The spatial context of burst pulse signals and whistles produced by Hawaiian spinner dolphins (*Stenella longirostris*)

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Michiel Schotten



Research report to K.N.A.W. Department of Marine Biology, University of Groningen Marine Mammal Research Program, University of Hawaii December 2003

ABSTRACT

Free-ranging dolphins produce three basic categories of signals: echolocation clicks, burst pulse clicks, and frequency modulated whistles. Lammers & Au (2003) hypothesized that whistles, by means of a mixed directionality of their harmonics, play an important role in maintaining group coordination for dolphins that are outside of each other's visual range. Based on this hypothesis, the prediction was tested that dolphins producing whistles are spaced more widely apart than dolphins that produce burst pulse signals, the latter of which may function as a more intimate type of signaling between adjacent individuals. A 3-hydrophone towed line array was used to record and localize spinner dolphin (Stenella *longirostris*) whistles, burst pulse signals, and echolocation clicks in 2-D up to a distance of 110 m from the array. From the x,y-coordinates of each presumed individual dolphin, distances were calculated between dolphins whose signals followed each other closely in time. Additionally, click source levels were calculated for burst pulse signals. The hypothesis of this study, i.e. that whistling dolphins are spaced more widely apart than burst pulsing dolphins, was supported by the data we collected from the field. Additionally, it was found that the closer two burst pulsing dolphins were to each other, the more quickly their burst pulses followed each other in time. This relationship could point to communicative exchanges of burst pulses between dolphins and was not found for whistles. Also, this study provides the first reported evidence that burst pulses are directional, which was expected from the signal transmission characteristics of the dolphin forehead, with indications that burst pulse clicks might have wider beam patterns than echolocation clicks. Finally, a logarithmic relationship was found between burst pulse source levels and the ranges at which they were produced. This finding could be an artifact, but if substantiated in future studies could have implications regarding the function of burst pulse signals.

ABSTRACT

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Michiel Schotten

Research report to K.N.A.W. December 2003

Research performed in partial fulfillment of the requirements to obtain a Ph.D. degree at the University of Groningen.

Ph.D. Committee:

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Front page: photo courtesy of Dr. Andre Seale.

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INTRODUCTION

Free-ranging dolphins produce a wide variety of sounds, which can be classified into three broad categories: echolocation clicks, burst pulse clicks, and whistles. Clicks are extremely short (~50 µs) and broadband signals, extending in frequency from 0 up to over 200 kHz (Au 1993, Lammers et al. 2003,) and emitted from the forehead in a narrow directional beam (Au 1993). The main feature used to distinguish between echolocation clicks and burst pulse clicks is the number of clicks produced per unit time (Lammers et al. 2004). Echolocation clicks are generally emitted only after the echo of the previous click has been received by the dolphin, plus some additional time (15-45 ms, Au 1993) to process the echo. Therefore, in echolocation click trains the interclick intervals (ICIs) exceed the 2-way transit time, i.e. the time needed for a signal to travel from a dolphin to the target and back to the dolphin, by at least 15 ms. In burst pulse click trains on the other hand, ICIs can be as small as 0.5 ms and generally do not exceed 10 ms (Lammers et al. 2004). While echolocation clicks are used to detect and recognize targets in the water column, burst pulse clicks are thought to be used mainly for social communication (Popper 1980, Lammers et al. 2003).

Furthermore, many dolphin species produce long-duration, frequency modulated tonal sounds known as whistles, which are also associated with social communication (Herman & Tavolga 1980) and which can be emitted simultaneously with burst pulse or echolocation clicks (Cranford 2000). One likely function of whistles is that dolphins use individually distinct "signature" whistles to identify one another (Caldwell & Caldwell 1965, Tyack 2000, but see McCowan & Reiss 2001 for a different view). Additionally, Lammers & Au (2003) found evidence that whistles may be used as a direction of movement cue, indicating the orientation and direction of travel of the signaling dolphin to nearby listeners, and thus facilitating group coordination for animals that are outside of each other's visual range. They speculated that listening dolphins may infer a change in the direction of the signaling dolphin by a shifting number of harmonics that they perceive in the whistle. While the fundamental frequency of FM whistle contours generally do not extend beyond 20 kHz, they also contain harmonics, which are multiple integers of the fundamental frequency and can extend in frequency up to as high as 100 kHz (Lammers et al. 2003). Lammers & Au (2003), who used a towed array of three hydrophones to record and localize signals from wild spinner dolphins (Stenella longirostris), found that whistles were directional, i.e. emitted in a beam. Directionality of a sound source is a measure of how much the received amplitude of the sound decreases as the receiver moves sideways of the sound beam axis. They also found that higher harmonics of the whistle were more directional, i.e. had a narrower beam pattern, than lower order harmonics.

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Therefore, the number and loudness of harmonics perceived by listening dolphins will change dependent on their relative position to the signaling dolphin's whistle beam pattern, which could thus act as a direction of movement cue to listening dolphins.

Since whistles because of their lower frequency content are thought to have wider beam patterns than broadband clicks, especially the fundamental contour and lower harmonics of the whistle, it is expected that they can be perceived by other dolphins over longer distances than burst pulse clicks. Based on the hypothesis that spinner 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.

An additional question was whether burst pulse clicks are directional, and if so whether they are equally, more, or less directional than echolocation clicks, i.e. whether burst pulse clicks are emitted by dolphins in a similar, narrower, or wider beam than echolocation clicks. The beam pattern of echolocation clicks has already been well documented from studies with captive dolphins by Au (1993), and Lammers & Au (2003) were the first to estimate a theoretical beam pattern for whistles. From the sound transmission properties of the dolphin forehead, it seems very likely that dolphin burst pulse clicks are also emitted in a beam, however, this has not yet been empirically confirmed in the existing literature. Also, it is unknown whether, and if so how the number of clicks emitted per unit time might affect the width of the emission beam of clicks, and therefore whether burst pulse clicks have a similar or different beam pattern compared to the echolocation click beam pattern.

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MATERIAL & METHODS

To establish whether or not whistles are exchanged from greater distances among individual dolphins than burst pulses, signals were recorded from free-ranging spinner dolphins (*S. longirostris*) using a 3-hydrophone line array towed behind a boat. A towed 3-hydrophone line array, as described by Lammers & Au (2003), enables one to localize dolphin signals in a 2-D plane up to distances over 100 m from the array, by using the differences in time of signal arrival at the 3 hydrophones. The localization error can range from 1-2 m up to >10 m, depending on the angle between dolphin and array as well as the dolphin's distance from the array. 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 at relatively large distances with medium accuracy, without providing information on depth of the dolphins or on the direction of their signal beam. Also, there is a left-right ambiguity in the localization, but efforts were made to keep dolphins on one side of the array.

Data collection

The 3-hydrophone array (Fig.1) was composed of three custom-made 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. At the front of the array a 15 X 30 cm PVC "towfish" with downward-angled wings and $\frac{1}{2}$ kg 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 and 10 cm apart was used to create drag and thus maintain tension on the array while being towed. To account for stretch of the nylon line from the towing, the tension on the line while traveling at different speeds was measured using a hand-held scale and subsequently the corresponding hydrophone displacements were measured. At the typical operating speed of 5 km/h, distance between hydrophones A and B and between B and C increased by 5 and 10 cm, respectively.

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 SemiconductorsTM ispPAC80 5th order filter chips were used to low-pass filter the signals at either 50 kHz or 150 kHz, depending on the A/D

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sample rate that was used, to avoid aliasing of the signals above the Nyquist frequency (which is half the sampling frequency). Additionally, a 3 kHz high-pass filter filtered out low frequency engine and water flow noise. During all recordings, the variable gain was set at 30 dB, providing a total of 70 dB of amplification with the pre-amplifier included. 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 an LED meter (which could also detect signals that were purely ultrasonic). A 4-channel simultaneous sampling Measurement ComputingTM analog-to-digital 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/sec (for field recordings made in May and June 2003) or 400,000 samples/sec (for the 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 ¹²⁶ MHz "lunchbox" computer, and the data acquisition and storage process was run by a custom-written LabView 6iTM program. Upon detection of dolphin signals, a 10-sec sampling period was initiated by a manual trigger and the resulting data files were automatically stored on the computer's hard drive.



Figure 1. Schematic of the 3-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 4-channel PCI-DAS4020/12 A/D board operated from a "lunchbox" computer running custom-written LabView $6i^{TM}$ data acquisition software, a manual TTL trigger (a) to initiate 10-sec 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 appr. 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 pre-amplification. 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.

The line array was towed from the research vessel "Meleana", a 9.8 m motorboat with an 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, and one person driving the boat from the flying bridge approximately 5 m above the water surface while simultaneously logging the presence of dolphins (unless a third person was present). Radio contact was maintained between bridge and cabin, and when the computer operator detected dolphin signals and started a recording period, the data logger was notified to log the number and positions of visible dolphins relative to the array. This was done to verify during the subsequent data analysis that dolphin positions calculated from the 3-hydrophone localization algorithm were approximately correct.

Acoustic recordings from spinner dolphins (*S. longirostris*) were obtained along the leeward coast of Oahu, Hawaii, on six separate days in May, June, and November 2003, while efforts made to encounter dolphins on eight different days were unsuccessful. Ideally, dolphins would be recorded when they traveled from their daytime resting grounds in shallow waters to their evening, offshore foraging grounds. In those cases, efforts were made to keep the boat positioned at one side and slightly ahead of the dolphins, while driving at approximately the same speed. A group of dolphins could often be maintained in this relationship for several minutes. When dolphins were encountered while they were not traveling, the array was also deployed in all cases when dolphins appeared to be socially (and therefore, acoustically) active. 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) to ascertain that localizations would be correct. When the computer operator could no longer detect signals, the boat driver was notified to make a gradual 180° turn and, depending on activity of the dolphins, drive by the group again. The dolphin pods that were recorded ranged in size from approximately 30 to 60 animals

Data analysis

Localizing signals

Recorded sounds were localized by using the differences in time of sound arrival at each hydrophone in standard equations (see Appendix). 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 dolphin-like FM 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.

The 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^{TM} software. Subsequently, whistles were analyzed using a custom-written Matlab 5.1^{TM} program that implemented the 3-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, those were not considered for further analysis 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 and could not be cross-correlated because of their short and transient nature. Therefore, unlike whistle localizations, click localizations could not be automated and were more tedious. First, to improve the signal-to-noise ratio of clicks (which have the major part of their energy in the ultrasonic range), low frequency noise and whistle fundamentals were filtered out by applying an artificial high-pass filter at 20 kHz in Cool Edit. Waveforms (i.e., amplitude plotted as a function of time) were compared in Cool Edit 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 later entered in another custom-written Matlab program to calculate the 2-D position of the sound-emitting dolphin, using the localization algorithm For each burst pulse, this was repeated for one up to several clicks, to ascertain that the localization for that burst pulse was correct.

In cases where the first and last few clicks were buried in the noise floor and it was unclear where the burst pulse signal started and ended, several clicks in the middle of the burst pulse were selected and the interclick intervals (ICIs) measured, to ascertain that the same click was being inspected on each channel. The sequence of ICIs should remain the same for the clicks arriving at each hydrophone, even though these sequences are shifted in time relative to each other because of the time of arrival differences. Therefore, only when the same sequence of a number of explicitly different ICIs were found on all three channels, it was assumed that the same series of clicks were being inspected on the three channels. In case a sequence of very similar ICIs were found, however, ICIs (and therefore clicks) could not be distinguished from each other among the three channels and these burst pulse signals were not considered for further analysis.

The Matlab localization programs plotted the position of a whistling or clicking dolphin in an x,ycoordinate system relative to the 3-hydrophone array on the x-axis, with the center hydrophone B (or h_1 in the Appendix) at the origin. The distances of the dolphin to each of the three hydrophones were also provided, as well as the "pole proximity". This parameter was used as a measure of how accurate the localization was. It was calculated by adding the time of arrival difference between channel A and B (t_{21}) to the difference between C and B (t_{31}) , and multiplying the resulting number with the Λ 'D sample rate to express "pole proximity" as a number of samples rather than as unit time (which made it easier to compare this parameter across the two sample rates used, 125 and 400 kHz, respectively). As can be seen from equations 4 and 5 in the Appendix, as the pole proximity approaches to zero (that is, $t_{21} = -t_{31}$), t_1 and s_x will explode to infinity (note that in this coordinate system $x_2 = -x_3 = -8$). This is the case as a sound either originates from a position close to the x-axis (i.e., the "pole" in equations 4 and 5, so at a relatively small angle to the array), or from a very large distance from the array. In both cases, the error in distance calculation becomes unacceptably large and localizations should be discarded. In the analysis, this error was noticed when a localization obtained from one click in a burst pulse differed considerably from the localization of another click within the same burst pulse, whereas these localizations should be approximately the same. The criteria used in this study were that only those signals were used for further analysis that had been localized with an absolute pole proximity of 15 or higher, and of which both the x and the y-coordinates did not exceed 110 m. The combination of these two criteria was found to yield localizations with sufficient localization accuracy for the hypothesis that was tested.

Source level and beam pattern analysis

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The x and y coordinates for each signal were entered into a spreadsheet program, as well as the pole proximity, and the time separation Δt between the signal and the signal just prior to it. Additionally, for each burst pulse and echolocation click train, several high amplitude clicks were selected that were not saturated on any of the three channels (i.e., the amplified amplitude of those clicks did not exceed the +/- 5 V input voltage of the A/D board). The minimum and maximum amplitude of such a series of several clicks were measured in CoolEdit for each channel and entered into the spreadsheet, as well as the three calculated distances of the dolphin to each hydrophone. From these, the received sound source level (SL) could be calculated, which is defined as the amplitude of a sound at 1 m from its source and can be expressed as:

 $SL = SPL + 20 \cdot \log R + \alpha \cdot R.$

In this equation, SPL is the peak-to-peak sound pressure level received by the hydrophone (expressed in dB re 1 μ Pa), which is equal to the absolute value of the hydrophone sensitivity $|H_s| = 205 \text{ dB re } 1 \text{ V}/\mu$ Pa, minus the gain G that was provided by the several amplifiers (40 dB pre-amplification + up to 35 dB re 1 µPa of additional gain), plus 20. logV_{pkpk} (where V_{pkpk} is the peak-to-peak voltage of the signal measured in CoolEdit). To determine the SL of a sound at its origin, one has to add the spherical spreading loss (20 logR) and the absorption loss (α · R) to the received SPL, where R is the calculated range or distance from the sound source to the hydrophone and α is the acoustic absorption coefficient, which was assumed to be 0.001 dB/m (Au 1993). If a different SL is received on each of the three hydrophones, this would point to directionality of the received sound, i.e. that a beam pattern is present in its emission characteristics. Thus, directionality could be compared between echolocation clicks and burst pulse clicks. Since no visual confirmation could be obtained regarding the direction of the heads of clicking dolphins, and hence the direction of their signal beams, this was only meant as a relative comparison averaged over many signals of either type, and not to establish an accurate beam pattern for burst pulse clicks. Besides the x,y-coordinates, pole proximity, Δt , and the SL information for each hydrophone, the number of clicks in a burst pulse or click train and the sequence of ICIs (measured using another customwritten Matlab program) were also entered into the spreadsheet program for later analysis. Those data have not been analyzed yet and are not presented in this report.

Establishing distances between signaling dolphins

Finally, to establish distances between dolphins exchanging burst pulses vs. those exchanging whistles, it needed to be determined for each signal whether it originated from the same dolphin or from a different dolphin than the signals immediately preceeding and following that signal. 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 maximum swimming speeds reported in the literature for various species of dolphins. 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 & 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.

Since the 3-hydrophone localization technique only allows to localize dolphins in 2 spatial dimensions, the depths of dolphins are not considered and the calculated distances between them are likely to be underestimates. Furthermore, although efforts were made to keep dolphins at one side of the array, d' can also be underestimated because of the left-right ambiguity of localizing with a 3-hydrophone array. However, since this is the case for localizations of both whistles and burst pulse signals, it should not affect a statistical comparison between them as long as the sample size of either signal type is large enough. If $d'/\Delta t \ge 8$ 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 criterium, since d' and therefore d'/ Δt are likely to be underestimates.

Besides considering the maximum swimming speed, another method used to determine whether two signals were emitted by different dolphins or by the same dolphin was to consider the angle between the calculated position of each signal and the center hydrophone. It was found that localization errors for a particular signal would only occur along the same line from its calculated position to the center hydrophone B. Therefore, angle localizations were found to be much more accurate and robust than range localizations, even for signals that had small pole proximity values. If two signals with relatively low pole proximity values (and therefore, relatively high localization errors) had different calculated positions along the same line from the center hydrophone, they were assumed to have originated from the same dolphin, even if the criterium of $d'/\Delta t \ge 8$ m/s was fulfilled. On the other hand, if two signals were localized at two different angles to the center hydrophone, they were sometimes assumed to have originated from two different dolphins even if $d'/\Delta t < 8$ m/s. This depended also on localizations of previous signals that were thought to have originated from one dolphin and the inferred direction of movement for that dolphin.

Other criteria were that only signals with both an absolute pole proximity ≥ 15 and x,y coordinates ≤ 110 m were used to calculate distance d' between two dolphins, with the additional criterium that they immediately followed each other (i.e. not interspersed by another signal) within a 3-sec time window. Therefore, mutual distances were only calculated for what were assumed to be direct signal "exchanges" between two dolphins, and not those cases where signals seemed to have been recorded from three or more dolphins. In the analysis, those cases were split up into a series of separate signal exchanges, so that distances d' were only calculated between two signal localizations that followed each other immediately in time, rather than calculating the mutual distances among all the different dolphins for which signals were recorded in a particular file. If two dolphins appeared to have been exchanging signals back and forth, d' was calculated for each separate signal exchange and then averaged for the subsequent statistical analysis.

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RESULTS

Spatial context of whistle and burst pulse exchanges

A total of 185 whistles and 172 burst pulse signals were localized. Whistle exchanges and burst pulse exchanges that met all criteria mentioned previously were selected and the distance d' between two dolphins that were assumed to have emitted the two recorded signals was calculated for each of these exchanges. Use of the term signal "exchange" here simply refers to two different dolphins each emitting a signal within 3 s of each other. For burst pulse exchanges, 27 distances were calculated (five of which represent average distances, for repeated signal exchanges by presumably the same two animals) and for whistle exchanges, 41 distances were calculated. Distributions of these distances are presented as histograms in Fig. 2 and were found to be slightly skewed towards lower distances both for whistle exchanges (Fig. 2A) and for burst pulse exchanges (Fig. 2B). The minimum distance d' was 4 m for whistle exchanges and 3 m for burst pulse exchanges, while the maximum calculated distance was 113 m for whistle exchanges and 72 m for burst pulse exchanges. Median distances were 23 m and 14 m for whistle and burst pulse exchanges, respectively. Overall, the distance d' apart between what were assumed to be two different dolphins was significantly larger for whistle exchanges than for burst pulse exchanges (p = 0.0054, Mann-Whitney test, 2-tailed). The non-parametric Mann-Whitney test was applied rather than the parametric Student's t-test, since distances calculated for both whistle and burst pulse exchanges appeared to have non-normal distributions.



Figure 2. Distributions of calculated distances apart between two dolphins for presumed whistle exchanges (A, N=41) and burst pulse exchanges (B, N=27).

Temporal context of whistle and burst pulse exchanges

Besides the spatial context, the temporal context of dolphin signal exchanges was also considered. More specifically, it was investigated whether the timing of signals had any relationship with the spatial separation between dolphins. For each presumed signal exchange, the calculated spatial separation d' was plotted as a function of the temporal separation Δt between the two signals, as presented in Fig. 3. For whistle exchanges (Fig. 3A), a very weak positive linear relationship was found ($R^2 = 0.05$), however, this relationship was not significant (regression test, p = 0.184). For burst pulse exchanges on the other hand (Fig. 3B), 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 exchanged 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 exchanges. Also recall that whistling dolphins were found to be spaced more widely apart than burst pulsing dolphins in general.



Figure 3. Calculated distances apart plotted as a function of the measured separation in time between two signals, for whistle exchanges (A) and burst pulse exchanges (B), with least square linear regression lines through the data points.

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Source levels and beam pattern of burst pulse clicks

Received peak-to-peak source levels of burst pulse signals were calculated for each of the three hydrophones, using the calculated distances of the dolphin to each hydrophone as specified previously. For all localized burst pulses, SLs received at hydrophones A and C (which were 16 m apart) were different. The mean absolute difference in received SL was 3.8 dB re 1 μ Pa, with a standard deviation of 3.68 dB (N = 123). This implies that burst pulse signals have directional properties like echolocation signals and are emitted in a beam, because if the sound source would be omni-directional (where the sound is not emitted in a beam but equally distributed over all angles), the SLs received at each hydrophone would have been similar instead of different. To make a relative comparison between the beam pattern of echolocation clicks (which has already been well documented by Au 1993) and that of burst pulse clicks, SLs were calculated for several echolocation click trains as well, which were defined as having interclick intervals \geq 15 ms. This analysis is still under progress, but there is preliminary evidence suggesting that burst pulse clicks might be less directional (i.e. have a wider beamwidth) than echolocation clicks. The mean absolute difference in SL received at hydrophones A and C for echolocation signals was 8.7 dB re 1 μ Pa, with an SD of 7.09 dB (N = 7). Although this larger difference in SL between channels A and C suggests that eholocation clicks have narrower beams than burst pulse clicks, due to the small sample size it was not significantly larger. However, the 0.05 significance criterium was barely missed (p = 0.059, 1-tailed Student's t-test with unequal variances) and is likely to be reached with an increasing sample size of echolocation click train SLs as the analysis progresses.

Additional evidence for burst pulse directionality is presented in Fig. 4. The absolute difference in SL received at hydrophones A and C was plotted as a function of the calculated range R of the dolphin to the center hydrophone B. This SL difference could be considered as a crude (although inverted) measure of burst pulse "beamwidth", where a smaller difference between hydrophones A and C indicates a wider beam. If burst pulses would be emitted in a beam, then as a dolphin is far away from the array, its burst pulse beam should cover a wide area. Therefore, a difference in received SL between two hydrophones of the array would be smaller than for a beam emitted by a dolphin close to the array. Indeed, the largest differences in SL between channels A and C were found for burst pulses with the smallest calculated ranges, which is another indication that burst pulses are directional. However, also note that small SL differences (< 1 dB) were found across all ranges, which will be discussed later.

In order to make an SL estimate for spinner dolphin burst pulse signals, the directionality of these signals had to be taken into account. Therefore, it was assumed that only burst pulses of which the highest SL was measured on the center hydrophone B were more or less aimed at the array, and thus represented signals that were approximately measured on the beam axis and the least distorted. Of those burst pulses, the mean SL on channel B was 178.6 dB re 1 μ Pa with an SD of 7.08 dB (N = 40).



Figure 4. A crude measure of "beamwidth" of burst pulse signals (the absolute difference in SL received at hydrophones A and C) plotted as a function of calculated range of each burst pulsing dolphin.

Furthermore, a post-hoc analysis of burst pulse SLs revealed a pattern in the data that might have implications regarding the function of burst pulse signals. When the SL received at hydrophone B was plotted as a function of calculated range R of the dolphin, this resulted in a logarithmic relationship with an R²-value of 0.53 (Fig. 5). These SL values include signals that did not have the highest measured SL on channel B, and that had therefore probably not been measured from the burst pulse beam axis. When off-axis SL values were not included in the plot, this caused the sample size to decrease from N=87 to N=33 with a resulting decrease of the R²-value to 0.10, but the same logarithmic relationship was found.

Finally, some evidence was found for the phenomenon of "chorusing" dolphins emitting burst pulse signals simultaneously and seemingly in synchrony, with clicks from two dolphins at different locations alternating at regular and very short intervals. These cases were difficult to distinguish from a single dolphin emitting burst pulse clicks that had intermediate reflections from the water surface and/or from the bottom (which could in theory be mistaken for clicks of another dolphin). However, at least one burst pulse was recorded on all three channels that showed intermediate clicks of different amplitude, presumably from a different dolphin 9 m away from the first one, that started only after the first three clicks from the first burst pulsing dolphin. These first three clicks from the first dolphin did not show reflections from the water surface or bottom on any of the channels. Therefore, it seems unlikely that the intermediate clicks starting after the third click were surface or bottom reflections. Since no simultaneous video recordings of dolphins were obtained in this study, no conclusions can be drawn from these occasional observations.



Figure 5. Peak-to-peak source level as received on hydrophone B plotted as a function of calculated range of burst pulsing dolphins (N=87).

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Figure 3. Peak-to-peak sinuse lifest arrangions in terministic of the contribution of plattic and individual statements of the second statement of

Spatial and temporal context of whistle and burst pulse exchanges

It was found that spinner dolphins emitted whistles at significantly greater distances from each other than burst pulse signals. This finding is further support for the hypothesis by Lammers & Au (2003) that whistles, by means of the mixed directionality of their harmonics, might function as a direction of movement cue for dolphins to maintain group coordination when they are outside of each other's visual range. If this hypothesis is correct, then one would expect whistles to be used amongst dolphins that are relatively far apart. Burst pulse signals on the other hand might function as a more "intimate" form of signaling between adjacent individual dolphins. This is in line with the finding that burst pulse signals from animals that were spaced more closely together followed each other more quickly in time, which suggests that burst pulses were actually exchanged between dolphins. Such a relationship between spatial and temporal separation between dolphins, beyond which the relation between distance and timing of the signals breaks down. Another possibility is that if whistles do indeed function as a direction of movement cue, there might be single dolphins leading the movement of larger groups and signaling a change in direction to the rest of the pod without the necessity that other dolphins respond.

Furthermore, the first evidence for burst pulse directionality is presented here, although as for whistles the exact beam pattern remains to be established. However, because of the physical properties of sound (with lower frequencies generally exhibiting wider beam patterns), whistles are likely to be less directional than burst pulse clicks, especially the fundamental contour and lower harmonics of the whistle. Since whistles are likely to have wider beam patterns than clicks, one would expect that they can be perceived by other dolphins over greater distances than burst pulse clicks, especially at angles away from the beam axis. A possible confounding factor to this notion, however, is that burst pulse signals have reportedly higher source levels than whistles, on average 203 dB re 1 μPa for burst pulses vs. 156 dB for whistles (Lammers & Au-2003). Until the exact properties of the emission beam pattern are established for spinner dolphin whistles and burst pulse signals, it is unknown how these two factors interact and whether either whistles or burst pulse clicks can be perceived from greater distances by other dolphins. However, this study does show that whistles are exchanged by spinner dolphins that are spaced more widely apart than those exchanging burst pulse signals. This finding might be related more to the different functions of these two types of signals than to their transmission characteristics.

As a final note, of course it can not be ascertained at this point that either whistles or burst pulses were actually "exchanged" between individual dolphins. This term implies a communicative function of signals, with information being transmitted from one animal to a receiving animal which then replies with another signal to the first animal. However, both burst pulse signals and whistles have repeatedly been recorded from wild dolphins engaged in different types of social interactions (e.g., Herzing 1996) and are therefore believed to serve a communicative function. Also, the significant difference in spatial separation between dolphins emitting these two types of signals, which suggests that these signals have different functions which are related to their proximity to one another, is an indication that they were exchanged. And for burst pulse signals in particular, the relationship between timing and distance from each other is additional evidence that they were exchanged.

Another relevant question for future research is what the spatial and temporal context is of echolocating dolphins relative to each other. This question is more difficult to address, since echolocation click trains are not as short as burst pulse click trains and therefore often localize to different points over their course as an echolocating dolphin moves. Also, they easily overlap with echolocation trains from other dolphins. Overlapping echolocation click trains cannot be separated automatically as can be done for whistles by using cross-correlation techniques, but have to be analyzed manually click by click, which can be a tedious and time-consuming process. It includes ICI sequence comparison among the three recording channels for trains that are thought to have originated from a single dolphin, as well as in some cases localizing each separate click of the overlapping trains to determine whether they were emitted by the same dolphin or by a different dolphin than the clicks prior and subsequent to it. This analysis is still in progress.

Source levels and beam pattern of burst pulse clicks

The source levels found for burst pulse signals in this study are much lower than those reported by Lammers (2003), with mean values of 179 vs. 203 dB re 1 μ Pa, respectively. However, many burst pulse recordings contained at least some clicks that were saturated on one or several channels, meaning that the amplified incoming signals exceeded the \pm 5V input voltage of the A/D board. Since saturated signals were not used for SL calculations, this means that the average SL reported in this study is an underestimate, although it is unknown by how much. An obvious solution to this for future recordings is to lower the variable gain setting on the signal conditioning unit. However, in this study a trade-off had to be made concerning the amount of amplification. In order to test the hypothesis that whistling dolphins are spaced more widely apart than burst pulsing dolphins, a sufficient number of both whistles and burst pulse signals needed to be recorded. Since spinner dolphin whistles have a low reported average SL of

156 dB (Lammers 2003), the variable gain was set to 30 dB so that whistles would be picked up easily. In fact, a similar average SL for spinner dolphin whistles was found in this study (M. Lammers pers. comm.). However, this high gain setting also caused many high SL burst pulse signals to be saturated on at least one of the channels. Therefore, although the gain setting suited the purpose of comparing distances between whistling dolphins vs. between burst pulsing dolphins, the actual SL estimate for burst pulses reported by Lammers (2003) seems more accurate than the one provided here.

Additionally, this study appears to be the first one to report empirical evidence for burst pulse directionality. This finding does not come as a surprise when considering the signal emission properties of the dolphin forehead, as well as the transmission beam pattern for echolocation clicks measured from captive dolphins by Au (1993) and the evidence for whistle directionality in wild spinner dolphins reported by Lammers & Au (2003). The exact transmission properties for both a whistle and burst pulse beam pattern remain to be established, but the high average difference in SL of echolocation clicks received at channels A and C, as compared to the relatively low average SL difference for burst pulse clicks, might be an indication that burst pulse clicks are less directional than echolocation clicks.

However, this finding can be interpreted in various ways. If it is assumed that burst pulse clicks are not used for echolocation, then echolocation click trains are more likely to be directed at the array than burst pulses by dolphins investigating the array acoustically. Since the measured properties of the echolocation transmission beam include a larger drop-off in amplitude at the side of the beam compared to the front of the beam (Au 1993), one would expect that the difference in SL received at hydrophones A and C would be smaller for echolocation clicks (of which the front of the beam is aimed at the array) than for burst pulse clicks, assuming they had similar beamwidths. A larger percentage of echolocation clicks is expected to be aimed at the array and thus to hit the array with the front of the beam (with a relatively small drop-off in SL with angle), whereas burst pulse clicks are thought to hit the array more often in a random fashion with the side of the beam (with a larger drop-off in SL with angle), thus causing the SL difference between channels A and C to be smaller for echolocation clicks than for burst pulse clicks. However, this is contrary to the finding in this study, of which the data are still being analyzed, that the SL difference between channels A and C is larger for echolocation clicks than for burst pulse clicks, although not significantly at this point. There could be three different explanations for this: (1) a smaller fraction of the analyzed echolocation click trains were aimed at the array compared to burst pulse signals (which, although unexpected, is possible considering the small sample size for echolocation click SLs), (2) echolocating dolphins were closer to the array than burst pulsing dolphins so that their beam covered a smaller area at the point of intersection with the array, or (3) echolocation clicks have sharper transmission beams than burst pulse clicks. To exclude either one of these interpretations, the sample size of echolocation click train SLs is currently being expanded.

Finally, a post-hoc analysis showed a logarithmic relationship between burst pulse SL and range R from the dolphin to the array up to ranges of about 120 m. Au & Benoit-Bird (2003) found a similar relationship for echolocation clicks recorded from different species of wild dolphins at relatively small ranges (< 25 m) and argued that this provided evidence for an automatic gain control system in dolphin echolocation. According to Au & Benoit-Bird, dolphins emit higher SL echolocation clicks at larger ranges to partly account for an increased transmission loss of the signal and echo (mainly in the form of the 2-way spherical spreading loss, $40 \cdot \log R$). They suggested that the SL of a click is automatically coupled to its interclick interval (ICI) and that as a dolphin approaches a target on which it echolocates, the ICIs decrease as the 2-way transit time becomes smaller (with echolocation clicks generally having ICIs that are larger than the 2-way transit time by about 15 to 45 ms, Au 1993) and consequently the SLs of the emitted clicks decrease as well.

The similar logarithmic relationship between SL and R that was found in this study for burst pulse clicks can be interpreted in several ways. At first sight, one might suggest that burst pulse clicks serve an hitherto unknown echolocation function, besides their more well-known assumed communicative function. Another possibility might be that this logarithmic relationship between SL and R found for both echolocation and burst pulse clicks is a built-in characteristic of the transmission system of dolphin clicks, even if these are not used for the purpose of echolocation such as burst pulse clicks. However, great care needs to be taken when interpreting these results. As discussed before, high SL burst pulse clicks produced at close ranges were likely to be recorded as saturated signals and would therefore not have been selected for SL analysis. As a result, high burst pulse SL values are likely to be underrepresented at relatively close ranges. Similarly, at large ranges low SL values might be underrepresented, because after the transmission loss only high SL values might be received by the hydrophones at sufficient levels to be detected. This seems less of a concern, however, because plotting the "plain" Sound Pressure Levels, which have not yet been corrected for transmission loss, as a function of R (not shown here) resulted in an approximately straight line. This suggests that the received SPL does not necessarily decline with increasing R. In any case, one should keep in mind that the found logarithmic relationship between burst pulse SL and range R might be an artifact rather than a real effect.

However, if it is a real effect this might have important implications for the function of burst pulse signals or for the production mechanism of both echolocation and burst pulse clicks. One might argue that if a mechanism of automatic gain control would apply to burst pulse clicks as well, then burst pulse clicks might also be used for echolocation (even if only a secondary function). Alternatively, it could be argued that this effect is simply a by-product of the production mechanism of both echolocation and burst pulse clicks, which is helpful for the function of echolocation clicks but not so much for that of burst pulse clicks. Whichever is the case, if the hypothesis of Au & Benoit-Bird is correct (i.e., the SL of echolocation clicks is automatically coupled to ICI) and would apply to the production of burst pulse clicks as well, then one might also expect to find a relationship between burst pulse ICI and SL. Although Lammers (2003) found only a weak positive relationship between ICI and SL for echolocation and burst pulse clicks of wild spinner dolphins ($R^2 = 0.20$), a rather crude measure of SL estimation was used in that study. The more accurate method of range and SL estimation in this study might result in better correlation between ICI and SL. Furthermore, this relationship between ICI and SL is expected to be logarithmic rather than linear, since a logarithmic relationship between SL and range R was found by Au & Benoit-Bird (2003), whereas Schotten et al. (2004) found that ICI increased linearly with R for wild spinner dolphin echolocation clicks.

The analysis of burst pulse ICIs, for which a separate Matlab program is used to extract the ICIs from the recordings, is currently under way. Besides a possible relationship between ICI and SL, it will also be investigated whether there is a relationship between ICI and a measure of "beamwidth" of the clicks (the SL difference between channels A and C), i.e. whether repetition rate affects the transmission beamwidth of clicks. For example, one might expect to find that the closer an echolocating dolphin is to a target, and the smaller therefore its ICIs and click SLs are, the wider its click beamwidth becomes. If this effect would extend to the production of burst pulse clicks, it would explain why burst pulse clicks appear to have a wider beamwidth than echolocation clicks.

Other ways to substantiate whether burst pulse click SL and beamwidth are coupled to ICI, is to use a self-contained 4-channel broadband acoustic/video recording system, which can be taken underwater while swimming to record and localize dolphins at close ranges, while simultaneously filming their behavior and head scanning movements. This needs to be a recording system with a wide dynamic range, to avoid the above mentioned issues of signal saturation on the one hand and the failure to detect weak signals on the other hand. Its construction is currently being completed for fieldwork in the near future, which should provide opportunities to answer some of the questions raised in this study. Finally, some occasional evidence for the phenomenon of "chorusing" dolphins was found, where two or more dolphins appeared to be producing burst pulse signals simultaneously and in synchrony. This is another finding which will only be possible to substantiate by using simultaneous broadband acoustic and video recordings.

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Conclusions

The main hypothesis of this study, i.e. that whistling dolphins are spaced more widely apart than burst pulsing dolphins because of a possible group coordinative function of whistles, was supported by the data that were collected from the field. Additionally, burst pulsing dolphins that were closer to each other were found to produce burst pulse signals that followed each other more quickly in time, a relationship which could point to communicative exchanges of burst pulses and which was not found for whistles. Also, burst pulses were found to be directional in nature, as was expected, with indications that burst pulse clicks might have wider beam patterns than echolocation clicks. Finally, a logarithmic relationship was found between burst pulse source levels and the ranges at which they were produced. This finding could be an artifact, but if substantiated in future studies could have implications regarding the assumed function of burst pulse signals.

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APPENDIX

The localization algorithm for a 3-hydrophone line array that was used in this study was developed by Lammers & Au (2003). This method enables one to localize signaling dolphins in a 2-D plane with a left-right ambiguity, by using the differences in time of signal arrival at the 3 hydrophones. The middle hydrophone h_1 (hydrophone B in Fig. 1 of Material & Methods) is assumed to be at the origin of an x,y coordinate plane (Fig. A-1). By using the relationship t = d/c, where t is the time for an acoustic signal of sound speed c to travel over a distance d, in combination with the Pythagorean theorem, the distance d_1 between the sound source and hydrophone h_1 can be expressed as

(1)
$$s_x^2 + s_y^2 = c^2 t_1^2$$

where s_x and s_y are the x and y-coordinates of the sound source and c = 1,533 m/s. Similarly, the distances d_2 and d_3 between the sound source and hydrophones h_2 and h_3 , respectively, can be expressed as

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

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

where $x_2 = -8$, $x_3 = 8$, $t_{21} = t_2 - t_1$ is the difference in the time of arrival of the sound between hydrophones h_2 and h_1 , and $t_{31} = t_3 - t_1$ is the time of arrival difference between hydrophones h_3 and h_1 . Using this set of three equations, the three unknown variables t_1 (the time it took the signal to travel to h_1), s_x and s_y can be algebraically solved for:

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

(5)
$$s_{x} = \frac{c^{2}(t_{21}t_{31}^{2} - t_{21}^{2}t_{31}) + (x_{2}^{2}t_{31} - x_{3}^{2}t_{21})}{2(x_{2}t_{31} - x_{3}t_{21})}$$

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

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Figure A-1. Geometry of a 3-hydrophone line array for localizing a sound source at position s(x,y). h₁, h₂, and h₃ correspond to hydrophones B, A, and C, respectively, in Fig. 1.