (H_4) harmonics always contained progressively less energy (Table II).

In whistles where one or more harmonics were present during 25%–75% of the signal's duration, there was a significant difference in the relative amplitude of segments that had a second harmonic versus those that did not (paired *t*-test, $P<0.001$). Segments of whistles with harmonics had a median amplitude (normalized to the maximum of each whistle) of 0.65 (S.D.=0.15) for spotted dolphins and 0.67 (S.D.=0.12) for spinner dolphins, while those without were only 0.48 (S.D.=0.19) and 0.53 (S.D.=0.14), respectively. In other words, harmonics consistently occurred at and around the maxima of amplitude modulation in the signal.

B. Burst pulses

Seventy-nine spinner dolphin and 73 spotted dolphin burst pulses were obtained that met the criteria set for quantitative analysis. Burst pulses were produced alone, in bouts or associated with whistles (Fig. 4). Spinner dolphins produced burst pulses that had on average approximately 30 clicks per train with a mean ICI of 3.85 ms (Table III). Spotted dolphin burst pulses averaged about 100 clicks per train with a mean ICI of 3.19 ms. The number of clicks in a burst pulse displayed an approximately bimodal distribution that distinguished burst pulses into low quantity (<70 clicks) and high quantity (>70 clicks) click trains (Fig. 5). Spotted dolphins produced significantly more high quantity burst pulses
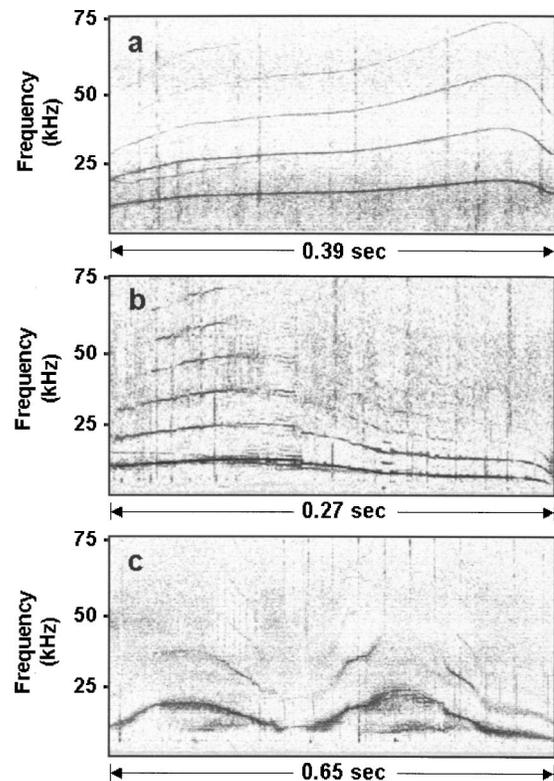

FIG. 3. Examples of the variation found in the harmonic composition of whistles: (a) spinner dolphin whistle with continuous harmonics throughout signal; (b) spotted dolphin whistle with harmonics emphasized on concave portion of the contour; and (c) spotted dolphin whistle with harmonics only on the slopes of the contour.

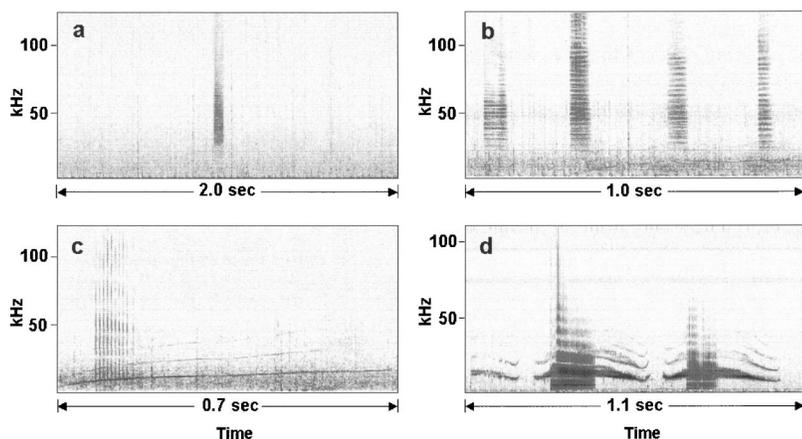Lammers *et al.*: Broadband social acoustic signals of dolphins

FIG. 4. Examples of the variation in burst pulse occurrence: (a) spinner dolphin burst pulse with minimal energy below 20 kHz occurring alone; (b) sequence of four spinner dolphin burst pulses with minimal energy below 20 kHz occurring within a one second period; (c) simultaneously occurring spinner dolphin whistle and burst pulse with energy both above and below 20 kHz; and (d) simultaneously occurring spotted dolphin whistle and burst pulse with energy mostly below 20 kHz. Individual clicks are not resolved in (a), (b), and (d) due to the inherent time/frequency resolution tradeoff of fast Fourier transforms.

($N=25/73$; $\bar{x}=239$ clicks; max$=958$ clicks) than spinner dolphins ($N=6/79$; $\bar{x}=116$; max$=168$ clicks) (chi-square test, $P<0.001$).

Peak and center frequencies for spinner dolphin burst pulses were on average 32.3 and 40.1 kHz, respectively. For spotted dolphins these were somewhat higher at 40.3 and 44.4 kHz, respectively. The rms bandwidths were roughly equivalent at 20.5 kHz for spinner dolphins and 18.1 kHz for spotted dolphins. Spectral energy distribution in clicks did not show any relationship to either the number of clicks in a train or the interclick interval.

Only 17.8% of spinner dolphin and 20.2% of spotted dolphin burst pulses had click trains with peak frequencies below 20 kHz (Table IV). On average, approximately 80% of the total energy in burst pulses was above 20 kHz for both species. Moreover, 39.2% of spinner dolphin and 60.3% of spotted dolphin burst pulses had less than 10% of their total energy below 20 kHz. Thus, while some burst pulses were clearly audible and prominent at sonic frequencies (<20 kHz), most were either barely detectable (aurally or visually on a sonogram) or completely devoid of energy at those frequencies [Figs. 4(a) and (b)]. When we digitally resampled each data file to reflect a 20-kHz bandwidth, we found that 40.5% of spinner dolphin and 30.1% of spotted dolphin burst pulses showed no evidence of being present within that frequency range (Fig. 6).

IV. DISCUSSION

A. Signal characteristics

Our results reveal that the whistles and burst pulses of these two species of dolphin span a broader frequency range than is traditionally reported for delphinids. Although the fundamental frequency contours of their whistles occur mostly in the human-audible range (as is typically assumed), their harmonics routinely reach 50 kHz and beyond. In addition, their burst pulse signals are predominantly ultrasonic, often with little or no energy below 20 kHz.

The spectral measures we have presented must be viewed with caution, however, due to the confounding effects of signal directionality. Dolphin clicks are well known to have directional properties (Au, 1993) and recent findings by Lammers and Au (2003) and Miller (2002) indicate that delphinids also project whistles in a frequency-dependent beam. We could not control for signaler orientation in our study. Therefore, our estimates of the energy content and the occurrence of harmonics and burst pulses are almost certainly underestimates of what these dolphins actually produce on-axis of their transmission beam. On the other hand, the temporal characteristics (number of clicks, interclick interval, etc.) of burst pulses are likely to be more robust to directional variations and can therefore be considered representative of what these two species produce.

1. Whistle harmonics

The majority of whistles recorded had one or more harmonics. Whistles without harmonics were generally fainter than those with them. These may have been signals that were produced by animals oriented away from the hydrophone rather than whistles truly lacking harmonic structure. Additionally, dolphins may also have exerted some control over the harmonic composition of their whistles, modulating their occurrence. Our finding that the presence or absence of a second harmonic was matched to amplitude maxima in the fundamental suggests that harmonics could be spectral byproducts of amplitude modulation. As a dolphin increases signal amplitude it may progressively lose its ability to pro-

TABLE III. The temporal and spectral characteristics of spinner and spotted dolphin burst pulses. All values are given as mean±standard deviation. No inference was attempted to distinguish the broadband spectral measures of the two species due to the potentially confounding effects of signal directionality (see discussion).

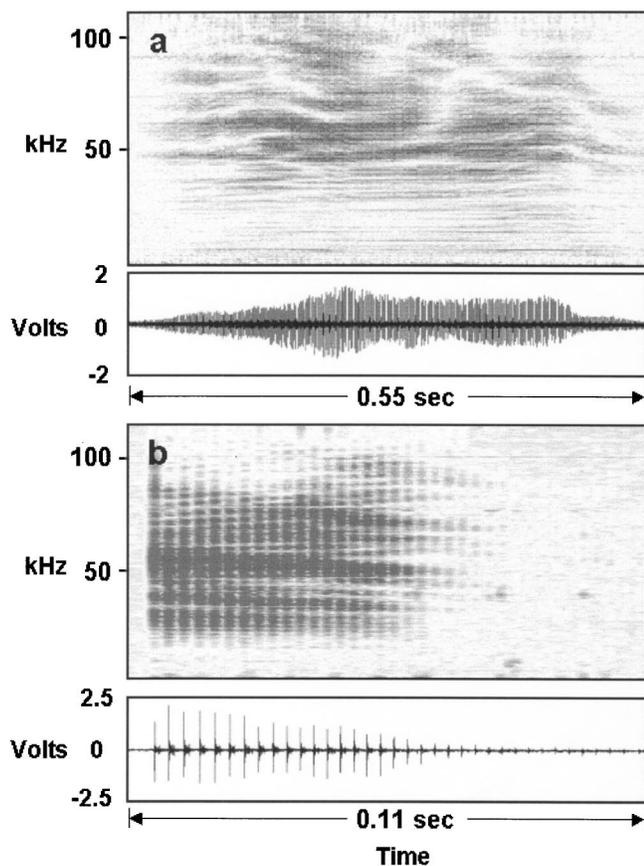|	N	No. of clicks/ burst pulse[b]	Mean interclick interval (ms)[a]	Peak frequency (kHz)	Center frequency (kHz)	rms bandwidth (kHz)
S. longirostris	79	29±29	3.85±1.67	32.3±12.5	40.1±12.1	20.5±4.3
S. frontalis	73	103±145	3.19±1.40	40.3±17.8	44.4±16.5	18.1±4.8

[a]$P<0.05$.
[b]$P<0.01$.

FIG. 5. Examples of high quantity (a) and low quantity (b) spotted dolphin burst pulses. Click train *a* has 255 clicks with mean ICI of 1.7 ms. Click train *b* has 35 clicks with a mean ICI of 2.9 ms.
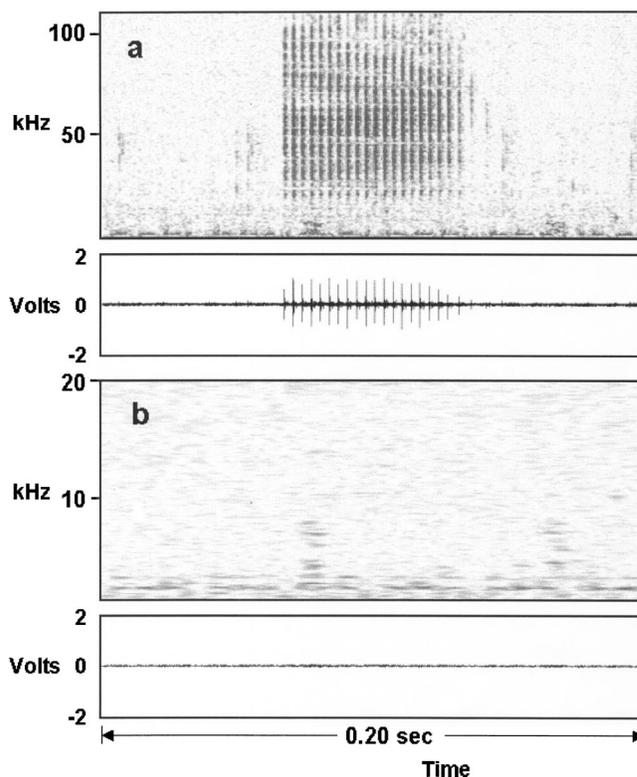

FIG. 6. The same spotted dolphin burst pulse represented both broadband (a) and downsampled to provide a narrow-band perspective (b). Note the lack of any evidence that a signal is present in the narrow-band view.

duce a pure tone, resulting in harmonic distortions. The variation in harmonic composition between and within whistles suggests that directionality and modulation probably both influence their occurrence. Empirical measurements of a whistle beam-pattern with a more detailed examination of how signal amplitude affects harmonic content will provide a more definitive explanation for the variability we observed.

An intriguing result was obtained when we used a delphinid audiogram to infer the way whistles with harmonics might be heard by nearby conspecifics. No audiograms specific to spinner or spotted dolphins presently exist, so we used one recently obtained for a species in the same genus, the striped dolphin (*Stenella coeruleoalba*) (Kastelein *et al.*, 2003). Adjusting the relative amplitude of each harmonic (from Table II) with respect to the striped dolphin's hearing sensitivity at the corresponding frequencies revealed that dolphins should be quite sensitive to harmonics. For almost all the frequencies examined, increased hearing sensitivity

more than compensated for the decreased amplitude of harmonics (Table V). In fact, at most harmonic frequencies the levels presumably received by listeners were between 3 and almost 7 dB higher than the fundamental

Whether listening dolphins hear the fundamental or a specific harmonic as the dominant frequency of a whistle depends on the perceived level and the signal-to-noise ratio of each signal component. Given the broad range in relative amplitudes of the harmonics we measured, it is entirely likely that harmonics sometimes are heard as the dominant frequency of a whistle. Figure 7 illustrates such a case. A whistle is presented as it was first recorded using a hydrophone with a flat frequency response and then bandpass filtered to approximate the striped dolphin's hearing sensitivity. In the filtered whistle the second and third harmonics are in fact higher in amplitude than the fundamental. We can conclude from this that how listening animals actually hear a whistle is greatly influenced by the signal's full spectral makeup, which is in turn determined by the listener's relative position to the emitting beam and perhaps also by active modulation on the part of the signaler.

TABLE IV. Narrow-band (20 kHz) versus broadband (130 kHz) bias of burst pulse spectral content and energy. Values presented as number of signals and % out of *N* or as mean±standard deviation.

	N	No. w/peak frequency below 20 kHz	% energy above 20 kHz	No. w/less than 10% energy below 20 kHz	No. not detectable narrow-band (<20 kHz)
S. longirostris	79	16 (20.2%)	78.7±19.6	31 (39.2%)	32 (40.5%)
S. frontalis	73	13 (17.8%)	80.4±27.8	44 (60.3%)	22 (30.1%)

TABLE V. Comparison of the relative amplitude of harmonics measured from the data (assuming equal sensitivity across all frequencies) and corrected for the hearing sensitivity of *S. coeruleoalba*.

		Mean frequency (kHz)	Mean amplitude of harmonics relative to F_0 (in dB)	
			Equal sensitivity across frequencies (from Table II)	Adjusted with *S. coeruleoalba* audiogram
S. longirostris	F_0	13.8	...	...
	H_1	27.6	−11.7	+3.3
	H_2	41.4	−18.4	+6.6
	H_3	55.2	−24.6	+2.4
	H_4	69.0	−28.7	−3.7
S. frontalis	F_0			
	H_1	10.9	−12.3	−0.3
	H_2	21.8	−19.0	+4.0
	H_3	32.7	−20.9	+6.1
	H_4	43.6	−24.1	+4.9

Whether whistle harmonics play a role in communication among dolphins is a question open for debate. To human listeners, harmonics provide the perceptual quality of timbre and offer qualitative cues that serve to distinguish between otherwise very similar sound patterns (e.g., the same word spoken by different individuals) (Handel, 1989). In many taxa, including other primates, harmonics are often associated with individual identity cues (Masters, 1991; Caudron *et al.*, 1998; Jouventin *et al.*, 1999; Charrier *et al.*, 2002). However, in dolphin signals the directionality of high-frequency spectral features probably result in whistle harmonics being poor indicators of identity due to azimuth-dependent degradation. On the other hand, cueing by listeners on the orientation-dependent amplitude of harmonics could play an important role in promoting group cohesion by revealing the orientation of signalers, as suggested by Miller (2002) and Lammers and Au (2003). Discrimination experiments with captive animals are needed to test whether dolphins in fact attend to changes in the harmonic structure of whistles.

2. Burst pulses

a. Energy distribution. The finding that burst pulses have the majority of their energy at ultrasonic frequencies is novel but comes as little surprise, given the properties of echolocation clicks (see Au, 1993). The burst pulse waveforms we recorded could not be readily distinguished from the other, presumably echolocation clicks that were obtained. Relatively few signals matched the traditional audio-range descriptions given for burst pulses, which often report peak frequencies of a few hundred to a few thousand hertz (e.g., Caldwell and Caldwell, 1967; McCowan and Reiss, 1995; Herzing, 1996). Only a minority of signals had peak frequencies below 20 kHz. However, numerous burst pulses displayed "breaks" in their energy distribution, reflecting a rippled spectrum caused by closely spaced surface and bottom reflections (Au, 1993). These often had a small energy peak in the audible range with considerably more energy distributed well above 20 kHz (Fig. 8). We presume that many of the previous narrow-band descriptions of burst
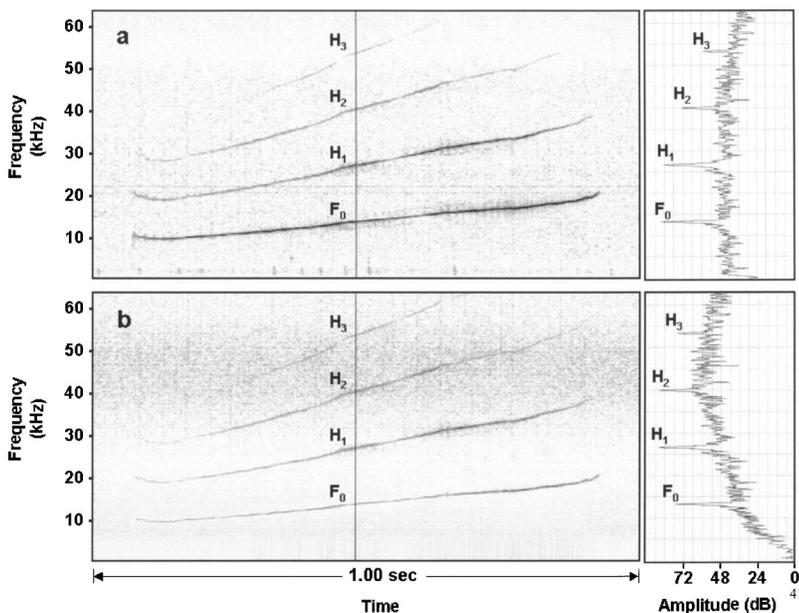

FIG. 7. Sonogram and power spectrum of a spinner dolphin whistle as it was recorded with a hydrophone flat in frequency response (a), and subsequently filtered with a frequency sensitivity curve approximating a striped dolphin's audiogram (b) (after Kastelein *et al.*, 2003). The solid vertical line represents where the 1024-point power spectrum was measured. Represented on the sonogram and power spectrum are the fundamental frequency (F_0), as well as the second (H_1), third (H_2), and fourth (H_3) harmonics. Note that the fundamental is approximately 10 dB lower that the second and third harmonics in the power spectrum of the filtered signal.
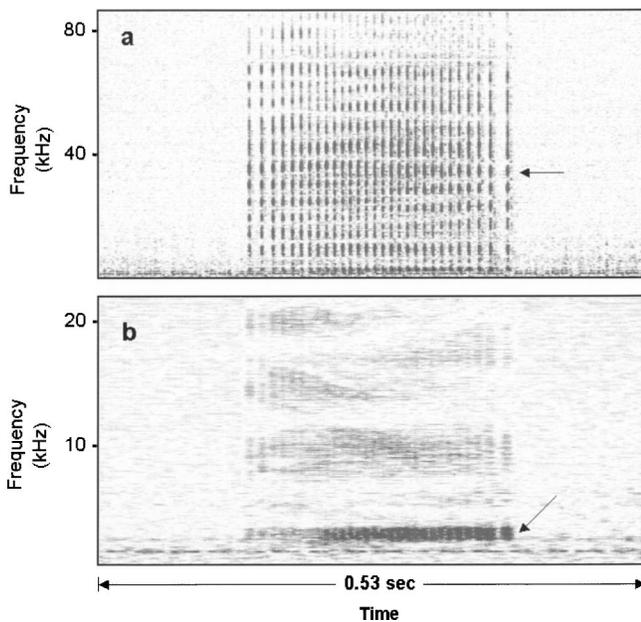
FIG. 8. A spotted dolphin burst pulse represented both broadband (a) and narrow-band (b). The banded pattern of individual clicks represents a rippled spectrum with multiple energy peaks of varying amplitude. The arrows indicate the location of the peak frequency in each case.

pulses may have been accounts of only these lower spectral peaks. In all likelihood, if a broader spectral analysis had been employed in earlier studies, considerably more energy would have been noted at the higher frequency bands.

Of particular interest is the proportion of burst pulses that had little or no energy at sonic frequencies. The fact that 30%–40% of burst pulses were undetectable below 20 kHz implies that they are probably a more common form of social signaling among delphinids than previously suspected. In our recordings, few whistling periods were observed that did not also coincide with at least some burst pulsing (sonic or ultrasonic). Consequently, it is our conclusion that at least in these two species burst pulses probably play an equally important if perhaps different social signaling role as do whistles.

b. Social signaling or echolocation? Given the similarities that exist between burst pulses and other click trains, a perplexing question invariably arises: what is the distinction between click trains presumably used for communication and those used for echolocation? The existing literature on this topic is vague because burst pulses have been traditionally discussed in terms of their sonic properties (Herman and Tavolga, 1980; Popper, 1980; Overstrom, 1983; Herzing, 1996; Van Parijs and Corkeron, 2001). In our analysis, we considered a signal to be a burst pulse if the interclick intervals did not exceed 10 ms. This criterion was based on a previous effort that examined patterns of click production in spinner dolphins which found a bimodal distribution of mean interclick intervals separated at around 10 ms (Lammers *et al.*, 2003). This bimodal distribution was interpreted as being indicative of two distinct patterns of click train production: a burst pulse pattern with interclick intervals consistently less than 10 ms and a sonar click train pattern with intervals greater than approximately 15 ms.

Admittedly, this distinction is not necessarily definitive because click trains are sometimes produced that begin with long interclick intervals (10–100+ ms) and end with very short ones (1.5–9 ms). These are often observed when animals are foraging and presumably echolocating on prey (Herzing, 1996). However, a rationale can be presented for the 10-ms distinction, given that it is not clear whether dolphins process the returning echoes from click trains with very short intervals. Experiments with free-swimming bottlenose dolphins (*Tursiops truncatus*) have shown that an echo-processing lag time of between 15 and 45 ms is always associated with successive clicks produced by animals echolocating on targets further than 0.4 m away (Evans and Powell, 1967; Au, 1993). As animals close in on a target (<0.4 m), interclick intervals as low as 2.5 ms have been observed (Evans and Powell, 1967; Morozov *et al.*, 1972), but whether dolphins are processing more than one echo at a time, selecting specific echoes or even using the returning echoes at all, is not known.

More telling perhaps is the fact that, even at close range, there is always a gradual progression towards shorter click intervals as the dolphin approaches a target (Evans and Powell, 1967; Morozov *et al.*, 1972). Therefore, trains characterized by variable ICIs considerably greater and less than 10–15 ms probably represent a type of echolocation not yet well understood rather than a functionally separate class of signals. However, no evidence presently exists to indicate that click trains that begin, persist, and end with interclick intervals less than 10 ms are ever used in contexts identified as echolocation. This does not exclude the possibility that an echolocation function may be associated, but rather implies that burst pulses, as defined here, form a class of click trains distinct in occurrence from those typically linked to echolocation. Their frequent incidence in highly social contexts (such as agonistic encounters) considered with their absence in controlled echolocation contexts strongly suggests that their primary function is likely communicative. In other words, burst pulses are probably signals intended to be heard by nearby animals. Additional broadband recordings coupled with underwater visual observations of socializing and echolocating animals will be needed to further explore the distinction between burst pulse and echolocation click train production, as well as to establish how burst pulses function in communication.

c. Nomenclature. Given that burst pulses are predominantly ultrasonic signals, we propose that the practice of discussing them in terms of their aural qualities should to be reconsidered in favor of a more quantitative approach. Terms such as "squawks," "squeaks," "creaks," and "yelps" commonly used to describe and distinguish burst pulses can result in misleading conclusions, as they primarily describe the subjective impressions of time separation pitch experienced by human listeners (McCellan and Small, 1965). Dolphins have better auditory time resolution capabilities than humans (Vel'min and Dubrovskiy, 1976; Ketten, 1992), so attempting to classify burst pulses on the basis of human-perceived aural qualities likely misrepresents how dolphins hear the sounds. As a start, forming classes on the basis of temporal characteristics, such as interclick intervals and total number of

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clicks, would lead to more meaningful comparative discussions between authors.

B. Species distinctions

Although some differences were noted in the broadband spectral properties of spinner and spotted dolphin signals, no attempt was made to formally define these distinctions due to the potentially confounding influences of signal directionality mentioned previously. However, differences in the more narrow-band and temporal properties of their whistles and burst pulses merit further comment.

1. Frequency of the fundamental

The fundamental whistle contours of spinner dolphins were on average 3 kHz higher in mean and maximum frequency than those of spotted dolphins. This can in part be explained by the disparity of their adult sizes. Hawaiian spinner dolphins range in length between 170 and 200 cm (Norris *et al.*, 1994), whereas Atlantic spotted dolphins are between 166 and 229 cm in length (Perrin *et al.*, 1994). Ding *et al.* (1995) established that a linear relationship exists between the typical body length of delphinid species and the maximum frequency of their whistle fundamentals. According to the formula they derived, the maxima of spinner dolphin whistles should fall between 14.9 and 15.9 kHz and those of spotted dolphins between 14.0 and 16.1 kHz. The fact that spinner dolphins consistently produced whistles higher in frequency than expected (95% C.I.=16.9–17.9 kHz) whereas spotted dolphins conformed to predicted values (95% C.I.=14.1–14.9 kHz) may reflect a response on the part of spinners to the noisy inshore waters typically found in Hawaii. Most of our recordings of spinner dolphins were made in shallow waters (<100 ft) near reefs where snapping shrimp (family: Alpheidae) produced a continuous stream of broadband clicks (Au and Banks, 1998). The resulting background noise in these areas was greatest below 10 kHz and decayed with increasing frequency. Bahamian waters were comparatively quieter, as spotted dolphins primarily occupied vast stretches of sandy bottom where snapping shrimp were rare. By producing whistles at higher frequencies, spinner dolphins improve their S/N ratio and may thus increase the range or ''active space'' of their signals (Janik, 2000b).

2. Amplitude modulation

Interference resulting from surface and bottom reflections can confound differences in the AM properties of whistles. However, the clear distinctions we found between the two species were sufficiently consistent to make us believe they were not simply artifacts of sound propagation. The pulselike qualities that characterized many spotted dolphin whistles support a contention previously made by Murray *et al.* (1998) that delphinid sounds are produced as a continuum of signals graded between exponentially damped sinusoidal pulses (clicks) and continuous sinusoidal tones (whistles). The AM whistles of spotted dolphins appear to be intermediary signals between the two ends of this continuum. To our knowledge, this is the first description of such signals obtained from the wild.

Whistles characterized by tonal pulses were produced commonly by spotted dolphins but rarely by spinners. This says something about the type of information that might be associated with the whistles of each species. Amplitude modulations in a tone degrade and become indistinct with increasing distance from the source (Urick, 1983). Spotted dolphin whistles with a high degree of AM may therefore be used more for communication with nearby listeners than for long-range signaling between individuals. This is consistent with their social structure, as spotted dolphins in the Bahamas occur in fairly small groups of 2–15 animals characterized by strong relationships between individuals (Herzing and Brunick, 1997). Communicating via AM cues about a behavioral, emotive, or referential condition to a nearby pair-mate or kin could be a primary function of their whistles. In contrast, spinner dolphins typically occur in much larger, dynamic aggregations of 20 to 100+ individuals (Ostman, 1994; Lammers, 2003) and rely heavily on the group's cohesion and coordination for defense against predators and cooperative foraging at night (Norris *et al.*, 1994; Benoit-Bird and Au, 2001). Spinner dolphin groups often travel with individuals spread over many hundreds of meters. Based on their social structure, communicating over longer ranges using signals designed to favor localization of the signaler is probably more adaptive and thus results in whistles produced with less AM but longer duration.

3. Click number and ICI

The typical number of clicks and the average interclick interval in burst pulses differed between the two species. Both produced relatively short burst pulses with less than 70 clicks, but spotted dolphins also produced many high quantity (>70 clicks) burst pulses whereas spinner dolphins did not. In addition, the interclick intervals of spotted dolphin burst pulses were somewhat shorter than those of spinner dolphin burst pulses.

Our surface behavioral observations were too limited in detail to match signals with the occurrence of specific behaviors; therefore our ability to speculate on the significance of these differences is limited. We suspect, however, that they may be tied to the daily patterns of activity characteristic of each species. Spotted dolphins were generally active during the day, spending much of their time foraging and socializing. Spinner dolphins, on the other hand, predominantly engaged in these activities in the late afternoon and at night, choosing to rest quietly during the middle of the day (Norris *et al.*, 1994). It is possible that spinner dolphins produced more high quantity burst pulses at night. However, since all spinner dolphin recordings were obtained during the day, we presently cannot address this question further.

Similarly, the difference in interclick intervals may also be a function of behavioral state. If burst pulses are indicators of emotive disposition, as has been suggested, then it is to be expected that variations would be tied to behavioral activities. Attempting to classify the fine scale temporal characteristics of burst pulses on the basis of their occurrence in specific behavioral contexts could be a fruitful avenue of future investigation.

V. CONCLUSION

If we presume that dolphins pay attention to the harmonic composition of whistles and if we accept that burst pulses play an important social role, then the evidence presented here indicates that there is considerably more to the social acoustic signaling behavior of spinner and spotted dolphins than meets the human ear. In future efforts to better understand the function of whistles and burst pulses we will need to more fully explore and appreciate their design. This will require that we take into account their broadband patterns of production and adopt methodologies that reflect the dolphin's auditory acuity. Recording signals in a manner consistent with how they are produced and ultimately heard by their intended listeners will be an important key to future efforts to accurately match them with their social context. Doing this will be as important for efforts to study spinner and spotted dolphin signaling as for those involving other species of delphinids.

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