

Phonation behavior of cooperatively foraging spinner dolphins

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Groups of spinner dolphins have been shown to cooperatively herd small prey. It was hypothesized that the strong group coordination is maintained by acoustic communication, specifically by frequency-modulated whistles. Observations of groups of spinner dolphins foraging at night within a sound-scattering layer were made with a multibeam echosounder while the rates of dolphin sounds were measured using four hydrophones at 6 m depth intervals. Whistles were only detected when dolphins were not foraging and when animals were surfacing. Differences in click rates were found between depths and between different foraging stages but were relatively low when observations indicated that dolphins were actively feeding despite the consistency of these clicks with echolocation signals. Highest click rates occurred within the scattering layer, during transitions between foraging states. This suggests that clicks may be used directly or indirectly to cue group movement during foraging, potentially by detecting other individuals' positions in the group or serving a direct communicative role which would be contrary to the existing assumption that echolocation and communication are compartmentalized. Communicating via clicks would be beneficial as the signal's characteristics minimize the chance of eavesdropping by competing dolphins and large fish. Our results are unable to support the established paradigm for dolphin acoustic communication and suggest an alternate coordination mechanism in foraging spinner dolphins. © 2009 Acoustical Society of America. [DOI: 10.1121/1.2967477]

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I. INTRODUCTION

Spinner dolphins, *Stenella longirostris*, are a pelagic subtropical species that feed on small mesopelagic prey one at a time (Cadenat and Doutre, 1959; Fitch and Brownell, 1968; Norris and Dohl, 1980; Perrin *et al.*, 1999). In Hawaiian waters, their prey migrate both vertically and horizontally and are only accessible to foraging dolphins for a limited amount of time during the night (Benoit-Bird and Au, 2003; Benoit-Bird *et al.*, 2001). Yet, spinner dolphins, as mammals, have relatively high energetic needs. Benoit-Bird (2004) used simple models to predict foraging needs of spinner dolphins in Hawaii and found that to meet its basic energetic needs, the average dolphin would need to consume 3–4 average sized prey/min during the time that the prey is shallow enough for feeding. This work suggests that spinner dolphins are limited by their feeding efficiency rather than by the abundance of food so that the density of prey rather than its total biomass determines feeding success (Benoit-Bird, 2004). Spinner dolphins in Hawaii seem to deal with this problem by actively aggregating their prey (Benoit-Bird and Au, 2003; Benoit-Bird and Au, 2009). They do so in highly stereotyped social behavior, foraging cooperatively at night in groups of 16–28 (Benoit-Bird and Au, 2009). Benoit-Bird and Au (2009) showed that groups of spinner dolphins used precise coordination in strict four-dimensional patterns to in-

crease prey density by up to 200 times using the prey's own avoidance behavior (Fig. 1). Dolphins then took turns feeding within the aggregation they created. As a result, each dolphin had more access to prey than it would if feeding individually, despite the costs of participating in the group, meeting the criteria for cooperation.

The highly coordinated foraging behavior of spinner dolphins leads us to ask how they facilitate these interactions. Vision is of limited utility underwater where light is attenuated rapidly and is probably particularly ineffective for these nocturnally foraging animals. Sound, however, travels well in the ocean and is important in mediating odontocete social interactions (Tyack, 1999). Delphinids produce sounds that can be classified into two categories; (1) tonal frequency-modulated whistles and (2) short broadband clicks (Herman and Tavolga, 1980). Whistles are used primarily in social contexts (Herman and Tavolga, 1980) and may play a key role in maintaining contact between individuals (Janik, 2000b). Broadband clicks can be further broken down into two groups based on both their acoustic characteristics and their hypothesized functions. Clicks can be used by dolphins to perceive their environment: to find prey, avoid obstacles and predators, termed echolocation (Au, 1993). Clicks used for echolocation are typically temporally spaced to allow the sound to travel to the object of interest, return to the dolphin, and be processed (Au, 1993). Clicks are also produced much more quickly in trains termed "burst pulses" (Herman and Tavolga, 1980) which are thought to play a role in social interactions and are often observed in agonistic interactions

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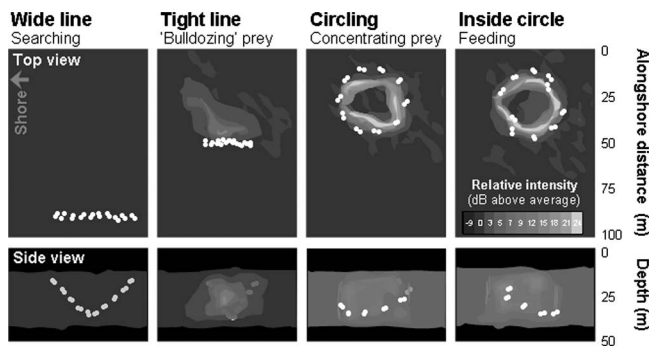


FIG. 1. Reprinted from [Benoit-Bird and Au \(2009\)](#) showing the four phases observed during spinner dolphin foraging from the top and side views. For the top view, scattering was integrated through the entire water column for each m^2 . For the side view, scattering was integrated for the 20 m immediately in front of the dolphin group. The relative scattering intensity of prey is indicated by grayscale. Prey density can be related to the scattering intensity with each 3 dB increase in scattering representing a doubling of prey density. The positions of the air passage echoes from dolphins are shown as dots. In the side view, the dolphins behind the integration plane are shown a darker shade.

([Caldwell and Caldwell, 1967](#); [Dawson, 1991](#); [Norris *et al.*, 1994](#)). Clicks may also produce in rapid trains in an echolocation role. Termed “terminal buzzes,” these short interclick interval pulsed signals are produced when a dolphin is within a few body lengths of a target and are thought to provide rapid information updates in the terminal phase of food capture ([Madsen *et al.*, 2005](#)). We hypothesize that foraging spinner dolphins maintain social cohesion through acoustic communication. We predict that the maintenance of group contact will lead to the production of many whistles within foraging groups and that echolocation clicks will be detected most often when animals are attempting to capture prey.

The relationship between dolphin vocalizations and behavior is difficult to assess because most behavior and acoustic signaling by wild dolphins occur underwater. A variety of approaches have been utilized to associate behavior with acoustic signals in natural settings. For example, tags capable of recording acoustic signals along with dive depth and orientation have elucidated much about beaked whale behavior (see [Madsen *et al.*, 2005](#), for example). Towed hydrophone arrays have been combined with observations of surface behavior to observe spatial relationships between animals and associated behaviors ([Lammers *et al.*, 2006](#)). Acoustic recordings have been combined with underwater video observations to associate specific sounds with behaviors ([Herzing, 1996](#); [Thomas *et al.*, 2003](#)). Each of these approaches has strengths and limitations. Tagging requires that the animal be capable of carrying the instrument package and is relatively invasive. Both the video and surface observation approaches require that animals be visually observed. Because of the small size of spinner dolphins and the limited success of previous tagging attempts in Hawaii ([Norris *et al.*, 1994](#)), tags are not currently a viable approach for studying the use of sound by foraging spinner dolphins. Their nocturnal habit and primarily underwater feeding make any visual approach ineffective as well. We used new sonar techniques to quantitatively track foraging dolphins and their prey simultaneously ([Benoit-Bird and Au, 2009](#)) while re-

cording their acoustic signals at four different depths. Our objective was to determine what sounds were being produced by foraging spinner dolphins and how these sounds were associated with various stages in their foraging pattern.

II. METHODS

To measure the distribution of dolphins and their prey, two sites along the leeward coast of Oahu were surveyed with active sonar techniques. Surveys were conducted between 2100 and 0300 h local time during ten nights in May and June of 2003. Sampling covered approximately 11 km surrounding Makua Bay and 10 km surrounding Electric Beach. All sampling was conducted on linear transects running parallel to the shoreline. These transects were located between 1.0 and 2.2 km from the shoreline and a total of 186 km were surveyed.

Surveying alternated between a 200 kHz Kongsberg-Simrad-Mesotech MS 2000 multibeam sonar and a Simrad EK-60 echosounder at 200 kHz. The instruments were selected because 200 kHz is outside the hearing range of this genus of dolphin and thus is likely to have the least impact ([Kastelein *et al.*, 2003](#)). The multibeam sonar provided three-dimensional information on the distribution of dolphins and their prey while the vessel was moving. The head of the multibeam sonar was mounted off the starboard side of the vessel, approximately 0.5 m below the water’s surface, at a 45° angle to the right of the direction of travel and 30° up from the vertical plane perpendicular to the bottom rather than looking directly downward from the vessel. This permitted us to observe animals from the side, rather than having to drive directly over them, which, based on previous experience, limits the potential impacts of the survey on the dolphins. The multibeam system used a $150 \mu s$ long outgoing pulse transmitted at a rate of 5.6/s with a source level of 215 dB re $1 \mu Pa$. The system had a resolution of 0.22 m in the direction 30° from vertical resulting in a true depth resolution of 0.19 m. The system had 120, $1.5^\circ \times 20^\circ$ beams that overlapped by 0.25° in the narrower, nearly across-track direction, providing an angular coverage 120° with a 1° resolution in this direction. Data were taken using the external imaging transducer of the sonar, thus forming a Mills Cross to provide the greatest spatial resolution, giving a received beam width of 1.5° in the direction 45° from along track. The sonar system was set to cover a range of 65 m. In the geometry used, the instrument thus had a maximum range of 37.5 m from the vessel, giving a swath width of 113 m at the furthest point in its range and a depth range of 50 m. Further technical details about the sonar can be found in [Cochrane *et al.* \(2003\)](#). As in [Benoit-Bird and Au \(2009\)](#), the multibeam echosounder system was calibrated using a reference sphere following the protocol established by [Foote *et al.* \(2005\)](#).

Data from the multibeam were displayed in real time using the system’s native software. The prey were sufficiently dense to be measured as volume scattering rather than as individual targets ([Benoit-Bird and Au, 2009](#)) while the dolphins were detected as single targets. The scattering characteristics of prey in terms of individual target strength can be found in [Benoit-Bird and Au \(2001\)](#) and in terms of vol-

ume scattering in several other papers (Benoit-Bird and Au, 2006; Benoit-Bird and Au, 2009; Benoit-Bird *et al.*, 2001). Previous active sonar studies have found that spinner dolphins have a unique set of scattering characteristics that allow them to be separated from other animals in the environment (Benoit-Bird and Au, 2003). The scattering strength of dolphins is much higher than that of their prey because of the difference in size between them (~ 2 m versus ~ 10 cm) and the air-filled lungs and sinus cavities of the dolphins. This permitted dolphins to be detected in real time with the multi-beam sonar. A total of 323 groups of dolphins were detected with the multibeam sonar. During some of these real-time detections, movement of the vessel was stopped with the dolphins within range of the multibeam and a series of hydrophones was used to record sounds produced by dolphins. Four BM8263 wideband omnidirectional hydrophones (Biomon, Santa Barbara, CA), each consisting of a 1.3 cm diameter PST spherical element with a sensitivity of -155 dB re $1\text{V}/\mu\text{PA}$, were deployed at 6.4 m depth intervals. The first hydrophone was deployed at a depth of 17 m if the top of the layer was at least 15 m deep or 3 m if the layer was close to the surface. The signals were low pass filtered at 50 kHz before recordings from each of the four hydrophones were made using a Measurement Computing PCI-DAS4020/12 analog to digital converter capable of simultaneous sampling on four channels. This board was operated using custom LABVIEW 6I software and a transportable computer. Each channel was sampled simultaneously for 34 s at a rate of 125 000 samples/s. This provided a Nyquist frequency of 64.5 kHz, precluding full spectral analysis of signals but not affecting temporal identification of clicks. Data collection alternated between recording from the hydrophones and the multibeam. The multibeam sonar collected for approximately 20 s of data between each of the hydrophone recordings. These combined hydrophone and multibeam sonar recordings were made from 56 groups of dolphins with each session lasting between 2 and 16 min (mean=7 min).

A. Multibeam sonar analysis

Details of data analysis can be found in Benoit-Bird and Au (2009). Briefly, raw data from the multibeam sonar were saved to hard disk, beam formed, and the amplitude and range of echoes in each beam were extracted using a MATLAB program. The range versus azimuth data were transformed into a rectangular coordinate system where one axis is along the direction of travel, the second is across the direction of travel, and the third is depth. To obtain three-dimensional information, six successive sonar returns, or about 1 s of data, were combined. All position data were corrected using coupled differential global positioning system (GPS) to eliminate the movement of the vessel. GPS readings were taken with each sonar signal, at a rate of 5.6/s. Using this transformed, averaged, and position corrected data, isoscattering surfaces could then be identified.

Dolphins were identified from the data based on their unique set of acoustic scattering characteristics (Benoit-Bird and Au, 2003), most notably, a very strong echo that is

caused by their air filled lungs (Au, 1996) and possibly their nasal passages that is surrounded by remarkably low-amplitude echoes presumably by their blubber which is nearly impedance matched to seawater. Echoes from spinner dolphins identified during daylight surfacings were taken nearly simultaneously with a calibrated 200 kHz echosounder (Simrad EK60) and the SM2000. Echoes from spinner dolphins SM2000 had values between -25.9 and -28.2 while the values measured with the EK60 were within 0.3 dB of -27.1 dB. The SM2000 echoes showed more variance in their amplitude, likely because of the increase in the variability in insonified angle relative to the narrow beam EK60. In both systems, the presumptive lung echo provided an extremely high target strength within this field of ~ -27 dB echoes. The length of animals measured with the multibeam was consistent with the size for adult spinner dolphins in Hawaiian waters. For analysis of dolphin position, the single strongest echo from each animal, likely its lungs, was utilized, creating a standardized method of locating the animal in space and measuring distance between animals.

The sonar system has a resolution of 1.5° in the azimuth and range direction and 9.6 cm in the range direction. To increase the resolution of measurement of animal spacing, information from six successive pings was used to calculate interanimal distances. Changes in spacing in this 1 s time period were assumed to be negligible. The movement of the sonar relative to the animals during this time, however, decreased the minimum interspacing distance that could be measured in all dimensions to approximately 10 cm.

Benoit-Bird and Au (2009) categorized the foraging behavior of these animals using the multibeam sonar into four distinct stages, summarized briefly here [Fig. 1, reprinted from Benoit-Bird and Au (2009)]. First, 8–14 pairs of dolphins swam in a widely spaced line in which they search for an existing patch within the prey field. Second, dolphins reduced their interpair spacing, a stage termed “tight line,” and began to undulate their swimming path up and down. During this phase of foraging, the density of prey began to increase as the prey avoided the dolphins and piled up on itself as snow in front of a plow. During the third phase of foraging, dolphins formed a circle around the increased density prey patch which distributed the prey more evenly over the circle. Finally, individual pairs of dolphins moved inside the circle to actively feed on the most dense regions of the patch while other animals continued to maintain the patch by swimming around it. Two pairs of dolphins moved into the circle at the same time, from opposite sides of the circle for about 10 s of feeding before taking their place at the circle’s edge and allowing the pairs behind them into the circle. Each pair of dolphins got an average of 45 s inside the region of most dense prey in each approximately 5 min foraging bout.

We used these categories to characterize the observed dolphins’ foraging stage observed with multibeam data taken immediately before and after each recording. If the stage before and after the recording was the same, the recording was labeled using that stage. If, however, the stage changed during the recording, the recording was labeled as the transition between the stages.

TABLE I. Univariate analysis of variance for dolphin click rate (clicks/hydrophone/30 s).

Source	SS	df	MS	F	p
Foraging stage	1 211 232	8	15 140	150.7	<0.001
			4	7	
Time	1 253	5	251	0.25	0.94
Date	6 800	8	850	0.85	0.56
Depth	10 338	7	1477	1.47	0.17
Hydrophone position	819 930	2	40 996	408.2	<0.001
			5	4	
Number of dolphins	10 030	6	1 672	1.66	0.13
Error	1 901 000	1893	1 004		
Total	7 117 561	1972			

B. Dolphin signal analysis

The waveforms and spectra from each hydrophone of 34 s recordings from 56 recording sessions were displayed using COOL EDIT software. Echolocation clicks and whistles were confirmed aurally and counted from the spectra. Any signal detected on more than one hydrophone was attributed to the hydrophone that received the highest amplitude whistle. Clicks were only rarely detected on more than one hydrophone and the number of whistles detected was low so no localizations were attempted.

Univariate analyses of variance (ANOVAs) were used to test the effects of the depth of the hydrophones, the position of hydrophones relative to the scattering layer, sampling day, sampling hour, the number of dolphins, and the foraging state of the dolphins on click and whistle rates (Tables I and II). Dunnett's *C post hoc* tests with Bonferonni corrections for multiple comparisons were used to test the effects of the position of hydrophones relative to the scattering layer on measured echolocation rates. Dunnett's *C post hoc* tests with Bonferonni corrections for multiple comparisons were conducted to test differences between foraging states using only the data from hydrophones within the scattering layer.

III. RESULTS

Direct testing of potential effects of the vessel and the sonars was not possible. Indications of changes in dolphin behavior—e.g., increases in audible surfacing rate, bowriding, playing at the surface, and swimming around the boat—were noticed during a few times when the vessel was moving unpredictably for reasons unassociated with sampling. However, these types of behaviors were not detected during nor-

TABLE II. Univariate analysis of variance for dolphin whistle rate (whistles/hydrophone/30 s).

Source	SS	df	MS	F	p
Foraging stage	37.53	8	4.7	138.02	<0.001
Time	0.01	5	0.0	0.04	0.99
Date	0.04	8	0.0	0.14	0.99
Depth	0.50	7	0.1	2.10	0.04
Hydrophone position	0.16	2	0.1	2.35	0.10
Number of dolphins	2.05	6	0.3	10.07	<0.001
Error	64.34	1 893	0.0		
Total	117.00	1 972			

mal transect sampling, suggesting limited effects of the vessel or the instruments on the dolphins during sampling.

Univariate ANOVAs were used to test the effects of the depth of the hydrophones, the position of hydrophones relative to the scattering layer, sampling day, sampling hour, the number of dolphins, and the foraging state of the dolphins on click and whistle rates (Tables I and II). For both clicks and whistles, there was a significant difference in their detected rate as a function of foraging stage. Note that there is no significant effect of the depth of the hydrophones on either click or whistle rate but there is a significant effect of the position of the hydrophones relative to the scattering layer on the rate of detected clicks.

Dunnett's *C post hoc* tests with Bonferonni corrections for multiple comparisons were used to test the effects of the position of hydrophones relative to the scattering layer on measured echolocation rates (Fig. 2). Echolocation rates measured by hydrophones within the scattering layer were significantly higher than the rates measured by hydrophones above and below the layer. No significant differences in echolocation rates were observed between hydrophones above and below the scattering layer (Fig. 3).

Dunnett's *C post hoc* tests with Bonferonni corrections for multiple comparisons were conducted to test differences

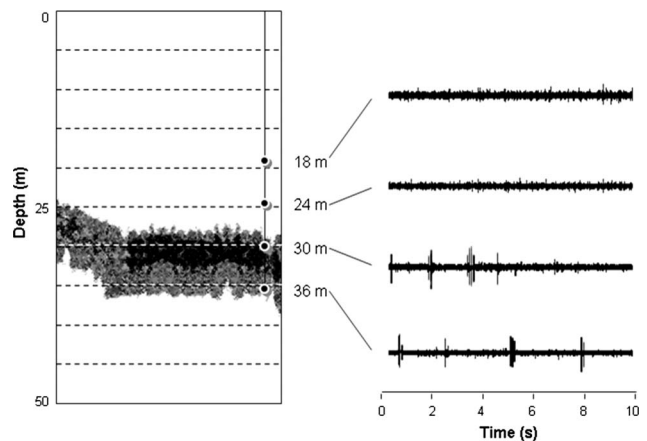


FIG. 2. A sample echogram showing the scattering layer over approximately 2 min while dolphins were circling. Local time was 22:18 h. The depths of deployed hydrophones are shown. Only the two lower hydrophones were within the scattering layer. Waveforms recorded from each of the four hydrophones are shown. The high amplitude pulses from the two deeper hydrophones are consistent with clicks from spinner dolphins.

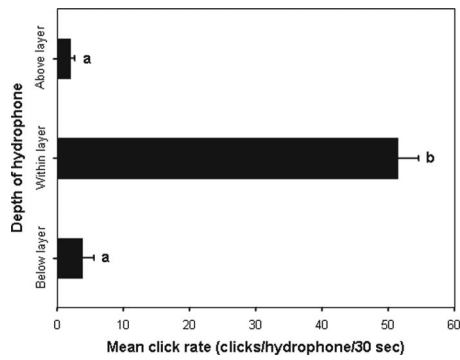


FIG. 3. Mean click rate recorded as a function of hydrophone position. Data that were statistically indistinguishable from each other but statistically distinct from other categories in the analysis are designated by lowercase letters ($p < 0.05$).

in click and whistle detections between foraging states using only the data from hydrophones within the scattering layer. Results are shown in Figs. 4 and 5.

The interval between clicks in series was measured to determine if clicks were consistent with echolocation or burst pulses and terminal buzzes. Because we were unable to record long click trains, the interclick interval was only measured when at least one other interval was observable before and after it. These beginning and end intervals were discarded. A histogram of the measured intervals is shown in Fig. 6.

The potential relationship between the spacing of circling dolphins and the spacing of clicks recorded during our observations was examined. The amount of time between pairs of dolphins passing a stationary point was compared with the time between recorded groups or bursts of clicks. Note that the term “click train” is not used here because we cannot be certain that entire trains were indeed recorded. The center of each recorded click series was used in this measurement (Fig. 7). The relationship between the spacing of dolphins and the spacing of clicks was linear with a slope of

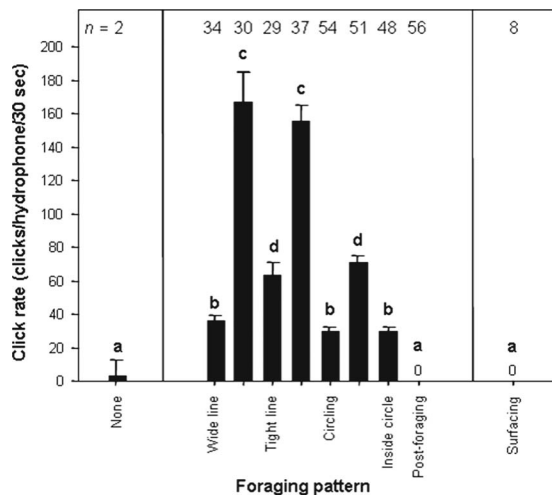


FIG. 4. Click rate as a function of foraging pattern. Error bars represent the 95% confidence interval about the mean. Data that were statistically indistinguishable from each other but statistically distinct from other categories in the analysis are designated by lowercase letters ($p < 0.05$).

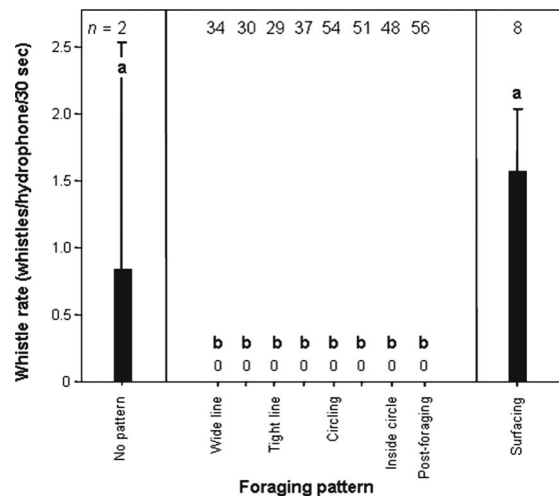


FIG. 5. Whistle rate as a function of foraging stage. Error bars represent the 95% confidence interval about the mean. Data that were statistically indistinguishable from each other but statistically distinct from other categories in the analysis are designated by lowercase letters ($p < 0.05$).

approximately 1 (interval between click bursts = 1.09 interval between dolphin pairs—0.19; $R^2 = 0.56$; F test of slope $p < 0.01$).

IV. DISCUSSION

As detailed in Benoit-Bird and Au (2009), the observed behavior of spinner dolphins is highly suggestive of foraging. The highly coordinated behavior of spinner dolphins during presumptive foraging suggests that there must be some method of synchronizing the activity of these cooperative groups. Animals were observed to transition from one distinct behavior to another nearly simultaneously with animals spread out over a distance of about 40 m. Vision is unlikely to be effective at these ranges underwater, especially at night. Based on previous studies of dolphin behavior, we propose that spinner dolphin acoustic methods of maintaining group cohesion while foraging. We hypothesized that whistles, shown to play a role in maintaining contact over these distances (Lammers *et al.* 2006), would be the primary type of acoustic signal used.

However, we recorded very few whistles and none when animals were engaged in behaviors identified with foraging.

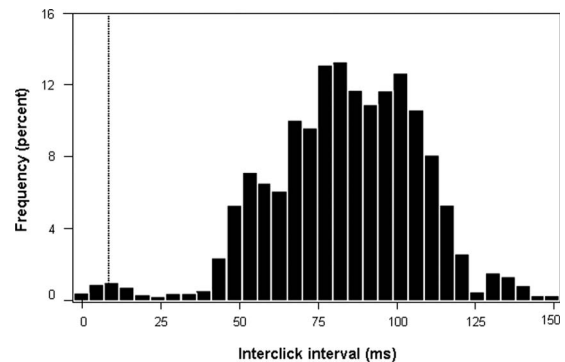


FIG. 6. Histogram of all measured interclick intervals. More than 95% of the clicks are at least 10 ms apart, indicated by the dashed line, consistent with echolocation signals rather than burst pulses.

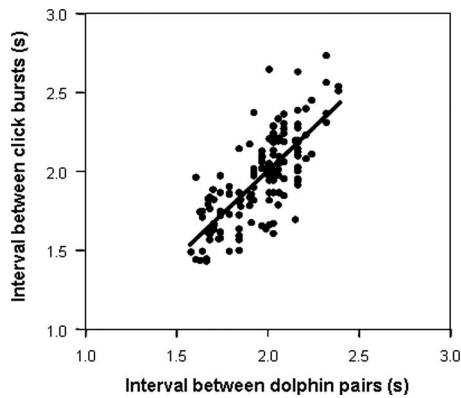


FIG. 7. The relationship between the interval between dolphin pairs swimming in a circle and the interval between detected click bursts. The relationship is linear with a slope of approximately 1.

This result is not likely an artifact of measurement technique or signal propagation. Spinner dolphin whistles are relatively low in frequency, tens of kilohertz (Bazua-Duran and Au, 2002), and are attenuated relatively slowly in seawater. While whistles have mixed directionality (Lammers and Au, 2003), they are omnidirectional at their lower frequencies which were well within our recording bandwidth. All of this suggests that if whistles were being produced by the observed groups, they would have been detected. The hypothesis that whistles are used for group coordination cannot be supported. However, this does not rule out acoustic signaling as a means of maintaining the behavior.

Click signals from spinner dolphins were recorded. Clicks in rapid repetition rate “burst pulsed” click trains have been observed to have a communicative function (Herman and Tavolga, 1980). These clicks are distinctive from clicks typically observed in echolocating animals in that their interclick interval is extremely short. Lammers *et al.* (2003) found that burst pulsed clicks in spinner dolphins typically had an interval less than 10 ms. Less than 2% of the clicks recorded had an interclick interval less than this threshold, suggesting that burst pulses are not a large component of signaling in these foraging groups. These results also suggest that terminal buzzes found which have been observed in other species of dolphins while feeding were either not produced or not recorded.

More than 98% of the clicks were consistent with echolocation based on their interclick interval. We hypothesized that echolocation would be used primarily to target individual prey before capture as spinner dolphins feed on prey one at a time. This would suggest that clicks should be identified most often when animals were inside the circle and actively feeding (Benoit-Bird and Au, 2009). However, the number of clicks detected when animals were inside the circle was amongst the lowest measured. In addition, interclick interval showed modes at 55, 80, and 100 ms. Given an approximately 20 ms processing lag time associated with echolocation clicks (Au, 1993), this suggests a two-way transit time equivalent to targets at approximately 26, 45, and 60 m, respectively. If these are indeed echolocation clicks, they are more consistent with animals echolocating off fea-

tures at the opposite side of the circle of dolphins (and the patch of prey) than with targets at close range that they are attempting to capture.

Further examination of the timing of click detection suggests another use for the detected clicks. Clicks were not produced most often within the discreet foraging stages but rather during the transitions between stages when animals were changing formation. A large number of clicks were detected when animals were moving from the wide line to the tight line and then again when the tight line began to form a circle. This suggests that clicks may be important in coordinating the group. Dolphins may be using clicks to gain information about the prey field at these critical decision points. Perhaps a threshold rule of prey density or distribution is employed for changing foraging stages and the animals are collectively testing for this threshold. They may also be using echolocation to track the changing positions of other members of the group which could be supported by the relatively long target ranges indicated by the measured interclick intervals. Another possibility is that the clicks themselves are being used to transfer information between individuals, serving as a form of communication rather than a sense. Information could be contained in any number of signal parameters of clicks including their temporal spacing that could serve to direct the movements of the group. Social communication via echolocationlike clicks has been suggested in cetaceans that do not produce whistles (Amundin, 1991; Dawson and Thorpe, 1990; Dawson, 1991) and in sperm whales (Watkins, 1980) supporting the hypothesis that these click signals that evolved for one purpose could be developed for others (Tyack, 1997).

The two possibilities raised here for the use of clicks in foraging spinner dolphins are difficult to test. While we were able to record clicks, we were unable to record single clicks on multiple hydrophones which would have allowed us to localize the signal to its production site and perhaps correlate that with the multibeam sonar observations to identify the individual signaler. This suggests that we likely missed many of the clicks produced. Dolphin clicks are high in frequency, typically with a peak frequency over 100 kHz, and thus attenuate rather quickly in water. In addition, clicks are highly directional with a half power (3 dB) beam angle of about 10° (Au, 1993), meaning that clicks are difficult to detect unless the receiver is within this narrow transmission cone. Further evidence of this can be seen in the depth at which clicks were recorded. Clicks were only recorded when the hydrophones were within the scattering layer which was also the depth range at which dolphins were present, suggesting we were only collecting clicks from animals close to the depth of each hydrophone. In addition, we were likely only recording clicks from animals directing their beam at the hydrophone. This is evidenced by the data shown in Fig. 7 relating the time interval between pairs of dolphins swimming in a circle past a fixed point and the interval between successive bursts of clicks. Individual pairs of dolphins within a foraging circle were probably each clicking in a directly relative to their position in the circle so as one pair passed, the hydro-

phone near that depth would be within the beams of those animals for a short period of time related to their distance and swimming speed.

After passing out of those individuals' beams, another pair slightly deeper in depth would pass similarly, providing a regular pattern to the collection of clicks as observed. Despite these difficulties in detecting clicks, the observed differences in click rate between different foraging stages likely represent important differences in how clicks are being used with these different behaviors, either through changes in click production rate or other changes such as sweeping of clicks over a wider area that might be detected as rate changes.

The potential use of clicks directly for communication has not been investigated. Most studies in dolphin echolocation have taken place under carefully controlled conditions with captive animals and artificial targets. We know very little about how wild dolphins use echolocation to solve tasks such as avoiding obstacles or detecting, selecting, and capturing prey (Tyack, 1999). Relatively recent field observations using arrays (e.g., Lammers *et al.*, 2006) and acoustic recording tags (e.g., Madsen *et al.*, 2005) are beginning to change this. However, concurrent observations of underwater behavior and acoustics of dolphins and prey behavior remain limited. The idea that dolphins could use existing signals for multiple purposes should not be surprising. Clicks have significant advantages for communication over whistles as pointed out specifically for burst pulsed signals by Lammers *et al.* (2006). For the same reasons that we had a difficult time detecting clicks, so would other animals in the habitat. Communication with clicks that have a relatively short active space, or radius of effective communication, of a few hundreds of meters at most (Au, 1993) and can be directed toward a recipient seems highly advantageous over using whistles which have a potential active space of a few tens of kilometers (Janik, 2000a) and cannot be focused when relaying information about a highly valuable resource. The animals in this group may keep noncooperative individuals from finding the highly dense prey patch they created by reducing eavesdropping. The mesopelagic prey layer that spinner dolphins feed upon is also an important food resource for a variety of fish including snappers (Haight *et al.*, 1993), tunas (He *et al.*, 1997), and billfish (Skillman, 1998). Most fish do not hear well at the high frequencies in dolphin clicks though they can likely hear the low-frequency components of whistles (Popper and Fay, 1999). Competing predatory fish would have even more difficulty than conspecifics using eavesdropping on a cooperating group of dolphins communicating via clicks, limiting the potential for the dolphins to lose the dense patch of prey they created. No information is available on the hearing of myctophid fishes, the primary prey found in these dense patches. However, most fish can only hear at frequencies up to a few kilohertz so it is possible that the use of high-frequency communication signals could limit the ability of the prey to detect the dolphins as well.

Group coordination of spinner dolphins during foraging may be maintained by other sensory modalities that cannot be examined in these data. For example, the prey of spinner

dolphins is bioluminescent with photophores that emit light when they are disturbed. Perhaps dolphins create a "wake of light" as they swim through the layer of prey. Dolphin-stimulated bioluminescence has been observed in bioluminescent zooplankton (Rohr *et al.*, 1998); however, there is no evidence available for the induction of bioluminescence by predators for the animals that serve as dolphin prey. Perhaps a combination of sensory stimuli play a role in both the decision making processes involved in prey herding and the communication, either intentional or as a by-product of other behavior, that occurs between individuals to maintain group coordination.

Our results suggest that while the acoustic signals that have been shown in other studies to serve a communicative role were noticeably absent, clicks consistent with echolocation were correlated with changes in coordinated groups of foraging spinner dolphins. These data cannot separate the use of these click signals for sensing of the prey field, leading to a decision of all individuals to exhibit a behavior from the direct use of the signals for communication. However, the extremely rapid and tightly synchronized movements observed among up to 28 individuals suggest that the mechanism is highly efficient. The changes in prey density observed were graded and varied over space which would make synchronized decision making via a threshold difficult. Some form of communication would seem necessary to coordinate the group unless the behavior is so highly stereotyped that no variability in the prey field is considered once the herding behavior begins and all individuals simply fulfill their expected roll. This is not supported by the variability in the timing between transitions in the greater data set presented in Benoit-Bird and Au (2009). Communication might be limited to a few simple cues at transitions, similar to a coach's command for a new play in a football game. All players (animals) would know what to do based on a single short command. This communication method would suggest that animals play a consistent part in the foraging from one bout to another and that groups are maintained over some time period longer than a single, 5 min foraging bout. Data are not available to evaluate these predictions. Whatever the mechanism by which clicks are involved in group coordination, the results highlight the potential flexibility of delphinid acoustic signals, contrary to the existing assumption that echolocation and communication are separate and compartmentalized (Tyack, 1997). Our results are unable to support the established paradigm for dolphin acoustic communication and suggest an alternate communication mechanism for foraging spinner dolphins.

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