

# Estimated communication range and energetic cost of bottlenose dolphin whistles in a tropical habitat

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(Received 4 May 2011; revised 26 September 2011; accepted 19 July 2011)

Bottlenose dolphins (*Tursiops* sp.) depend on frequency-modulated whistles for many aspects of their social behavior, including group cohesion and recognition of familiar individuals. Vocalization amplitude and frequency influences communication range and may be shaped by many ecological and physiological factors including energetic costs. Here, a calibrated GPS-synchronized hydrophone array was used to record the whistles of bottlenose dolphins in a tropical shallow-water environment with high ambient noise levels. Acoustic localization techniques were used to estimate the source levels and energy content of individual whistles. Bottlenose dolphins produced whistles with mean source levels of  $146.7 \pm 6.2$  dB re.  $1 \mu\text{Pa}(\text{RMS})$ . These were lower than source levels estimated for a population inhabiting the quieter Moray Firth, indicating that dolphins do not necessarily compensate for the high noise levels found in noisy tropical habitats by increasing their source level. Combined with measured transmission loss and noise levels, these source levels provided estimated median communication ranges of 750 m and maximum communication ranges up to 5740 m. Whistles contained less than 17 mJ of acoustic energy, showing that the energetic cost of whistling is small compared to the high metabolic rate of these aquatic mammals, and unlikely to limit the vocal activity of toothed whales. © 2012 Acoustical Society of America.

[DOI: 10.1121/1.3662067]

PACS number(s): 43.80.Ka, 43.80.Lb, 43.60.Jn [WWA]

Pages: 582–592

## I. INTRODUCTION

Group living offers many evolutionary advantages that may include various strategies for decreasing predation, increasing foraging efficiency, or evolving cooperative breeding or nursing systems (Norris and Schilt, 1988; Krebs and Davies, 1993; Gowans *et al.*, 2007). Social groups are common in many animal species, ranging from small, single-celled algae over eusocial insects, to large African elephants (Hamilton, 1964; Anderson and McShea, 2001). One of the key requisites of group living is the ability to locate and remain in contact with other individuals, leading to the evolution of signaling mechanisms to facilitate these tasks (Da Cunha and Byrne, 2009). Acoustic signals are well suited for rapid, long-range communication in many habitats and are consequently used to mediate group cohesion in

many insect, bird and mammalian species (e.g., Brenowitz, 1982; Boinski, 1993; Cortopassi and Bradbury, 2006). This is especially true for mammals in aquatic habitats where acoustic signals propagate faster and attenuate less rapidly than in air (Urlick, 1983; Janik, 2005). Cetaceans, for example, rely heavily on acoustic signals for communicating with conspecifics and, in the case of toothed whales, for actively sensing their environment using highly directional echolocation signals (Tyack, 2000).

The effective range over which a communication signal can be detected by a conspecific is termed the active space (Marten and Marler, 1977). This communication range can play an important role in shaping the structure and dispersal of social groups as well as the vocal behavior of individuals. Low-frequency acoustic signals of animals such as elephants and baleen whales are likely to be detected over very long distances of tens to thousands of kilometers (Payne and Webb, 1971; Garstang *et al.*, 1995), and such long-range communication may result in very extensive social networks

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as seen in African savannah elephants (McComb *et al.*, 2000; McComb *et al.*, 2003). In contrast, Asian corn borer moths produce very silent acoustic signals for courting females at a distance of 2 cm in order to prevent eavesdropping by conspecifics or detection by predators (Nakano *et al.*, 2009). Such large differences in active spaces are determined by a variety of physical, behavioral and ecological factors. In isolation, the benefits of social communication, such as finding a mate or maintaining cohesion within a social group, will select for higher amplitude signals as this will increase the chance of detecting the signal in ambient noise and consequently increase the active space of the signal. On the other hand, the potential energetic costs of generating the signal (Prestwich *et al.*, 1989) as well as the increased risk of being detected by predators (Ryan *et al.*, 1982; Deecke *et al.*, 2002; Morisaka and Connor, 2007; Nakano *et al.*, 2009), prey (Deecke *et al.*, 2005), or social competitors (McGregor, 2005) will select for lower amplitude and consequently a smaller active space.

The bottlenose dolphin (*Tursiops* sp.) is one of the most studied toothed whale species (Connor *et al.*, 2000). Studies in Sarasota Bay (Florida) and Shark Bay (West Australia) have shown that these animals are organized in fission-fusion societies where animals leave and rejoin associates frequently (Wells and Scott, 1999; Connor *et al.*, 2000). Interactions between groups and between individuals are primarily mediated by acoustic signals (Herzing, 2000; Tyack, 2000; Watwood *et al.*, 2004) where individually specific signatures of whistles (Sayigh *et al.*, 1999; Janik *et al.*, 2006) may facilitate maintenance of long-term social bonds despite periodic separations (Connor *et al.*, 1992; Tyack, 2008a). These whistles are reported to have a large active space that may facilitate long-range group cohesion (Janik and Slater, 1998; Janik, 2000).

The active space of whistles will determine the maximum separation distances over which individuals may still remain in acoustic contact as well as the maximum distances over which conspecifics may eavesdrop on vocal interactions (Janik, 2000). Estimating the range over which conspecifics can detect or discriminate acoustic signals requires either careful playback experiments (McComb *et al.*, 2003) or modeling (Brenowitz, 1982). While playback experiments may reveal biologically relevant communication ranges (McComb *et al.*, 2003), they necessitate clearly quantifiable reactions to the playbacks. Alternatively, the active space can be estimated using knowledge on the psychophysical detection and discrimination of calls in noise (Brumm and Slabbekoorn, 2005), as well as careful measurements of signal source properties, sound propagation (Marten and Marler, 1977) and background noise levels (Brenowitz, 1982).

A signal broadcast into the environment with a given source level (SL) will attenuate gradually when propagating through the environment and eventually become masked by the background noise. At any given distance from the source, the received level (RL) of the signal can be estimated by the signal SL minus the transmission loss (TL) from source to receiver. A conspecific is expected to detect this signal if the received sound pressure level exceeds the psychophysical detection threshold (DT) of the animal on a statistical basis (Eq. (1)) (all values in decibel units):

$$DT \leq SL - TL. \quad (1)$$

For a pure tone with a received level exceeding the hearing threshold of young individuals, the detection threshold can be estimated as the sum of the spectral noise level ( $N_0$ ) and the critical ratio (CR). The transmission loss is the sum of spreading loss and frequency-dependent absorption, both increasing as a function of range (R), so that Eq. (1) can be rewritten as:

$$N_0 + CR \leq SL - (k \times \log_{10}(R) + \alpha R). \quad (2)$$

The spreading loss constant  $k$  depends on habitat and bathymetry, but normally it ranges from spherical spreading loss ( $k=20$ ) in deep water, to cylindrical spreading loss ( $k=10$ ) in very shallow water for continuous signals (Urlick, 1983).

The first study to investigate the range of *Tursiops* whistles estimated an active space of up to 25 km in calm weather (sea state 0) in the Moray Firth, Scotland (Janik, 2000). This estimate was based on measurements of whistle source levels combined with assumptions on shallow water sound propagation (Marsh and Schulkin, 1962) and noise level profiles for deep water (Knudsen *et al.*, 1948). In contrast, Quintana-Rizzo and colleagues (2006) reported much smaller estimates of communication ranges on the order of 500 m in a shallow habitat with high noise levels, but with the potential for long-range (>20 km) signal transmission through sound channels (Quintana-Rizzo *et al.*, 2006). However, while Quintana-Rizzo and colleagues measured both habitat-specific sound propagation and noise levels dominated by snapping shrimp, they could not address whether the resident dolphin populations had adapted to these higher noise levels by increasing whistle source levels as seen in non-human primates, birds, and killer whales (Sinnott *et al.*, 1975; Brumm, 2004; Holt *et al.*, 2009). Given that most research on the social organization of bottlenose dolphins comes from tropical, shallow habitats such as Shark Bay and Sarasota Bay (the field site studied by Quintana-Rizzo and colleagues), a detailed understanding of communication ranges in these habitats may help uncover the spatial limits of contact between individuals and further advance our understanding of the evolutionary factors shaping different levels of sociality in odontocetes. However, to do so reliably, it is important to measure the whistle source levels, ambient noise levels and transmission loss for the habitat in question.

In this study, we attempt to meet these requirements by integrating measurements of environmental background noise levels and transmission loss with estimates of source parameters of bottlenose dolphins (*Tursiops* sp.) in a shallow-water tropical habitat to test whether tropical bottlenose dolphins use whistles of higher source level than populations living in more temperate, and less noisy, habitats. We estimate the active space and metabolic energy cost for *Tursiops* whistles and discuss implications for communication range and acoustic behavior in this habitat.

## II. MATERIALS AND METHODS

### A. Recording habitat

The study was conducted in the shallow waters of Koombana Bay, Bunbury, Western Australia (33°17'S, 115°39'E) in

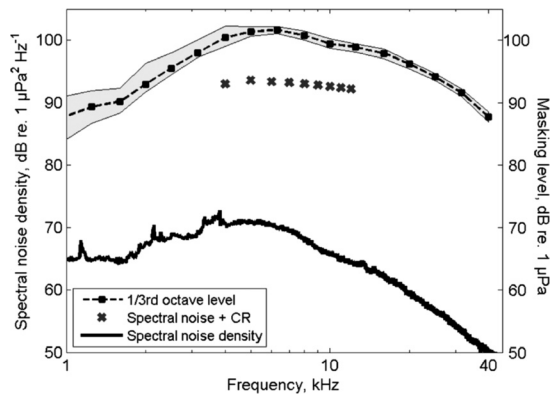


FIG. 1. Background noise in the study area of Bunbury Bay measured as spectral noise levels (black, solid line) and one-third octave noise levels (squares)  $\pm 95\%$  confidence intervals (grey area). Also included is the effective masking noise (crosses) given by the sum of spectral noise and bottlenose dolphin critical ratios (CR) (from Johnson *et al.*, 1968).

February 2007. A population of coastal bottlenose dolphins (*Tursiops* sp.), possibly *T. aduncus* or a species of South Australian bottlenose dolphins (Möller *et al.*, 2008) numbering a few hundred individuals inhabits the nearby coastline and frequently forages in the recording area. Background noise levels in this subtropical habitat are high (Fig. 1), generally dominated by the sounds of snapping shrimp, but also influenced by the close proximity of the coast and a busy harbor (Jensen *et al.*, 2009b).

## B. Sound propagation measurements

Sound transmission experiments were conducted using two small aluminium-hulled vessels as transmission and reception platforms. Sound propagation was investigated for a nearly homogenous water depth of 5–7 m along a transect line running approximately 270 m parallel to the coast. Along this transect, the bottom consisted primarily of sand with occasional patches of sea grass. Transmission source levels were  $<162$  dB re. 1  $\mu\text{Pa}$  (RMS), less than the source levels of dolphin whistles reported previously (Janik, 2000). To minimize the risk that the playback signals significantly affected any nearby dolphins, one observer on each vessel continuously scanned the area for dolphins throughout the experiment so that transmissions could be halted if dolphins were closer than 100 m.

One anchored vessel deployed a recording array of three calibrated B&K 8101 hydrophones with a sensitivity of  $-184$  dB re 1 V/ $\mu\text{Pa} \pm 2$  dB from 0.1 to 80 kHz. The three hydrophones were suspended at depths of 0.5 m, 3 m and 5.5 m between a surface buoy and a 0.5 kg lead weight (water depth 6 m). The hydrophones were connected through custom-built low-noise amplifiers (20–40 dB gain, 4-pole bandpass filter,  $-3$  dB points: 100 Hz to 50 kHz) to a four-channel, 12-bit analogue-to-digital converter (ADlink Technology, Chungo City, Taiwan), digitizing each channel with a sample rate of 150 kHz and writing data to a laptop computer via a PCMCIA interface (Magma, San Diego, CA, USA).

A second vessel deployed an underwater speaker and power amplifier set (Lubell 3300, Lubell Labs, Columbus, OH, USA) [300 Hz to 20 kHz,  $\pm 4$  dB], connected to a stereo

compact-flash playback device (M-Audio Microtrack 24/96: M-Audio, Irwindale, CA, USA) for sound transmission. The transmitting vessel was anchored at distances of 6 m, 20 m, 50 m, 100 m, and 250 m along the transect line from the recording array, measured with a measuring rope (6 m and 20 m) or a laser rangefinder ( $\pm 1$  m accuracy). At each location, transmissions were conducted at each of three depths: At the surface (0.5 m depth), in the middle of the water column (2.5 m–3.5 m depth), and near the bottom (0.5 m from the bottom), mirroring the setup of the recording array. Each transmission consisted of an upsweep (sweeping from 1–21 kHz over a period of 0.5 s duration) followed by individual pure-tone signals (0.5 s duration) spanning the frequencies from 1–21 kHz in 2 kHz steps. Transmissions were repeated ten times at each location and at each transmitting depth.

### 1. Pure-tone TL

Each 0.5 s tone was extracted and windowed with a Tukey window (length 75 000 samples, total 128 points tapering). To obtain the power spectrum, a Discrete Fourier Transform was performed (DFT size 75 000, spectral resolution 2 Hz). The received level of the test tone was found as the spectral sound pressure level at the test frequency (dB re 1  $\mu\text{Pa}$  RMS). Finally, transmission loss was calculated as the slope of a linear regression of received level against log-transformed distance using the ten transmissions.

### 2. Sweep TL

Each 0.5 s upsweep was extracted and filtered with a matched filter (400 Hz bandwidth, centered on the instantaneous frequency of the upsweep) to maximize signal-to-noise ratio (SNR). Subsequently, a power spectrum (DFT size 75 000, spectral resolution 2 Hz) was derived and averaged over ten repeated transmissions. The averaged power spectrum was down-sampled with a factor of 50, for a final spectral resolution of 100 Hz, and corrected for amplification and hydrophone sensitivity. Transmission loss was then calculated as the difference between the averaged power spectra for the 250 m and the 20 m transmission. To get the transmission loss coefficient  $k$ , we then corrected for the difference between the actual range increase (a factor 10.25) and a ten-fold range increase.

### 3. Whistle recording setup

Bottlenose dolphin whistles were recorded using a dispersed array of four GPS synchronized hydrophones (Møhl *et al.*, 2001). The recording array consisted of four small anchored vessels, each deploying a calibrated B&K 8101 hydrophone with a recording sensitivity of  $-184$  dB re 1 V/ $\mu\text{Pa}$  at a recording depth of 3 m which was approximately in the middle of the water column. Each hydrophone was connected to a custom made conditioning box (20–40 dB gain, 4-pole bandpass filter,  $-3$  dB points: 100 Hz to 50 kHz) and recorded with a sampling rate of 96 kHz on one channel of a 16 bit stereo sigma-delta recorder (M-Audio Microtrack 24/96: M-Audio, Irwindale, CA, USA). Recording stations were GPS synchronized using the methodology

of Møhl *et al.* (2001): A GPS antenna and receiver (Garmin GPS25 LV, 12-channel receiver) on each vessel received GPS position and GPS time continuously. The GPS unit was connected to a custom built frequency-shift keying device (Møhl *et al.*, 2001), converting the serial GPS information into a tone signal where information was coded in binary form as a series of 17 kHz (ones) and 20 kHz (zeroes) components. The GPS unit emitted a 20 ms timing pulse each second, synchronized to the atomic clocks of the satellites, that was encoded by the frequency-shift keying device as an abrupt decrease in signal amplitude. The final frequency-encoded signal was recorded on the second channel of the sound recorder so that sound and GPS information was sampled simultaneously and so that sound recordings from all platforms could be synchronized using the GPS pulse to within 50  $\mu$ s.

### C. Acoustic localization

Recordings were examined in custom written MATLAB 6.5 (MathWorks) software. Whistles were identified in synchronized spectrograms (FFT size 2048, 75% overlap) of all four recording stations and stored for subsequent analysis. Receiver locations were extracted from the GPS information and converted from spherical WGS84 data into Cartesian coordinates. A source location estimate for each whistle was derived using time-of-arrival differences for a two-dimensional array of receivers (Møhl *et al.*, 2001; Wahlberg *et al.*, 2001).

To improve the localization accuracy of whistles recorded at a low SNR on some receivers, time-of-arrival differences (Fig. 2) were found by cross-correlating each synchronized recording with a replica of the whistle constructed by filtering the whistle with best SNR with a frequency-modulated filter tracing the whistle fundamental frequency contour (Beedholm *et al.* in prep). This step was used to remove unnecessary noise as well as to remove broadband dolphin clicks that correlate well between channels and return an erroneous time difference for the whistle in question.

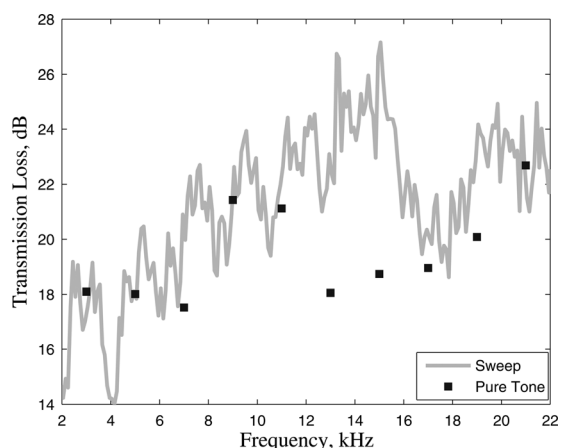


FIG. 2. Transmission loss coefficients estimated using sweeps (grey line) or pure tone (black squares) playbacks over a range of 250 m. The dip in transmission loss at 4 kHz is due to low S/N ratio of the playbacks at this particular frequency.

For each pair of receivers, a hyperboloid curve of possible locations of the source can be constructed from the time-of-arrival difference, sound speed and receiver locations (Spiesberger and Fristrup, 1990). Localization was constrained to two dimensions because of the shallow depth compared to the large aperture of the recording array. With four receivers, three independent hyperbola equations can be derived, yielding an overdetermined 2D localization system (Wahlberg *et al.*, 2001; Madsen and Wahlberg, 2007). The hyperbola equations were examined graphically and the source position was estimated as the mean intersection between hyperbolas (Fig. 2). In cases where the array geometry was quasi-linear, hyperbolas might intersect once on each side of the array and the location of the source would be ambiguous. In such cases, ambiguity was solved by selecting the set of intersections with the smallest least-squared distance between them, and locations of dolphins confirmed by examining records of visual observations taken from the recording vessels.

### D. Derivation of whistle source parameters

Whistles were subdivided into three groups based on their fundamental time-frequency contour (following Janik *et al.*, 1994). A fundamental frequency contour increasing throughout most of the whistle was classified as a rise or up-sweep whistle. A fundamental frequency contour with small variations in frequency content was classified as a flat or constant-frequency (CF) whistle. An ascending/descending fundamental frequency contour, often with several repetitions, was classified as a sine or loop whistle. Temporal gaps between repetitions of the same whistle may be important for the information conveyed between dolphins (Esch *et al.*, 2009). However, since this study focused on the source level of whistles rather than their information content, similar but unconnected whistles were regarded as discrete entities for the analysis.

Whistles with a successful source location estimate were analyzed for source parameters using one recording station. The localization accuracy varied due to the changing spatial relationship between the four receivers. To minimize the influence of localization errors on source level estimates, if the sound source was localized within 30 m of the recording station with the highest SNR, a more distant recording station was used for source level estimates.

To maximize the SNR, whistles were filtered with a 6-pole bandpass filter with corner frequencies adjusted to the minimum and maximum fundamental frequencies estimated from the whistle model. A root-mean-square (RMS) noise measure was derived from a 0.1s window following each whistle, and the whistle duration was then defined as the length of the smallest window containing 95% of the total signal energy after subtracting the noise power (Madsen and Wahlberg, 2007). The SNR was calculated as the difference in RMS signal amplitude and RMS noise amplitude on a dB scale, and signals with less than 6 dB SNR were removed from further analysis.

A spectrogram was computed with 5 ms Hann windows (480 samples, zero-padded to 4096 samples for FFT

computation) with 50% overlap for an interpolated spectral resolution of 24 Hz and a temporal resolution of 2.5 ms. A supervised trace of the fundamental frequency contour (similar to Deecke *et al.*, 1999) was used to derive the fundamental minimum ( $F_{\min}$ ), mean ( $F_{\text{mean}}$ ) and maximum ( $F_{\max}$ ) frequency over the 95% energy window. Power spectra within the 95% energy window were summed to estimate the spectral power distribution across the entire whistle according to the Welch method (Welch, 1967). The peak frequency,  $F_p$  (defined as the frequency with highest spectral power) and the centroid frequency,  $F_c$ , (defined as the frequency separating the power spectrum into two halves with the same amount of total energy) were computed from the Welch power spectrum (Au, 1993).

### 1. Source levels

Two amplitude measures were extracted: First, the average sound pressure was calculated as the RMS amplitude over the 95% energy window. Second, the highest sound pressure level was calculated as the maximum value of a running-average RMS sound pressure level with a duration of 200 ms (95% overlap), corresponding to the pure-tone integration time of dolphins around the frequencies measured here (Johnson, 1968b). Absolute RLs were then computed from the calibrated recording chain clip level. Finally, source levels were estimated from received levels by compensating for the transmission loss (TL) using Eq. (1):

$$SL = RL + TL = RL + k \times \log_{10}(R), \quad (3)$$

where  $k$  is the frequency-dependent transmission loss coefficient extrapolated from pure tone TL estimates in Fig. 2 (18 log  $R$ ) using the derived centroid frequency of each whistle,  $R$  is the range between source and receiver in meters, and all sound level values are in dB re. 1  $\mu\text{Pa}$  (RMS).

### 2. Active space

Communication ranges were modeled based on the measured source levels, estimated masking noise levels based on the measured background noise, and the measured habitat-specific transmission loss. When detecting a pure tone in noise, the masking noise depends on the spectral noise level as well as the bandwidth around the frequency of the tone over which noise is integrated, called the critical bandwidth. To estimate the masking noise level, Fletcher (1940) defined the critical ratio (CR) as the ratio of tone power to noise power spectral density at threshold (Fletcher, 1940). That means that a tone in white noise would be correctly detected 50% of the time if the received level equaled the sum of noise spectral density and the critical ratio for the frequency in question. The detection levels or masking levels used in this study (Fig. 1) were therefore calculated as spectral levels of background noise added to the auditory critical ratios measured for bottlenose dolphins (Johnson, 1968a). The appropriate detection level for a given whistle was derived by interpolating estimated masking levels (Fig. 1) to the centroid frequency of each whistle. Detection levels estimated from the spectral noise levels and critical ratios were

somewhat below the 1/3rd octave noise levels that are often used to estimate communication distances (Fig. 1).

### 3. Energy content

The average source level energy flux density ( $SL_{95\%EFD}$ : dB re. 1  $\mu\text{Pa}^2\text{s}$ ) was calculated for each whistle as the sum of the squared instantaneous sound pressure integrated over the 95% energy window (Madsen *et al.*, 2006; Madsen and Wahlberg, 2007). The total radiated acoustic energy ( $E_{95\%}$ : J) was then calculated as the energy flux density (on a linear scale) divided by the acoustic impedance of seawater, and multiplied by the surface area of a sphere with a radius of 1 m (reference distance for source level) (Fig. 4). This assumes that whistles are omnidirectional, a fair approximation for the fundamental frequency range studied here (Lammers and Au, 2003).

The vocal efficiency is defined as the ratio of the produced acoustic energy to the required metabolic ratio for a sound production system. The vocal efficiency of toothed whales is currently unknown, both for the production of bio-sonar clicks and tonal communication sounds. In frogs, vocal efficiencies vary between 0.8%–5% (Prestwich *et al.*, 1989). To estimate metabolic energy costs, we therefore assumed a conservative 1% vocal efficiency for a toothed whale well-adapted to underwater sound production (Cranford *et al.*, 1996).

## III. RESULTS

### A. Sound propagation

Transmissions conducted with the transducer and receiver located at different depths yielded very similar average transmission loss coefficients. TL estimates from sweeps and pure tones corresponded well with each other (Fig. 2) up to 11 kHz, but deviated from each other at higher frequencies. This high-frequency deviation may be caused by the different approaches to estimating transmission loss coefficients. For sweeps, the transmission loss coefficient was based on a comparison of sound levels at 250 m with those at 20 m, placing more emphasis on the longer distance transmissions (that suffer more frequency-dependent absorption) than the regression of sound levels against distance that was used for calculating pure-tone transmission loss. However, the transmission loss coefficient with both receiver and transducer located in the middle of the water column was estimated at 18 dB per 10-fold increase in distance for frequencies equal to and below 8 kHz for both pure tone and sweep transmissions (Fig. 2). Since this covered most of the energy contained in the whistles (Table I), we used this transmission loss coefficient for estimating active space.

### B. Whistles

A total of 180 whistles (consisting of 134 rise, 24 flat, and 22 sine whistles) were successfully localized (Fig. 3) with a sufficient SNR for analysis. Whistles covered a frequency range from a minimum frequency of  $5.2 \pm 1.0$  kHz to a maximum frequency of  $9.8 \pm 2.1$  kHz, with centroid frequencies around  $6.7 \pm 1.1$  kHz. No significant differences in source

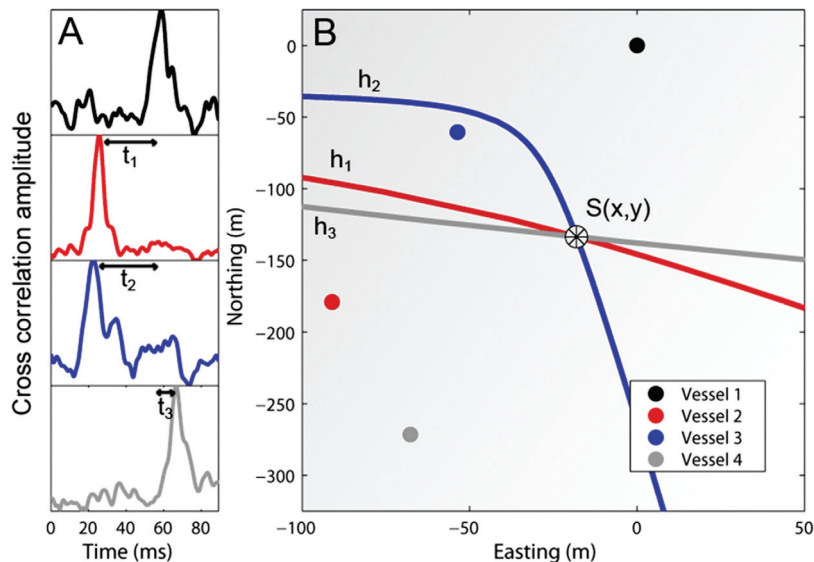


FIG. 3. Acoustic localization of bottlenose dolphin whistle. A: Cross correlations of signals from four GPS synchronized recorders with time-of-arrival differences ( $t_1$ – $t_3$ ) given by the time difference of cross correlation peaks. B: Two-dimensional localization plot relative to the northermost receiver (note the different scaling in the two axes). Each time-of-arrival difference gives rise to a hyperbola ( $h_1$ – $h_3$ ), and the source location  $S$  is estimated as the mean hyperbola intersection.

levels were found between the three different classes of whistles (Fig. 5: Kruskal-Wallis:  $p=0.73$ ) and the three classes were pooled accordingly. Results of the pooled whistle analyses are summarized in Table I. RMS source levels were measured to be  $146.7 \pm 6.2$  (max 164) dB re.  $1 \mu\text{Pa}$  using the 95% energy RMS measure and at  $147.6 \pm 6.4$  dB re.  $1 \mu\text{Pa}$  when evaluated over a 200 ms time window (mean difference  $+0.9$  dB, greatest difference  $+4.1$  dB). These source levels were significantly lower than the mean found for bottlenose dolphin whistles in the Moray Firth (Wilcoxon signed-rank test:  $p < 0.0001$ ). Since RMS measures depend on the window length (Madsen *et al.*, 2006), comparisons between studies are hampered somewhat by the use of different windows. Source levels for toothed whale whistles have been quantified using windows covering 100 ms (Rasmussen *et al.*, 2006) to 125 ms (Janik, 2000) and in some cases using undefined windows presumably covering the length of the signal (Lammers and Au, 2003; Miller, 2006). Window lengths smaller than the pure-tone integration time, such as the 125 ms of Janik (2000) (corresponding to the integration time of a tone around 20 kHz: Johnson, 1968b), may also lead to overestimates of source levels that are not representative for how the animals detect whistles in noise. Furthermore, small windows will also be more sensitive to overlying transients and to sporadic amplitude variations caused by multipath propagation. While there are only small differences between source levels found using a well-defined 95% energy

window and a 200 ms integration window, we did not test shorter window lengths and it is plausible that at least part of the explanation for the higher source levels of Janik (2000) may relate to using very short windows.

### C. Active space

The active space of each whistle was estimated under optimal noise conditions, with noise levels recorded in Sea State 0 and no nearby vessels (Jensen *et al.*, 2009b). Active space estimates based on the 95% energy RMS source levels were highly variable, with 95% of all whistles detectable at a range of 220 m, median communication ranges of 740 m, and 5% of whistles detectable at a range of 3240 m. The highest source level whistle had a modeled communication range of 5740 m.

### D. Energy

As a consequence of the relatively low SL, both acoustic power and total energy content (Fig. 4) was found to be very low. Mean backcalculated  $SL_{95\% \text{ EFD}}$  were at  $142.0 \pm 6.6$  dB re.  $1 \mu\text{Pa}^2\text{s}$ , and 95% of whistles were found to have  $SL_{95\% \text{ EFD}}$

TABLE I. Source parameters of bottlenose dolphin (*Tursiops* sp.) whistles recorded in Bunbury Bay, West Australia.

Parameter	Mean $\pm$ std	[ $P_5$ : $P_{95}$ ]
$F_{\min}$ (kHz)	$5.2 \pm 1.0$	[4.4:6.5]
$F_{\text{centroid}}$ (kHz)	$6.7 \pm 1.1$	[5.4:8.1]
$F_{\max}$ (kHz)	$9.8 \pm 2.1$	[5.8:12.8]
$SL_{200\text{ms}}$ (dB re. $1 \mu\text{Pa}$ )	$147.6 \pm 6.4$	[137.9:159.0]
$SL_{95\% \text{ RMS}}$ (dB re. $1 \mu\text{Pa}$ )	$146.7 \pm 6.2$	[136.8:158.0]
$SL_{95\% \text{ EFD}}$ (dB re. $1 \mu\text{Pa}^2\text{s}$ )	$142.0 \pm 6.6$	[131.4:153.3]
Active Space (m)	$10^{(2.9 \pm 0.34)}$	[218:3244]
$E_{95\%}$ (J)	$10^{(-2.9 \pm 0.66)}$	[0.0001:0.017]
N	180	

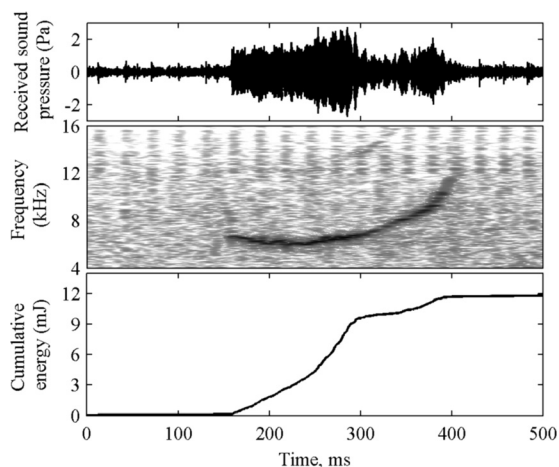


FIG. 4. Whistle waveform (top), spectrogram (sample rate 48 kHz, FFT size 2048 samples, 95% overlap) (middle) and back-calculated cumulative acoustic energy radiated from the source (bottom).

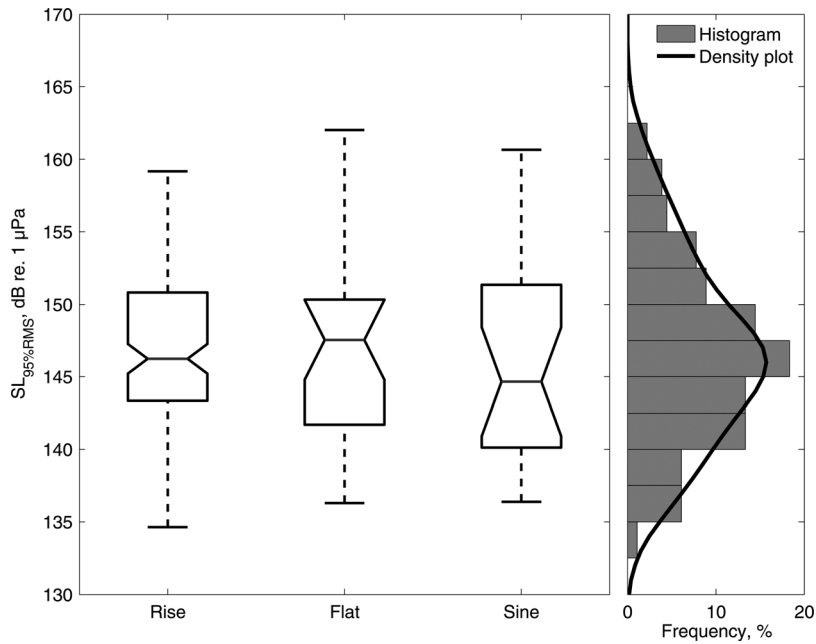


FIG. 5. (a) Source levels of whistles classified as either rise (upsweep), flat (constant frequency) or sine (loop) whistles. Lower and upper bounds on box indicate quartiles, and middle line and notch indicates the median and 95% confidence interval of the median. Whiskers show furthest point within 1.5 x interquartile range. No points lie outside the whiskers. (b) Histogram and smoothed density plot (2.5 dB Gaussian Kernel) of all whistles (N=180).

less than 153.3 dB re. 1  $\mu\text{Pa}^2\text{s}$ . Assuming an omnidirectional sound radiation for whistles, the total radiated acoustic energy was calculated to be very low, with a median of 1.1 mJ of energy contained in whistles, and 95 percent of all whistles containing less than 17 mJ of acoustic energy.

Assuming a vocal efficiency of 1%, we estimate that less than 1.7 J of metabolic energy is invested in the production of 95% of the whistles recorded here. Published estimates of the resting oxygen consumption of adult bottlenose dolphins are around 5 mL $\text{O}_2$  kg $^{-1}\text{min}^{-1}$  (Williams *et al.*, 1993), corresponding to a resting metabolic rate of approximately 104 J kg $^{-1}\text{min}^{-1}$ . A 180-kg adult female in Shark Bay (Reeves *et al.*, 2002) whistling continuously (60 whistles per minute) at the highest outputs measured here (1.7 J per whistle) would therefore increase its resting metabolic rate with 0.5% (Table II). For a 15-kg newborn calf in Shark Bay (Reeves *et al.*, 2002) with a mass-specific metabolic rate corrected for size (approx. 6x higher than the mass-specific metabolic rate of an adult when scaled with  $M^{0.75}$ ), continuous whistling at the levels reported here for adults would still only lead to a 1% increase in metabolic rate (Table II).

TABLE II. Estimated costs of whistling for Bunbury Bay mother and newborn calf.

	Mass-specific metabolic rate <sup>a</sup> J kg $^{-1}$ min $^{-1}$	Weight <sup>b</sup> kg	Resting metabolic rate J min $^{-1}$	Near-constant whistling <sup>c</sup> J min $^{-1}$	Cost
Adult	104	180	18720	18822	+0.54%
Calf	670	15	10058	10160	+1.01%

<sup>a</sup>Calculated from Williams *et al.*, 1993 for adult dolphin. For calf, adult resting metabolic rate was scaled to the different body mass (M) according to a scaling coefficient of  $M^{0.75}$ .

<sup>b</sup>Reeves *et al.*, 2002.

<sup>c</sup>Assuming whistle rate of 60 whistles per minute with a metabolic energy cost of 1.7 J per whistle derived from the radiated acoustic energy exceeding 95% of whistles recorded here, divided by an assumed acoustic efficiency of a conservative 1%.

#### IV. DISCUSSION

All animals communicating acoustically face the challenge of getting a signal through to the receiver in a dynamic acoustic environment with fluctuating ambient noise levels. The severity of these challenges are likely to increase with the rising noise levels caused by anthropogenic activities, especially in urban areas and in the ocean (Tyack, 2008b). One way of dealing with masking effects caused by increasing ambient noise is to adjust the amplitude of calls. A short-term increase in call intensity during periods of higher noise levels has been observed across a wide range of animals. This includes many avian and primate species (Sinnott *et al.*, 1975; Brumm and Slabbekoom, 2005), but also cetaceans such as right whales (Parks *et al.*, 2011), belugas (Scheifele *et al.*, 2005) and killer whales (Holt *et al.*, 2009). However, little is known about the maximum range at which animals may need to communicate or to what extent they can compensate for elevated noise levels vocally (Tyack, 2008b). Due to the high ambient noise levels from snapping shrimp in tropical waters (Fig. 1), we expected that tropical bottlenose dolphins would produce higher source levels than temperate conspecifics as a possible long-term adaptation to higher noise levels. In contrast to this expectation, we found that the source levels of  $146.7 \pm 6.4$  (max 164) dB re. 1  $\mu\text{Pa}$  were significantly lower than the source levels of  $158 \pm 6.4$  (max 169) dB re. 1  $\mu\text{Pa}$  previously estimated for *Tursiops truncatus* in the Moray Firth, Scotland (Janik, 2000). This would indicate that long-term vocal changes in habitats of higher ambient noise do not necessarily include increasing the vocalization intensity.

Alternative strategies for overcoming masking of ambient noise might be to alter the frequency of vocalizations, shifting call energy into frequency bands where noise levels are lower. This is a common long-term strategy for animals, such as songbirds and frogs, inhabiting urban areas (Slabbekoom and den Boer-Visser, 2006; Parris *et al.*, 2009). Similarly, right whales have increased their fundamental frequency over time,

as a possible adaptation to increases in vessel noise (Parks *et al.*, 2007). It has been suggested that ambient noise also shapes the vocalization frequency of bottlenose dolphin populations (Morisaka *et al.*, 2005; May-Collado and Wartzok, 2008). However, this does not seem to be the case for bottlenose dolphins in our study, since minimum frequency and centroid frequency of whistles (Table 1) is in the frequency band with highest ambient noise levels (Fig. 1). One reason for this might be that the adaptive value of changing frequency parameters will depend on the shape of ambient noise and the habitat-specific propagation conditions. Because the noise generated by snapping shrimp is very broadband, the advantage of increasing frequency seems to be minimal as masking levels do not decrease much with increasing frequencies (Fig. 1). In contrast, calls would suffer more attenuation from the increasing frequency-dependent absorption (Fig. 2) and ultimately not propagate further at all.

The apparent higher intensity of whistles recorded in Moray Firth (Janik, 2000) might be explained in part by the greater body size of animals compared to the dolphins studied here. Bottlenose dolphins in the northeastern Atlantic Ocean (including the Moray Firth) are among the largest *Tursiops* populations, reaching lengths of 350–410 cm (Fraser, 1974; Lockyer and Morris, 1985). In contrast, bottlenose dolphins on the west coast of Australia are much smaller, reported to reach lengths of 220–230 cm (Cockcroft and Ross, 1990; Hale *et al.*, 2000). It has been shown across species that acoustic power scales with body mass (Gillooly and Ophir, 2010; Ophir *et al.*, 2010) and it is possible that the different source levels may reflect the maximum acoustic power output of these animals.

The high noise levels and lower source levels found in this study inevitably results in much lower estimates of active space than in studies of delphinid communication in more temperate areas (Janik, 2000; Miller, 2006). The noise levels in this study are about 6 dB lower than used to model communication ranges in Sarasota (Quintana-Rizzo *et al.*, 2006), but are comparable to noise levels found in other subtropical habitats with snapping shrimp (Au *et al.*, 1985). Noise levels in this study were obtained under ideal, low-noise conditions (Sea State 0: flat sea with no vessels and no wind), so if anything, the active space will likely be lower than reported here due to increased noise from wind, waves and rain. Together, these results imply that communication range of tropical, coastal dolphins is inherently short-range where 50% of the whistles are unlikely to be detected beyond a range of 800 m, more than an order of magnitude lower than some previous estimates for delphinids (Janik, 2000; Miller, 2006), and much closer to the ranges estimated in Sarasota Bay (Quintana-Rizzo *et al.*, 2006).

In the studies of Janik (2000) for bottlenose dolphins and Miller (2006) for killer whales, theoretical deep sea noise levels were used (Knudsen *et al.*, 1948; Wenz, 1962). These low deep sea noise profiles are considerably lower than the spectral noise levels normally measured at more shallow depths, especially in the frequency range where delphinids vocalize (Wenz, 1962; Piggott, 1964; McConnell *et al.*, 1992). A one-year study of ambient noise in the Gulf of Finland, with little vessel noise and few loud, biological

sources of noise, demonstrates a variation in the spectral noise levels of up to 40 dB (Poikonen and Madekivi, 2010; Poikonen, 2010). Even the lowest noise levels measured (when the Gulf had frozen over) still exceed the Knudsen curves above 2 kHz (Poikonen, 2010). We therefore argue that the actual differences in active space estimates for the temperate and tropical regions are smaller than the order of magnitude difference appearing when comparing the present results with studies using Knudsen curves. While our estimate of an active space smaller than 3 km (including all relevant habitat-specific parameters measured) is likely short for delphinids because of snapping shrimp noise, it is probably very rare that active spaces of dolphin whistles in general reach the maximum of 20–25 km estimated by Janik (2000).

Differences in active space between different studies not only hinge on SL differences and the noise profiles in question, but also on the models used for transmission loss in the habitat and on how delphinids are able to detect and decode signals in different types of noise. In this study, we measured an average transmission loss of  $18\log(R)$  which is very close to spherical spreading. At short ranges, this corresponds well with the transmission loss predicted using the Marsh and Shulkin (1962) model for continuous sounds as employed by Janik (2000) and Miller (2006). The existence of sound channels might increase the transmission of signals drastically for very specific frequencies (Quintana-Rizzo *et al.*, 2006). However, sound transmission in such channels is often unpredictable and varied, and received levels can change quickly even over short distances and depths (Quintana-Rizzo *et al.*, 2006). Using general models or extrapolating between habitats may easily lead to transmission loss errors, and we therefore recommend that transmission loss is measured in the habitats for which the active space estimation takes place, if at all possible. Furthermore, the low transmission loss of sound channels inherently implies multipath propagation and hence contour degradation that may impede information transfer even when the signal exceeds detection levels (Dabelsteen *et al.*, 1993; Blumenrath and Dabelsteen, 2004). It is even possible that very extensive propagation range might pose problems for the animals themselves by interfering with the detection of signals from conspecifics (Janik, 2000, 2009).

Most studies of masking in delphinids are based on the equal power model of masking (Fletcher, 1940). However, this model does not apply well to non-Gaussian broadband noise such as that produced by snapping shrimp (Hall *et al.*, 1984). Recent psychophysical experiments have demonstrated masked thresholds in comodulated noise well below masked thresholds in Gaussian noise of equivalent spectral noise density and bandwidth for synthetic maskers (Branstetter and Finneran, 2008). The only experimental study with actual environmental noise profiles (including snapping shrimp noise) seems to indicate a 6 dB threshold decrease for 10 kHz tones (Trickey *et al.*, 2010). It is possible that this comodulation masking release would apply for this study habitat too, potentially doubling communication range estimates. Whether and how such masking release depends on signal type and frequency remains undetermined, however.



For a communicating animal, there may be indirect costs of vocalizing due to eavesdropping conspecifics or predators and direct costs given by the metabolic energy consumed by sound production. These costs are of interest to the scientific community because of their importance for evaluating population level effects of acoustic changes in response to disturbance such as caused by anthropogenic activity (NRC, 2005).

In toothed whales, the energetic costs of communication have remained unexplored so far. Here we have provided the first energy content estimates of dolphin whistles where 95 percent of whistles contain less than 17 mJ of radiated acoustic energy. In comparison, the highest on-axis biosonar clicks have been measured at  $SL_{EFD}$  of 160 dB re.  $1 \mu Pa^2 s @ 1m$  (Jensen *et al.*, 2009a). When corrected for a biosonar directionality index of 29 dB (Wahlberg *et al.* accepted) and typical repetition rates between 10–50 clicks per second (Jensen *et al.*, 2009a), this gives a total radiated energy for a 1-second echolocation click sequence of only 1–5 mJ. From a production point of view, it therefore seems less costly to echolocate than to communicate. This is further corroborated by studies showing that a higher nasal pressure is required to produce a whistle compared to an echolocation sequence (Ridgway and Carder, 1988).

The direct metabolic costs of sound production have been heavily debated in songbirds and insects. Some species of songbirds increase calling rates when provided with abundant food, suggesting indirectly that call activity may be energy-limited (Strain and Mumme, 1988). Our study indicates that the direct, metabolic costs of communication in delphinids may be of relatively little importance (Table II). However, investigations of the vocal efficiency of toothed whales and direct measurements of metabolic costs of vocalizations at varying source levels are needed to confirm our estimates and form a thorough representation of the energetic costs of communicating for these animals. Our estimates suggest that other ecological costs, such as detection by predators (Deecke *et al.*, 2002; Morisaka and Connor, 2007), prey (Deecke *et al.*, 2005) or eavesdropping by conspecifics (Janik, 2009) are much more likely to shape the acoustic behavior of delphinids. Bottlenose dolphins in particular may have many social interactions that are not beneficial to every individual, including for example the cooperative herding of females by male alliances (Connor *et al.*, 2000), and it may be envisioned that animals may limit the rate or amplitude of whistling when faced with such intraspecific interactions.

In conclusion, we have shown that whistling bottlenose dolphins in a shallow-water, noisy habitat do not use higher source levels to compensate for the high background noise levels in the area compared to more temperate areas. The low source levels found here combined with the high background noise levels in the habitat leads to low communication ranges for these animals that might influence the structure of social groups and the contact between individuals. It seems unlikely that the low source levels is a result of high metabolic costs of whistling, as the acoustic energy in whistles, and the metabolic energy required to produce them, would be very low compared to the field metabolic rate of a

normal bottlenose dolphin. Other ecological factors such as increased risk of being detected by predators, prey, or social competitors, are probably more important in shaping the acoustic behavior of these animals.

## ACKNOWLEDGMENTS

This study received support from the Danish Ph.D. School of Aquatic Sciences (SOAS), Aarhus University, DK, WWF Verdensnaturfonden and Aase & Ejnar Danielsens Foundation, the Siemens Foundation, the Faculty of Science at the University of Aarhus, DK, and the Danish Natural Science Foundation via a Steno scholarship and a logistics grant to PTM. We greatly appreciate the assistance in the field provided by M. Hansen, M. Wilson, H. Schack, H. Smith and J. Knust, the technical help given by N. U. Kristiansen and J. Svane, as well as the logistical support provided by Murdoch University and Bunbury Dolphin Discovery Center. Two anonymous reviewers and Dr. D. Noren, Dr. V. Janik, and Dr. P. Nachtigall provided valuable comments to previous versions of the manuscript. Research in Australia was conducted under a permit to LB from the Department of Environment and Conservation and Ethics Approval from Murdoch University.

- Anderson, C., and McShea, D. W. (2001). "Individual versus social complexity, with particular reference to ant colonies," *Biol. Rev. Cambridge Philos. Soc.* **76**, 211–237.
- Au, W. W. L. (1993). *The Sonar of Dolphins* (Springer-Verlag, New York), p. 277.
- Au, W. W. L., Carder, D. A., Penner, R. H., and Scronce, B. L. (1985). "Demonstration of adaptation in beluga whale echolocation signals," *J. Acoust. Soc. Am.* **77**, 726–730.
- Blumenrath, S. H., and Dabelsteen, T. (2004). "Degradation of great tit (*Parus major*) song before and after foliation: Implications for vocal communication in a deciduous forest," *Behaviour* **141**, 935–958.
- Boinski, S. (1993). "Vocal coordination of troop movement among white-faced capuchin monkeys, *Cebus capucinus*," *Am. J. Primatol.* **30**, 85–100.
- Branstetter, B. K., and Finneran, J. J. (2008). "Comodulation masking release in bottlenose dolphins (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **124**, 625–633.
- Brenowitz, E. A. (1982). "Long-range communication of species identity by song in the Red-winged Blackbird," *Behav. Ecol. Sociobiol.* **10**, 29–38.
- Brumm, H. (2004). "The impact of environmental noise on song amplitude in a territorial bird," *J. Anim. Ecol.* **73**, 434–440.
- Brumm, H., and Slabbekoorn, H. (2005). "Acoustic communication in noise," in *Advances in the Study of Behavior*, edited by P. J. B. Slater, C. T. Snowdon, T. J. Roper, H. J. Brockmann, and M. Naguib (Elsevier, New York), pp. 151–209.
- Cockroft, V. G., and Ross, G. J. B. (1990). "Age, growth, and reproduction of bottlenose dolphins *Tursiops truncatus* from the east coast of southern Africa," *Fish. Bull.* **88**, 289–302.
- Connor, R. C., Smolker, R. A., and Richards, A. F. (1992). "Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.)," *Proc. Natl. Acad. Sci.* **89**, 987–990.
- Connor, R. C., Wells, R. S., Mann, J., and Read, A. J. (2000). "The Bottlenose Dolphin," in *Cetacean Societies: Field Studies of Whales and Dolphins*, edited by J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (Univ. Chicago, Chicago), pp. 91–126.
- Cortopassi, K. A., and Bradbury, J. W. (2006). "Contact call diversity in wild orange-fronted parakeet pairs, *Aratinga canicularis*," *Anim. Behav.* **71**, 1141–1154.
- Cranford, T. W., Amundin, M., and Norris, K. S. (1996). "Functional morphology and homology in the odontocete nasal complex: Implications for sound generation," *J. Morphol.* **228**, 223–285.
- Da Cunha, R. G. T., and Byrne, R. W. (2009). "The use of vocal communication in keeping the spatial cohesion of groups: Intentionality and specific functions," in *South American Primates*, edited by P. A. Garber,

- A. Estrada, J. C., Bicca-Marques, E. W., Heymann, and K. B., Strier (Springer, New York), pp. 341–363.
- Dabelsteen, T., Larsen, O. N., and Pedersen, S. B. (1993). "Habitat-induced degradation of sound signals - quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song." *J. Acoust. Soc. Am.* **93**, 2206–2220.
- Deecke, V. B., Ford, J. K. B., and Slater, P. J. B. (2005). "The vocal behaviour of mammal-eating killer whales: communicating with costly calls." *Anim. Behav.* **69**, 395–405.
- Deecke, V. B., Ford, J. K. B., and Spong, P. (1999). "Quantifying complex patterns of bioacoustic variation: Use of a neural network to compare killer whale (*Orcinus orca*) dialects." *J. Acoust. Soc. Am.* **105**, 2499–2507.
- Deecke, V. B., Slater, P. J. B., and Ford, J. K. B. (2002). "Selective habituation shapes acoustic predator recognition in harbour seals." *Nature* **420**, 171–173.
- Esch, H. C., Sayigh, L. S., and Wells, R. S. (2009). "Quantifying parameters of bottlenose dolphin signature whistles." *Marine Mammal Sci.* **25**, 976–986.
- Fletcher, H. (1940). "Auditory Patterns." *Rev. Mod. Phys.* **12**, 47.
- Fraser, F. C. (1974). "Report on Cetacea stranded on the British coasts from 1948–1966." Publications of the British Museum of Natural History **14**, 1–65.
- Garstang, M., Larom, D., Raspet, R., and Lindeque, M. (1995). "Atmospheric controls on elephant communication." *J. Exp. Biol.* **198**, 939–951.
- Gillooly, J. F., and Ophir, A. G. (2010). "The energetic basis of acoustic communication." *Proc. R. Soc. London, Ser. B* **277**, 1325–1331.
- Gowans, S., Würsig, B., Karczmarski, L., and David, W. S. (2007). "The social structure and strategies of delphinids: Predictions based on an ecological framework." *Adv. Mar. Biol.* **53**, 195–294.
- Hale, P. T., Barreto, A. S., and Ross, G. J. B. (2000). "Comparative morphology and distribution of the *aduncus* and *truncatus* forms of bottlenose dolphin *Tursiops* in the Indian and Western Pacific Oceans." *Aquat. Mamm.* **26**, 101–110.
- Hall, J. W., Haggard, M. P., and Fernandes, M. A. (1984). "Detection in noise by spectro-temporal pattern analysis." *J. Acoust. Soc. Am.* **76**, 50–56.
- Hamilton, W. D. (1964). "The genetical evolution of social behaviour. II." *J. Theor. Biol.* **7**, 17–52.
- Herzing, D. L. (2000). "Acoustics and social behavior of wild dolphins: implications for a sound society," in *Hearing by Whales and Dolphins*, edited by W. W. L. Au, A. N. Popper, and R. E. Fay (Springer, New York), pp. 225–272.
- Holt, M. M., Noren, D. P., Veirs, V., Emmons, C. K., and Veirs, S. (2009). "Speaking up: Killer whales (*Orcinus orca*) increase their call amplitude in response to vessel noise." *J. Acoust. Soc. Am.* **125**, EL27–EL32.
- Janik, V., Todt, D., and Dehnhardt, G. (1994). "Signature whistle variations in a bottlenosed dolphin, *Tursiops truncatus*." *Behav. Ecol. Sociobiol.* **35**, 243–248.
- Janik, V. M. (2000). "Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland." *J. Comp. Physiol. [A]* **186**, 673–680.
- Janik, V. M. (2005). "Underwater acoustic communication networks in marine mammals," in *Animal Communication Networks*, edited by P. K. McGregor (Cambridge University, Cambridge), pp. 390–415.
- Janik, V. M. (2009). "Acoustic communication in delphinids," *Advances in the study of behavior*, edited by M. Naguib, V. Janik, N. Clayton, and K. Zuberbuhler (Academic, New York), pp. 123–157.
- Janik, V. M., Sayigh, L. S., and Wells, R. S. (2006). "Signature whistle shape conveys identity information to bottlenose dolphins." *Proc. Natl. Acad. Sci. U.S.A.* **103**, 8293–8297.
- Janik, V. M., and Slater, P. J. (1998). "Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls." *Anim. Behav.* **56**, 829–838.
- Jensen, F. H., Bejder, L., Wahlberg, M., and Madsen, P. T. (2009a). "Biosonar adjustments to target range of echolocating bottlenose dolphins (*Tursiops* sp.) in the wild." *J. Exp. Biol.* **212**, 1078–1086.
- Jensen, F. H., Bejder, L., Wahlberg, M., Soto, N. A., Johnson, M., and Madsen, P. T. (2009b). "Vessel noise effects on delphinid communication." *Mar. Ecol.: Prog. Ser.* **395**, 161–175.
- Johnson, C. S. (1968a). "Masked tonal thresholds in bottlenosed porpoise." *J. Acoust. Soc. Am.* **44**, 965–967.
- Johnson, C. S. (1968b). "Relation between absolute threshold and duration-of-tone pulses in the bottlenosed porpoise." *J. Acoust. Soc. Am.* **43**, 757–763.
- Knudsen, V. O., Alford, R. S., and Emling, J. W. (1948). "Underwater ambient noise." *J. Mar. Res.* **7**, 410–429.
- Krebs, J. R., and Davies, N. B. (1993). *An Introduction to Behavioural Ecology* (Blackwell Publishing, Oxford), p. 420.
- Lammers, M. O., and Au, W. W. L. (2003). "Directionality in the whistles of Hawaiian spinner dolphins (*Stenella longirostris*): A signal feature to cue direction of movement?," *Marine Mammal Sci.* **19**, 249–264.
- Lockyer, C., and Morris, R. J. (1985). "A wild but sociable dolphin off Porthreath, north Cornwall." *J. Zool.* **207**, 605–607.
- Madsen, P. T., and Wahlberg, M. (2007). "Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales." *Deep-Sea Res. I* **54**, 1421–1444.
- Madsen, P. T., Wahlberg, M., Tougaard, J., Lucke, K., and Tyack, P. (2006). "Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs." *Mar. Ecol.: Prog. Ser.* **309**, 279–295.
- Marsh, H. W., and Schulkin, M. (1962). "Shallow-water transmission." *J. Acoust. Soc. Am.* **34**, 863–864.
- Marten, K., and Marler, P. (1977). "Sound transmission and its significance for animal vocalization." *Behav. Ecol. Sociobiol.* **2**, 271–290.
- May-Collado, L. J., and Wartzok, D. (2008). "A comparison of bottlenose dolphin whistles in the Atlantic Ocean: Factors promoting whistle variation." *J. Mammal.* **89**, 1229–1240.
- McComb, K., Moss, C., Sayialel, S., and Baker, L. (2000). "Unusually extensive networks of vocal recognition in African elephants." *Anim. Behav.* **59**, 1103–1109.
- McComb, K., Reby, D., Baker, L., Moss, C., and Sayialel, S. (2003). "Long-distance communication of acoustic cues to social identity in African elephants." *Anim. Behav.* **65**, 317–329.
- McConnell, S. O., Schilt, M. P., and Dworski, J. G. (1992). "Ambient noise measurements from 100 Hz to 80 kHz in an Alaskan fjord." *J. Acoust. Soc. Am.* **91**, 1990–2003.
- McGregor, P. K. (2005). *Animal Communication Networks* (Cambridge University, Cambridge), p. 672.
- Miller, P. (2006). "Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations." *J. Comp. Physiol., A* **192**, 449–459.
- Morisaka, T., and Connor, R. C. (2007). "Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes." *J. Evol. Biol.* **20**, 1439–1458.
- Morisaka, T., Shinohara, M., Nakahara, F., and Akamatsu, T. (2005). "Effects of ambient noise on the whistles of Indo-Pacific bottlenose dolphin populations." *J. Mammal.* **86**, 541–546.
- Møhl, B., Wahlberg, M., and Heerfordt, A. (2001). "A large-aperture array of nonlinked receivers for acoustic positioning of biological sound sources." *J. Acoust. Soc. Am.* **109**, 434–437.
- Möller, L. M., Bilgmann, K., Charlton-Robb, K., and Beheregaray, L. (2008). "Multi-gene evidence for a new bottlenose dolphin species in southern Australia." *Mol. Phylogenet. Evol.* **49**, 674–681.
- Nakano, R., Takanashi, T., Fujii, T., Skals, N., Surlykke, A., and Ishikawa, Y. (2009). "Moths are not silent, but whisper ultrasonic courtship songs." *J. Exp. Biol.* **212**, 4072–4078.
- Norris, K. S., and Schilt, C. R. (1988). "Cooperative societies in three-dimensional space - on the origins of aggregations, flocks, and schools, with special reference to dolphins and fish." *Ethol. Sociobiol.* **9**, 149–179.
- NRC (2005). *Marine Mammal Populations and Ocean Noise: Determining when Noise Causes Biologically Significant Effects* (National Academy, Washington, DC)
- Ophir, A. G., Schrader, S. B., and Gillooly, J. F. (2010). "Energetic cost of calling: general constraints and species-specific differences." *J. Evol. Biol.* **23**, 1564–1569.
- Parks, S. E., Clark, C. W., and Tyack, P. L. (2007). "Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication." *J. Acoust. Soc. Am.* **122**, 3725–3731.
- Parks, S. E., Johnson, M., Nowacek, D., and Tyack, P. L. (2011). "Individual right whales call louder in increased environmental noise." *Biol. Lett.* **7**, 33–35.
- Parris, K. M., Velik-Lord, M., and North, J. M. A. (2009). "Frogs call at a higher pitch in traffic noise." *Ecol Soc* **14**, (1); <http://www.ecologyandsociety.org/vol14/iss1/art25/>. (Last viewed September 26th, 2011).
- Payne, R., and Webb, D. (1971). "Orientation by means of long range acoustic signalling in baleen whales." *Ann. N.Y. Acad. Sci.* **188**, 110–141.
- Piggott, C. L. (1964). "Ambient sea noise at low frequencies in shallow water of the scotian shelf." *J. Acoust. Soc. Am.* **36**, 2152–2163.

- Poikonen, A., and Madekivi, S. (2010). "Wind-generated ambient noise in a shallow brackish water environment in the archipelago of the Gulf of Finland," *J. Acoust. Soc. Am.* **127**, 3385–3393.
- Poikonen, A. A. (2010). "High-frequency wind-driven ambient noise in shallow brackish water: Measurements and spectra," *J. Acoust. Soc. Am.* **128**, EL242–EL247.
- Prestwich, K. N., Brugger, K. E., and Topping, M. (1989). "Energy and communication in three species of hylid frogs - power input, power output and efficiency," *J. Exp. Biol.* **144**, 53–80.
- Quintana-Rizzo, E., Mann, D. A., and Wells, R. S. (2006). "Estimated communication range of social sounds used by bottlenose dolphins (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **120**, 1671–1683.
- Rasmussen, M. H., Lammers, M., Beedholm, K., and Miller, L. A. (2006). "Source levels and harmonic content of whistles in white-beaked dolphins (*Lagenorhynchus albirostris*)," *J. Acoust. Soc. Am.* **120**, 510–517.
- Reeves, R. R., Stewart, B. S., Clapham, P. J., and Powell, J. A. (2002). *Sea Mammals of the World: A Complete Guide to Whales, Dolphins, Seals, Sea Lions and Sea Cows* (A & C Black, London), p. 528.
- Ridgway, S. H., and Carder, D. A. (1988). "Nasal pressure and sound production in an echolocating white whale, *Delphinapterus leucas*," in *Animal Sonar: Processes and Performance*, edited by P. E. Nachtigall, and P. W. B. Moore (Plenum, New York), pp. 53–60.
- Ryan, M. J., Tuttle, M. D., and Rand, A. S. (1982). "Bat predation and sexual advertisement in a neotropical anuran," *Am. Nat.* **119**, 136–139.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D., and Irvine, A. B. (1999). "Individual recognition in wild bottlenose dolphins: a field test using playback experiments," *Anim. Behav.* **57**, 41–50.
- Scheifele, P. M., Andrew, S., Cooper, R. A., Darre, M., Musiek, F. E., and Max, L. (2005). "Indication of a Lombard vocal response in the St. Lawrence River beluga," *J. Acoust. Soc. Am.* **117**, 1486–1492.
- Sinnott, J. M., Stebbins, W. C., and Moody, D. B. (1975). "Regulation of voice amplitude by the monkey," *J. Acoust. Soc. Am.* **58**, 412–414.
- Slabbekoorn, H., and den Boer-Visser, A. (2006). "Cities change the songs of birds," *Curr. Biol.* **16**, 2326–2331.
- Spiesberger, J. L., and Fristrup, K. M. (1990). "Passive localization of calling animals and sensing of their acoustic environment using acoustic tomography," *Am. Nat.* **135**, 107–153.
- Strain, J. G., and Mumme, R. L. (1988). "Effects of food supplementation, song playback, and temperature on vocal territorial behavior of Carolina Wrens," *Auk* **105**, 11–16.
- Trickey, J. S., Branstetter, B. K., and Finneran, J. J. (2010). "Auditory masking of a 10 kHz tone with environmental, comodulated, and Gaussian noise in bottlenose dolphins (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **128**, 3799–3804.
- Tyack, P. L. (2000). "Functional aspects of cetacean communication," in *Cetacean Societies: Field Studies of Dolphins and Whales*, edited by J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (Univ. Chicago, Chicago), pp. 270–307.
- Tyack, P. L. (2008a). "Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals," *J. Comp. Psych.* **122**, 319–331.
- Tyack, P. L. (2008b). "Implications for marine mammals of large-scale changes in the marine acoustic environment," *J. Mammal* **89**, 549–558.
- Urick, R. J. (1983). *Principles of Underwater Sound* (Peninsula, Los Altos), p. 423.
- Wahlberg, M., Mohl, B., and Madsen, P. T. (2001). "Estimating source position accuracy of a large-aperture hydrophone array for bioacoustics," *J. Acoust. Soc. Am.* **109**, 397–406.
- Watwood, S. L., Tyack, P. L., and Wells, R. S. (2004). "Whistle sharing in paired male bottlenose dolphins, *Tursiops truncatus*," *Behav. Ecol. Sociobiol.* **55**, 531–543.
- Welch, P. D. (1967). "Use of Fast Fourier Transform for estimation of power spectra - a method based on time averaging over short modified periodograms," *IEEE Trans. Audio Electroacoust.* **AU-15**, 70–73.
- Wells, R. S., and Scott, M. D. (1999). "Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821)," in *Handbook of marine mammals*, edited by S. H. Ridgway, and R. Harrison (Academic, New York), pp. 137–182.
- Wenz, G. M. (1962). "Acoustic ambient noise in ocean - spectra and sources," *J. Acoust. Soc. Am.* **34**, 1936–1956.
- Williams, T. M., Friedl, W. A., and Haun, J. E. (1993). "The physiology of bottlenosed dolphins (*Tursiops truncatus*) - Heart rate, metabolic rate and plasma lactate concentration during exercise," *J. Exp. Biol.* **179**, 31–46.