DIRECTIONALITY IN THE WHISTLES OF HAWAIIAN SPINNER DOLPHINS (*STENELLA LONGIROSTRIS*): A SIGNAL FEATURE TO CUE DIRECTION OF MOVEMENT?

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ABSTRACT

Dolphins produce frequency modulated (FM) whistles that are thought to promote the synchrony and coordination of behavior between members of a group. How whistles are used in this regard remains poorly understood. One possibility is that whistles have directionality and thereby convey the orientation and direction of movement of the signaler to nearby listeners. To explore this possibility, whistles from free-ranging Hawaiian spinner dolphins (*Stenella longirostris*) were obtained using a towed, three-hydrophone line array and examined for the presence of directionality. Both the estimated source level and harmonic content of whistles produced by animals traveling with or toward the array were greater than those of animals moving ahead or away from it. In addition, signals produced by animals near the array (within 20 m) were received differently on the three hydrophones spaced 11.5 m apart. These differences were greater than would be expected from transmission loss disparities alone. The results indicate that directivity is present in the transmission pattern of whistles. To infer the form of this directivity, a theoretical whistle beam pattern was established based on the assumption that the dolphin's sound source is approximated by a circular piston transducer (Au 1993). The resulting beam indicates that spinner dolphin whistles become increasingly directional with frequency, especially with respect to harmonics. The orientation-dependent harmonic structure of whistles thus presents a potential cue that listening animals could interpret to infer the direction of movement of signalers. Harmonics are present in the whistles of many dolphin species and may represent an inherent signal design feature that promotes coordination between animals.

Key words: directionality, whistles, spinner dolphins, *Stenella longirostris*, harmonics, towed hydrophone array, source level, group coordination.

Dolphins live in fluid social groups and produce complex FM whistles that play an important role in maintaining communication between individuals and other groups (Herman and Tavolga 1980). One likely function of whistles is to provide conspecifics with information about the identity and location of signaling animals. There is compelling evidence to suggest bottlenose dolphins (*Tursiops truncatus*), and possibly other species, use individually distinct "signature" whistles to identify one another (Caldwell and Caldwell 1965, Tyack 1986, Caldwell *et al.* 1990, Sayigh *et al.* 1990, Tyack 2000, but see McCowan and Reiss 2001 for a divergent view). These whistles are produced in a manner consistent with promoting social contact between group members both in captivity and in the wild (Smolker *et al.* 1993, Janik and Slater 1998, Janik 2000).

For animals dependent on group membership, however, maintaining contact with others is only one part of the challenge of staying integrated with the group. Establishing physical coordination and synchrony with other members is another important requirement. Many species of dolphins travel in pods over large distances while foraging and protecting themselves from predation in a coordinated and/or cooperative fashion (Norris and Døhl 1980, Norris and Schilt 1988). Individuals in such groups must know not only the location of their pod-mates, but must also be able to detect alterations in their trajectories. It is thought that during the day and at close range visual cues play an important role in this regard among dolphins (Madsen and Herman 1980, Pryor 1990, Würsig *et al.* 1990). However, at night or over larger distances it is generally assumed that whistles, in addition to maintaining contact, also serve to facilitate coordination. But exactly how they function in this regard is not yet clear.

A commonly held belief among many researchers studying dolphin social acoustic behavior is that whistles are more or less omnidirectional signals (see Norris *et al.* 1994, p. 168). However, this assumption has never been empirically verified and is inconsistent with the directional transmission properties of the dolphin's anatomical sound generating and focusing structures (Aroyan *et al.* 1992, 2000; Cranford 2000). Directional cues could play a role in providing information to listening animals about the orientation of the signaler and, as a result, convey information about direction of movement. Consequently, such cues could represent a salient feature of whistles that promotes group cohesion and the coordination of behavior.

In the present study we examine the transmission characteristics of whistles produced by free-ranging Hawaiian spinner dolphins (*Stenella longirostris*). Spinners are gregarious and at times vociferous animals that epitomize the kind of delphinids that depend on acoustic signaling to promote the coordination of a group. They are most active at night, relying heavily on group membership for cooperative foraging and protection from predators such as large sharks, false killer whales (*Pseudorca crassidens*), and pygmy killer whales (*Feresa attenuata*) (Norris *et al.* 1994). Spinner dolphins are tropical to subtropical in their distribution and occur worldwide (Perrin and Gilpatrick 1994). They can be found in both pelagic waters and associated with continents, islands, and reefs.

In Hawaii, spinner dolphins usually occur in aggregations of 20–100 animals (Östman 1994). They are often found quietly resting inshore along the leeward coasts of the main islands during the morning and midday hours. Groups tend to become very active behaviorally and acoustically in the late afternoon as they join other pods and begin travel toward their evening foraging grounds farther offshore (Norris *et al.* 1994). Whistling activity reaches a peak during travel and stays high throughout the night while the animals are feeding (Brownlee 1983). Unlike some

species of dolphins, spinners never occur alone. In fact, their dependence on the group is thought to be so great that Norris and his colleagues, in their 1994 review of spinner dolphin natural history, suggested that a single spinner, "... when taken from the group, is much less than a complete animal" (p. 347). Recent studies of spinner dolphin foraging behavior highlight this dependency. Observations of foraging pods using a modified echosounder have shown that spinners almost always occur as pairs while feeding and coordinate their behavior within the context of a larger group to actively concentrate their prey (Benoit-Bird and Au 2000).

Given these life history traits, we expected that if dolphins convey orientation of movement information via directional cues in whistles this would be apparent in the signals of spinners. The objectives of this study were two-fold: first, to determine whether spinner dolphin whistles exhibit directional properties, and second to infer how the transmission pattern of whistles might contribute to their communicative value as coordination promoting signals.

We investigated whistle transmission using both an empirical and theoretical approach. To establish whether whistles exhibit directional characteristics, signals were collected from free-ranging animals using a towed, three-hydrophone line array. This allowed us to localize signaling animals in two dimensions and compare the properties of whistles as they were received on separate, spaced hydrophones. Then, to infer the form of whistle directivity, we used known and assumed properties of the dolphin's anatomical sound emission structures to approximate the beam pattern of dolphin whistles.

Methods

Empirical Approach

The presence or absence of directivity in signals obtained from the field was established by examining signal propagation in two separate recording contexts. Each of these had alternative outcomes dependent on the transmission properties of the signals. In the first situation we examined the whistles of animals moving in opposite directions with respect to the array. The two scenarios compared were of animals swimming with or towards (W/T) the array with those moving ahead or away (A/A) from it. Signals for each scenario were evaluated for source level and harmonic content. We expected that if whistle transmission were omnidirectional no significant differences would be found between each scenario, whereas notable disparities would be present in the case of signal directivity.

The second recording context considered was of whistles produced by animals localized to a position near the array (within 20 m of the middle hydrophone) where the differences in propagation angles from the dolphin to each hydrophone would be relatively large. Here we expected that, if whistles were omnidirectional in their transmission, the estimated root mean square (rms) source level from each channel would be the same for a particular signal. Alternatively, if whistles were emitted in a beam, estimated source levels for the three channels would be different, particularly between the two most widely spaced hydrophones.

Data Collection

The towed array (Fig. 1) was composed of three spherical 2.5-cm hydrophones flat (±3 dB) to 150 kHz spaced 11.5 m apart from each other along a neutrally
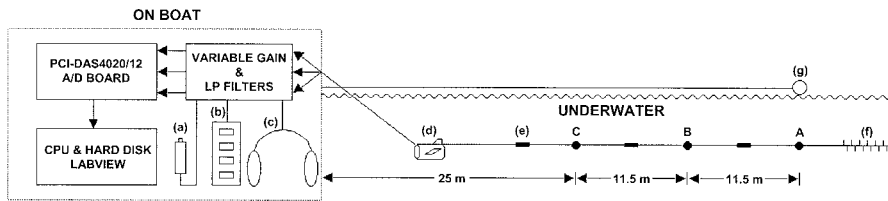
Figure 1.   Schematic of the towed three-hydrophone line array system. On the vessel the system is composed of a signal-conditioning unit with variable gain and low-pass filters, a four-channel A/D board operated with a desktop computer running custom LabView 6i data acquisition software, a manual TTL trigger (a) used to initiate the recording process, an LED meter (b) to monitor the level of incoming signals and a headset (c) to alert the system's operator to the presence of signals. Below water, a PVC "tow-fish" (d) is used to sink the array. Signals are collected on three hydrophones (A, B, and C). Each channel is coupled to an amplifier-line driver (e) that provides 20 dB of gain and high-pass filters received signals at 3 kHz. A tattletale (f) at the end array is used to maintain tension and prevent undulations. Above water, a 40-cm diameter buoy (g) is towed to mark the end of the array as a reference for the observers.

buoyant 1.2-cm thick nylon line. Two of the hydrophones (A and C) were identical ITC 1094A models with a calibrated sensitivity of -200 dB re 1 µPa, while the third (hydrophone B) was a custom model with a sensitivity of -197 dB re 1 µPa. Each hydrophone was coupled to a custom-built amplifier-line driver stage that provided 20 dB of gain and also high-pass filtered the signal at 3 kHz. At the front of the array a custom-made 15 cm $\times$ 30 cm PVC "tow-fish" with downward-angled wings and 5 kg of attached 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, 1.0-cm thick nylon "tattletale" line with 20 cm-long cable ties attached 10 cm apart was placed to create drag and maintain tension on the array. To account for stretch in the nylon line while being towed, we measured the tension on the array while traveling at different speeds using a hand-held scale. We then compensated our hydrophone distance measurements according to the corresponding displacement. At our typical operating speed of 5 km/h (3 knt), the distance between hydrophones A and B and B and C increased by 5 cm and 10 cm, respectively.

The signal from each channel was filtered and amplified using a custom-built, signal-conditioning unit. A variable gain amplifying circuit provided up to 35 dB of additional amplification in 5 dB steps. We used a Lattice Semiconductors™ ISPpac80 filter chip as a 5th order, 50-kHz low-pass filter. To detect the presence of signals, the middle hydrophone (channel B) was monitored using both headphones and an LED meter. Each channel was recorded 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 Pentium 133 MHz desktop computer. Each channel was sampled simultaneously at a rate of 125,000 samples/sec, providing a Nyquist frequency for all recordings of 62.5 kHz. Upon detection of a signaling bout, a manual trigger was used to initiate a 10-sec sampling period. The resulting data files were stored on the computer's hard drive.

The array was towed using a 9.8-m motorboat with a single, inboard 120-hp diesel engine. A team of three individuals was used for data collection. Two observers were positioned on the vessel's flying bridge, approximately five meters above the water line, while a computer operator was located in the cabin below. Communication between the bridge and cabin was maintained via two-way radios. During a recording

session, one of the observers would log the number and position of visible animals relative to the array every two minutes or when prompted by the computer operator. As a reference, a separately towed buoy was used to mark the end of the array. Direction of movement of the animals relative to the array was also recorded.

Spinner dolphins were acoustically sampled on ten separate occasions along the leeward coast of the island of Oahu between February and June of 2001. We generally sought out groups of animals traveling from their daytime resting grounds in shallow waters to their evening, offshore foraging grounds. Animals were usually recorded in waters greater than 30 m deep where ambient noise from snapping shrimp was reduced or absent. Recorded noise levels were approximately equivalent across all ten sampling periods. Noise from the vessel's engine could not be detected above 3 kHz.

The dolphin pods that were recorded ranged in size from 15 to 80+ animals. Our approach was to position the vessel to one side and ahead of a traveling group. This placed the array more or less adjacent and moving parallel to the animals. If approached carefully, a group could be maintained in this relationship for several minutes. At times, groups and individuals would make sudden turns and swim out of our view. When this occurred their position and orientation to the array was logged as uncertain. When recording larger groups, the animals were often too spread out to maintain the same relationship with the entire group. The array was then oriented relative to the largest visible subgroup. Recordings of signals were made only when the vessel and the array were traveling in a straight line, as indicated by the towed buoy.

Data Analysis

Localizations were made using time of arrival difference cues. Differences in the time of arrival of whistles at each hydrophone were measured by cross-correlating segments of the data files containing signals obtained for channels A and C with the ones obtained for channel B (Spiesberger and Fristrup 1990). The largest peak in the resulting cross-correlation vector was used to establish the time lags between channels A and B and C and B. Freitag and Tyack (1993) have shown that multipath reflections from the surface can produce ambiguous cross-correlation results with multiple peaks. In addition, poor signal-to-noise ratio on one or more of the channels can result in low and/or uncertain cross-correlation results. Therefore, to maintain a high degree of confidence in the localizations, signals with low cross-correlation maxima or more than one equivalent peak were not considered. Once the time delay between channels was established, standard equations (see the Appendix) were used to model the location of the signaler on an x-y coordinate axis. This provided the animal's position relative to the array and its distance to each hydrophone. Signals that localized to a position closely in line with the array (ahead or behind) were not considered in the analysis because even small errors in their time of arrival measures would result in considerable range estimation errors.

The system's ability to localize signals was tested using an artificial, omnidirectional source producing dolphin-like FM tones. While maintaining the array stationary at a depth of two meters, the source was placed at different angles and distances (maximum 30 m) away from the middle hydrophone. In each case, localizations were determined to be accurate to within 1–2 m of the actual location of the source. Calculated estimates of the test signal's rms source level for each channel were consistently found to be within 1 dB of one another.

All localization and analysis algorithms were implemented using custom-written Matlab 6.0[TM] programs. Cool Edit 96[TM] was used for the initial visualization of recordings and for comparing the spectrum of signals across the three channels. All FFT calculations used a 1,024-point Hanning window. The speed of sound used for localizations was 1,533 m/sec. This was calculated assuming a typical local salinity of 34.9 ppt and a water temperature of 24.5°C (Urick 1983). All source-level calculations assumed a 20 log(R) spherical spreading loss model and an absorption coefficient of 0.001 dB/m.

Theoretical Estimation of Whistle Directivity

Directivity is a measure of how much more a directional source concentrates its available acoustic power in a specific direction than an omnidirectional source. The directivity factor (d) is defined as the ratio of the intensity of a source at a particular point along its acoustic axis (I_{ax}) to the intensity at that same point due to an omnidirectional source (I_o) radiating the same total acoustic power. Mathematically, this can also be expressed as:

$$d = \frac{I_{ax}}{I_o} = \frac{p_{ax}^2}{p_o^2}$$

where p_{ax} and p_o are the respective rms pressure values. A source's directivity is usually represented in terms of its directivity index (DI), which is simply:

$$DI = 10 \ \log(d).$$

By definition, an omnidirectional source has a directivity index of zero. Any source with a DI value greater than zero is directional and therefore has a definable beam. The larger the directivity index, the sharper the signal's beam.

To infer the transmission characteristics of dolphin whistles we assumed that both clicks and whistles originate from the same location in the dolphin's head. Using high-speed video endoscopy, Cranford *et al.* (2000) recently provided evidence of this by demonstrating that both classes of sounds are produced at the so-called "phonic lips" (formerly the monkey lips; Cranford *et al.* 1996) in odontocetes. We interpret this finding to suggest that the transmission path into the surrounding environment of both whistles and clicks is likely very similar. Consequently, a circular disk transducer can be used to estimate a whistle beam pattern. Au (1993) calculated a directivity index of 25.8 dB for an echolocating *Tursiops* producing clicks with peak frequencies close to 120 kHz. He also determined that a 4-cm radius circular disk projector emitting a continuous wave (cw) signal at 120 kHz would have the same directivity index as the dolphin. Therefore, beam patterns for a 4-cm radius disk projector operating at typical whistle fundamental and harmonic frequencies were calculated to gain insight on how a dolphin's beam might change with frequency. All the calculations were based on equations presented in Au (1993, pp. 109–111). Standard deviation is given with means.

RESULTS

Field Data

A total of 1,136 whistles of varying signal to noise ratio quality were collected on one or more of the three channels. Of these, only 79 (7%) met the criteria
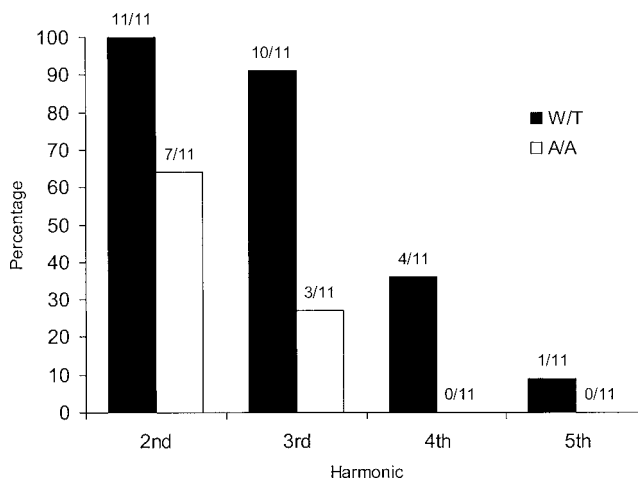
Figure 2. The occurrence of higher order harmonics in the whistles of dolphins confirmed to be swimming either with/toward (W/T, $n = 11$) or ahead/away from (A/A, $n = 11$) the array.

required for a confident localization of the animal's position. Out of these, 38 were deemed to be repeated whistles in a signaling bout, leaving 41 separately occurring whistles to be analyzed.

An approximate direction of movement (either W/T or A/A) was established for 22 signals using either the log entries made by the observers at the time of the recording, or the track provided by consecutive localizations of an animal repeating its whistle during a signaling bout. Eleven signals were associated with each orientation. The mean distance from the middle hydrophone to the signaling animals was 31.2 ± 13.0 m for W/T signals and 32.4 ± 9.4 m for A/A signals.

There was a significant difference in the mean source levels estimated at the middle hydrophone in each case (two sample t-test, $P = 0.03$). Whistles from animals moving with or towards the array had a mean source level of 153.9 ± 4.47 dB, while those moving ahead of or away from it were on average only 150.2 ± 2.78 dB. The harmonic content of the whistles in each case was also notably different. Figure 2 illustrates how often a second, third, fourth, and fifth harmonic were present in the recordings. Ten out of 11 (91%) of the W/T whistles had a visible second and third harmonic. This was the case for only three out of eleven (27%) of the A/A whistles (Fisher's exact test, $P = 0.008$). In addition, fourth, and fifth order harmonics occurred only in whistles produced by animals moving with or towards the array. On average, W/T whistles had 3.3 ± 1.0 harmonic elements (including the fundamental) while A/A whistles only had 1.9 ± 0.8 (two sample t-test, $P = 0.003$).

Although most animals tended not to approach the array very closely, whistles from nearby (<20 m) signalers were obtained on a total of eight occasions. Figure 3 depicts the sonogram and spectrum of one of these whistles as it was received on channels A and C. This signal was localized to a dolphin swimming in an unknown direction relative to the array at a distance of 19, 17, and 23 m from hydrophones A, B, and C, respectively. Although the animal was only 4 m closer to hydrophone
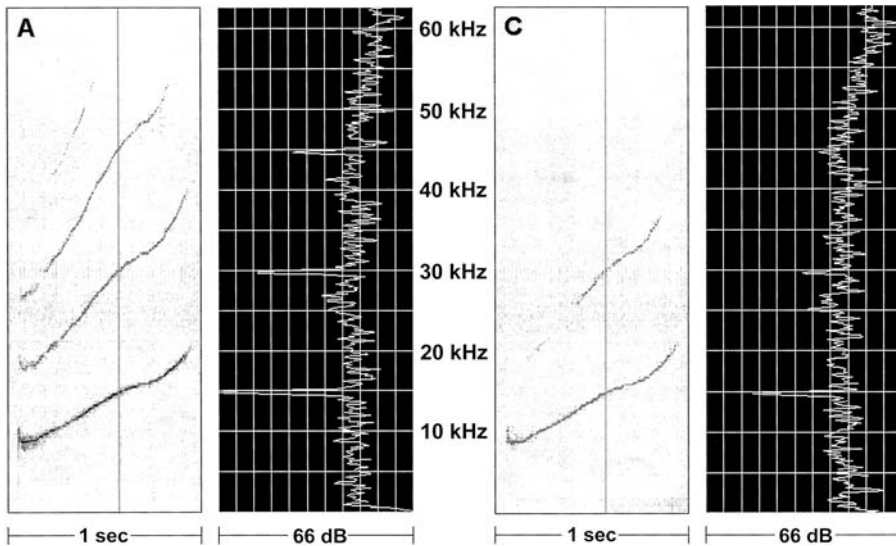
Figure 3.   Sonogram and spectrum of a whistle produced by a signaler less than 20 m from the arrays middle hydrophone. Note the disparity in level of the fundamental and harmonics received on channels A and C, approximately 23 m apart. The difference is greater than would be expected from only a variation in transmission loss.

A than to C, the signal was received quite differently on the two channels. The source level estimated on channel A was 155.8 dB re 1 μPa, while on channel C it was 146.1 dB, an almost 10 dB difference. Moreover, the harmonic structure of the two recordings was visibly different. The level of the second harmonic, even when adjusted for the additional transmission loss, was at least 17 dB lower on channel C than on A, and the third harmonic appeared to be completely absent from the recording on channel C.

Source level estimates calculated for each of these eight nearby signals revealed a regular disparity between channels A and C. While neither channel had significantly different source-level estimates overall (paired *t*-test, $P = 0.12$), each individual signal always resulted in unequal estimates between the two channels. The difference between them was on average 6.3 ± 2.8 dB. The channel with the higher source level had a mean value of 156.0 ± 4.0 dB while the lower one was 149.7 ± 3.2 dB.

An analysis of the spectrum of each of these eight signals further showed that the harmonic structure received on the two channels was also not equivalent. Measurements of the level of the second harmonic made at the beginning, middle, and end of each signal revealed an average difference of 8.0 ± 5.5 dB between channels A and C. The third harmonic was usually too attenuated on one or both of the channels for such comparisons.

Beam Pattern of a Circular Disk

To account for the bandwidth of a whistle with multiple harmonics, the beam pattern and directivity index of a circular piston transducer was calculated for cw
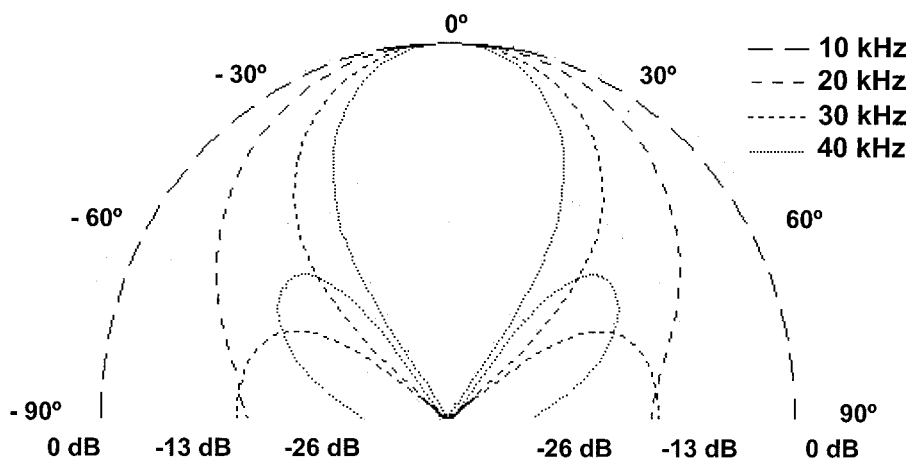
Figure 4. Beam pattern of a 4-cm radius circular piston transducer at frequencies of 10 kHz (*DI* = 6.3 dB), 20 kHz (*DI* = 10.8 dB), 30 kHz (*DI* = 13.7 dB) and 40 kHz (*DI* = 16.5 dB).

signals with a frequency of 10, 20, 30, and 40 kHz. This approximated the frequencies typically observed for the fundamental, second, third, and fourth harmonics of spinner dolphin whistles (Lammers *et al.* 1997). The theoretical beam pattern obtained assuming a 4-cm radius disk is presented in Figure 4. The beam is relatively broad at 10 kHz, but narrows considerably with each increasing octave. The directivity indices of the source at each frequency are presented with the figure.

DISCUSSION

The results obtained from the field data do not fit an omnidirectional whistle transmission model. Whistles from dolphins swimming toward the array were on average higher in amplitude and richer in harmonic structure than those from animals moving away from it. Furthermore, the levels of attenuation observed on separate channels for nearby whistles indicate that, particularly at harmonic frequencies, spinner dolphin whistles have directivity. We therefore conclude that a whistle beam is present.

This finding does not come as a surprise. Simple physics dictates that only a spherical source could produce an omnidirectional signal with a bandwidth equivalent to a spinner dolphin's whistle (Urick 1983). No spherical tissue structure or air space exists in the spinner dolphin's head that could be associated with whistle production (Dormer 1979, Cranford 1988). In addition, shading from cranial bones and nasal air sacs would make it very difficult for a broadband signal to radiate equally in all directions (Aroyan *et al.* 1992, 2000; Cranford 2000). Therefore, some level of directivity should be expected regardless of the precise anatomical origin of whistles.

A more dubious issue concerns the actual form of the whistle beam. The field data obtained did not allow us to empirically derive the spinner dolphin's whistle beam pattern because the orientation of signaling animals could not be precisely

established. However, the source level differences observed between the end hydrophones (A and C) when animals were nearby (mean = 6.3 dB) are consistent with the directivity predicted from the theoretical 10-kHz beam (*DI* = 6.3 dB). Ten kHz corresponds well with the typical fundamental frequency of the whistles we analyzed. Moreover, the mean difference (8 dB) in the levels observed for the second harmonic at hydrophones A and C is not far from the directivity predicted for the 20-kHz beam (*DI* = 10.8 dB). Therefore, in the absence of an empirically measured transmission pattern, the theoretical beam we have presented does seem to serve as a reasonable proxy.

Biological Significance

The results presented suggest that spinner dolphin whistles have what is referred to as "mixed directionality" (Larsen and Dabelsteen 1990, Miller 2002). This term was initially coined to describe the transmission properties of certain bird songs that were found to be omnidirectional at low frequencies and directional at higher frequencies (Larsen and Dabelsteen 1990). In the case of spinner dolphin whistles, we apply it to mean that the lower frequency elements of a whistle radiate with less directivity than those of higher frequency. In other words, the fundamental is less directional than the second harmonic, which is less directional than the third, and so on. This finding is consistent with the results reported by Evans *et al.* (1964) who found a similar trend by projecting artificial sounds through the heads of both *Stenella* and *Tursiops* cadavers.

An important consequence of this type of transmission is that nearby listeners will not always receive the same signal equally. Rather, they will hear it in a manner consistent with their position relative to the signaler's transmission beam. Our recordings on the three spaced hydrophones illustrate this point. What each hydrophone received when a signaling dolphin was close by was determined by its location relative to the animal's beam. Coincidentally, this helps to explain why so many whistles were too faint on one or more channels to be localized.

A Direction of Movement Cue

The relative presence or absence of harmonic energy in a whistle is potentially a valuable source of information for animals listening nearby. Assuming pod-mates are familiar with one another's on-axis whistle structure (its typical harmonic composition and source level) and transmission beam, a change in the perceived level of harmonics received off-axis would provide information to the listener about a signaler's orientation. Consequently, whistles with harmonics probably contain an inherent direction of movement cue. We propose that, by simply interpreting the spectral composition of a received whistle, a listening dolphin would be able to infer its own position relative to the whistling animal, as well as detect changes in the signaler's direction of travel. The whistle beam of a dolphin may therefore provide an important acoustic cue that facilitates the coordination of movements between animals (Fig. 5).

By being broadband and increasingly directional with frequency, the whistles of spinner dolphins make better carriers of direction of movement information than simple, narrowband, omnidirectional whistles. This is because the orientation-
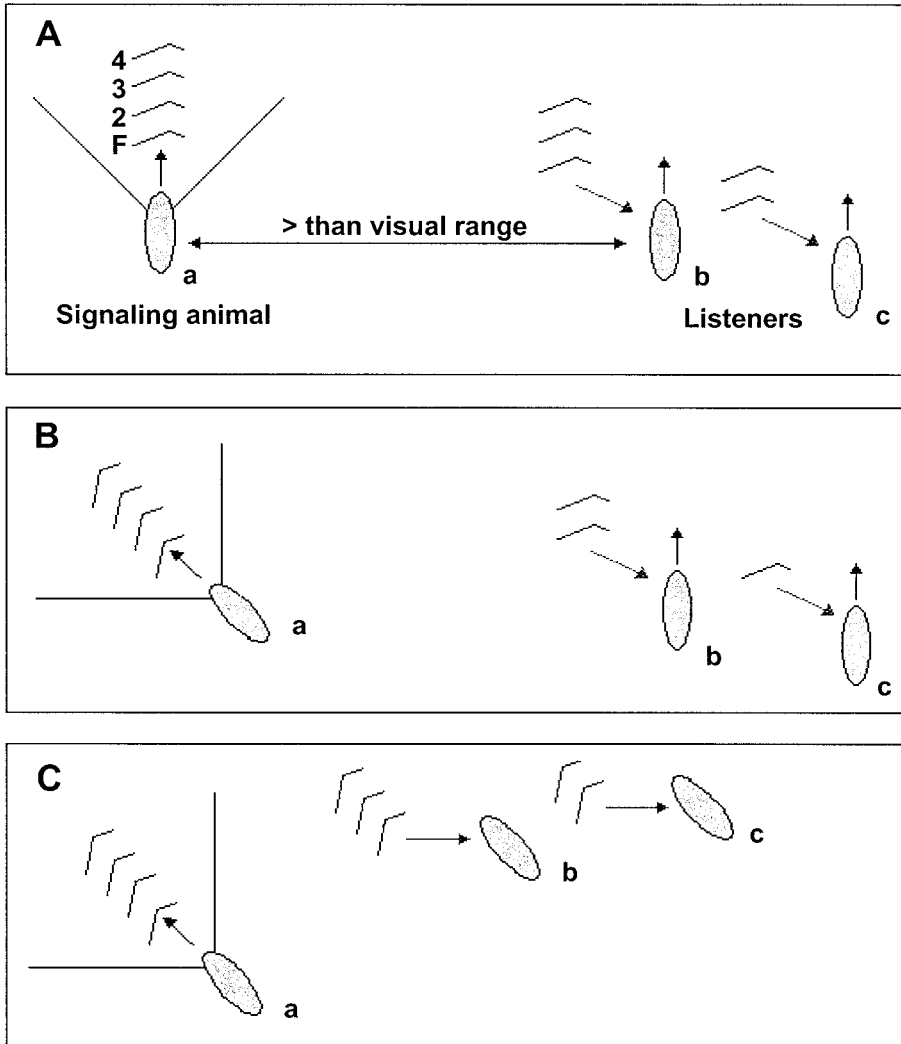
Figure 5. A simple model for the function of whistle harmonics in coordinating group navigation. The ovals represent dolphins while the chevrons symbolize the fundamental (F) and higher order harmonics (2, 3, and 4) of a whistle contour. (A) A whistle with a specific harmonic composition is received by adjacent listeners in a manner determined by their relative position to a whistle beam pattern. (B) As the signaler's orientation to the listeners changes so does the perceived level of higher frequency harmonics. (C) The listeners respond to this cue by re-orienting themselves relative to the whistle beam, re-establishing the original condition.

dependent changes in the amplitude of harmonics produce a more qualitatively distinguishable signal feature than does the attenuation of the fundamental alone. An attenuated fundamental does not allow a listener to distinguish between an increase in distance to the signaler and a change in its orientation. Conversely, the relative level of one or more harmonics will result in a change in the perceived

timbre of the whistle that is indicative of the signaler's orientation relative to the listener.

In addition, the directivity of the dolphin's receiving beam may also come into play (Au and Moore 1984, Au 1993). For *Tursiops*, hearing directivity increases with frequency in a manner similar to the outgoing sonar beam (Au 1993). At 30 and 60 kHz (frequencies commonly associated with harmonics) the directivity indices are 10.4 and 15.3 dB, respectively. Consequently, a listening dolphin will probably hear a whistle as the product of the interaction between the signaler's emission beam and its own receiving beam. This will most likely result in the perceived timbre of repeated signals to change as a function of even small changes in the spatial relationship between signaler and listener.

Other Species

Harmonics are a common feature in the whistles of many dolphin species. Yet, until recently, most researchers paid little attention to them, mostly because of the challenge of obtaining broadband recordings in the field (Au *et al.* 1999). If the ideas presented above prove correct, the presence of harmonics could represent an adaptive signal design trait shared throughout much of the Delphinidae family. There is evidence from at least one other species to suggest this may be the case. Miller (2002) recently presented findings of mixed directionality in the calls of killer whales (*Orcinus orca*). Using a towed beamforming array to localize calling whales, he demonstrated that the higher frequency (>5 kHz) elements of calls are considerably more directional than the lower frequency (1–5 kHz) components. His conclusion mirrored ours: the mixed directionality of killer whale calls is likely a direction of movement cue that facilitates group coordination.

Conclusions and Future Research

A common observation is that dolphins are capable of maintaining tight coordination and synchrony even when spread out over large distances or restricted visually (Norris *et al.* 1994). An acoustic direction of movement cue is the most likely explanation for this ability. Assuming that the cue is signal directivity, a whistle (signature or otherwise) not only identifies the location of an individual, but also inherently informs others of that animal's direction of travel. We propose that dolphins listen to one another's whistle spectral structure in order to infer both the present and future locations of their pod-mates.

It is still too early to fully appreciate all the biological consequences of whistle directionality. However, a theoretical basis for its role in delphinid communication certainly exists. Whether dolphins actually attend to the information present in the directional cues of their whistles remains open for debate and further study. Clearly, more work is needed to fully evaluate the merits of the ideas presented here and by Miller (2002). An empirically established whistle-beam must be obtained to improve the one estimated here. Also, controlled experiments need to be performed to establish whether dolphins do in fact discriminate changes in the harmonic structure of whistles. Finally, additional field observations and localization data will be needed to better understand the behavioral contexts in which whistles are produced.

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APPENDIX

A detailed discussion of the theory associated with localizing an acoustic source using a sparse array is beyond the scope of this appendix. Interested readers should refer to Watkins and Scheville (1972) and Spiesberger and Fristrup (1990) for a more detailed treatment on how to localize and track signaling whales and dolphins.

The localizations reported here were obtained using a linear equation approach adapted for a three-hydrophone line array after Spiesberger and Fristrup (1990). This approach allows simple, two-dimensional locations to be established along an x-y coordinate plane. To use this approach, one of the hydrophones is assumed to be at the origin as shown in Figure A-1. By convention, the origin is placed at the middle hydrophone, but any of the three hydrophones could be used.

Using the relationship $t = r/c$, where t is the time for an acoustic signal of speed c to travel over a distance r, and the Pythagorean theorem, the distance between the sound source and hydrophone h_1 (d_1 in Fig. A-1) can be expressed as

$$s_x^2 + s_y^2 = c^2 t_1^2 \tag{1}$$

where s_x and s_y are the x-axis and y-axis coordinates of the source. Likewise, the distances of hydrophones h_2 and h_3 from the source (d_2 and d_3, respectively) are equivalent to
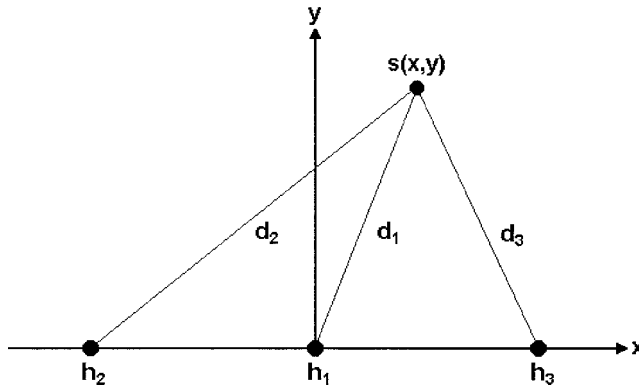

Figure A-1. Geometry of a three-hydrophone line array for localizing a sound source at position *s(x,y)*.

$$(s_x - x_2)^2 + s_y^2 = c^2(t_1 + t_{21})^2 \tag{2}$$

$$(s_x - x_3)^2 + s_y^2 = c^2(t_1 + t_{31})^2 \tag{3}$$

where t_{21} is the difference in the time of arrival of the sound between hydrophones h_2 and h_1 and t_{31} is the time of arrival difference between hydrophones h_3 and h_1. Using liner algebra, the above equations can then be used to solve for the three unknown variables: t_1 (the time it took the signal to travel to h_1), s_x and s_y. These become

$$t_1 = \frac{c^2(x_3 t_{21}^2 - x_2 t_{31}^2) + (x_2 x_3^2 - x_2^2 x_3)}{2c^2(x_2 t_{31} - x_3 t_{21})} \tag{4}$$

$$s_x = \frac{c^2(t_{21} t_{31}^2 - t_{21}^2 t_{31}) + (x_2^2 t_{31} - x_3^2 t_{21})}{2(x_2 t_{31} - x_3 t_{21})} \tag{5}$$

$$s_y = \pm\sqrt{c^2 t_1^2 - s_x^2} \tag{6}$$

It should be noted that the solutions for t_1 and s_x contain "poles" that will cause equations 4 and 5 to explode to infinity when $t_{31} = -t_{21}$. This situation cannot be avoided with a three- hydrophone line array, and there will be locations on the x-y plane where $t_{31} = -t_{21}$. When these occurred in the present study, the signals associated were not considered for analysis.