The spatial context of free-ranging Hawaiian spinner dolphins (*Stenella longirostris*) producing acoustic signals

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To improve our understanding of how dolphins use acoustic signals in the wild, a three-hydrophone towed array was used to investigate the spatial occurrence of Hawaiian spinner dolphins (*Stenella longirostris*) relative to each other as they produced whistles, burst pulses, and echolocation clicks. Groups of approximately 30 to 60 animals were recorded while they traveled and socialized in nearshore waters off Oahu, Hawaii. Signaling animals were localized using time of arrival difference cues on the three channels. Sequences of whistles occurred between dolphins separated by significantly greater distances than animals producing burst pulses. Whistles typically originated from dolphins spaced widely apart (median = 23 m), supporting the hypothesis that whistles play a role in maintaining contact between animals in a dispersed group. Burst pulses, on the other hand, usually came from animals spaced closer to one another (median = 14 m), suggesting they function as a more intimate form of signaling between adjacent individuals. The spacing between echolocating animals was more variable and exhibited a bimodal distribution. Three quarters of echolocating animals were separated by 10 m or more, suggesting that the task of vigilance in a pod may not be shared equally by all members at all times. © *2006 Acoustical Society of America.* [DOI: 10.1121/1.2151804]

I. INTRODUCTION

Dolphins communicate using a combination of the visual, tactile, acoustic, and possibly chemosensory channels (Herman and Tavolga, 1980). Of these, only the acoustic modality allows for signaling over ranges greater than tens of meters. It can therefore be assumed that acoustic signals are the primary means by which delphinids mediate social processes that involve group coordinated behaviors (e.g., foraging and predator defense), navigation, and maintaining contact between widely dispersed individuals.

Dolphins produce a variety of sounds, which can be classified broadly into three categories: Echolocation click trains, burst pulse click trains, and whistles (Fig. 1). The clicks of most species are extremely short ($\sim$50 μs), broadband signals, extending in frequency from 2 to over 200 kHz (Au, 1993) and are emitted from the animal's forehead in a narrow directional beam (Au, 1993). The primary difference between echolocation clicks and burst pulse clicks is the number of clicks produced per unit time (Lammers *et al.*, 2004) and difference in amplitude (Au *et al.*, 1987). Echolocation clicks are used for sensing the surrounding environment, so they are generally emitted only after the echo of the previous click has been received by the dolphin, plus an

additional period [15–45 ms (Au, 1993)] used to process the echo. Burst pulse signals are broadband click trains similar to those used in echolocation, but with interclick intervals of only a few (0.5–10) milliseconds (Lammers *et al.*, 2004). Because these intervals are considerably shorter than the processing period generally associated with echolocation, and because they are often recorded during periods of high social activity, burst pulse click trains are thought to instead play an important role in communication (Popper, 1980; Overstrom, 1983; Herzing, 1988).

In addition to clicks, many dolphin species produce long-duration frequency-modulated whistles, which are also associated with social communication (Herman and Tavolga, 1980), and which can be emitted simultaneously with burst pulse or echolocation clicks (Cranford, 2000). Whistles are among the most variable signals produced by dolphins. Perhaps the most common explanation for their function is that of "signature" signals that allow individuals to identify themselves to one another (Caldwell and Caldwell, 1965; Caldwell *et al.*, 1990; Tyack, 2000). The so-called "signature whistle hypothesis" has received support from numerous studies involving captive and restrained animals (Tyack, 1986; Caldwell *et al.*, 1990; Sayigh *et al.*, 1990; Janik *et al.*,
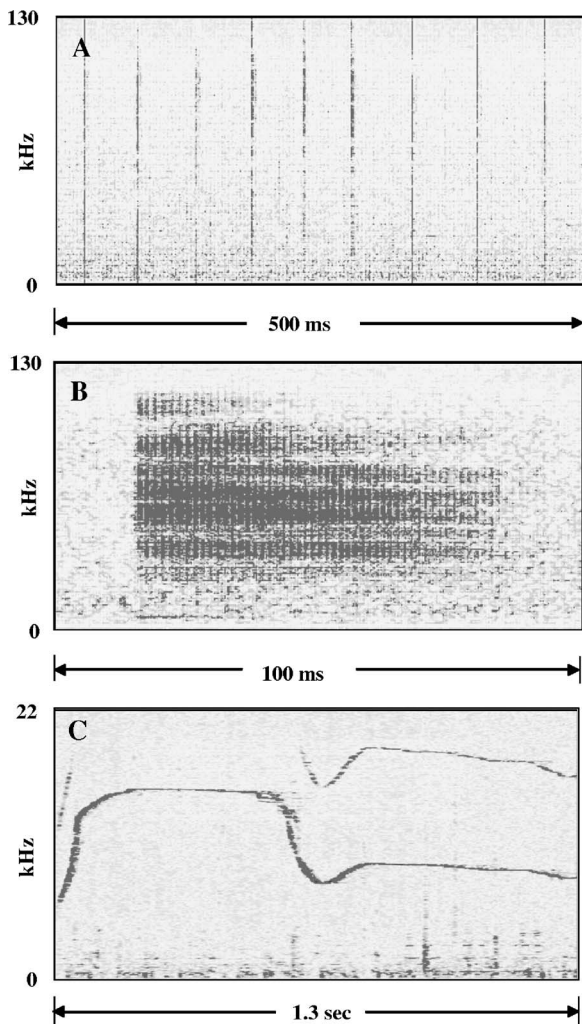
FIG. 1. Spectrogram examples of a dolphin echolocation click train (A), a burst pulse click train (B), and whistle harmonics (C).

1994; Janik and Slater, 1998), as well as from field studies of free-ranging animals (Smolker *et al.*, 1993; Herzing, 1996; Janik, 2000). Some, however, have argued that a simple signature function alone cannot account for the diversity of signals observed in socially interactive dolphin groups (McCowan and Reiss, 1995a, 2001), and that additional communicative functions are therefore likely also involved.

Dolphins produce whistles with fundamental frequencies that are usually in the human audible range (below 20 kHz). However, whistles typically also have harmonics, which occur at integer multiples of the fundamental and extend well beyond the range of human hearing (Lammers *et al.*, 2003). Harmonics are integral components of tonal signals produced by departures of the wave form from a sinusoidal signal. It has been proposed that this signal feature could function as a cue that allows listening animals to infer the orientation and direction of movement of a signaling dolphin (Miller, 2002; Lammers and Au, 2003). Whistles and their harmonics may therefore be important in mediating group cohesion and coordination.

Simple modeling of the dolphin's sound generator suggests that whistles have a wider beam pattern than clicks, especially at the fundamental and lower harmonic frequencies of the whistle (Au *et al.*, 1999; Lammers and Au, 2003). It is therefore typically presumed that whistles are perceived by listening dolphins over longer ranges than burst pulse clicks. Based on the hypothesis that dolphins use whistles to maintain group coordination when they are outside of each other's visual range, the prediction tested in the current study is that whistles are produced by dolphins that are spaced more widely apart from each other than dolphins exchanging burst pulse signals, which may function as a more "intimate" form of signaling between adjacent individuals. In addition, the spatial relationship is examined between dolphins that echolocated simultaneously to determine whether spacing between them is random, or whether it tends to follow patterns that could suggest how echolocation is used within a group of dolphins.

II. MATERIALS AND METHODS

To examine the spatial context of acoustic signaling in dolphins, signals were recorded from free-ranging Hawaiian spinner dolphins (*Stenella longirostris*) resident along the leeward coast of the island of Oahu, Hawaii. Spinner dolphins are a gregarious island-associated species commonly found along many of Hawaii's coastlines (Norris *et al.*, 1994). Their occurrence and daily behavioral cycle tend to follow predictable patterns, marked by periods of rest, travel, and socializing during different times of the day (Lammers, 2004). Their social and echolocation signals have been previously characterized by Lammers *et al.* (2003) and Schotten *et al.* (2004), respectively. Acoustic signals produced by spinner dolphins were recorded using a three-hydrophone line array towed behind a boat, as described by Lammers and Au (2003). A towed three-hydrophone line array enables one to localize dolphin signals in a two-dimensional (2D) plane by using the differences in time of signal arrival at the three hydrophones. This method can be used to record dolphins that are traveling in the same direction as the boat (since the array has to be towed), and generally to localize dolphins up to distances of approximately 12^*S away, where S represents the spacing between hydrophones.

A. Data collection

The hydrophone array used (Fig. 2) was composed of three ITC 1094A spherical omnidirectional hydrophones, with a calibrated sensitivity of approximately −205 dB re 1 V/μPa. The hydrophones were spaced 8 m apart from each other, with the cable attached to a 1.2 cm thick nylon line. A custom-made amplifier/line driver was coupled to each hydrophone, providing 40 dB of gain, as well as a 3 kHz high-pass filter to eliminate engine and water flow noise. At the front of the array, a 15×30 cm polyvinyl chloride (PVC) "towfish" with downward-angled wings and 6 kg of lead weight was used to sink the array to an operating depth of approximately 2 m. At the end of the array, a 3 m long 1.0 cm thick nylon "tattletale" line—with 20 cm long cable ties attached perpendicularly to the line 10 cm apart—was used to create drag and thus maintain tension on the array while being towed.

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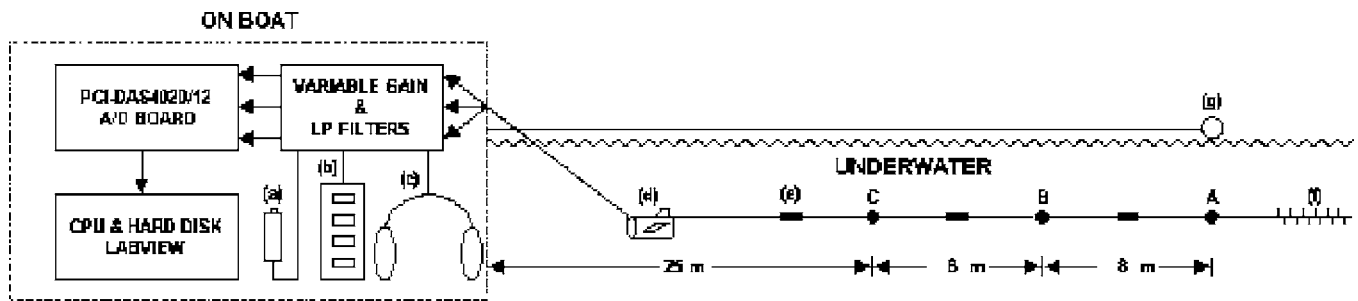Lammers *et al.*: Spatial context of dolphin acoustic signalling   1245

FIG. 2. Schematic of the three-hydrophone line array recording unit. The system is composed of a signal conditioning unit with low-pass filters and variable gain up to 35 dB, a four-channel PCI-DAS4020/12 A/D board operated from a lunchbox computer running custom-written LABVIEW6i^{TM} data acquisition software, a manual TTL trigger (a) to initiate 10 s recording periods, and an LED meter (b) and headset (c) to detect and monitor the level of incoming dolphin signals. Underwater, a PVC tow-fish (d) sinks the array to a depth of approximately 2 m while being towed, and signals are collected on hydrophones A, B, and C, that are each coupled to amplifier/ line drivers (e) providing 40 dB of preamplification as well as 3 kHz high-pass filters. A tattletale (f) at the end maintains tension on the array during towing, and a 40 cm diameter buoy (g) above water marks hydrophone A for the observers on board (from Lammers and Au, 2003).

A custom-built signal conditioning unit on board the research vessel amplified and low-pass filtered the incoming signals from the three channels. There was the option of providing 35 dB of additional amplification in 5 dB steps, and programmable Lattice Semiconductors^{TM} ispPAC80 fifth-order filter chips were used to low-pass filter the signals at either 50 kHz or 150 kHz, depending on the analog/digital (A/D) sample rate that was used, to avoid aliasing. During all recordings, the variable gain was set at 30 dB, providing a total of 70 dB of amplification. The middle hydrophone (Channel B) was used to detect the presence of dolphin signals, by means of both headphones (for signals that had energy in the human audio range) and a light-emitting diode (LED) meter (which could also detect signals that were purely ultrasonic). A four-channel simultaneous sampling Measurement Computing^{TM} A/D converter board, the PCI-DAS4020/12, was used to digitize incoming signals on the three channels, at a sample rate of either 125,000 samples/s (for field recordings made in May and June 2003) or 400,000 samples/s (for recordings in November 2003) providing a Nyquist frequency of 62.5 and 200 kHz, respectively. This A/D board provided 12-bit resolution and had an input voltage of ±5 V. It was operated from a Pentium 850 MHz "lunchbox" computer, and the data acquisition and storage process was run by a custom-written LABVIEW6i^{TM} program. Upon detection of dolphin signals, a 10 s sampling period was initiated by a manual trigger, and the resulting data files were automatically stored on the computer's hard drive.

The line array was towed from a 9.8 m boat powered by a 120 hp inboard diesel engine. A buoy towed separately and parallel to the array marked the position of the furthest hydrophone. Data collection was accomplished by either two or three persons, with one person operating the computer from the cabin below, one person driving the boat from the flying bridge, approximately 5 m above the water surface, and a third person who logged the presence of dolphins. In the absence of a third person, the boat operator logged the presence of dolphins. Radio contact was maintained between the bridge and the cabin, and when the computer operator detected dolphin signals and started a recording period, the data logger was notified to log the number and position of visible dolphins relative to the array. This was done to verify that

dolphin positions calculated from the three-hydrophone localization algorithm were approximately correct.

Acoustic recordings from spinner dolphins were obtained along the leeward coast of Oahu, Hawaii, on six separate days in May, June, and November 2003. Dolphins were recorded when they traveled from their daytime resting areas in shallow waters to their evening offshore foraging grounds. To mitigate the potentially confounding effects of right-left ambiguity inherent in working with a line array, efforts were made to keep the boat positioned at one side and slightly ahead of all the dolphins in a pod, while traveling at approximately the same speed as the pod. If approached carefully, a group of dolphins could often be maintained in this relationship for several minutes. The array was also deployed in cases when dolphins appeared to be socially (and therefore, acoustically) active, but not traveling. The approach in those cases was to pass the group of dolphins on one side, while keeping the array in a straight line behind the boat (as indicated by the towed buoy). When the computer operator could no longer detect signals, the boat driver was notified to make a gradual 180° turn and, depending on the activity of the dolphins, drive by the group again. The dolphin pods recorded ranged in size from approximately 30 to 60 animals.

B. Data analysis

Recorded sounds were localized by evaluating the differences in time of sound arrival at each hydrophone using standard equations as described in Lammers and Au (2003). The speed of sound in water (c) used in the localization algorithm was 1533 m/s, which was calculated assuming a typical water temperature of 24.5 °C and a salinity of 34.9 ppt (Urick, 1983). The system's localization accuracy was calibrated by using an artificial omnidirectional sound source that produced dolphinlike frequency-modulated signals, which was placed at different angles and distances away from the center hydrophone up to a maximum of 30 m, while the array was kept stationary at a depth of 2 m. In all cases, localizations proved to be accurate to within $1-2$ m from the actual position of the sound source.

Field recordings were initially inspected for the presence

of dolphin whistles and burst pulse signals of sufficient signal-to-noise ratio on all three channels, and accordingly categorized using COOL EDIT 96™ software. Subsequently, whistles were analyzed using a custom-written MATLAB 5.1™ program that implemented the three-hydrophone localization algorithm. Differences in time of whistle arrival at each hydrophone were obtained by cross correlating a particular whistle in the data files from Channels A and C with the same whistle in the file from Channel B. The largest peak of the resulting cross-correlation vector was used to establish the time of arrival difference between Channels A and B and between B and C. Since acoustic reflections from the water surface and poor signal-to-noise ratio can result in ambiguous or low cross-correlation results, recordings with those attributes were not considered for further analysis in order to maintain a high degree of confidence in the localizations.

For the analysis of burst pulse and echolocation clicks, arrival times had to be measured directly from the original data files. Wave forms were compared among the three channels to measure time of arrival differences between the three hydrophones. This was done by inspecting the first (or last) click of a particular burst pulse signal or echolocation click train on each channel, and logging the sample value of the first peak in amplitude of that click. The three logged sample values for a particular click were then entered in another custom-written MATLAB program to calculate the 2D position of the sound-emitting dolphin, using the localization algorithm. For each click train (both echolocation and burst pulse), this was repeated for up to several clicks, to ascertain that the localization for that train was correct. The x and y coordinates for each signal were then logged together with the time separation (Δt) between the localized signal and the signal produced just prior to it.

Finally, to establish distances between dolphins producing acoustic signals, it is necessary to determine whether the signal originated from the same dolphin or from a different dolphin than the signal immediately preceding and/or following it. For both whistles and burst pulses, this was accomplished by considering both their spatial and temporal relationships, as inferred from the calculated x, y coordinates for each signal, in combination with their measured time separation Δt, as well as the presumed maximum swimming speed. Bottlenose dolphins (*Tursiops truncatus*) can easily sustain a swimming speed of 2 m/s (Williams *et al.*, 1992), and have been reported capable of sustaining speeds over 8 m/s (Lang and Pryor, 1966). The smaller harbor porpoises (*Phocoena phocoena*) have reported mean swimming speeds of around 1 m/s and a maximum reported speed of 4.3 m/s (Otani, 2000). Therefore, in this study, it was assumed that spinner dolphins—which are intermediate in size compared to these other two species—do not swim faster than 8 m/s. Using the Pythagorean theorem, the distance d between two subsequent Signals A and B was calculated from their x, y coordinates as $d = \sqrt{(x_A - x_B)^2 + (y_A - y_B)^2}$, with a ± 1 m accuracy. If $d/\Delta t \geq 8$ m/s (where Δt is the measured time separation between Signals A and B), it was assumed that Signals A and B originated from two different dolphins and the distance d was used for subsequent statistical analysis. This was

a conservative criterion, since d and, therefore, $d/\Delta t$ are likely to be underestimates.

Echolocation click trains were often considerably longer in duration than whistles and burst pulses (up to several seconds), allowing time for spatial relationships to potentially change during the course of a click train. Therefore, to examine the spatial relationship between echolocating individuals, only click trains that overlapped in time with each other were considered. This ensured that separate animals were actually involved and that their spatial relationship did not change appreciably during the period examined.

III. RESULTS

The spatial context of whistle and burst pulse production

A total of 185 whistles, 172 burst pulse signals, and 94 echolocation click trains were localized. Signals that met the conditions mentioned previously were selected, and the distance d between the two dolphins that were assumed to have emitted the recorded signals was calculated for each of these exchanges. Distances were calculated for 27 burst pulse sequences, (5 of which represent average distances, for repeated signal sequences produced by presumably the same 2 animals) and 41 whistle sequences. Distances between animals echolocating concurrently were established in 44 cases. Examples of localizations for each type of signal are represented in Fig. 3, and the distributions of distances in each case are presented as histograms in Fig. 4. The distributions for both whistles and burst pulses were somewhat skewed toward shorter distances [Figs. 4(a) and 4(b)]. The minimum distance d was 4 m for whistle sequences and 3 m for burst pulse sequences, while the maximum calculated distance was 113 m for whistle sequences and 72 m for burst pulse sequences. Median distances were 23 m and 14 m for whistle and burst pulse sequences, respectively. Overall, the distance d between two dolphins was significantly larger for whistle sequences than for burst pulse sequences ($p = 0.0054$, Mann–Whitney test, two tailed).

The distribution of distances for concurrently echolocating animals was distinctly bimodal [Fig. 4(c)]. The median distance between animals was 24 m, but two peaks occurred centered around 10 m and 40 m. In addition, 34 of the 44 instances (77%) were localized to animals separated by a distance greater than 10 m. Therefore, concurrent echolocation occurred primarily between individuals separated by several body lengths.

A. The temporal context of whistle and burst pulse sequences

In addition to the spatial context, the temporal context of dolphin signal sequences was also considered for whistles and burst pulses. Specifically, the timing of signals was investigated to determine whether any relationship exists with the spatial separation between dolphins. For each signal sequence, the calculated spatial separation d was plotted as a function of the temporal separation Δt between the two signals, as presented in Fig. 5. For whistle sequences [Fig. 5(a)], a very weak positive linear relationship was found (R^2

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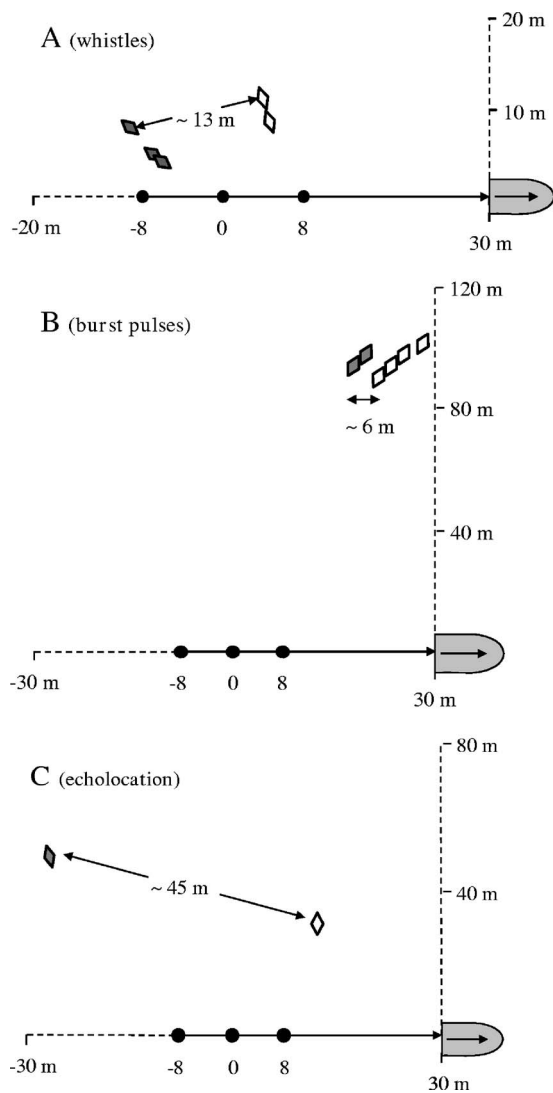Lammers *et al.*: Spatial context of dolphin acoustic signalling   1247

FIG. 3. Representative examples of localizations obtained for a whistle exchange (A), burst pulses exchange (B), and concurrent echolocation by two dolphins (C). The grey and white diamonds represent the successive positions of the two animals involved in the exchange, relative to the towed array and towing vessel. The black circles represent the hydrophones of the array, with the center hydrophone serving as the origin in the coordinate axes used to plot localizations.
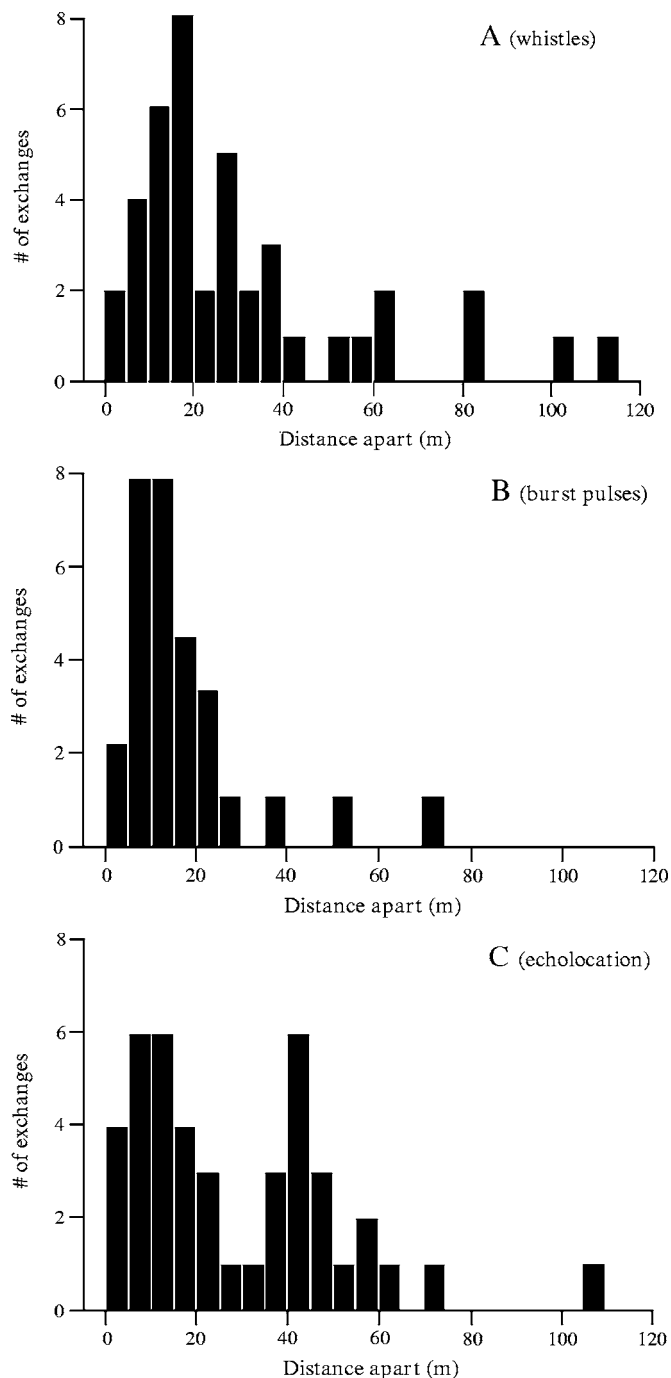

FIG. 4. Distributions of calculated separation distance between two dolphins for whistle sequences (A, $N=41$), burst pulse sequences (B, $N=27$), and concurrent echolocation click trains (C, $N=44$).

$=0.05$), however, this relationship was not significant ($P =0.148$). For burst pulse sequences on the other hand [Fig. 5(b)], a slightly stronger positive linear relationship was found between spatial and temporal separation of the signals ($R^2=0.21$) and this relationship proved to be significant ($P =0.013$). Therefore, burst pulse signals that were produced between two dolphins that were closer to each other were found to also follow each other more quickly in time, while this was not the case for whistle sequences.

IV. DISCUSSION

The results reveal that the production of whistles among spinner dolphins tends to take place between individuals separated by significantly greater distances than between animals producing burst pulses. It cannot be established at this point whether either whistles or burst pulses were "exchanged" between individual dolphins, since the term im-

plies that information is transmitted from one animal to another, which then replies with a signal back to the first animal. However, the significant difference in spatial separation between dolphins emitting whistles versus those emitting burst pulses, does suggest that these signals have different functions which are directly related to the dolphins' proximity to one another, thus suggesting communicative exchanges. Additionally, evidence of whistle matching by wild bottlenose dolphins (*Tursiops truncatus*) suggests that dolphins, in fact, do address one another acoustically (Janik, 2000), leaving open the possibility that the sequences observed do represent exchanges of signals.
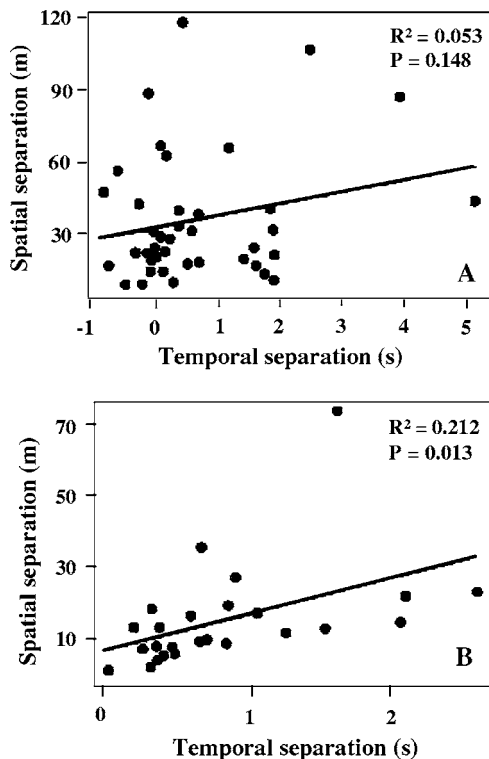
FIG. 5. Calculated separation distances plotted as a function of the measured separation in time between two signals, for whistle sequences (A) and burst pulse sequences (B), with least-square linear regression lines through the data points.

Our findings provide empirical evidence that whistles and burst pulses play distinct functional roles. Specifically, most whistling appears to take place near or beyond the periphery of visual contact, whereas burst pulsing typically occurs within it (assuming a visual range of ~20 m in local inshore waters). Whistles, therefore, are likely important in signaling between individuals dispersed in a pod (Fig. 6).This supports the hypothesis that whistles, and the acoustic cues present in them, play an important role in mediating group behavior and cohesion (Norris *et al.*, 1994; Lammers and Au, 2003). Janik and Slater (1998) previously found evi-
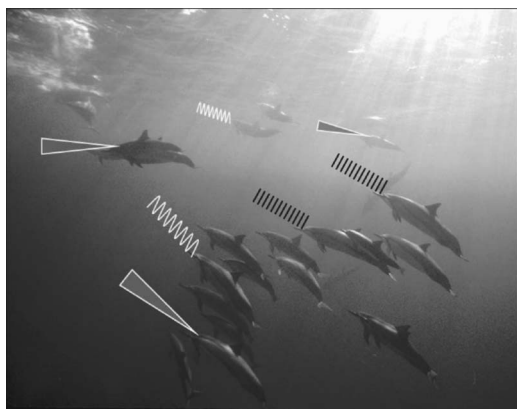

FIG. 6. A hypothetical example of the proposed spatial occurrence of acoustic signals in a spinner dolphin pod. The white sinusoids represent whistle production, the black bars represent the production of burst pulses, and the outlined gray cones are the occurrence of echolocation click trains (photo courtesy of Andre Seale).

dence for this through acoustic observations of a group of captive dolphins, and Smolker *et al.* (1993) documented the use of contact calls between mothers and calves, but this is the first known evidence from free-ranging pods.

Burst pulsing, on the other hand, takes place primarily between nearby animals in a group (Fig. 6). This is consistent with their hypothesized function as "emotive" signals, as several researchers have previously suggested (Lilly and Miller, 1961; Herzing, 1988, 1996; Bloomqvist and Amundin, 2004). Burst pulses have been implicated primarily in aggressive or agonistic contexts, such as confrontational "head-to-head" behaviors between individuals (Caldwell and Caldwell, 1967; Overstrom, 1983; McCowan and Reiss, 1995b; Bloomqvist and Amundin, 2004). However, contexts ranging from courtship behaviors to alarm responses have also been associated with burst pulsing (Herzing, 1996). Their occurrence, primarily among closely spaced individuals, is consistent with the task of communicating emotively charged information to potential mates or affiliated individuals, or to perhaps support visual displays. In addition, by presumably being more directional than whistles, burst pulses may function as more intimate forms of signaling than whistles, and be meant primarily for individuals in the immediate vicinity.

The bimodal distance distribution of concurrently echolocating dolphins is interesting and potentially revealing of how echolocation is used in a pod. Specifically, the fact that over three-quarters of cases were of animals separated by 10 m or more suggests that the task of vigilance in a pod may not be shared equally by all members simultaneously. Spinner dolphins rarely swim alone for any length of time, but rather occur in pairs or small clusters of several animals that are usually separated by less than one body length from each other (Norris *et al.*, 1994). It is therefore somewhat surprising that very little concurrent echolocation was observed between closely spaced individuals. Rather, the first peak—occurring around 10 m—is consistent with the approximate horizontal diameter of a spinner dolphin subpod (as personally observed by one of the authors—M. L.). Therefore, the results suggest that vigilance through echolocation may be maintained by animals strategically located in a subpod rather than by all individuals echolocating at random (Fig. 6). Furthermore, the second peak at 40 m likely represents echolocating animals in adjacent subpods.

Finally, the timing of signals relative to the physical separation of the signalers was examined to determine whether they are related. It has been suggested that spinner dolphin chorusing during certain times of the day may be important in the process of coordinating group behavior (Norris *et al.*, 1994). The timing of signals might play a role in this process by cueing nearby dolphins on the physical proximity of the signalers to one another, and thereby communicate their general behavioral disposition (resting, traveling, socializing, etc.). As an example, signals closely timed (or overlapping) might be indicative of close proximity, which is characteristic of resting and/or social behavior. Conversely, widely spaced signalers (together with widely timed signals) could represent a traveling pod, or one not very synchronized. For whistles, however, no such correlation was

noted between separation and timing. Burst pulses, on the other hand, did exhibit a weak but significant correlation, and followed each other more quickly in time when they were exchanged by two dolphins that were closer to one another. While perhaps not sufficient to warrant assuming a direct relationship, this result does suggest that a more detailed examination of the timing of burst pulses within various behavioral contexts could be fruitful.

ACKNOWLEDGMENTS

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