Echolocation parameters of Australian humpback dolphins (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the wild

Mafalda de Freitas[a)]
Zoophysiology, Department of Bioscience, Aarhus University, Building 1131, C.F. Moellers Alle 3, DK-8000 Aarhus C, Denmark

Frants H. Jensen[b)]
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544, USA

Julian Tyne and Lars Bejder
Murdoch University Cetacean Research Unit, School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, Western Australia 6150, Australia

Peter T. Madsen[c)]
Zoophysiology, Department of Bioscience, Aarhus University, Building 1131, C.F. Moellers Alle 3, DK-8000 Aarhus C, Denmark

(Received 21 October 2014; revised 13 April 2015; accepted 29 April 2015)

Echolocation is a key sensory modality for toothed whale orientation, navigation, and foraging. However, a more comparative understanding of the biosonar properties of toothed whales is necessary to understand behavioral and evolutionary adaptions. To address this, two free-ranging sympatric delphinid species, Australian humpback dolphins (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), were studied. Biosonar clicks from both species were recorded within the same stretch of coastal habitat in Exmouth Gulf, Western Australia, using a vertical seven element hydrophone array. *S. sahulensis* used biosonar clicks with a mean source level of 199 ± 3 dB re 1 μPa peak-peak (pp), mean centroid frequency of 106 ± 11 kHz, and emitted at interclick intervals (ICIs) of 79 ± 33 ms. These parameters were similar to click parameters of sympatric *T. aduncus*, characterized by mean source levels of 204 ± 4 dB re 1 μPa pp, centroid frequency of 112 ± 9 kHz, and ICIs of 73 ± 29 ms. These properties are comparable to those of other similar sized delphinids and suggest that biosonar parameters are independent of sympatric delphinids and possibly driven by body size. The dynamic biosonar behavior of these delphinids may have, consequently, allowed for adaptations to local environments through high levels of control over sonar beam properties. © *2015 Acoustical Society of America*.
[http://dx.doi.org/10.1121/1.4921277]

[WWA] Pages: 3033–3041

I. INTRODUCTION

Toothed whales currently comprise 67 species, exhibiting a vast morphological diversity that is defined by the foraging niches they have evolved to exploit. Deep-diving open water species, such as sperm whales (*Physeter macrocephalus*) and beaked whales, have been selected for a large body size and extended breath holding abilities that allow them to execute long dives and target deep prey layers (Watwood *et al.*, 2006). Other species, such as many phocoenids or coastal delphinids that inhabit near-shore shallow-water environments, are smaller and exhibit lower diving capacities (Akamatsu *et al.*, 2002). Across all toothed whales, however, is a ubiquitous reliance on echolocation for orientation, navigation, and foraging (Au, 1993; Madsen and Surlykke, 2013).

Echolocation is an active sense where a short, high-intensity acoustic signal is emitted and reflected off ensonified objects, producing a returning echo that is subsequently detected and processed by the echolocating animal (Griffin, 1958; Au, 1993). This process has been studied in detail in bats where the primary determinants of their biosonar characteristics are considered to be habitat type and foraging mode. Bat species use different biosonar parameters depending on ranges to prey, background vegetation, and foraging behavior (Denzinger and Schnitzler, 2013). As a result, bats are assigned into guilds independent of phylogeny, but rather based on common adaptations to environmental resources. Moreover, bat biosonar is further shaped within the same guild. Sympatric bat species change biosonar parameters, such as frequency, duration, and bandwidth, allowing for niche partitioning and avoiding competition for the same limited resources (Siemers and Schnitzler, 2004; Denzinger and Schnitzler, 2013). In contrast, toothed whales are comparatively understudied, and it remains unclear whether such

[a)]Electronic mail: mafalda.df@gmail.com
[b)]Also at: Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.
[c)]Also at: Murdoch University Cetacean Research Unit, School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, Western Australia 6150, Australia.

adaptations have similarly shaped odontocete biosonar source parameters given the general functional convergence in bat and toothed whale biosonars (Madsen and Surlykke, 2013).

To date, studies on odontocete biosonar suggest four signal types: multi-pulsed clicks produced by sperm whales (*P. macrocephalus*) (Møhl *et al.*, 2003); long frequency-modulated clicks produced by beaked whales (Johnson *et al.*, 2004); narrowband high frequency (NBHF) clicks produced by a polyphyletic group of porpoises (Møhl and Andersen, 1973), non-whistling delphinids (Kyhn *et al.*, 2009), pygmy sperm whales (Madsen *et al.*, 2005), and the Franciscana dolphin (Melcon *et al.*, 2012); and, last, short broadband transient clicks produced by whistling delphinids (Au, 1993). With the exception of the NBHF species, whose sonar signals are thought to have evolved in part as a form of acoustic crypsis to avoid predation from killer whales (Morisaka and Connor, 2007; Kyhn *et al.*, 2013), mapping the different biosonar signal types onto the odontocete phylogeny highlights that phylogeny plays an important role as a primary determinant of signal type within toothed whales. Size, too, appears an important factor in shaping basic biosonar parameters. The increasing number of odontocete biosonar studies indicates an overall inverse scaling of frequency with body size (Au *et al.*, 1999; Møhl *et al.*, 2003; Kyhn *et al.*, 2009; Wahlberg *et al.*, 2011a). Since the directionality of a biosonar is determined largely by the frequency of the biosonar signal relative to the size of the emitting aperture (Au, 1993; Madsen and Wahlberg, 2007), this inverse scaling of frequency to size results in a relatively constant biosonar directionality across toothed whale species (Madsen and Surlykke, 2013). Consequently, this finding has led to the suggestion that directionality is a major driving force for biosonar frequency in both bats and toothed whales (Madsen and Surlykke, 2013).

Recent studies have also demonstrated that toothed whales, like bats, have a high level of dynamic control over both the spectral composition and directionality of biosonar signals (Moore *et al.*, 2008; Wisniewska *et al.*, 2012; Wisniewska *et al.*, 2015; Kloepper *et al.*, 2014; Jensen *et al.*, 2015), allowing them to potentially adapt their biosonar performance to different environmental conditions. A recent study showed that toothed whales inhabiting shallow, acoustically complex environments produced lower source level signals and higher repetition rates than similar sized oceanic delphinids, suggesting a potential influence of environment on biosonar search range and, thus, biosonar parameters (Jensen *et al.*, 2013). In addition to environmental adaptations, species specific shifts in centroid frequency have been observed in sympatric NBHF species, possibly reflecting character displacement and hypothesized to facilitate species recognition (Kyhn *et al.*, 2013). However, no such biosonar adaptations have been documented in sympatric broadband transient species.

Therefore, to understand the influence of sympatric species and shallow habitat on delphinid biosonar properties, we recorded the biosonar signals of two free-ranging sympatric delphinid species, the Australian humpback dolphin (*Sousa sahulensis*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), within Exmouth Gulf, Western Australia. *S. sahulensis* is a newly described delphinid species (Jefferson and Rosenbaum, 2014) and its biosonar signals are essentially unknown. Both species grow to a similar size of some 2.8 m and overlap in distribution within the Gulf, but *S. sahulensis* are thought to prefer shallower coastal waters (Parra *et al.*, 2004). Using these two sympatric species in the same habitat, we show that sympatric competition has little influence on the biosonar source parameters of broadband transient species. Rather, source parameters emitted by both species are comparable to similar sized delphinids, suggesting that biosonar source parameters of broadband transient species is possibly driven by body size.

II. MATERIALS AND METHODS

A. Recording site and platform

Recordings were carried out during daylight hours in Exmouth Gulf (21.91°S, 114.15°E) North West Cape (NWC), Western Australia, between Exmouth boat harbor and Bundegi boat ramp. A 6 m steel-hulled research boat was used as the recording platform from the 11th to 25th September, 2013. The littoral zone surrounding the NWC consists of a shallow reef followed by a gently sloping sand bottom. Animals were frequently found foraging on the reef or traveling the length of the coast adjacent to it. Single species groups were most common and occasional mixed-species groups were always ignored. Depending on group behavior, animals were approached and arrays deployed in different manners. For traveling groups, the research boat was placed 100–200 m ahead of the group's projected travel path, engine and echosounder switched off, and recording equipment promptly deployed and initiated to record echolocation clicks as the group approached the boat. Milling and feeding groups were slowly approached, engine and echosounder switched off, and recording equipment deployed and initiated once within 20–50 m of individuals. Immediately after a recording was initiated, start time, group behavior, group size, and subsequent end time were all noted for each event. Only single species groups were recorded. The arrival of a new species in the recording area resulted in the termination of the recording session and a search for a new isolated group. Recordings were terminated either (1) once animals were out of recording range ($\geq$100 m), (2) no echolocation was seen on the recording screen for $\geq$3 min, or (3) another species came into the recording area (500 m from array). Due to the length of the array, recordings were limited to depths $>$5 m, representing the area of water adjacent to the reef.

B. Recording equipment

A dedicated vertical array of seven Neptune Sonar D/140 spherical hydrophones (Neptune Sonar Ltd., East Yorkshire, UK) was custom built on a 14 m, 16 wire single cable (Cortland Cable Company, Cortland, NY). The hydrophones were soldered to breakouts, with 0.6 m spacing between each hydrophone, along one end of the cable, starting 0.4 m in. A clear Plexiglas cylinder was placed around the breakout and electronics, and subsequently filled with

polyurethane while the hydrophone element extended out from the cylinder parallel to the array cable.

The array was suspended from a surface buoy with the first hydrophone positioned at 1 m depth, and the last at 4.6 m, following the 0.6 m spacing. A 3 kg weight was attached to the bottom, 0.4 m below the final hydrophone, in order to maintain the array as linear as possible within the water column. For recordings, the array was connected to a custom-made eight-channel amplifier and filtering box (1-pole 1 kHz high pass, 4-pole 180 kHz low pass, 20 dB gain), which then connected to a National Instruments USB-6356 analog-to-digital converter (National Instruments, Austin, TX) with a sampling rate of 500 kHz and 16 bit resolution. The recording chain had a resulting clip level of 204 dB re 1 μPa, as set by the maximum voltage of ± 5 V in the analog to digital converter. The recording chain was connected to a Dell (Round Rock, TX) laptop, via USB (universal serial bus), where a custom-made recording programme (LabView, Metrotech, Denmark) was used for data acquisition. All recordings were manually started and ended, with files stored every 30 s.

The hydrophones were calibrated individually against a Reson TC-4034 hydrophone (Teledyne RESON A/S, Slangerup, Denmark) and an average frequency response of the Neptune D/140 (Neptune Sonar Ltd., East Yorkshire, UK) and the amplifier-filter box was determined in the range of 80–180 kHz, with the profile outside of this range set to 1. Before analysis, recorded clicks were corrected for the hydrophone frequency response by dividing the complex spectra with the average frequency profile and then back transforming the result into the time domain. The resulting effective frequency response of the array was then flat within ± 2 dB from 1 to 200 kHz.

C. Click analysis

Prior to analysis, recordings were visually inspected in Adobe Audition 3.0 (Adobe Systems Incorporated, CA). Files with echolocation signals were isolated and labeled accordingly, while files with a low signal-to-noise ratio or lack of signal were omitted from further analysis. Interference from overlapping click trains of multiple individuals did not appear to pose a problem for any of the *S. sahulensis* recordings, and were easily distinguishable during the extraction process in the few *T. aduncus* recordings in which they occurred. A standard detection threshold, the level above noise where all relevant peaks can be detected, was set for each species and used in the click analysis procedure. Click analysis was carried out with a custom written click extraction and analysis toolbox for delphinid echolocation clicks (Biosonar array toolbox, F. H. Jensen) in MATLAB 7.0 (Mathworks, Inc., Natwick, MA). An automated click detector identified echolocation clicks on the central hydrophone whenever the signal envelope exceeded a detection threshold of 150 dB re 1 μP. Each detected click was localized and further analyzed if present on all seven hydrophones.

D. Localization

The source of each click was localized acoustically using a least-squares solution of time-of-arrival differences (TOADs) (Madsen and Wahlberg, 2007). Individual TOADs for each pair of hydrophones were estimated by cross-correlating the signal recorded on the central hydrophone with the signal received on the remaining hydrophones. Differences in arrival time for each pair of receivers generated a hyperbolic curve that represented the possible location of the source. Additional receivers produced more hyperbolic curves where the source of the signal should, ideally, be restricted to the intersection of the different curves (Wahlberg *et al.*, 2001). The seven receivers generated an over-determined system that was solved with a least squares method and resulted in an estimate of the unknown source position (Madsen and Wahlberg, 2007).

The localization accuracy of the array was calibrated in Aarhus Harbour, Denmark. A 2-cycle 80 kHz sine burst pulse was produced by a random waveform generator (model 33220A, Agilent Technologies, CA) and emitted from an HS70 hydrophone (Sonar Research and Development Ltd, Beverly, East Yorkshire, UK). Pulses were emitted at the depth of the middle hydrophone, 2.8 m, and at a horizontal range from 10 m to 60 m. The speed of sound for the calibration period was calculated using measured water temperature and salinity values in the Leroy equation. The range within which the transmission loss root-mean-square (rms) error relative to the known range was <3 dB was considered a reliable localization range, and all *T. aduncus* and *S. sahulensis* clicks recorded beyond the precise localization range were omitted from further analysis.

Localization calibrations of the recording array (Fig. 1) showed that clicks could be localized with a transmission loss rms error <3 dB out to 60 m from the seven element array with a corresponding 3.6 m aperture. As a result, only clicks recorded within 60 m from the array were used for further analysis.

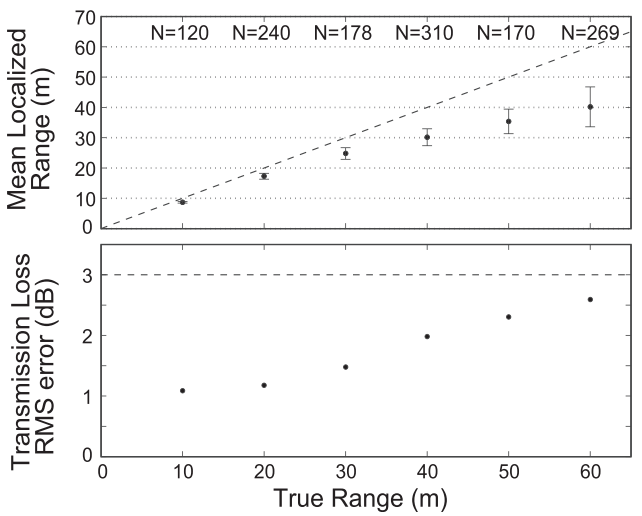

FIG. 1. Localization accuracy of a 3.6 m aperture seven element array. (Top) Mean localized range and standard deviation for (N) number of measurements made at each distance against the true range. The expected localized range at a given distance is depicted by the broken line. (Bottom) Transmission loss rms error, expressed in dB, of the localization procedure as a function of range. Broadband clicks could be localized with a ± 3 dB error on source level estimates out to 60 m. Therefore, only clicks localized within this range were used in this study.

E. Source parameters

As a consequence of the high directionality of odontocete clicks, clicks recorded off acoustic axis are not only prone to distortion, but can result in much lower apparent source level (ASL) and parameters than those recorded on-axis (Au, 1993; Madsen and Wahlberg, 2007) posing a problem when assessing sonar potential. Therefore, in order to ensure that only clicks recorded as close to the acoustic axis as possible were used in the analysis, a set of established criteria (Madsen and Wahlberg, 2007; Kyhn *et al.*, 2009) was implemented to determine on-axis clicks. Due to the boat-shy and skittish nature of *S. sahulensis*, long recordings where individuals properly investigated the array were not possible for this species. Clicks were identified as on-axis if (i) they were successfully localized within 60 m range (the localization range corresponding to a maximum 3 dB source level error: Fig. 1), (ii) they were part of a scan—a series of clicks consisting of a minimum of five, which first increase and then decrease in amplitude, indicative of an animal passing its acoustic beam across the array, (iii) the click had the highest amplitude within a scan, (iv) the highest amplitude across hydrophones was recorded by either of the inner hydrophones rather than by the outer hydrophones (vertically on-axis), and (v) reflections were of lower amplitude than the direct click.

For each click identified as on-axis, source parameters were derived *sensu* Au (1993) and Madsen and Wahlberg (2007). Interclick intervals were computed from the time interval between the peak envelope of adjacent clicks. Clicks were high pass filtered at 10 kHz to exclude low frequency electrical noise. The power spectrum of recorded clicks was calculated as the squared fast Fourier transform (FFT) of a 320-point Hanning window centered on the mean energy of the envelope, resulting in a factor 10 Sinc interpolation. Both peak frequency, defined as the center frequency of the band in the spectrum with the highest amplitude, and centroid frequency, defined as the point dividing the spectrum into equal energy halves (Madsen and Wahlberg, 2007), were determined from the normalized power spectrum. The 3 dB, 10 dB, and rms bandwidths were also computed from the spectrum. The Q factor of each click, defined as the ratio of the centroid frequency to the rms bandwidth, was computed and provided an indication of how broadband the projected signals were (Au, 1993, 2004). Finally, the click waveform was interpolated with a factor 10 (linear interpolation) and the duration of the signal was determined by the time interval between the -10 dB end points of the signal relative to the peak of the signal envelope (Madsen and Wahlberg, 2007). Extracted parameters for each species were then tested for normality of distribution.

F. Source level estimations

The orientation of echolocating individuals with respect to the array was not known in this study. ASLs, defined as the back-calculated sound pressure level at one meter in any direction from the source (Møhl *et al.*, 2000; Wahlberg *et al.*, 2011b), were therefore computed following the equation: $\mathrm{ASL} = \mathrm{RL} + \mathrm{TL}$, where RL is the peak-peak (pp) received level. Transmission loss (TL) was estimated from spherical spreading and absorption (α) loss at the given range (R) following: $\mathrm{TL} = 20\log(R) + \alpha R$. The absorption coefficient, α, of 0.025 dB m^{-1} was calculated using an average water temperature of 23 °C and a centroid frequency of 90 kHz. Peak-peak ASL (dB re1 μPa, pp), measured from the maximum and minimum peak pressures of the waveform, and energy flux density (EFD) ASL, calculated from the sum of squared sound pressure values within the 10 dB time window, were both computed for this study (Madsen and Wahlberg, 2007; Jensen *et al.*, 2013).

III. RESULTS

Throughout the 14-day study period, a total of 27 *S. sahulensis* approaches were recorded, resulting in 3 h and 22 min of recordings. From these, a total of 1572 clicks were detected, 42 of which were considered to be on-axis following the predefined criteria. For *T. aduncus*, 12 recorded approaches yielded 2 h and 12 min of recordings where 5573 clicks were detected, 58 of which were classified as being on-axis.

S. sahulensis group sizes ranged from one to five individuals, with calves occasionally present, whereas *T. aduncus* groups ranged from two to ten individuals, with calves also occasionally present. Groups of both species were most commonly encountered in traveling modes along the coast, with milling and feeding groups seen periodically. Population structure of either species in the area is currently unknown and, therefore, identification of recorded individuals is not possible at present. As groups were at times re-approached to ensure successful recordings, it is possible that some individuals may have been recorded more than once.

Both species produced broadband transient clicks (Fig. 2) of equally short duration ($15 \pm 2\,\mu$s and $14 \pm 2\,\mu$s for *S. sahulensis* and *T. aduncus*, respectively), with *S. sahulensis* using marginally longer interclick intervals (ICIs) (79 ± 33 ms) than *T. aduncus* (73 ± 29 ms). The corresponding mean EFD source level for *S. sahulensis* was 141 ± 3 dB re 1 μPa^2 s and 146 ± 5 dB re 1 μPa^2 s for *T. aduncus*. ASLs (pp) were lower for *S. sahulensis* (199 ± 3 dB re 1 μPa pp) than *T. aduncus* (204 ± 4 dB re 1 μPa pp) (Table I). The power spectra of on-axis clicks appear unimodal with particular emphasis between 120 kHz and 130 kHz for both species (Fig. 2). However, occasional bimodal spectra are also present in both species, particularly in *T. aduncus*. The steep decline in the power spectra around 180 kHz is attributed to the steep low pass filter of the recording system. Centroid frequencies of *S. sahulensis* were lower than those of *T. aduncus* (106 ± 11 kHz and 112 ± 19 kHz, respectively) and *S. sahulensis* displayed marginally narrower rms bandwidths (29 ± 4 kHz) than *T. aduncus* (34 ± 3 kHz). Consequently, *S. sahulensis* displayed a higher Q factor than *T. aduncus*.

The test for normality of distribution showed that all residuals were normally distributed. The distribution of centroid and peak frequencies, as well as rms bandwidth, for both species can be seen in Fig. 3. Monte Carlo permutation tests for equal median without replacement ($n = 5000$) (Manly, 2007) showed that peak frequencies and rms bandwidth varied

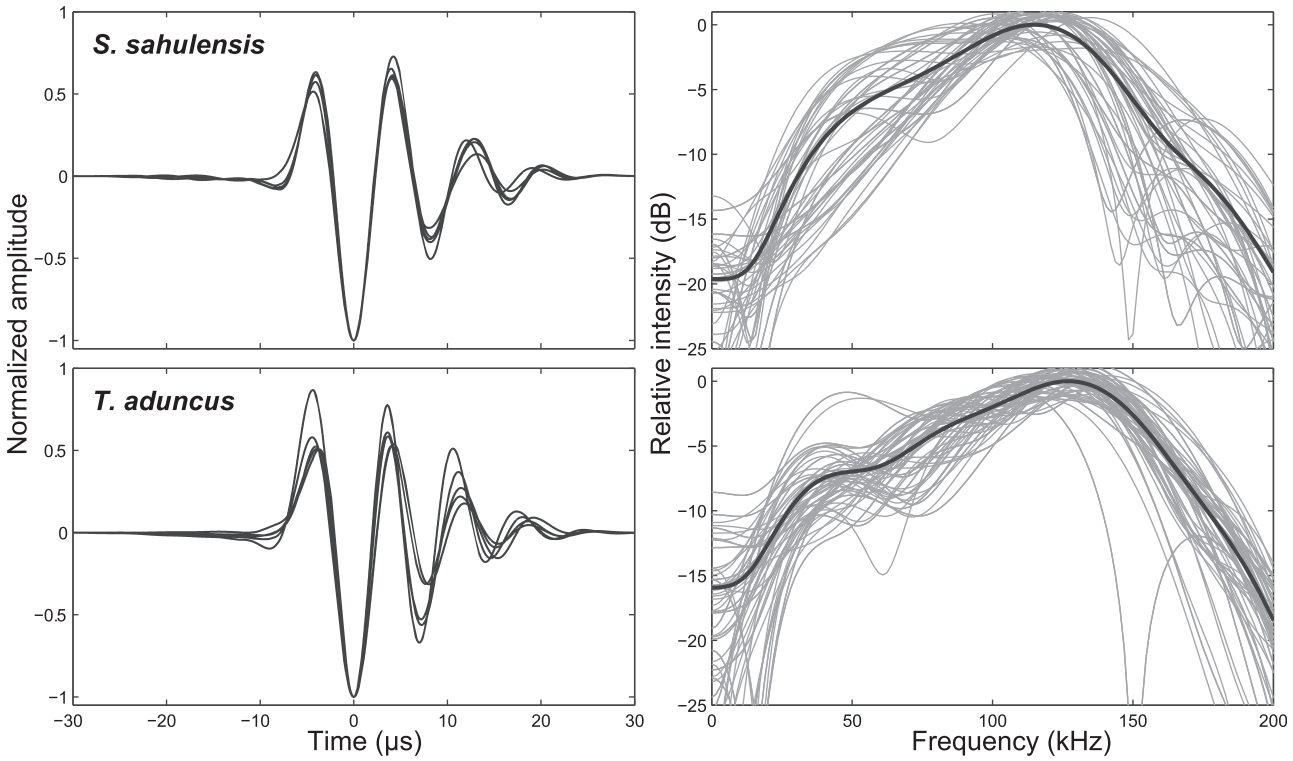

FIG. 2. Time domain and power spectrum of on-axis echolocation clicks from *Sousa sahulensis* and *T. aduncus*. Signal waveforms of the five clicks with the highest source level are plotted for each species (centered to the peak of the signal). Adjacent are the corresponding individual power spectra of all on-axis clicks (grey lines) with average power spectrum (black line) overlaid. (Sampling rate 500 kHz, FFT size 32-points, Hanning window, interpolation factor of 10, normalized around the mean of the spectrum.)

significantly between the two species ($p < 0.001$ for both), but with no significant difference between click centroid frequencies ($p = 0.1440$). Centroid frequencies for both species increased ~1 kHz (*T. aduncus*: $\alpha = 0.84$; *S. sahulensis*: $\alpha = 1.09$) per 1 dB increase in ASLpp (Fig. 4), and regression lines were significantly different from 0 (*T. aduncus*: $p = 0.0020$; *S. sahulensis*: $p = 0.0384$). However, r^2 values were very low and account for little of the variation (*T. aduncus*: $r^2 = 0.17$; *S. sahulensis*: $r^2 = 0.10$). ICI and source levels were plotted as a function of range to test whether either species exhibited range locking or automatic gain control (Fig. 5). Both species decreased ICIs as a function of decreasing range (*T. aduncus*: $\alpha = 0.78$; *S. sahulensis*: $\alpha = 0.56$), but with very low r^2 values (*T. aduncus*: $r^2 = 0.09$; *S. sahulensis*: $r^2 = 0.03$). *T. aduncus* and *S. sahulensis* both exceeded the two way travel time (TWT) and only *T. aduncus* showed a regression line significantly different from 0 ($p = 0.0182$). Source levels of both species increased as a function of range. Regression lines were significantly different from 0 ($p < 0.001$ for both) and *S. sahulensis* displayed a larger increase in ASL (dB re 1 μPa pp) per increasing log unit of range (*T. aduncus*: $\alpha = 10.61$, $r^2 = 0.23$; *S. sahulensis*: $\alpha = 20.18$, $r^2 = 0.47$). An unrestricted permutation of observations ($n = 5000$) (Manly, 2007) highlighted source levels as being significantly different

TABLE I. Mean (±standard deviation) echolocation source parameters of *Sousa sahulensis* and *Tursiops aduncus*.

	Humpback dolphin (*Sousa sahulensis*)		Bottlenose dolphin (*Tursiops aduncus*)	
Parameters	Mean (±standard deviation)	Range	Mean (±standard deviation)	Range
ASL_{pp} (dB re 1 μPa pp)	199 (±3)	194–208	204 (±4)	193–214
ASL_{rms} (dB re 1 μPa rms)	189 (±3)	183–198	195 (±4)	183–204
ASL_{EFD} (dB re 1 μPa^2 s)	141 (±3)	136–149	146 (±5)	134–156
$D_{-10\ dB}$ duration (μs)	15 (±2)	10–20	14 (±2)	10–19
Centroid frequency (kHz)	106 (±11)	86–125	112 (±9)	82–129
Peak frequency (kHz)	114 (±12)	86–135	124 (±13)	53–141
−3 dB bandwidth (kHz)	59 (±18)	42–114	62 (±17)	40–108
−10 dB bandwidth (kHz)	116 (±20)	86–163	140 (±17)	92–178
rms. bandwidth (kHz)	29 (±4)	24–39	34 (±3)	29–40
Q_{rms}	3.7 (±0.7)	2.6–4.7	3.3 (±0.4)	2.3–4.3
Range (m)	32 (±10)	24–60	26 (±10)	9–55
N	42		54	

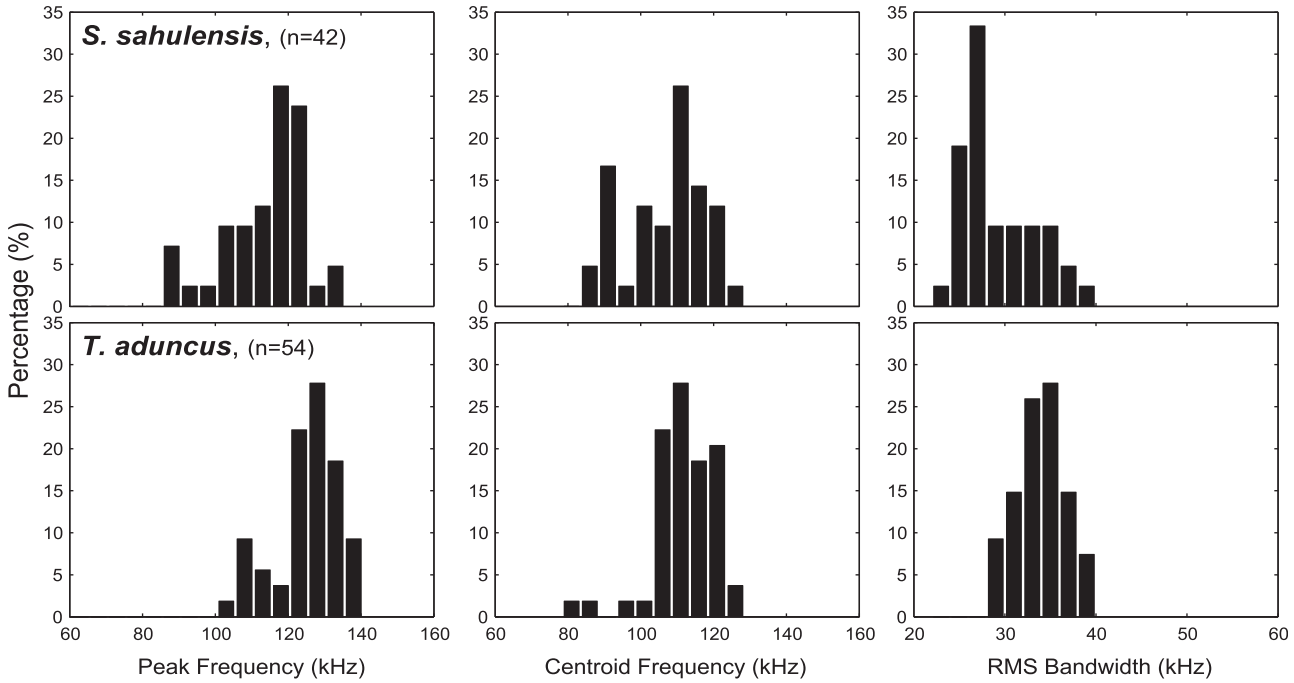

FIG. 3. Histogram of peak frequency, centroid frequency, and rms bandwidth for on-axis clicks of both species. Binwidths for both peak and centroid frequencies are 5 kHz, while binwidth for rms bandwidth is 2 kHz.

between the two species ($p < 0.001$) and significantly dependent on range ($p = 0.0062$). The interaction between species and range, however, was not significant ($p = 0.062$).

IV. DISCUSSION

Despite the role of echolocation as a key sensory modality, the evolutionary pressures that define the variation in toothed whale biosonar parameters remain largely unknown. More specifically, there is a paucity of knowledge on how sympatric delphinids and local environments have shaped the evolution and operation of biosonar source parameters in toothed whales. In an attempt to address this, we identified two small delphinids of similar phylogeny inhabiting the same shallow coastal environment, and to test the hypothesis that, similarly to bats, habitat and sympatric species competition will provide the greatest influence in shaping toothed whale biosonar source parameters.

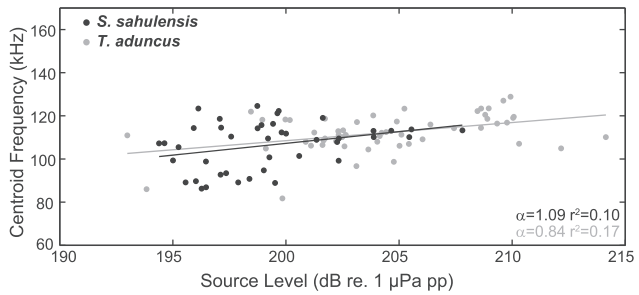

FIG. 4. Centroid frequency of on-axis clicks as a function of source level (pp). Clicks of both species increase in centroid frequency with increasing SLpp. Linear regression of *S. sahulensis* (black) is significant from a slope of 0 ($p = 0.0384$) with the equation $f_c = 0.109\text{SLpp} - 110$ and $r^2 = 0.10$. *T. aduncus* (grey) linear regression has the equation of $f_c = 0.84\text{SLpp} - 60$ with an r^2 value of $r^2 = 0.17$. It is also significant from a slope of 0 ($p = 0.002$).

The present study provides the first high-quality multihydrophone array recording of *S. sahulensis*. Free-ranging *S. sahulensis* emitted short-duration (~15 μs), broadband (Q factor of 3–4) echolocation clicks (Fig. 2), characteristic of all whistling delphinids (Au, 1993). The source levels of *S. sahulensis* in this study are 17 dB higher than those previously reported for the sister species, *Sousa chinensis*. Kimura *et al.* (2014) measured source levels from *S. chinensis* of

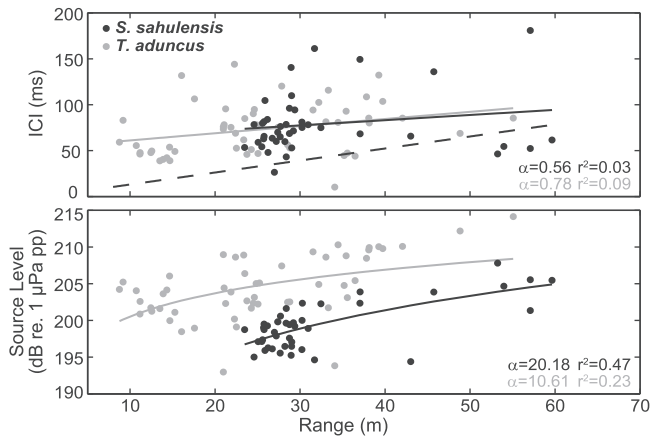

FIG. 5. ICI and source levels as a function of range. (Top) ICIs as a function of range from the array. The broken black line represents the TWT if both species were focusing on the array. Linear regression line of *S. sahulensis* has the equation $\text{ICI} = 0.56\text{Range} + 60$ with a fit of $r^2 = 0.03$. It is not significantly different from 0 ($p = 0.2003$). The linear regression line for *T. aduncus* has the equation $\text{ICI} = 0.78\text{Range} + 53$ and a fit of $r^2 = 0.09$, and is not significantly different from 0 ($p = 0.0182$). (Bottom) Source levels as a function of log range from the array. The two pools of *S. sahulensis* data at both extremes of the trend line are what have given rise to a sharper increase in SL with increasing range. The regression line of *S. sahulensis* has the equation $\text{SL} = 20\log\text{Range} + 169$ and a fit of $r^2 = 0.47$. The regression line for *T. aduncus* is $\text{SL} = 11\log\text{Range} + 190$ with a fit of $r^2 = 0.23$. Both regression lines are significantly different from 0 ($p < 0.001$).

$\sim$182 $\pm$ 7 dB re 1 μPa (pp), which is lower than the minimum source levels reported here. However, Kimura *et al.* (2014) had technical limitations including a limited frequency range and low clipping level. This may have resulted in clicks with high source levels being excluded and, conversely, the inclusion of low source level buzz clicks in the analysis.

Small but statistically significant variation was found between the source levels, peak frequencies, and rms bandwidths of *S. sahulensis* and *T. aduncus*. These parameters are intrinsically linked and ultimately behavior dependent. Increasing source levels result in greater levels of energy at high frequencies, which, in turn, increases the bandwidth and gives rise to the positive correlation between centroid frequency and source level (Fig. 4). The significantly higher peak frequency and rms bandwidth measured in *T. aduncus* may, therefore, be a consequence of the higher source levels recorded for this species. Source levels are, in turn, highly behavior dependent. Lower source levels are known to be produced at close target ranges and in foraging situations (Au and Benoit-Bird, 2003; Au, 2004; Jensen *et al.*, 2009) (Fig. 5). While we did find lower source levels for *S. sahulensis* compared to *T. aduncus*, there was significant overlap in the range of values, and it is difficult to say, if the differences we found may be due to uncontrollable behavioral differences. Nevertheless, results suggest that in contrast to NBHF species (Kyhn *et al.*, 2013) acoustic character displacement is less important for these two sympatric delphinids as no significant difference was found between emitted centroid frequencies. One important explanation for this is that the spectral content of a broadband delphinid echolocation click is linked to other source properties such as source level and directionality (Au, 1993; Madsen *et al.*, 2013; Finneran *et al.*, 2014). This means that dynamic changes in the acoustic gaze (Au *et al.*, 1995; Wisniewska *et al.*, 2012; Jensen, *et al.*, 2015) may result in, or require, spectral changes to the outgoing signals. Perhaps more importantly, the spectrum of a broadband click is strongly affected by the off-axis angle (Wahlberg *et al.*, 2011b; Au *et al.*, 2012). Successful spectral discrimination, despite large changes in frequency depending on aspect and behavior, is likely to require a relatively large difference in frequency (Ibsen *et al.*, 2013). Such a change would interfere with biosonar operation by changing directionality and, hence, the detection range of prey, rendering character displacement undesirable in species that emit broadband echolocation signals. Furthermore, delphinid species that rely on broadband biosonar clicks for echolocation also use frequency-modulated whistles for mediating social interactions, and may rely on these for species recognition (Soto *et al.*, 2014). It should also be noted that species in the present study are often found in mixed species groups (Brown *et al.*, 2012), highlighting that it may be very challenging or impossible from a passive acoustic monitoring perspective to discriminate correctly between species in these sympatric delphinids.

The different environments inhabited by odontocetes may provide constraints on biosonar operations and have been hypothesized to influence biosonar parameters. Whereas species inhabiting open oceanic waters are likely limited by noise, those in shallow waters likely negotiate a more complex acoustic scene in close proximity to surfaces and vegetation. The detection range of these species is, therefore, likely to be limited by clutter and reverberation (Jensen *et al.*, 2013). If habitat-specific limitations are correct, we can make two predictions about source parameters. First, the echo-to-clutter or echo-to-reverberation ratio is not improved by increasing the outgoing source level, meaning that echolocating animals in a clutter-limited scenario may not increase detection range by increasing source level. Thus, animals in shallow habitats would be expected to use lower source levels than animals in open-ocean environments where higher source levels would mean longer prey detection range. Second, to avoid confusing a returning echo from echoes produced by subsequent clicks (range ambiguity), echolocating species typically wait a time period that exceeds the TWT to the target and back, before emitting subsequent clicks (Au, 1993; Wisniewska *et al.*, 2012). Animals that are limited to shorter echolocation distances would, therefore, be expected to produce clicks at faster repetition rates.

Both species presented here produced ICIs longer than those reported for riverine species, such as Irrawaddy or Ganges River dolphins (Jensen *et al.*, 2013), but shorter than ones produced by oceanic species [Atlantic bottlenose dolphins (*Tursiops truncatus*): 80–120 ms, Wahlberg *et al.*, 2011b]. The minimum and maximum ICI values produced by both *T. aduncus* and *S. sahulensis* illustrate the flexibility in repetition rates and, therefore, search ranges. A range dependent decrease in ICIs was found for both species as ICIs exceeded the TWT (Fig. 5). The low r^2 values of the two species (*T. aduncus*: $r^2 = 0.09$; *S. sahulensis*: $r^2 = 0.03$) indicate a high level of spread in the data, and likely highlight that individuals may not have been focusing on the array, but rather beyond it. However, it may also be due to a longer time being required to process the acoustically complex environment. Overall, both species' ICIs are comparable to those previously reported for *T. aduncus* foraging in a similar habitat (median: 52 ms, Jensen *et al.*, 2009), suggesting a reduced search range and a demand for fast update rates for successful orientation and navigation in such shallow complex environments.

Parallel with short ICIs, echolocating animals in shallow water seem to emit clicks with reduced levels as seen in Irrawaddy dolphins [195 $\pm$ 4 dB re 1 μPa (pp)] and Ganges River dolphins [183 $\pm$ 3 dB re 1 μPa (pp)] (Jensen *et al.*, 2013), indicating reduced search ranges in an acoustically complex environment. Both species studied here produced peak to peak source levels higher than those observed for riverine species, Irrawaddy dolphin, and Ganges River dolphin, likely due to the less acoustically complex coastal habitat. The present source levels are consistent with those found by Wahlberg *et al.* (2011b) for *T. aduncus* in a similar habitat [205 $\pm$ 7 dB re 1 μPa (pp)], but lower than source levels produced by similar sized deep water delphinids [oceanic bottlenose dolphin (*Tursiops truncatus*): 212 dB re 1 μPa (pp), Wahlberg *et al.*, 2011b; white beaked dolphins (*Lagenorhynchus albirostris*): up to 219 dB re 1 μPa (pp), Rasmussen *et al.*, 2002; and spotted dolphins (*Stenella frontalis*): up to 223 dB re 1 μPa (pp), Au and Herzing, 2003],

suggesting imposed constraints of different habitats on source levels by rendering high levels futile in cluttered environments.

Toothed whales have also been shown to decrease source levels and ICIs with decreasing target range as a means of maintaining echo levels constant (Au and Benoit-Bird, 2003; Jensen *et al.*, 2009; Wisniewska *et al.*, 2012) and producing a simpler auditory scene for processing and evaluation. In addition to the observed decrease in ICIs, both species studied here showed an apparent reduction in source levels with decreasing range (*T. aduncus*: 11 log Range; *S. sahulensis*: 20 log Range; Fig. 5). The lack of statistical significance of the interaction term between species and range suggests no differences in the way the two study species decrease source levels with range. The observed difference in coefficient may, therefore, be due to the clustering of data points at the extreme ends of the line which pull the line artificially. Furthermore, a lot of variability is present in the data as indicated by the low r^2 values (*T. aduncus*: $r^2 = 0.23$; *S. sahulensis*: $r^2 = 0.47$). This may suggest that individuals studied here do not always show range adjustments in the form of a range dependent, cognitive gain control (Au and Benoit-Bird, 2003; Jensen *et al.*, 2009; Kloepper *et al.*, 2014) due to the already low levels utilized in this clutter limited environment. Alternatively, the animals may not have locked their biosonars on the array, but happened to scan it while focusing on a different target. In spite of this, our results appear to support the hypothesis that habitat will influence biosonar source parameters through different selection pressures imposed by local acoustic properties. More specifically, odontocetes inhabiting cluttered shallow water environments will tend to produce lower source levels than similar sized deep-water delphinids as a likely consequence of limitations on detection range due to clutter.

It is becoming increasingly evident that odontocete biosonar behavior is very dynamic. Echolocating toothed whales readily adjust their acoustic sampling of the environment through changes to biosonar update rate, output level, and beam width (Wisniewska *et al.*, 2012, 2015; Finneran *et al.*, 2014; Kloepper *et al.*, 2014). Increasing repetition rates lead to a higher temporal resolution of their auditory scene and the simultaneous reduction in output levels reduces the ensonified range and, therefore, number of echoes detected (Wisniewska *et al.*, 2012), allowing echolocating animals to successfully navigate complex environments. Sympatric competition appears to play a very small role in driving biosonar signal parameters for delphinids with a broadband biosonar. The high level of control over biosonar source properties, combined with the strong off-axis distortion encountered by nearby odontocetes may explain why this would not be a very reliable cue for species identification. To attribute signal diversity purely to habitat shaping may be tempting, but the apparent convergence of all odontocetes on a high directionality suggests that biosonar parameters may mostly be driven by the inverse scaling of frequency to body size. To further ascertain the role of habitat and scaling in driving biosonar diversity, additional studies on species recorded across several diverse habitats, or of individuals moving between different habitats, would provide a powerful comparison and help separate the effects of phylogeny, habitat, and body size as the drivers of diversity in biosonar parameters and operation.

ACKNOWLEDGMENTS

We are deeply thankful to the following persons for logistic and technical support: Kristian Beedholm for help with equipment corrections and calibrations, John Svane and Niels Kristiansen for help building the array, Line Hermannsen and Nina Iversen for help with in-field calibrations and data collection, Danuta Wisniewska and Laia Rojano-Donate for stimulating discussions, and Tim Hunt for information on the local populations and advice on both species. Field work and equipment was funded by the National Danish Research Council via grants to P.T.M., and by an Honorary Walter Murdoch Professorship to P.T.M. F.H.J. was funded by postdoctoral fellowships from the Danish Council for Independent Research | Natural Sciences and the Carlsberg Foundation. This research was carried out under the approval of Murdoch University Animal Ethics Committee (Permit No. W2342/10) and approved by the Western Australian Department of Parks and Wildlife (Permit Nos. SF009373 and CE004048).

Akamatsu, T., Wang, D., Wang, K., Wei, Z., Zhao, Q., and Naito, Y. (**2002**). "Diving behaviour of freshwater finless porpoises (*Neophocaena phocaenoides*) in an oxbow of the Yangtze River, China," ICES J. Mar. Sci. **59**, 438–443.

Au, W. W. L. (**1993**). *The Sonar of Dolphins* (Springer, New York), pp. 1–277.

Au, W. W. L. (**2004**). "Echolocation signals of wild dolphins," Acoust. Phys. **50**, 454–462.

Au, W. W. L., and Benoit-Bird, K. J. (**2003**). "Automatic gain control in the echolocation system of dolphins," Nature **423**, 861–863.

Au, W. W. L., Branstetter, B., Moore, P. W., and Finneran, J. J. (**2012**). "Dolphin biosonar signals measured at extreme off-axis angles: Insights to sound propagation in the head," J. Acoust. Soc. Am. **132**, 1199–1206.

Au, W. W. L., and Herzing, D. L. (**2003**). "Echolocation signals of wild Atlantic spotted dolphin (*Stenella frontalis*)," J. Acoust. Soc. Am. **113**, 598–604.

Au, W. W. L., Kastelein, R. A., Rippe, T., and Schooneman, N. M. (**1999**). "Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*)," J. Acoust. Soc. Am. **106**, 3699–3705.

Au, W. W. L., Pawloski, J. L., Nachtigall, P. E., Blonz, M., and Gisner, R. C. (**1995**). "Echolocation signals and transmission beam pattern of a false killer whale (*Pseudorca crassidens*)," J. Acoust. Soc. Am. **98**, 51–59.

Brown, A., Bejder, L., Cagnazzi, D., Parra, G. J., and Allen, S. J. (**2012**). "The North West cape, Western Australia: A potential hotspot for Indo-Pacific humpback dolphins *Sousa Chinensis*?," Pac. Conserv. Biol. **18**, 240–246.

Denzinger, A., and Schnitzler, H. U. (**2013**). "Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats," Front. Physiol. **4**(164), 1–15.

Finneran, J. J., Branstetter, B. K., Houser, D. S., Moore, P. W., Mulsow, J., Martin, C., and Perisho, S. (**2014**). "High-resolution measurement of a bottlenose dolphin's (*Tursiops truncatus*) biosonar transmission beam pattern in the horizontal plane," J. Acoust. Soc. Am. **136**, 2025–2038.

Griffin, D. R. (**1958**). *Listening in the Dark: The Acoustic Orientation of Bats and Men* (Yale University Press, New Haven, CT), pp. 1–413.

Ibsen, S. D., Muller, M. W., Au, W. W. L., Nachtigall, P. E., and Breese, M. (**2013**). "Discrimination of phase altered targets by an echolocating Atlantic bottlenose dolphin," J. Acoust. Soc. Am. **133**, 1135–1140.

Jefferson, T. A., and Rosenbaum, H. C. (**2014**). "Taxonomic revision of the humpback dolphins (*Sousa* spp.), and description of a new species from Australia," Mar. Mammal Sci. **30**, 1494–1541.

Jensen, F., Rocco, A., Mansur, R. M., Smith, B. D., Janik, V. M., and Madsen, P. T. (**2013**). "Clicking in shallow rivers: Short-range

echolocation of Irrawaddy and Ganges River dolphins in a shallow, acoustically complex habitat," PloS ONE **8**, e59284.
Jensen, F. H., Bejder, L., Wahlberg, M., and Madsen, P. T. (**2009**). "Biosonar adjustments to target range of echolocating bottlenose dolphins (*Tursiops* sp.) in the wild," J. Exp. Biol. **212**, 1078–1086.
Jensen, F. H., Wahlberg, M., Beedholm, K., Johnson, M., de Soto, N. A., and Madsen, P. T. (**2015**). "Single-click beam patterns suggest dynamic changes to the field of view of echolocating Atlantic spotted dolphin (*Stenella frontalis*) in the wild," J. Exp. Biol. **218**, 1314–1324.
Johnson, M., Madsen, P. T., Zimmer, W. M., De Soto, N. A., and Tyack, P. L. (**2004**). "Beaked whales echolocate on prey," Proc. R. Soc. London, Ser. B: Biolog. Sci. **271**(Suppl. 6), S383–S386.
Kimura, S., Akamatsu, T., Fang, L., Wang, Z., Wang, K., Wang, D., and Yoda, K. (**2014**). "Apparent source level of free-ranging humpback dolphin, *Sousa chinensis*, in the South China Sea," J. Mar. Biol. Assoc. U. K. **FirstView**, 1–7.
Kloepper, L. N., Smith, A. B., Nachtigall, P. E., Buck, J. R., Simmons, J. A., and Pacini, A. F. (**2014**). "Cognitive adaptation of sonar gain control in the bottlenose dolphin," PloS ONE **9**, e105938.
Kyhn, L. A., Tougaard, J., Beedholm, K., Jensen, F. H., Ashe, E., Williams, R., and Madsen, P. T. (**2013**). "Clicking in a killer whale habitat: Narrow-band, high-frequency biosonar clicks of harbour porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*)," PloS ONE **8**, e63763.
Kyhn, L. A., Tougaard, J., Jensen, F., Wahlberg, M., Stone, G., Yoshinaga, A., Beedholm, K., and Madsen, P. T. (**2009**). "Feeding at a high pitch: Source parameters of narrow band, high-frequency clicks from echolocating off-shore hourglass dolphins and coastal Hector's dolphins," J. Acoust. Soc. Am. **125**, 1783–1791.
Madsen, P. T., Carder, D. A., Bedholm, K., and Ridgway, S. H. (**2005**). "Porpoise clicks from a sperm whale nose—Convergent evolution of 130 kHz pulses in toothed whale sonars?," Bioacoustics **15**, 195–206.
Madsen, P. T., Lammers, M., Wisniewska, D., and Beedholm, K. (**2013**). "Nasal sound production in echolocating delphinids (*Tursiops truncatus* and *Pseudorca crassidens*) is dynamic, but unilateral: Clicking on the right side and whistling on the left side," J. Exp. Biol. **216**, 4091–4102.
Madsen, P. T., and Surlykke, A. (**2013**). "Functional convergence in bat and toothed whale biosonars," Physiology **28**, 276–283.
Madsen, P. T., and Wahlberg, M. (**2007**). "Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales," Deep-Sea. Res., Part I **54**, 1421–1444.
Manly, B. F. (**2007**). *Randomization, Bootstrap and Monte Carlo Methods in Biology* (Chapman and Hall–CRC, Boca Raton, FL), pp. 1–456.
Melcon, M. L., Failla, M., and Iniguez, M. A. (**2012**). "Echolocation behavior of franciscana dolphins (*Pontoporia blainvillei*) in the wild," J. Acoust. Soc. Am. **131**, EL448–EL453.
Møhl, B., and Andersen, S. (**1973**). "Echolocation: High frequency component in the click of the harbor porpoise," J. Acoust. Soc. Am. **54**, 1368–1372.
Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A., and Lund, A. (**2003**). "The monopulsed nature of sperm whale clicks," J. Acoust. Soc. Am. **114**, 1143–1154.
Møhl, B., Wahlberg, M., Madsen, P. T., Miller, L. A., and Surlykke, A. (**2000**). "Sperm whale clicks: Directionality and source level revisited," J. Acoust. Soc. Am. **107**, 638–648.
Moore, P. W., Dankiewicz, L. A., and Houser, D. S. (**2008**). "Beamwidth control and angular target detection in an echolocating bottlenose dolphin (*Tursiops truncatus*)," J. Acoust. Soc. Am. **124**, 3324–3332.
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.
Parra, G. J., Corkeron, P. J., and Marsh, H. (**2004**). "The Indo-Pacific Humpback Dolphin, *Sousa chinensis* (Osbekc, 1765), in Australian Waters: A summary of current knowledge," Aquat. Mamm. **30**, 197–206.
Rasmussen, M. H., Miller, L. A., and Au, W. W. L. (**2002**). "Source levels of clicks from free-ranging white-beaked dolphins (*Lagenorhynchus albirostris* Gray 1846) recorded in Icelandic waters," J. Acoust. Soc. Am. **111**, 1122–1125.
Siemers, B. M., and Schnitzler, H. U. (**2004**). "Echolocation signals reflect niche differentiation in five sympatric congeneric bat species," Nature **429**, 657–661.
Soto, A. B., Marsh, H., Everingham, Y., Smith, J. N., Parra, G. J., and Noad, M. (**2014**). "Discriminating between the vocalizations of Indo-Pacific humpback and Australian snubfin dolphins in Queensland, Australia," J. Acoust. Soc. Am. **136**, 930–938.
Wahlberg, M., Beedholm, K., Heerfordt, A., and Møhl, B. (**2011a**). "Characteristics of biosonar signals from the northern bottlenose whale, *Hyperoodon ampullatus*," J. Acoust. Soc. Am. **130**, 3077–3084.
Wahlberg, M., Jensen, F. H., Soto, N. A., Beedholm, K., Bejder, L., Oliveira, C., Rasmussen, M., Simon, M., Villadsgaard, A., and Madsen, P. T. (**2011b**). "Source parameters of echolocation clicks from wild bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*)," J. Acoust. Soc. Am. **130**, 2263–2274.
Wahlberg, M., Møhl, 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., Miller, P. J., Johnson, M., Madsen, P. T., and Tyack, P. L. (**2006**). "Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*)," J. Anim. Ecol. **75**, 814–825.
Wisniewska, D. M., Johnson, M., Beedholm, K., Wahlberg, M., and Madsen, P. T. (**2012**). "Acoustic gaze adjustments during active target selection in echolocating porpoises," J. Exp. Biol. **215**, 4358–4373.
Wisniewska, D. M., Ratcliffe, J. M., Beedholm, K., Christensen, C. B., Johnson, M., Koblitz, J. C., Wahlberg, M., and Madsen, P. T. (**2015**). "Range-dependent flexibility in the acoustic field of view of echolocating porpoises (*Phocoena phocoena*)," eLife 2015;10.7554/eLife.05651.