

Echolocation signals of Heaviside's dolphins (*Cephalorhynchus heavisidii*)^{a)}

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Field recordings of echolocation signals produced by Heaviside's dolphins (*Cephalorhynchus heavisidii*) were made off the coast of South Africa using a hydrophone array system. The system consisted of three hydrophones and an A-tag (miniature stereo acoustic data-logger). The mean centroid frequency was 125 kHz, with a -3 dB bandwidth of 15 kHz and -10 dB duration of 74 μ s. The mean back-calculated apparent source level was 173 dB re 1 μ Pa_{p-p}. These characteristics are very similar to those found in other *Cephalorhynchus* species, and such narrow-band high-frequency echolocation clicks appear to be a defining characteristic of the *Cephalorhynchus* genus. Click bursts with very short inter-click intervals (up to 2 ms) were also recorded, which produced the "cry" sound reported in other *Cephalorhynchus* species. Since inter-click intervals correlated positively to click duration and negatively to bandwidth, Heaviside's dolphins may adjust their click duration and bandwidth based on detection range. The bimodal distribution of the peak frequency and stable bimodal peaks in spectra of individual click suggest a slight asymmetry in the click production mechanism.

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I. INTRODUCTION

Heaviside's dolphins (*Cephalorhynchus heavisidii*) are endemic to the west coast of southern Africa and typically occur within a few kilometers off the shore in waters less than 180 m deep (Best and Abernethy, 1994). Although our knowledge of this species remains limited, its ecology and behavior seem broadly similar to those of the other *Cephalorhynchus* species (Dawson, 2009), with individuals displaying relatively small home ranges and engaging in diurnal inshore-offshore movements that are apparently driven by the diurnal cycle of

their main prey, juvenile hake (*Merluccius* spp.) (Sekiguchi *et al.* 1992; Best and Abernethy, 1994; Elwen *et al.*, 2006). Prior to the current study, the sounds made by Heaviside's dolphins received very little attention; some three decades ago Watkins *et al.* (1977) described the sounds made by four Heaviside's dolphins temporarily held in a rock pool. The authors noted low-level clicks with various repetition rates, ranging from 2 to over 100/s, short (0.3–0.5 s) bursts of clicks at 50–70 clicks per second, and "cry" sounds made up of a rapid series of pulses, up to 500/s and 0.4–2 s in duration. The limited bandwidth (BW) of the recording equipment used (60 Hz to 10 kHz) meant that the high-frequency click components, since described for other *Cephalorhynchus* species (e.g., Dawson, 1988), could not be recorded.

All *Cephalorhynchus* species except Heaviside's dolphins have been reported to produce narrow-band high-frequency (NBHF, *sensu* Madsen *et al.*, 2005) clicks. The echolocation clicks of Hector's dolphins (*Cephalorhynchus hectori*) (Dawson, 1988; Dawson and Thorpe, 1990; Thorpe and Dawson, 1991; Thorpe *et al.*, 1991), Commerson's dolphins (*Cephalorhynchus commersonii*) (Kamma and

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Wiersma, 1982; Yeh *et al.*, 1982; Evans and Awbrey, 1988; Evans *et al.*, 1988, Hatakeyama *et al.*, 1988; Dziedzic and De Buffrenil, 1989; Nakamura, 1999, Kyhn *et al.*, 2010), and Chilean dolphin (*Cephalorhynchus eutropia*) (Götz *et al.*, 2010) have been described in detail. Compared to the very short ($<50 \mu\text{s}$), intense (often $>200 \text{ dB re } 1 \mu\text{Pa}$) broadband ($-3 \text{ dB BW } >10 \text{ of kHz}$) clicks typical of other delphinids (Au, 1997; 2002), NBHF clicks are longer ($>125 \mu\text{s}$), typically $>20 \text{ dB}$ less intense signals with one peak above 100 kHz and with narrower BWs (-3 dB BW typically $<10 \text{ kHz}$). The main pulse of delphinid broadband clicks usually contains one or two cycles with the first cycle achieving maximum amplitude. In contrast, NBHF clicks typically have a waveform whose amplitude increases over the first five cycles and then decays exponentially (Nakamura and Akamatsu, 2004). Recently, hourglass dolphins (*Lagenorhynchus cruciger*) (Tougaard and Kyhn, 2010) and Peale's dolphins (*Lagenorhynchus australis*) (Kyhn *et al.*, 2010), whose taxonomy is currently debated, were reported to produce NBHF clicks. These data support the argument of May-Collado and Agnarsson (2006), which was made on the basis of molecular phylogeny inferred from cytochrome *b* that hourglass dolphins and Peale's dolphins be transferred to the *Cephalorhynchus* genus. If click characteristics are potentially important for taxonomic considerations, descriptions of these clicks are necessary for the lesser known cetaceans, such as Heaviside's dolphins.

Species producing NBHF clicks are found in at least three different odontocete groups, Kogiidae, Phocoenidae, genus *Cephalorhynchus*, and possibly Pontoporiidae (Madsen *et al.*, 2005; Morisaka and Connor, 2007). It is hypothesized that the convergent evolution of NBHF clicks may have evolved for acoustic crypsis as an anti-predator strategy against killer whales (*Orcinus orca*) (Morisaka and Connor, 2007).

Here we describe in detail the echolocation clicks of Heaviside's dolphins, so that they may be compared with those of other species known to produce NBHF clicks.

II. MATERIALS AND METHODS

A. Study area and equipment

Acoustic recordings were made in January and February 2008 at Table Bay ($33^{\circ}89'S$, $18^{\circ}40'E$) and St. Helena Bay ($32^{\circ}76'S$, $18^{\circ}03'E$), on the southwest coast of South Africa, in water depths ranging from 5 to 32 m. The two delphinid species most frequently encountered in this area, Heaviside's dolphins and dusky dolphins (*Lagenorhynchus obscurus*), can be easily distinguished by their dorsal fins. Recordings were done during the sole presence and in close proximity to Heaviside's dolphins.

Recordings were made with a T-shaped array (Fig. 1) consisting of one miniature stereo acoustic data-logger ([A-tag; ML200-AS2: Marine Micro Technology, Saitama, Japan; Akamatsu *et al.* (2008)], sensitivity $-201 \text{ dB re } 1 \text{ V/1 } \mu\text{Pa}$ between 100 and $160 \text{ kHz} \pm 5 \text{ dB}$) and three calibrated hydrophones: one Reson TC 4012 hydrophone with VP 2000 amplifier (Reson A/S, Slangerup, Denmark; sensitivity $-211 \text{ dB re } 1 \text{ V/1 } \mu\text{Pa}$ between 70 and $160 \text{ kHz} \pm 3 \text{ dB}$) and one Aquafeeler III system (System Intech, Co., Ltd., Tokyo,

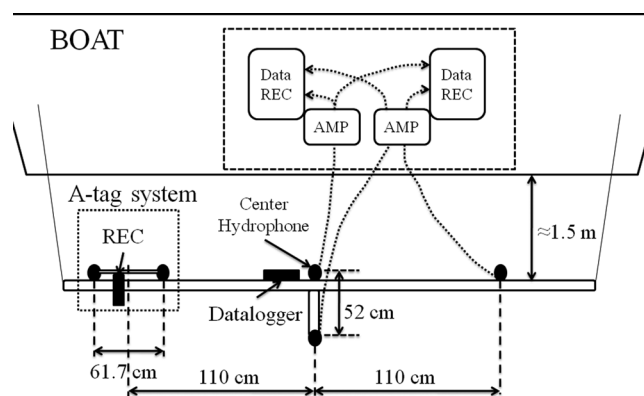


FIG. 1. Recording system. One miniature stereo acoustic data-logger (A-tag) and three hydrophones attached to a 3 m pole. Black circles indicate hydrophones. Acoustic data were recorded on two data-recorders. One data-logger monitored system movement. AMP: amplifier, REC: recorder.

Japan) with two hydrophones (SH200K-0801 and SH200K-0802; sensitivity -213 dB and $-216 \text{ dB re } 1 \text{ V/1 } \mu\text{Pa}$ between 70 and $160 \text{ kHz} \pm 3 \text{ dB}$, respectively). The A-tag is a miniature high-frequency pulse event recorder, which stored the intensity of the received pulse every 0.5 ms along with the difference in the arrival time of each pulse between the two hydrophones with a resolution of 271 ns (Akamatsu *et al.*, 2008; Li *et al.*, 2009). High-pass filters were set at 100 Hz for the Reson and at 200 Hz for the Aquafeeler III. The Reson hydrophone was the center hydrophone and was used for measurements of click characteristics. This hydrophone's output was low-pass filtered at 250 kHz to avoid aliasing.

The array, attached to 3 m stainless steel pole, was suspended in the water so that its long axis was parallel to the water surface at a depth of approximately 2 m, and it was approximately 1.5 m from the bottom of the boat. Straight reflections from the bottom of the boat would only be recorded if signals approached vertically from -45° to -90° , and these angles were not used in the analysis. Two 1 kg (at both sides) and one 2 kg (at center bottom) weights were added to the T-array to stabilize it in the water column, and a data-logger (PD2GT; Little Leonardo, Tokyo, Japan) was attached to record the depth and movement of the array. Data recorded at times when the array moved back and forth, or rolled strongly, were not used for the analysis described below.

Acoustic data from the three hydrophones were recorded on two stereo EZ 7510 (NF corporation, Yokohama, Japan) data-recorders which consist of an analog-to-digital converter (sampled at 500 kHz, 16 bit resolution) with data stored on a 40 GB hard disk drive (HDD). Output from the central Reson hydrophone was amplified via a VP2000 amplifier and then recorded on channel 1 of each of stereo recorders. Output from each of the other two hydrophones was amplified via the stereo Aquafeeler III system and then recorded on the remaining channel of each of the recorders. The relative gain of each amplifier was recorded in the field notes. For the calculation of the receiver level, these gains were used to compare between different channels. The sound intensity received by the two hydrophones and the sound arrival time difference between the two hydrophones of the A-tag were stored in the A-tag itself when the received level was larger than the trigger level (129 dB).

B. Estimation of source level

The sound source level (SL) is defined as the sound pressure level back-calculated to 1 m from the sound source. Due to the directionality of the beam pattern, the sound pressure level should be measured in front of the phonating dolphin on its acoustic axis (see the last sentence of this section). The distance between the array and the dolphin was calculated independently using the hydrophone array system. The distance calculation was performed using a custom-built Igor Pro (WaveMetrics, Lake Oswego, OR) routine, based on time-of-arrival differences (TOADs) of the same signal from three pairs of hydrophones; the two hydrophones of the A-tag, the center and right hydrophones, and the center and bottom hydrophones. Simulations of a 170 dB (re 1 μPa @ 1 m) signal using the Cramer-Rao Bound estimation (System Intech Company Limited, 2009) suggest that this system has less than ± 1 m distance error within 50 m from the array. Because the array is two dimensional, it cannot estimate exact three-dimensional positions.

The speed of sound in the water was calculated at 1505 m/s from salinity (36 ppt) and temperature (14°C) measurements based on the Medwin equation (Medwin, 1975). Transmission loss (TL) was estimated by $TL = 20 \log(R) + R\alpha$, where R is the estimated distance between the dolphin and the center hydrophone, and α is the frequency-dependent absorption at α 125 kHz signal calculated using previously described methods (Francois and Garrison, 1982).

The SL can be calculated from the sonar equation, $SL = RL + TL$, where RL is the received sound level. Dolphin clicks are directional, and it is important to select clicks as close to on-axis as possible (Au, 1993; Madsen and Wahlberg, 2007). Since it was impossible to accurately determine whether the phonating dolphin faced directly toward the center hydrophone (on-axis), we refer to our measurements as the “apparent source level” (ASL) (Møhl *et al.*, 2000; Madsen and Wahlberg, 2007). The ASL has been defined as the back-calculated peak-to-peak sound pressure level at a distance of 1 m from a directional source in an unknown (off-axis or on-axis) direction (*sensu* Møhl *et al.*, 2000).

In order to choose clicks as close to on-axis as possible, we followed the selection criteria of Villadsgaard *et al.* (2007) and Kyhn *et al.* (2009) after selecting clicks with regular inter-click intervals (ICIs), which are considered to be produced by an individual, not multiple individuals (Akamatsu *et al.*, 1998). Thus, measured clicks had to: (1) be detectable on all hydrophones, (2) have greater amplitude on the direct path than any other reflections, (3) have the maximum amplitude in a click train series, and (4) show maximum amplitude on the center hydrophone. In addition, we required measured clicks to (5) have a waveform consisting only of a single pulse (clicks whose waveforms contained double or more pulses were removed) and (6) be localized within 50 m of the center hydrophone.

C. Click analysis

Click parameters were analyzed with a custom-built Igor Pro (WaveMetrics) routine (Madsen and Wahlberg, 2007). We measured the same parameters of previous studies

(Villadsgaard *et al.*, 2007; Kyhn *et al.*, 2009) to facilitate comparisons with other species.

Following Kyhn *et al.* (2009) we measured click duration at 10 dB below the peak of the click envelope (-10 dB duration). The centroid frequency (f_c) represented the frequency that divides the spectrum into two halves of equal energy, and the peak frequency (f_p) was the highest frequency at the highest spectrum energy. The BW was parameterized by the -3 dB_BW (kHz; frequency range within 3 dB below the maximum spectral peak), -10 dB_BW (kHz; 10 dB below the spectral peak), and the root-mean-square BW of the spectrum (rms_BW, in kHz, which provides a measure of the spectral standard deviation around the centroid frequency). The quality factor (Q_{rms} ; Au, 1993) was the value of the centroid frequency divided by the rms_BW. A large Q -factor means a narrow-band signal since most of the sound energy is concentrated in a narrow frequency band.

ASLs were obtained as the peak-to-peak sound pressure level [ASL_pp (dB re 1 $\mu\text{Pa}_{\text{p-p}}$)], rms sound pressure level calculated over the -10 dB duration of the signal (ASL_ -10dB [dB re 1 μPa rms]), and energy flux density which was the signal energy integrated over the -10 dB duration [EFD_ -10dB [dB re 1 μPa^2 s]].

ICIs were determined as the average of the two intervals between (1) the on-axis click and the click preceding the on-axis click and (2) between the on-axis click and the click following the on-axis click.

Since individual clicks often had second peak in their spectra, the frequency of second peak was manually measured from each spectrum with second peak. The second peak is defined here as obvious spectral peak having an amplitude $>25\%$ of the highest spectral peak.

All statistical analyses were conducted using JMP 7 (SAS Institute, Inc., Cary, NC).

III. RESULTS

Total sound recording time was 9 h 55 min 23 s. No pure tonal whistles were recorded. Since Table Bay had a worse signal-to-noise ratio than St. Helena Bay, we only used acoustic data from St. Helena Bay. After excluding recordings in which other delphinid species were seen or suspected to be present, 2 h 34 min of recordings remained for further analysis. These recordings were from 7 groups of 2–13 dolphins. Animals were engaged in various behaviors, including travelling, resting, milling, and socializing.

We analyzed 372 click train series from Heaviside’s dolphins. Ninety-nine clicks were selected as on-axis signals for further analysis. An example of a Heaviside’s dolphin click is shown in Fig. 2. All click parameters are summarized in Table I. The estimated range from the array was from 1.8 to 45.8 m (mean, 12.7 ± 8.0 m).

Peak frequency formed a bimodal distribution, with histogram peaks at 122 and 130 kHz (Fig. 3). The clicks with a higher peak frequency (>125 kHz) tended to have stronger ASL_pp than those with a lower peak frequency (≤ 125 kHz); however, the difference was not statistically significant (two-tailed t -test, $t = 1.94$, $f = 97$, $p = 0.056$). The centroid frequency was significantly correlated with ASL_pp

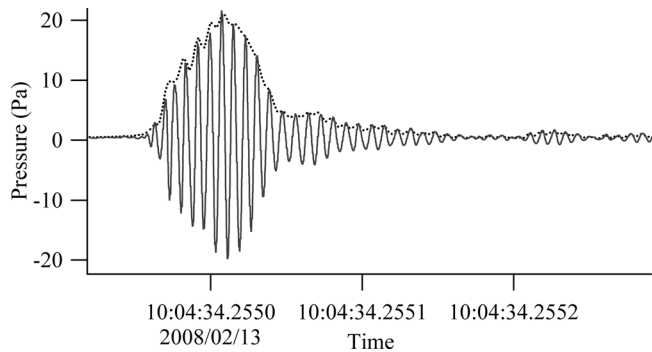


FIG. 2. An example of a waveform of a Heaviside's dolphin click. The dotted line indicates the signal envelope.

[analysis of variance (ANOVA), $F = 4.48$, $f = 97$, $p = 0.037$; Fig. 4). Individual clicks showed either a single peak or bimodal peaks in their spectra at around 122 and 130 kHz. Four different click types were classified based on the amplitude difference between second peak and highest spectral peak (Fig. 5).

ICIs varied between 2 and 113 ms (Fig. 6). Six click sequences had ICIs of less than 10 ms, but only two were included for ICI analysis. There was a gap at 10–20 ms of the ICI distribution. Clicks made in rapid series tended to be shorter; ICIs showed significant positive relationships to -3 and -10 dB BWs and to -10 dB duration (ANOVA, $F = 21.8$, 39.2 , and 26.9 , respectively, all $p < 0.0001$; Fig. 7). All three BW measurements (-3 dB, -10 dB, and rms) were negatively correlated to the -10 dB duration (ANOVA, $F = 58.5$, 206.3 , and 4.1 , $p < 0.0001$, 0.0001 , and 0.05 , respectively).

IV. DISCUSSION

A. NBHF clicks of Heaviside's dolphins

Similar to other *Cephalorhynchus* species, Heaviside's dolphins produced NBHF clicks and did not produce whistles. NBHF clicks and the lack of whistles are thus distinctive features of the genus *Cephalorhynchus* (Kyhn *et al.*, 2009; Götz *et al.*, 2010; Tougaard and Kyhn, 2010). In one study, Dawson and Thorpe (1990) analyzed a large sample of recordings made with a single hydrophone, and although they could not be sure of the orientation of the phonating animal toward the hydrophone, the Heaviside's dolphin sounds found in our study are very similar to the single pulses described by Dawson and Thorpe. More recently, Kyhn *et al.* (2009) used a hydrophone array to record sounds produced by Hector's dolphins and could eliminate the off-axis clicks. The parameters measured by Kyhn *et al.* for Hector's dolphins are very similar to those reported here for Heaviside's dolphins (Table I).

The average ASL of Heaviside's dolphin clicks is 173 dB (161–186) re $1 \mu\text{Pa}_{\text{p-p}}$, which is similar to reported values for coastal Hector's dolphins of 177 dB (161–187) (Kyhn *et al.*, 2009) and Commerson's dolphins of 177 dB (165–190) (Kyhn *et al.*, 2010). However, the source level is lower than those for some other NBHF species—197 dB (190–203) for hourglass dolphins (Kyhn *et al.*, 2009); 185

dB (169–196) for Peale's dolphins (Kyhn *et al.*, 2010); 178–205 dB for harbour porpoises, *Phocoena phocoena* (Villadsgaard *et al.*, 2007); and 197 dB (180–209) for riverine finless porpoises, *Neophocaena phocaenoides asiaorientalis* (Li *et al.*, 2009)—and also much lower than the broadband clicks made by other delphinid species, such as bottlenose dolphins (228 dB, Au, 1993).

Three possible mechanisms could be here considered to explain these source level variations: phylogenetic, body length, and environmental difference. There seems to be a phylogenetic difference between the family Phocoenidae and genus *Cephalorhynchus* in terms of click source level, i.e., weaker clicks produced by the genus *Cephalorhynchus* than other species mentioned above. The family Phocoenidae, Monodontidae, and Delphinidae are estimated to share a common ancestor until about 20 million years ago (Nikaido *et al.*, 2001). The Delphinidae diverged after the Phocoenidae and Monodontidae, and then the genus *Cephalorhynchus* emerged from the Delphinidae, and the Phocoenidae split from the Monodontidae. As the weak NBHF clicks were thought to emerge independently in the Phocoenidae and the genus *Cephalorhynchus* (Morisaka and Connor, 2007), the reduction rate of click source level could be different in the Phocoenidae and the genus *Cephalorhynchus*.

However, as Kyhn *et al.* (2010) suggested, the body size, which is known to influence the sound intensity in several animals (e.g., birds, Brumm, 2004), could also explain the weak clicks produced by the genus *Cephalorhynchus* because members of this genus are smaller (Heaviside's dolphins, maximum 1.7 m; Hector's dolphins, maximum 1.5 m; Commerson's dolphins, maximum 1.5 m) than other NBHF species (harbour porpoises, maximum 2.0 m; finless porpoises, maximum 1.9 m; hourglass dolphins, maximum 1.8 m; Peale's dolphins, maximum 2.2 m; size data from Jefferson *et al.*, 1993). Phylogenetic constraints or body size differences might be among the factors controlling the click source level, especially in genus *Cephalorhynchus*.

However, both phylogeny and body size explanation fail to explain the high source levels of hourglass and Peale's dolphins. Although both species have been proposed for transfer to the *Cephalorhynchus* genus (May-Collado and Agnarsson, 2006), the source levels of these species' clicks are obviously higher than those of the genus *Cephalorhynchus*.

The genus *Cephalorhynchus* produce weaker clicks but inhabit a similarly cluttered acoustic environment to harbour porpoise and the riverine finless porpoise. Akamatsu *et al.* (2007) reported that harbour porpoises produce clicks with longer ICIs than riverine finless porpoise, suggesting that there is environmental difference between their habitats. Nevertheless, these porpoises produce clicks with similar source levels, which suggest that environmental differences do not explain the source level differences between the *Cephalorhynchus* dolphins and these two phocoenids. Environmental differences might, however, explain the relatively stronger clicks produced by hourglass dolphins. Kyhn *et al.* (2009) hypothesized that offshore NBHF species produce clicks with higher source levels than coastal species. As Kyhn *et al.* (2009) suggested, further acoustic studies of offshore NBHF species, such as Dall's porpoise (*Phocoenoides dalli*),

TABLE I. Average (\pm standard deviation) and range of echolocation click source parameters produced by Heaviside's dolphins (*C. heavisidii*). Additional *Cephalorhynchus* species (*C. hectori*, *C. commersonii*, and *C. eutropia*) and other NBHF species (*L. cruciger*, *L. australis*, *P. phocoena*, and *N. phocaenoides*) are listed for comparison.

Source parameters	Heaviside's dolphin, <i>C. heavisidii</i> This study		Hector's dolphin, <i>C. hectori</i> Kyhn <i>et al.</i> (2009)	Commerson's dolphin, <i>C. commersonii</i> Kyhn <i>et al.</i> (2010)	Chilean dolphin, <i>C. eutropia</i> Götz <i>et al.</i> (2010)	Hourglass dolphin, <i>L. cruciger</i> Kyhn <i>et al.</i> (2009)	Peale's dolphin, <i>L. australis</i> Kyhn <i>et al.</i> (2010)	Harbour porpoise, <i>P. phocoena</i> Villadsgaard <i>et al.</i> (2007)	Finless porpoise	
	Average \pm SD	Range	Average \pm SD	Average \pm SD	Average	Average \pm SD	Average \pm SD	Range	<i>N. p. asiaeorientalis</i> Li <i>et al.</i> (2005, 2009)	<i>N. p. sunameri</i> Li <i>et al.</i> (2007)
ASL_pp (dB re 1 μ Pa _{p.-p.})	173 \pm 5	161–186	177 \pm 6	177 \pm 5	n.a.	197 \pm 4	185 \pm 6	178–205	197 ^a	n.a.
ASL ₋₁₀ dB (dB re 1 μ Pa _{rms})	161 \pm 5	149–174	166 \pm 6	166 \pm 5	n.a.	186 \pm 4	173 \pm 6	166–194	n.a.	n.a.
EFD ₋₁₀ dB (dB re 1 μ Pa ² s)	120 \pm 5	108–135	121 \pm 4	125 \pm 5	n.a.	146 \pm 3	133 \pm 6	123–150	n.a.	n.a.
–10 dB duration (μ s)	74 \pm 9	53–115	57 \pm 6	78 \pm 1	83 \pm 30 ^b	115 \pm 24	92 \pm 2	44–113	68 \pm 14 ^c	80 \pm 11 ^c
Peak Frequency (kHz)	125 \pm 4	118–132	129 \pm 5	132 \pm 6	126 \pm 2	126 \pm 2	126 \pm 3	129–145	125 \pm 7	121 \pm 4
Centroid Frequency (kHz)	125 \pm 2	121–130	128 \pm 3	133 \pm 2	126 \pm 2	128 \pm 2	129 \pm 3	130–142	n.a.	n.a.
–3 dB _{BW} (kHz)	15 \pm 3	6–21	20 \pm 3	21 \pm 3	18 \pm 5	8 \pm 2	15 \pm 4	6–26	20 \pm 4	18 \pm 3
–10 dB _{BW} (kHz)	23 \pm 2	17–30	30 \pm 10	n.a.	34 \pm 8	13 \pm 2	n.a.	14–46	n.a.	n.a.
RMS _{BW} (kHz)	15 \pm 6	7–33	18 \pm 5	12 \pm 3	12 \pm 2	11 \pm 4	12 \pm 3	5–12	n.a.	n.a.
<i>Q</i> _{rms}	9 \pm 3	4–18	8 \pm 2	12 \pm 3	8 \pm 3 ^d	13 \pm 5	12 \pm 3	12–30	7 \pm 2	7 \pm 1
ICI (ms)	58 \pm 22	2–113	n.a. ^e	n.a. ^f	2–?	n.a.	n.a.	6–200	n.a.	n.a.
Range from array (m)	13 \pm 8	2–46	11 \pm 4	21	n.a.	50 ^g	16	5–75	n.a. ^h	n.a. ⁱ
<i>n</i>	99		16	94	83	58	87	37	548 ^j	71
Recordings	6 hydrophones		4 hydrophones	6 hydrophones	1 hydrophone	4 hydrophones	6 hydrophones	3–4 hydrophones	1 hydrophone ^j	1 hydrophone

^aRange 180–209 dB.

^bDuration 20 dB below the peak of the click envelope.

^cDuration between two points where the click oscillations rose from the background noise and descended into the background noise.

^d*Q*_{-3dB}.

^eMedian value 27 and range 1–60 in Thorpe *et al.* (1991) using 7661 clicks.

^f22 \pm 2.5 ms in average and SD, range 2–30 in Hatakeyama *et al.* (1988).

^gEstimated minimum range.

^hRange 25–73 m.

ⁱRange 5–50 m.

^j*n* = 34, 4-hydrophone recording for ASL measurement in Li *et al.* (2009).

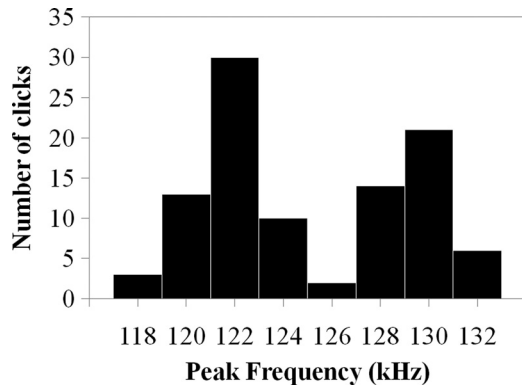


FIG. 3. Histogram of peak frequency from 99 on-axis clicks produced by Heaviside's dolphins. Bin width is 2 kHz.

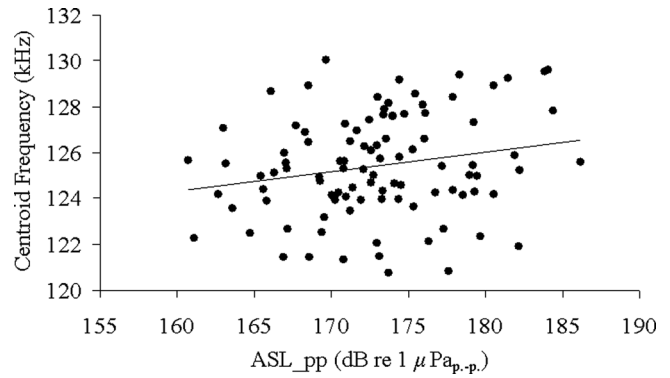


FIG. 4. Centroid frequency as a function of the ASL of Heaviside's dolphins. Regression line: $y = 0.086x + 111$, $R^2 = 0.04$.

would be helpful to answer this question. Thus, multiple mechanisms could be controlling the source level of the clicks produced by those species. Further comparisons of source level among species should consider sonar gain control, which is the mechanism by which the amplitude increases with increasing target range.

There is a high degree of similarity in the peak frequency of clicks made by *Cephalorhynchus* species, including Heaviside's dolphin, Hector's dolphin, and Chilean dolphin, as well as hourglass dolphin and Peale's dolphin (Table I). Harbour porpoises appear to have a higher peak frequency than *Cephalorhynchus*. Finless porpoises, which belong to the same family as harbour porpoises (Phocoenidae), produce clicks with similar peak frequency as *Cephalorhynchus*, and thus the high peak frequency in clicks of harbour porpoises cannot be explained by a phylogenetic difference. Clearly, the slightly higher peak frequency of clicks produced by Commerson's dolphins cannot be explained by a phylogenetic difference either. Kyhn *et al.* (2010) proposed that character displacement mechanisms might work on the centroid frequencies of the clicks of two sympatric NBHF species, such as Peale's dolphins and Commerson's dolphins. If true, this would not be the case with harbour por-

poise in Denmark where the harbour porpoises were recorded (Villadsgaard *et al.*, 2007) because no sympatric NBHF species occur there. Further detailed researches for each species are needed for exact comparisons of the peak frequencies produced by NBHF species.

The duration measurement of Heaviside's dolphin clicks was, however, different from those of Hector's, Peale's and hourglass dolphins and similar to those of Commerson's dolphins and harbour porpoises. Kyhn *et al.* (2009) suggested that hourglass dolphin clicks have a longer duration than clicks of two other NBHF species (Hector's dolphin and harbour porpoise), which likely facilitates a longer detection range in their pelagic environment. This could also be the case with continental shelf-living Peale's dolphins. However, those authors did not discuss the differences in click duration displayed by Hector's dolphins and harbour porpoises. As harbour porpoises and Heaviside's, Hector's, and Commerson's dolphins all inhabit coastal shallow waters, there is no obvious difference in their environments. The recording context could potentially explain the difference in click durations between Hector's dolphins in the study by Kyhn *et al.* (2009) and other species, i.e., Heaviside's dolphins (present study), Commerson's dolphins (Kyhn *et al.*, 2010), and harbour

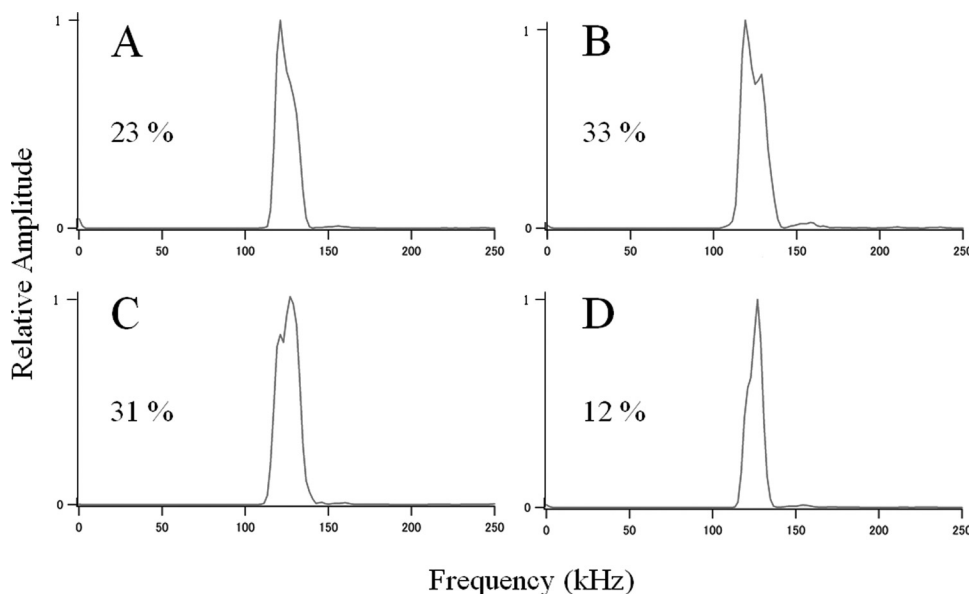


FIG. 5. Spectra of four examples of Heaviside's dolphin clicks [fast Fourier transform (FFT) size 256, spectrum interpolated with a factor of 10, sampling rate of 500 kHz, and Hanning window]. (A) A single peak spectrum with a peak frequency at around 122 kHz; (B) a bimodal spectrum with a peak frequency at around 122 kHz and a second peak at around 130 kHz; (C) a bimodal spectrum with a peak frequency at around 130 kHz and a second peak at around 122 kHz; (D) a single peak spectrum with a peak frequency at around 130 kHz. The percentage of the click type is also shown to the left of the spectrum.

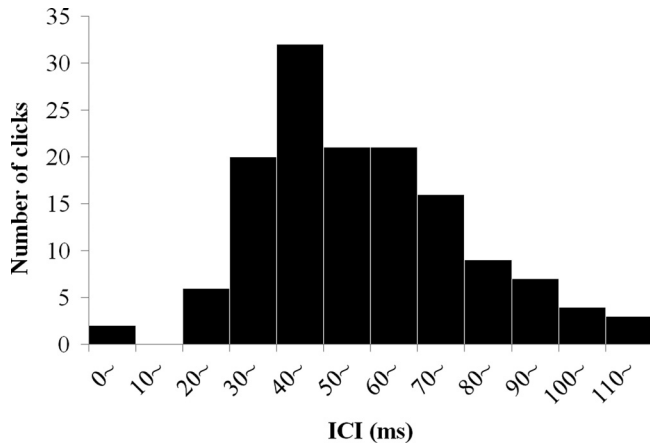


FIG. 6. Histogram of ICIs from Heaviside's dolphins ($n = 141$; average 58 ms; standard deviation 22 ms; bin width 10 ms).

porpoises (Villadsgaard *et al.*, 2007). In Heaviside's dolphins, click duration shortens when ICIs decrease. Because ICIs usually correlate with the distance between the dolphin and its sonar target (Au, 1993), the Hector's dolphins recorded in the study by Kyhn *et al.* (2009) may have been closer to the recording array than the animals recorded in this study by Kyhn *et al.* (2010) and by Villadsgaard *et al.* (2007).

Heaviside's dolphins thus produce NBHF clicks that are very similar to those of other *Cephalorhynchus* species.

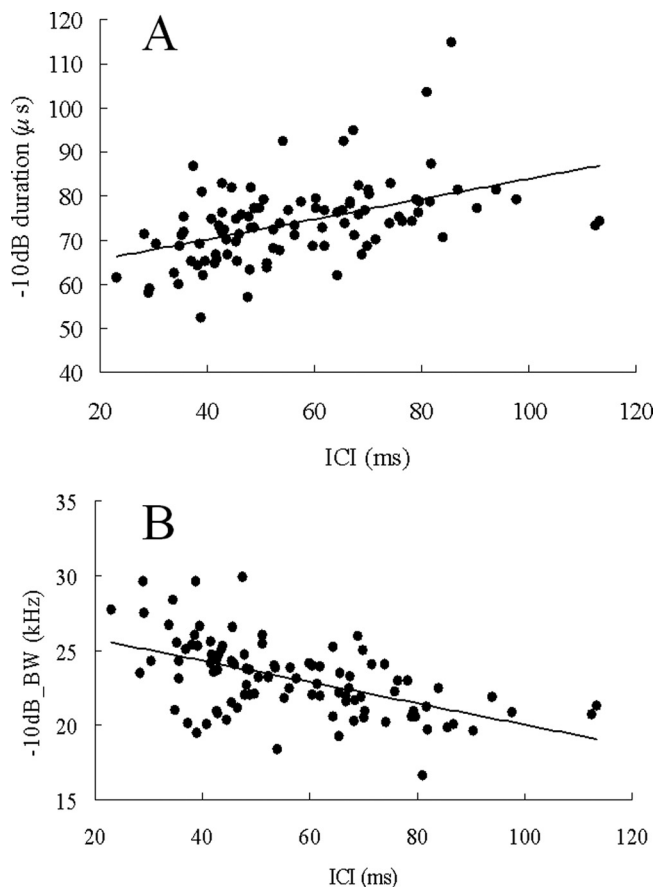


FIG. 7. (A) 10 dB duration as a function of ICI. Regression line: $y = 0.23x + 61$, $R^2 = 0.22$; (B) 10 dB_BW as a function of ICI. Regression line: $y = -0.07x + 27$, $R^2 = 0.29$.

Heaviside's dolphins are currently considered the basal species in the genus *Cephalorhynchus* (Pichler *et al.*, 2001). Moreover, a recent study by May-Collado and Agnarsson (2006) suggested that *L. cruciger* and *L. australis*, which also produce NBHF clicks (Tougaard and Kyhn, 2010, Kyhn *et al.*, 2010), might need to be reclassified taxonomically into the genus *Cephalorhynchus* and that Heaviside's dolphins may be one of the closest relatives to these (currently) *Lagenorhynchus* species. Such NBHF echolocation clicks with weaker source levels appear to be an important defining characteristic of this genus.

B. Relationships among ICIs, durations, and BWs of the Heaviside's clicks

The ICIs of the Heaviside's clicks significantly correlated with click duration (positively) and BW (negatively). In other words, clicks had longer duration and narrower BW, as successive clicks are spaced further apart. These relationships have also been observed in bats, another taxa known to echolocate (Kalko and Schnitzler, 1993; Surlykke and Moss, 2000). Dolphins normally space their clicks apart so that the previous pulse's echo returns before the next pulse is emitted (Au *et al.*, 1982). Hence, in most species ICIs linearly correlate to the target range (Au, 1993). It is possible that Heaviside's dolphins, and possibly other *Cephalorhynchus* species, can lengthen their echolocation clicks in order to detect distant targets. Using longer duration clicks increases the energy of the signal without increasing its amplitude. Narrowing the BW should improve the signal to noise ratio. Increasing click energy increases the likelihood that at least some will be reflected back, and narrowing the BW is advantageous to extract signal out of broadband noise. This may also allow for acquisition of relative target velocity via Doppler shift (Thorpe *et al.*, 1991).

All BW measurements were negatively correlated to click duration. This is expected because a signal of a very short duration has too few cycles to precisely encode frequency information.

C. Bimodal peak frequency in Heaviside's dolphin clicks

The distribution of the peak frequency of Heaviside's dolphin clicks was bimodal, with 122 and 130 kHz peaks. As shown in Figure 5, each individual click appeared to have either a single peak or a bimodal spectrum with two stable peaks at around 122 and 130 kHz. NBHF click spectra have been previously described as single peaked (Au *et al.*, 1999; Nakamura and Akamatsu, 2004). Bimodal peak frequency has often been observed in broadband click species, such as bottlenose dolphins, belugas, and false killer whales (Au, 2000), and is proposed to be due to asymmetry in the sound generator (Cranford *et al.*, 1996; Lammers and Castellote, 2009). Cranford *et al.* (1996) suggested that the length of the fatty dorsal bursae within the monkey lips/dorsal bursae (MLDB) complex, which plays a central role in the production of clicks, is related to peak frequency. The size of the right dorsal bursae is about twice as large as that of the left in the broadband click species, while the dorsal bursae in

NBHF click species, like the harbour porpoise and Commerson's dolphin, are only slightly asymmetric. These species make NBHF clicks with a single peak or two indistinguishable peaks (Cranford *et al.*, 1996). The bimodal peak frequency in clicks made by Heaviside's dolphins suggests that the dorsal bursae could be asymmetric. Similar to our findings for Heaviside's dolphins, Au *et al.* (2005) found a positive relationship between peak-to-peak source level and centroid frequency of clicks in false killer whales. This suggests that, at low impulse levels (i.e., the driving force in click production) the pair of larger dorsal bursae is involved, producing a lower frequency click at a lower sound pressure level. Conversely, at high impulse levels the pair of smaller dorsal bursae is involved, producing a higher frequency click at a higher sound pressure level. The positive correlation between peak-to-peak source level and centroid frequency of clicks in Heaviside's dolphins reported here suggests that similar mechanisms underlie click production in Heaviside's dolphins.

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Akamatsu, T., Teilmann, J., Miller, L. A., Tougaard, J., Dietz, R., Wang, D., Wang, K., Siebert, U., and Naito, Y. (2007). "Comparison of echolocation behaviour between coastal and riverine porpoises," *Deep-Sea Res., Part II* **54**, 290–297.

Akamatsu, T., Wang, D., Nakamura, K., and Wang, K. (1998). "Echolocation range of captive and free-ranging baiji (*Lipotes vexillifer*), finless porpoise (*Neophocaena phocaenoides*) and bottlenose dolphin (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **104**, 2511–2516.

Akamatsu, T., Wang, D., Wang, K., Li, S., Dong, S., Zhao, X., Barlow, J., Stewart, B. S., and Richlen, M. (2008). "Estimation of the detection probability for Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*) with a passive acoustic method," *J. Acoust. Soc. Am.* **123**, 4403–4411.

Au, W. W. L. (1993). *The Sonar of Dolphins* (Springer-Verlag, New York, NY), pp. 98–228.

Au, W. W. L. (1997). "Echolocation in dolphins with a dolphin-bat comparison," *Bioacoustics* **8**, 137–162.

Au, W. W. L. (2000). "Echolocation in Dolphins," in *Hearing by Whales and Dolphins*, edited by W. W. L. Au, A. N. Popper, and R. R. Fay (Springer, New York, NY), pp. 364–408.

Au, W. W. L. (2002). "Echolocation," in *Encyclopedia of Marine Mammals*, edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen (Springer-Verlag, New York, NY), pp. 358–367.

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 phocaena*)," *J. Acoust. Soc. Am.* **106**, 3699–3705.

Au, W. W. L., Pawloski, J. L., Nachtigall, P. E., Blonz, M., and Gisner, R. C. (2005). "Echolocation signals and transmission beam pattern of a false killer whale (*Pseudorca crassidens*)," *J. Acoust. Soc. Am.* **98**, 51–59.

Au, W. W. L., Penner, R. H., and Kadane, J. (1982). "Acoustic behavior of echolocating Atlantic bottlenose dolphins," *J. Acoust. Soc. Am.* **71**, 1269–1275.

Best, P. B., and Abernethy, R. B. (1994). "Heaviside's dolphin, *Cephalorhynchus heavisidii* (Gray, 1828)," in *Handbook of Marine Mammals, vol. 5. The First Book of Dolphins*, edited by S. H. Ridgway and M. Harrison (Academic Press, New York, NY), pp. 393–416.

Brumm, H. (2004). "The impact of environmental noise on song amplitude in a territorial bird," *J. Anim. Ecol.* **73**, 434–440.

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.

Dawson, S. M. (1988). "The high frequency sounds of free-ranging Hector's dolphin, *Cephalorhynchus hectori*," *Rep. Int. Whal. Comm.* **9**, 339–341.

Dawson, S. M. (2009). "Cephalorhynchus dolphins," in *Encyclopedia of Marine Mammals*, edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen (Academic Press, San Diego, CA), pp. 191–196.

Dawson, S. M., and Thorpe, C. W. (1990). "A quantitative analysis of the acoustic repertoire of Hector's dolphin," *Ethology* **86**, 131–145.

Dziedzic, A., and De Buffrenil, V. (1989). "Acoustic signals of the Commerson's dolphin, *Cephalorhynchus commersonii*, in the Kerguelen Islands," *J. Mamm.* **70**, 449–452.

Elwen, S., Mejer, M. A., Best, P. B., Kotze, P. G. H., Thornton, M., and Swanson, S. (2006). "Range and movements of female Heaviside's dolphins (*Cephalorhynchus heavisidii*), as determined by satellite-linked telemetry," *J. Mamm.* **87**, 866–877.

Evans, W. E., and Awbrey, F. T. (1988). "Natural history aspects of marine mammal echolocation: Feeding strategies and habitat," in *Animal Sonar: Processes and Performance*, edited by P. E. Nachtigall and P. E. B. Moore (Plenum Press, New York, NY), pp. 521–534.

Evans, W. E., Awbrey, F. T., and Hackbarth, H. (1988). "High frequency pulses produced by free-ranging Commerson's dolphin (*Cephalorhynchus commersonii*) compared to those of Phocoenids," *Rep. Int. Whal. Comm.* **9**, 173–181.

Francois, R. E., and Garrison, G. R. (1982). "Sound absorption based on ocean measurements. Part II: Boric acid contribution and equation for total absorption," *J. Acoust. Soc. Am.* **72**, 1879–1890.

Götz, T., Antunes, R., and Heinrich, S. (2010). "Echolocation clicks of free-ranging Chilean dolphins (*Cephalorhynchus eutropia*)," *J. Acoust. Soc. Am.* **128**, 563–566.

Hatakeyama, Y., Ishii, K., Soeda, H., and Shimamura, T. (1988). "Acoustic surveys on Commerson's dolphin," Document Submitted to the International North Pacific Fisheries Commission, Fisheries Agency of Japan, Tokyo, Japan, pp. 1–21.

Jefferson, T. A., Leatherwood, S., and Webber, M. A. (1993). *FAO Species Identification Guide. Marine Mammals of the World* (FAO, Rome, Italy), pp. 148–193.

Kalko, E. K. V., and Schnitzler, H. U. (1993). "Plasticity in echolocation signals of European pipistrelle bats in search flight: Implications for habitat use and prey detection," *Behav. Ecol. Sociobiol.* **33**, 415–428.

Kamminga, C. E., and Wiersma, H. (1982). "Investigations on cetacean sonar V. The true nature of the sonar sound of *Cephalorhynchus commersonii*," *Aquat. Mamm.* **9**, 95–104.

Kyhn, L. A., Jensen, F. H., Beedholm, K., Tougaard, J., Hansen, M., Madsen, P. T. (2010). "Echolocation in sympatric Peale's dolphins (*Lagenorhynchus australis*) and Commerson's dolphins (*Cephalorhynchus commersonii*) producing narrow-band high-frequency clicks," *J. Exp. Biol.* **213**, 1940–1949.

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.

Lammers, M. O., and Castellote, M. (2009). "The beluga whale produces two pulses to form its sonar signal," *Biol. Lett.* **5**, 297–301.

Li, S., Akamatsu, T., Wang, D., and Wang, K. (2009). "Localization and tracking of phonating finless porpoises using towed stereo acoustic dataloggers," *J. Acoust. Soc. Am.* **126**, 468–475.

Li, S., Wang, D., Wang, K., Akamatsu, T., Ma, Z., and Han, J. (2007). "Echolocation click sounds from wild inshore finless porpoise (*Neophocaena phocaenoides sunameri*) with comparisons to the sonar of riverine *N. p. asiaeorientalis*," *J. Acoust. Soc. Am.* **121**, 3938–3946.

- Li, S., Wang, K., Wang, D., and Akamatsu, T. (2005). "Echolocation signals of the free-ranging Yangtze finless porpoise (*Neophocaena phocaenoides asiaorientalis*)," *J. Acoust. Soc. Am.* **117**, 3288–3296.
- 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., and Wahlberg, M. (2007). "Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales," *Deep-Sea Res., Part I* **54**, 1421–1444.
- May-Collado, L., and Agnarsson, I. (2006). "Cytochrome *b* and Bayesian inference of whale phylogeny," *Mol. Phylogenet. Evol.* **38**, 344–354.
- Medwin, H. (1975). "Speed of sound in water: A simple equation for realistic parameters," *J. Acoust. Soc. Am.* **58**, 1318–1319.
- 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.
- 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.
- Nakamura, K. (1999). "A functional and morphological study of clicks in odontocetes: Physical characteristics and structure of sound source," Ph.D. dissertation, Hokkaido University, Hokkaido, pp. 100–145.
- Nakamura, K., and Akamatsu, T. (2004). "Comparison of click characteristics among odontocete species," in *Echolocation in Bats and Dolphins*, edited by J. A. Thomas, C. F. Moss, and M. Vater (The University of Chicago Press, Chicago, IL), pp. 36–40.
- Nikaido, M., Matsuno, F., Hamilton, H., Brownell, R. L., Jr., Cao, Y., Ding, W., Zuoyan, Z., Shedlock, A. M., Fordyce, R. E., Hasegawa, M., and Okada, N. (2001). "Retroposon analysis of major cetacean lineages: the monophyly of toothed whales and the paraphyly of river dolphins," *Proc. Natl. Acad. Sci. U.S.A.* **98**, 7384–7389.
- Pichler, F. B., Robineau, D., Goodall, R. N., Meyer, M. A., Olivarria, C., and Baker, C. S. (2001). "Origin and radiation of Southern Hemisphere coastal dolphins (genus *Cephalorhynchus*)," *Mol. Ecol.* **10**, 2215–2223.
- Sekiguchi, K., Klages, N. T. W., and Best, P. B. (1992). "Comparative analysis of the diets of smaller odontocete cetaceans along the coast of Southern Africa," *S. Afr. J. Mar. Sci.* **12**, 843–861.
- Surlykke, A., and Moss, C. F. (2000). "Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory," *J. Acoust. Soc. Am.* **108**, 2419–2429.
- System Intech Company Limited (2009). *Report of Position Accuracy Estimation of the Hydrophone Array System* (System Intech Company Limited, Tokyo, Japan), pp. 1–6.
- Thorpe, C. W., Bates, R. H., and Dawson, S. M. (1991). "Intrinsic echolocation capability of Hector's dolphin, *Cephalorhynchus hectori*," *J. Acoust. Soc. Am.* **90**, 2931–2934.
- Thorpe, C. W., and Dawson, S. M. (1991). "Automatic measurement of descriptive features of Hector's dolphin vocalizations," *J. Acoust. Soc. Am.* **89**, 435–443.
- Tougaard, J., and Kyhn, L. A. (2010). "Echolocation sounds of hourglass dolphins (*Lagenorhynchus cruciger*) are similar to the narrow band high-frequency echolocation sounds of the dolphin genus *Cephalorhynchus*," *Marine Mammal Sci.* **26**, 239–245.
- Villadsgaard, A., Wahlberg, M., and Tougaard, J. (2007). "Echolocation signals of wild harbour porpoises, *Phocoena phocoena*," *J. Exp. Biol.* **210**, 56–64.
- Watkins, W. A., Schevill, W. E., and Best, P. B. (1977). "Underwater sounds of *Cephalorhynchus heavisidii* (Mammalia: Cetacea)," *J. Mamm.* **58**, 316–320.
- Yeh, S., Zbinden, K., Kraus, C., Gahr, G., and Pilleri, G. (1982). "Characteristics and directional properties of the sonar signals emitted by the captive Commerson's Dolphin, *Cephalorhynchus commersonii* (Gray 1846)," *Invest. Cetacea* **18**, 177–204.