

Source parameters of echolocation clicks from wild bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*)

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The Indian Ocean and Atlantic bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*) are among the best studied echolocating toothed whales. However, almost all echolocation studies on bottlenose dolphins have been made with captive animals, and the echolocation signals of free-ranging animals have not been quantified. Here, biosonar source parameters from wild *T. aduncus* and *T. truncatus* were measured with linear three- and four-hydrophone arrays in four geographic locations. The two species had similar source parameters, with source levels of 177–228 dB re 1 μ Pa peak to peak, click durations of 8–72 μ s, centroid frequencies of 33–109 kHz and rms bandwidths between 23 and 54 kHz. *T. aduncus* clicks had a higher frequency emphasis than *T. truncatus*. The transmission directionality index was up to 3 dB higher for *T. aduncus* (29 dB) as compared to *T. truncatus* (26 dB). The high directionality of *T. aduncus* does not appear to be only a physical consequence of a higher frequency emphasis in clicks, but may also be caused by differences in the internal properties of the sound production system. © 2011 Acoustical Society of America. [DOI: 10.1121/1.3624822]

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I. INTRODUCTION

Echolocation has evolved as the primary sensory modality in both toothed whales and bats. Since the discovery of echolocation in bats in the 1930s (summarized by Griffin, 1958) and dolphins in the 1950s and 1960s (Kellogg, 1958;

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Norris *et al.*, 1961), this sensory system has been under intense scientific investigation both in the field and in the laboratory. Trained bats and dolphins in captivity have been studied to quantify their hearing, target detection and target discrimination abilities (Griffin, 1958; Au, 1993; Supin *et al.*, 2001). These findings have been complemented with acoustic recordings and behavioral studies of animals both in captivity and in the field, with a main focus on addressing how echolocation is used when the animal is stationary or approaching targets, and quantifying the types of echolocation signals used under different circumstances (e.g., Evans and Powell, 1967; Evans 1973; Johnson *et al.*, 2006; Verfuss *et al.*, 2009; Jakobsen and Surlykke, 2010).

In field studies of echolocation signals, data can be obtained from animals under natural conditions for which their sonar evolved. However, in field studies there is limited or no experimental control to test specific features of echolocation. Therefore, carefully designed laboratory studies are needed to understand the basic functions of echolocation, such as the hearing and target detection abilities of the animal. On the other hand, in the laboratory there is always the doubt of whether trained and well-fed animals will use their sonar in a manner that is representative of free-ranging animals. Studies made both in captivity and in the field are therefore important for our understanding of animal echolocation and how it evolved.

Among toothed whales, captive bottlenose dolphins have been the favorite study object over the last 60 yr (Au, 1993). Bottlenose dolphins, which are grouped into the Atlantic (*Tursiops truncatus*) and Indian Ocean (*Tursiops aduncus*) species, lend themselves well to captivity and are ideal for training using methods of positive reinforcement. *T. truncatus* was the first toothed whale species in which biosonar was unequivocally demonstrated (Kellogg, 1958; Norris *et al.*, 1961). Since then, there has been a large range of studies on the hearing abilities and biosonar performance of bottlenose dolphins (reviewed by Au, 1993, and Supin *et al.*, 2001).

From early recordings of bottlenose dolphin biosonar, click source levels were estimated to be ~ 170 dB re $1 \mu\text{Pa}$ peak to peak (pp), with a frequency emphasis ~ 35 – 60 kHz (Norris, 1967, 1969). These measurements were made of an animal in a relatively small and highly reverberant tank. To test the biosonar capabilities of bottlenose dolphins under much less reverberant conditions, Au *et al.* (1974), Au (1980) and Murchinson (1980) performed long-range target detection experiments with animals in a relatively shallow, open-water environment. In these experiments the dolphins emitted clicks with source levels of up to 228 dB re $1 \mu\text{Pa}$ pp at 1 m and peak frequency above 100 kHz when successfully echolocating a 5 cm steel sphere out to ranges of 89 m.

Later laboratory and field studies have shown that dolphins not only modulate their click source levels and frequency content but also their interclick intervals. These characteristics depend on the echolocation task, the range to the target, the background noise level, and the amount of clutter (Penner, 1988; Moore and Pawloski, 1990; Au, 1993; Supin *et al.*, 2001; Jensen *et al.*, 2009b; Ibsen *et al.*, 2010). The direction and width of the transmitted beam can be altered to facilitate the detection of targets slightly off the dolphin

body axis (Moore *et al.*, 2008; Starkhammar *et al.*, 2011). For many species of toothed whales there is a positive correlation between the frequency weight of the emitted clicks and their directionality, as well as between their frequency weight of the clicks and source level (Au, 1993; Au *et al.*, 1995; Møhl *et al.*, 2000; Madsen *et al.*, 2002). The variability of signal waveforms and spectral patterns has been used to define different click types for automated classification of bottlenose dolphin echolocation signals (Houser *et al.*, 1999; Muller *et al.*, 2008). However, these studies were carried out in pools and pens with relatively short target ranges to biosonar targets, resulting in most clicks having low source levels, low centroid frequencies and narrow frequency bandwidths compared to the clicks recorded in the open water experiments of Au *et al.* (1974), Au (1980), and Murchinson (1980).

There is thus a clear discrepancy in the shape and intensity of the signals produced by dolphins kept in small tanks and by dolphins swimming in shallow open water conditions. These differences are probably due to strong echoes from nearby structures interfering with the biosonar performance of dolphins in confined spaces. As a result animals may reduce the output level and the frequency content of the signals. This has a significant effect on the biosonar performance, as both factors influence target discrimination and target ranging abilities (Au, 1993; Siemers and Schnitzler, 2004; Kloepper *et al.*, 2010). This raises the question of whether the results from psychophysical echolocation trials made on bottlenose dolphins in captivity are directly applicable when trying to understand the biosonar performance of free-ranging animals. In fact, the properties of captive *T. truncatus* clicks have been used to estimate the echolocation performance in terms of detection ranges (Au *et al.*, 2007; Madsen *et al.*, 2007) and target discrimination abilities in the wild (Au *et al.*, 2009; Yovel and Au, 2010). Although such ecophysiological inferences are important for understanding the evolution and use of biosonar in the wild, they critically hinge on the fact that the chosen assumptions (out of many) from the captive *T. truncatus* are representative for their wild conspecifics.

The danger in extrapolating from laboratory studies to the wild is that laboratory settings may inadvertently (clutter, noise) or on purpose have led the animals to produce signals with source properties that are not representative for wild conspecifics. Some aspects of the acoustic behavior of echolocating free-ranging bottlenose dolphins have been described already by Norris (1967, 1969). More recent and detailed information has been provided by Jensen *et al.* (2009b) for *T. aduncus* and Simard *et al.* (2009) for *T. truncatus*. However, some of the basic source parameters of the clicks from free-ranging bottlenose dolphins are still unknown, despite the bottlenose dolphin being the most studied of all cetacean species.

This paper presents for the first time detailed source properties of echolocation signals from free-ranging *T. aduncus* and *T. truncatus*. Recordings were collected using a vertical hydrophone array in four different geographical areas of the Atlantic and Indian Oceans. Results are compared to what is known about the echolocation signals of bottlenose dolphins from animals held in captivity, and we discuss implications for how to interpret and use acoustic recordings made under different circumstances.

II. MATERIALS AND METHODS

Recordings of *T. aduncus* and *T. truncatus* were made at four field sites by different research teams. The field work was not coordinated in terms of data collection techniques and use of equipment. Therefore there are some discrepancies in the methods as described in detail here.

A. *Tursiops aduncus*

Indian Ocean bottlenose dolphins were recorded in February 2007 (Koombana Bay, Bunbury, West Australia, 33°17'S, 115°39'E) in 6 m (± 1 m) deep water on sandy bottom. Small groups of dolphins frequently approached the recording platform. Data acquisition was manually initiated when dolphins were observed surfacing within 100 m of and toward the array. Acquisition lasted until the dolphins had passed the recording platform, interrupted ~ 5 s every minute for data storage. The acoustic background noise level, measured with a B&K 8101 hydrophone (receiving sensitivity -184 dB re $1 \mu\text{Pa/V}$) was high, up to 60 dB re $1 \mu\text{Pa}/\sqrt{\text{Hz}}$ in the measured frequency range 0.2–40 kHz, and probably below this level in the whole frequency range of interest for *Tursiops* echolocation (up to some 120 kHz). The main component of ambient noise was broad spectral noise from snapping shrimps (for details on noise measurements, see Jensen *et al.*, 2009a).

The recordings were made with a linear four-hydrophone array (Fig. 1). The hydrophones were spaced 1 m apart and aligned by mounting them with an interconnected set of PVC pipes. The hydrophone array was suspended vertically between a surface buoy and a 0.5 kg lead weight, the top hydrophone held at a depth of a few meters. The hydrophones (TC4034, RESON) were connected to a four-channel custom-built amplifier, containing noise rejecting and anti-aliasing filters (40 dB amplification, one-pole high pass filter with a -3 dB cutoff frequency at 1 kHz, and a four-pole low pass filter with a -3 dB cutoff frequency of 200 kHz). An analog-to-digital (A/D) converter (sampling frequency 800 kHz, 12 bits, ± 5 V input voltage, ADLink Technology) was used to store data in a laptop computer via a PCMCIA interface (Magma). The recording system was calibrated prior to

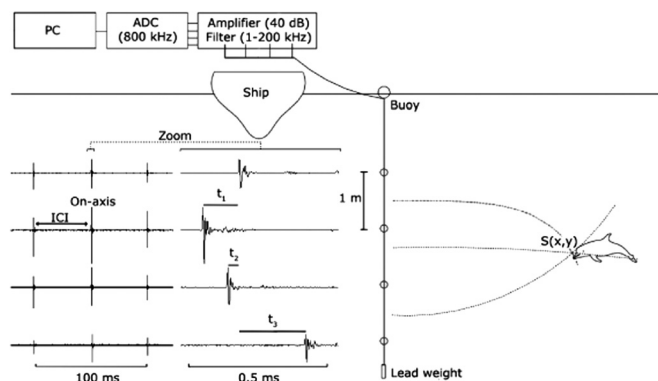


FIG. 1. Setup for recordings of *Tursiops aduncus*. The recording setup was similar for the *T. truncatus* recordings reported in the text. t_1 , t_2 , and t_3 are the time-of-arrival differences between the same click arriving on the four different hydrophones. [Jensen *et al.* (2009b), reprinted with permission from J. Exp. Biol.]

and after each recording session by emitting a two-cycle click centered at 80 kHz with an omnidirectional hydrophone and comparing the sensitivity of the recording system with the known sensitivity of a RESON TC4014 hydrophone. The hydrophone sensitivity of the measurement hydrophones was -220 dB re $1 \text{ V}/\mu\text{Pa}$, with an omnidirectional receiving characteristic (spherical element) in the relevant frequency range from below 1 to 200 kHz (± 2 dB). The frequency response of the amplifier was partially corrected for during postprocessing, giving an overall flat frequency response of the recording chain (± 2 dB) between 1 and 200 kHz, with a maximum received level of 194 dB re $1 \mu\text{Pa}$ peak dictated by the peak voltage that can be handled by the A/D converter.

B. *Tursiops truncatus*

Recordings of Atlantic bottlenose dolphins were made at three field sites: off Tenerife, Canary Islands (28°15'N, 16°53'W) in March 2006; off Pico Island, Azores (38°22'N, 28°23'W) in June 2006; and in Cardigan Bay, Wales, UK (52°30'N, 04°21'W) in July 2005. The recordings off Tenerife were made with four hydrophones spaced 2 m apart using a PVC rig. The top hydrophone was at a depth of a couple of meters. The water depth was deeper than 800 m and recordings were only made in Sea State 2 or less. The recording chain was identical to the Australian system described earlier, except that a sampling rate of 500 kHz was used and the amplifier was set at 30 dB. The same frequency response compensation of the conditioning box was made as in the Australian recordings, giving the system a flat frequency response (± 2 dB) between 1 and 200 kHz with a clipping level of 204 dB re $1 \mu\text{Pa}$ peak dictated by the peak voltage that can be handled by the A/D converter. The Azorean recordings were made with a three-hydrophone array in waters of several hundreds meters depth and in Sea State 1. The hydrophone spacing was 1 and 2 m (with the 2 m spacing closer to the surface), and the hydrophones (same model as in the Australian and Tenerife recordings) were aligned using a PVC pipe rig. The highest hydrophone was at a couple of meters depth. The hydrophones were connected to a custom-built signal conditioning box (amplification 30 dB, one-pole high pass filter with a -3 dB cutoff frequency of 10 Hz, and a four-pole low pass filter with a -3 dB cutoff frequency of 200 kHz) similar to the one used in Australia and sampled with a 12-bit A/D converter (voltage input range ± 0.5 V, sampling rate 330 kHz; Wavebook 512, Iotech). The setting of the low pass filter protected the recordings from antialiasing effects below 120 kHz. Aliasing may have occurred in the frequency interval 120–165 kHz, but this had only a minor effect of the results presented below as most energy in bottlenose dolphin clicks is found below 120 kHz. The field site in Wales was set on a sand and mud bottom area at 10–25 m water depth. Recordings were made in Sea State 2 or less. The hydrophones were identical to the ones used in Australia. The three hydrophones were spaced 2 m apart and suspended on a line with a 2 kg weight without using a rig, resulting in less accurate acoustic localization than at the other three sites. The top hydrophone was

at a depth of a few meters. The hydrophones were connected to a multichannel signal conditioning box (amplification 30 dB, high pass filter 10 Hz) and recorded on a lunch-box computer containing an A/D converter identical to the one used in Australia (sampling rate 800 kHz, 12 bits; voltage input range ± 5 V; for a more thorough description of the recording system, see [Rasmussen et al., 2004](#)). No low pass (anti-aliasing) filter was used in the Welsh recordings, but the signals were sampled at such a high sample rate that any aliasing would be negligible (the hydrophone sensitivity starts dropping at around the Nyquist frequency of the recording system at 400 kHz). The signal-to-noise ratio is likely poorer in these recordings due to high frequency electrical noise being folded down into the recording band.

C. Analysis

All signal analysis was made with custom-written routines in MATLAB 6.5 and 7.5 (The MathWorks, Inc.). First, echolocation click sequences were identified from the repetition rate patterns. Besides being used for echolocation, clicks are also used in communication signals, so-called burst-pulsed calls, which are quite stereotyped and hence easy to tell apart from regular echolocation click trains ([Thomson and Richardson, 1995](#)). From each sequence that could be sorted out, echolocation clicks recorded on each dolphin recording event were identified for further analysis with an automated click-detector set to a minimum detectable received level on the top hydrophone. The threshold varied between the recordings depending on the signal-to-noise ratio and the received level of the dolphin clicks. Only clicks that could be located in all channels were considered for further analysis, except in the recordings from Wales. The localization was not optimal in the recordings from Wales due to variations in the alignment of the hydrophones. However, these recordings were still used to assess frequency and duration properties of presumably on-axis signals as explained in the following.

The position of the click source relative to the receivers was estimated using acoustic localization techniques based on time-of-arrival differences of the same click on the four receivers ([Madsen and Wahlberg, 2007](#)). Time-of-arrival differences were determined by cross-correlating the signal recorded on the top hydrophone with the signals recorded at the other hydrophones, excluding surface reflections. In addition to the time-of-arrival differences and the receiver spacing, the sound speed must (at least approximately) be known to accurately localize the sound source ([Madsen and Wahlberg, 2007](#)). This was calculated from the Leroy equation ([Urlick, 1983](#)) to 1520 m/s using measurements of the water temperature (23.5 °C) and salinity (35 parts per million) at the Australian recording sites. The sound velocity at the other recording sites may have been slightly different, but this slight error has an extremely small (less than 1%) effect on the localization results derived in the following.

For each pair of hydrophones the difference in time-of-arrival is limiting the localization of the source to a single hyperboloid surface. Three independent hyperboloids are generated by four receivers. For each receiver pair, the corre-

sponding hyperboloid indicates the surface to which the source is restricted, given the measured time-of-arrival difference. Ideally, all three hyperboloids intersect on a horizontal circle parallel to the water surface. For recordings with three hydrophones, two hyperboloids are generated, also intersecting on a circle. As the array is oriented vertically in the water, the circle defines the depth and the vertical bearing to the source. The source coordinates can either be solved for geometrically, by inspecting the intersection of the three hyperboloids, or analytically by, e.g., the method of least-squares ([Madsen and Wahlberg, 2007](#)).

For the Australian recordings, the accuracy and precision of acoustic localizations was tested in shallow water by transmitting artificial dolphin clicks (two cycles, centroid frequency 70 kHz) at a depth of 3 m using an omnidirectional hydrophone (HS70, Sonar Products, Ltd.) lowered from a small boat at distances between 10 and 60 m from the array, measured with a stretched rope from the two boats. The rms error, defined as the root-mean-squared range deviations from the true range, was below 9% for range estimates within 40 m from the array, but increased significantly beyond this range. A too large ranging error would give a large bias to the estimated source levels and directionality pattern from the dolphins, as these measures critically depend on the transmission loss and (in the case of directionality) the angle between the hydrophones as seen from the dolphins' location. To reduce this source of bias we only included clicks from dolphins localized at ranges closer than 40 m from the array in the analysis. This ranging procedure and range criterion result in an rms error < 1 dB in the estimation of the transmission loss using $20 \log R + \alpha R$, where R is the range to the dolphin and α is the absorption loss. In all, for the Australian recordings, the combined sources of bias results in an uncertainty of less than 2 dB when backcalculating the sound pressure level to a distance of 1 m of the clicking dolphins. The precision in the estimated sound levels was probably at least as good for the Tenerife recordings (larger aperture), but slightly worse for the Azorean recordings (as three receivers were used there as compared to four receivers at the other sites). The precision for the Welsh recordings was assumed to be much worse due to the misalignment of the hydrophones.

Click source parameters were calculated using equations in [Madsen and Wahlberg \(2007\)](#). The apparent source level (ASL_{pp}) is defined as the backcalculated sound pressure level 1 m from the source at an unknown angle from the acoustic axis ([Møhl et al., 2000](#)). It was calculated using the following equation:

$$\text{ASL} = \text{RL} + \text{TL} = \text{RL} + 20 \log R + \alpha R,$$

where RL is the received level. The transmission loss (TL) was estimated from spherical spreading and frequency-dependent absorption of the range $R(m)$, using an absorption coefficient α of 0.025 dB m^{-1} at 90 kHz (close to the centroid frequency of most on-axis *Tursiops* clicks).

When investigating source properties of directional biosonar signals, it is essential to quantify the signal as close to the acoustic axis as possible due to strong off-axis distortion.

Including off-axis clicks in the analysis leads to underestimating source levels and a lowered frequency emphasis of the clicks (Madsen and Wahlberg, 2007). With a one-dimensional array, it is difficult to ensure that a given click is on-axis, and most recorded clicks will be recorded at various degrees off the acoustic axis. We identified click sequences, here called scans, most likely associated with the acoustic beam of the animal passing across the axis of the hydrophone array. Provided that the animal maintains the same source level and directionality, the click with highest amplitude within a click sequence has the highest likelihood of being on-axis. This assumption may not always be correct, as the source level and directionality may vary between clicks. However, for consecutive clicks in a click train, such changes are usually relatively small so we believe this is still an efficient method to extract on-axis signals. In this study, we defined a scan as any sequence of 10 or more clicks with interclick intervals of less than 1 s. For each scan we then classified a click as on-axis and used it for further analysis if it fulfilled the following criteria:

- (1) The click had the highest apparent source level (pp) in a scan;
- (2) The highest backcalculated source level was recorded on one of the central hydrophones; and
- (3) The source position was estimated to be within 40 m of the array.

In the Welsh recordings we used the received level rather than the apparent source level for these criteria, as it was not possible to localize the animals with sufficient localization accuracy. Due to the high directionality of the signals, the error of classifying clicks using received, rather than source levels, is small for the short ranges of interest here: for source locations in front of the array the transmission loss compensation will be relatively constant across all channels compared to the effects of directionality on the signal levels in most cases.

The directionality of the signals was estimated from the measurements of apparent source level as a function of the calculated off-axis direction to each hydrophone for each click. Only the Australian and Tenerife data were used for this calculation, as the quality of the data from Wales and the Azores was insufficient for analysis of directionality. Each click was aligned relative to the estimated on-axis direction and normalized so that they all had a maximum level of 0 dB in the on-axis direction. The peak intensity and the angle were adjusted using Lagrange interpolation in which a second degree polynomial is fitted to the three points made up by the peak ASL on one hydrophone and the ASLs on the two neighboring hydrophones (Menne and Hackbarth, 1986). This means that the highest measured value was not necessarily set to 0 dB and 0°. Thereafter, all off-axis levels were plotted as a function of the off-axis angle in one single diagram. The transmission beam pattern was fitted to the beam pattern of a generic on-axis click exiting a spherical piston of the diameter that resulted in the least squared error. The circular piston model was used to estimate the directionality properties of the measured beam pattern, such as the -3 and -10 dB beam width and the directionality index

using the methods described in Møhl *et al.* (2003). For statistical analysis we used analysis of variances (ANOVA) (Zar, 1996).

The accuracy of our beam pattern estimation technique was investigated using a transducer of known directionality (TC 2116, RESON) emitting sound pulses of 200 μ s duration centered at 50 kHz with a repetition rate of 10 Hz. The transducer was held at a 7.6 m horizontal distance from a horizontal hydrophone array of 4 TC4034 RESON hydrophones at a 75 cm interreceiver distance. The depth of both array and transducer was 1.5 m. The transducer was moved back and forth and up and down to simulate the movements of a dolphin approaching the array. From the recordings, clicks with the highest apparent source level on any of the central hydrophones, and surrounded by lower apparent source level clicks in the same channel, was regarded as being recorded close to on-axis, following the criteria for the field data. An analysis identical to that outlined above for the field data gave a -3 dB beam width of 14° compared to the actual -3 dB beam width of 15° from the factory calibration of this transducer. Thus, the techniques used here for beam pattern estimation are reliable.

III. RESULTS

In Australia, a total of 5 h of recordings were made during 2 days of encounters with dolphins during field work, and a total of 4202 clicks were detected. Out of these, 89 clicks from 26 different dolphin approaches fitted the on-axis and range criteria given previously and thus were used for measurements of ASL and directionality index. Seven well-known individuals from the population were identified and represented in this sample. None of these animals continuously visited the recording station throughout the recording sessions, making it unlikely that only a few animals contributed to the bulk of the data set.

In Tenerife a total of 5 min of recordings were made during 2 days, resulting in 742 clicks, out of which 95 were regarded as being on-axis. More than two groups of presumably different dolphin individuals were recorded during 2 consecutive days. In the Azores, a total of 8 min of recordings during 1 day resulted in 569 clicks out of which 9 were classified as being on-axis. All the recordings were made of the same groups of bottlenose dolphins consisting of at least 5 individuals. In Wales, 17 min of recordings resulted in 1697 clicks, out of which 145 were regarded as recorded on-axis. The recordings were made during 1 day and were presumably made from more than five individuals.

The measured click source parameters of the two species and the four different recording sites are detailed in Table I, also including a comparison with click parameters on trained bottlenose dolphins echolocating in open waters during psychophysical tasks and on animals recorded in small tanks.

Examples of waveforms of *T. aduncus* and *T. truncatus* echolocation clicks are shown in Fig. 2. The structure of the clicks of both species is similar, but *T. aduncus* clicks have a higher frequency emphasis than *T. truncatus* clicks. The normalized spectra of all measured on-axis clicks are shown in

TABLE I. Source parameters of bottlenose dolphin (*Tursiops aduncus* and *T. truncatus*) echolocation signals recorded at different field locations compared to studies made with animals in captivity.

Parameters	<i>Tursiops aduncus</i>		<i>Tursiops truncatus</i>			
	Australia	Tenerife	Azores ^a	Wales	Trained animals in open water ^{b,c}	Animals in tank ^c
Number of analyzed clicks	4202	742	569	1697
Number on axis clicks	89	95	9	145
Source level (dB re 1 μ Pa pp at 1 m) ^d	205 \pm 7 (177–219)	199 \pm 6 (186–214)	212 \pm 11 (196–228)	...	217–228 ^f	170 ^g
Energy density (dB re 1 μ Pa ² s at 1 m) ^{d,e}	146 \pm 7 (122–160)	147 \pm 6 (134–161)	132 \pm 15 (114–164)	...	Up to 162 ^g	...
Duration (μ s) ^d	18 \pm 6 (8–48)	21 \pm 8 (13–72)	22 \pm 11 (13–50)	23 \pm 8 (12–46)	35–45 ^f	50–250 ^g
Centroid frequency (kHz) ^d	91 \pm 13 (45–109)	80 \pm 9 (55–95)	82 \pm 8 (62–90)	75 \pm 16 (33–102)	93–101 ^f	30–60 ^{g,h} and 100–130 ⁱ
rms BW ^j (kHz) ^d	35 \pm 3 (25–43)	28 \pm 3 (23–38)	29 \pm 2 (27–32)	34 \pm 6	21.4–28 ^f	...
$Q^{\text{d,k}}$	2.3 \pm 0.3 (1.6–3.1)	2.8 \pm 0.4 (1.5–3.4)	2.9 \pm 0.3 (2.2–3.3)	2.2 \pm 0.6 (0.8–3.6)	3.6–3.8 ^f	...
Interclick interval (ms) ^d	63 \pm 45 (3–255)	80 \pm 59 (3–526)	120 \pm 56 (43–282)	96 \pm 98 (7.1–481)	20–180 ^f	...
–3 dB BW	8°	9°	8–40° ^{l,m}	...
–10 dB BW	10°	16°	21° ^f	30° at –19 dB ^g
Directionality index (dB)	29	26	25.8 ^f	...

^aAzorean data contained aliased energies in the frequency range of 120–165 kHz. This may have had a slight, but probably insignificant, influence on the derived source parameters.

^bThe trained animal was recorded when performing a psychophysical echolocation task.

^cFor animals in captivity, see original references to obtain the relevant measures used.

^dResults are given as mean \pm 1 standard deviation and as the range from minimum to maximum value. For animals in captivity only ranges are given.

^eFor the free-swimming animals, the energy source level was measured within the 95% energy content of the accumulated energy, and the duration was measured as the 95% energy content of a 100 μ s window around the peak of the signal (for details, see Madsen and Wahlberg, 2007).

^fSee Au (1993).

^gSee Norris (1967, 1969).

^hSee Hol and Kamminga (1979).

ⁱSee Poche *et al.* (1982).

^jThe rms BW is the root-mean-square bandwidth.

^k Q is the centroid frequency divided by the rms BW.

^lSee Au *et al.* (1978).

^mSee Zaytzeva *et al.* (1975).

Fig. 3. The shape of the spectra is very stereotyped, almost always unimodal and with a high-frequency emphasis, both for low level and high level clicks. Note that Figs. 3(a) and 3(b) show the power spectra, and thus have a logarithmic y axis. Care must be taken when comparing this figure with

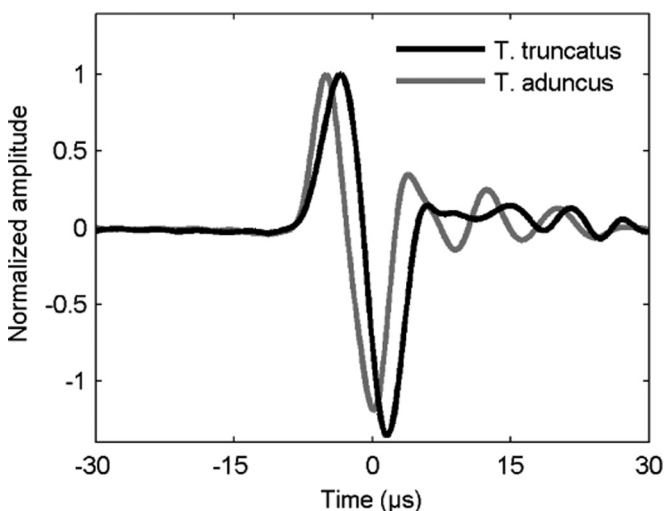


FIG. 2. Echolocation click signal waveform from *T. aduncus* and *T. truncatus*.

many previously published spectra of *Tursiops*, which are sometimes given as amplitude spectra with a linear amplitude axis (e.g., Au, 1993).

The clicks differed significantly in duration, sound level, peak frequency, and bandwidth in on- and off-axis directions of the dolphin in both the *T. aduncus* and *T. truncatus* recordings. There is a notch present in spectra of off-axis directions that is consistently progressing toward lower frequencies for larger off-axis angles (Fig. 4).

The centroid frequency of the clicks increased as a function of the click source level (Fig. 5). A least-square regression line on data from *Pseudorca* (Au *et al.*, 1995) is included in Fig. 5 for comparison. The least-square regression line of the *T. aduncus* data has a significantly (ANOVA, $p < 0.05$) smaller slope than the *Pseudorca* regression line. The least-square regression line from the *T. truncatus* data is not significantly different from a line with slope 0 (ANOVA, $p > 0.05$) and therefore not depicted in Fig. 5, whereas the regression line of *T. aduncus* is significantly different from 0 (ANOVA, $p < 0.05$). This means that there is a significant relationship between the centroid frequency and ASL for *T. aduncus*, but not for *T. truncatus*.

The composite transmission beam pattern of *T. aduncus* has a –3 and –10 dB beam width of 8° and 10.5°, respectively, and a directivity index of 29 dB [Table I, Fig. 6(a)].

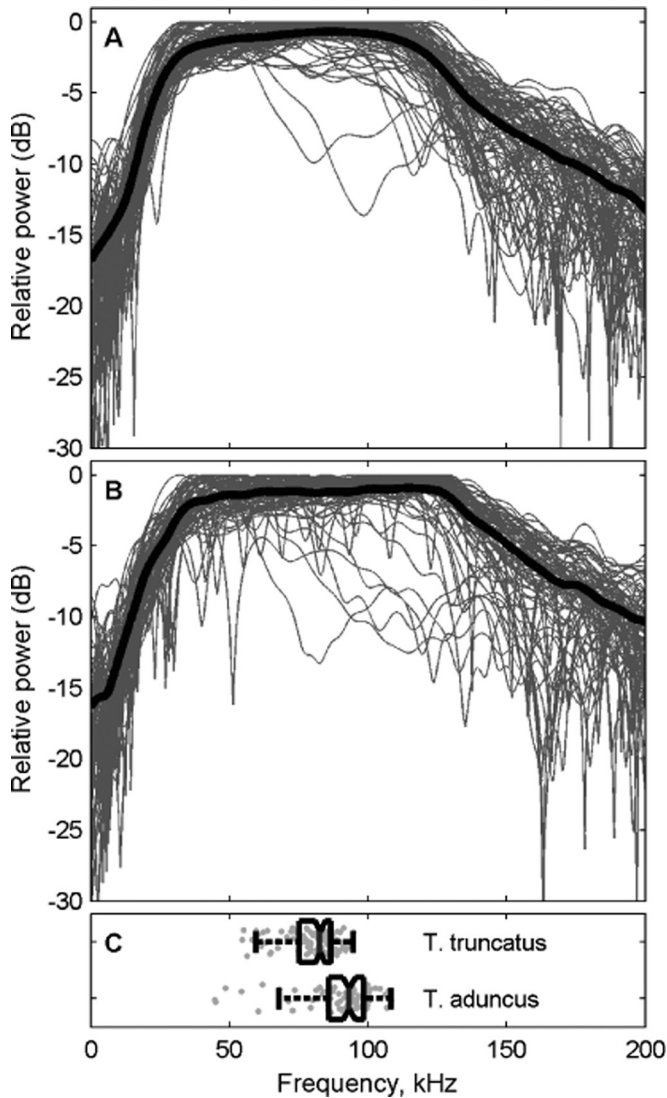


FIG. 3. Individual power spectra (gray lines) and averaged power spectrum (black line) of all on-axis echolocation clicks from bottlenose dolphins. (a) *Tursiops truncatus*, recorded off Los Gigantes, Tenerife, Spain. Sampling rate 500 kHz, fast Fourier transform (FFT) size 128 points, Hann window, spectrum interpolated 10 times. (b) Indian Ocean bottlenose dolphins, *Tursiops aduncus*. Sampling rate 800 kHz, FFT size 128 points, Hann window, spectrum interpolated 10 times. (c) Notched box plot indicating the distribution of centroid frequency estimates for the two species overlaid on top of individual estimates. Box plot shows 25th, 50th (median), and 75th percentile of data. Whiskers indicate the most extreme data point within 1.5 interquartile range of the median.

The corresponding beam widths of *T. truncatus* clicks were 9° and 16° and the directionality index 26 dB [Table I, Fig. 6(b)].

IV. DISCUSSION

Over the last six decades, bottlenose dolphins have been used as the most common laboratory animal in experimental studies of toothed whale biosonar. It is for this species that we have the most detailed measurements of the directionality pattern and characteristics of the ultrasonic echolocation signals available, as well as the most profound knowledge of their biosonar performance in terms of detection, discrimination, and ranging abilities. However, essentially all these

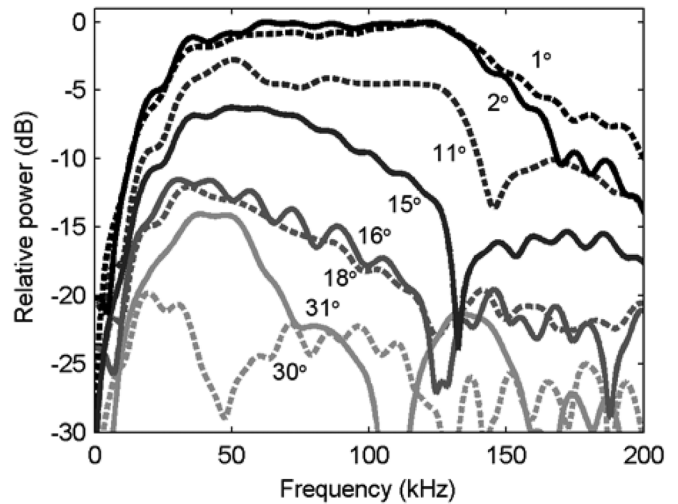


FIG. 4. Spectra of echolocation clicks recorded from bottlenose dolphins, *Tursiops aduncus*, shown for various degrees of off-axis recordings for two clicks recorded on the four-channel array. Sampling rate 800 kHz, FFT size 128 points, Hann window, spectrum interpolated 10 times. The off-axis angle in the vertical plane, calculated from a Lagrange interpolation of each click measurement (see the text for details), is indicated for each spectrum.

measurements have been made on animals in captivity as they were performing echolocating tasks in a stationary position. The study presented here is the first to present detailed biosonar source parameters recorded from free-ranging bottlenose dolphins.

When comparing the source properties measured from animals in the field with previous measurements from captive animals, it is important to read the references in the footnotes in Table I. The signals have not been measured using exactly the same metrics in the various studies. Still, there are some clear similarities and differences between the measurements from the different studies. The signal shape is similar in our recordings from the field, with clicks from *T. aduncus* having a slightly higher frequency emphasis than

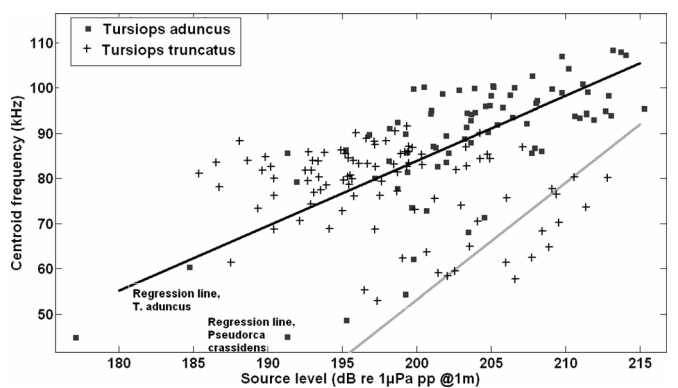


FIG. 5. The centroid frequency of on-axis clicks as a function of the apparent source level (see the text for details) of clicks from *Tursiops aduncus* (recorded in Australia) and *T. truncatus* (recorded off Los Gigantes, Tenerife, Spain). The linear regression line of the *T. aduncus* data has the equation $f_0 = 1.26 \cdot \text{ASL} - 166$ with a fit of $R^2 = 0.6$. It is significantly different from a line with slope zero (ANOVA, $p < 0.05$). The linear regression line of the *T. truncatus* data is not significantly different from a line of slope zero and therefore not shown. The linear regression line of data from a false killer whale (*Pseudorca crassidens*) from Au et al. (1995) is given as comparison ($f_0 = 2.55 \cdot \text{ASL} - 456$ with $R^2 = 0.8$).

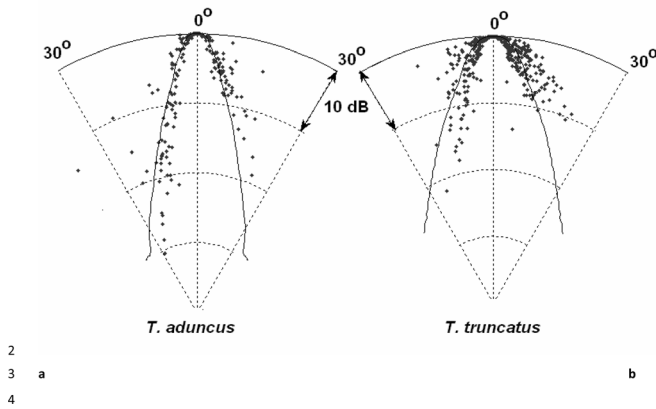


FIG. 6. Composite directionality plot of signals from (a) *Tursiops aduncus* (recorded in Australia) and (b) *T. truncatus* (recorded off Tenerife). The off-axis angle for each click has been adjusted by finding the maximum of a Lagrange interpolated quadratic curve through the measurements (see the text for detail). Solid line is a piston model using an on-axis click from a free-ranging bottlenose dolphin, assuming a piston radius of 12.7 cm for *T. aduncus* and 8.4 cm for *T. truncatus* (for details, see Au, 1993).

the ones from *T. truncatus* (Figs. 2 and 3). The clicks from both species are similar to the ones recorded from captive *T. truncatus* involved in long-range target detection in open-water conditions (Table I). This shows that *T. truncatus* in the field and in captivity use a similar palette of possibilities for modulating the signal shape, duration, and frequency content. However, there are very noticeable differences in the way bottlenose dolphins make use of their echolocation signals in the field as compared to a specimen in a smaller tank: The source level and frequency content of the signals are much higher for free-ranging animals (Table I). The low source levels reported in Norris' (1967) study are most likely due to the dolphins reducing their output level to minimize echo levels from the tank walls. In a tank where the echoes from the walls were minimized, Poche et al. (1982) actually observed peak frequencies of *Tursiops* clicks resembling those of the present study. The lower frequency content of the clicks recorded in tanks both by Norris (1967), as well as by Hol and Kamminga (1979), may be explained by the source level and frequency emphasis being positively correlated, as seen in *T. aduncus* (Fig. 5). An additional explanation may be the animals adjusting the frequency content of the signals to fit the region of best hearing, which may be considerably lowered in older individuals (Klopper et al., 2010).

The source levels of free-ranging *Tursiops* clicks (*T. truncatus* 196–228 and *T. aduncus* 177–219 dB re 1 μ Pa pp, from Table I) are similar to the source levels reported from other delphinids of similar size, such as the white-beaked dolphin [*Lagenorhynchus albirostris* (Rasmussen et al., 2002), source level of 194–211 dB re 1 μ Pa pp], the Risso's dolphin [*Grampus griseus* (Madsen et al., 2004a), 201–225 dB re 1 μ Pa pp] and the pygmy killer whale [*Feresa attenuata* (Madsen et al., 2004b), 197–223 dB re 1 μ Pa pp]. There is an \sim 10 dB difference in the maximum level of signals recorded from the various field sites, with the Azorean *T. truncatus* reaching the highest source levels and the Australian *T. aduncus* having the lowest ones. The Azorean levels may be less accurate than the levels recorded in Tenerife and

Australia, as only three hydrophones were used instead of four. However, this is probably not the only explanation for the discrepancy in source levels: the localization error should be of 100% to cause a 6 dB overestimation of ASL, and the estimated localization error was much less than this for all recordings analyzed here.

The long-range detection experiments with trained animals reported higher maximum source levels than the source levels recorded from free-ranging dolphins both off Tenerife and in Australia (Table I). One may envision this to be caused by our methodology and on-axis criteria not being strict enough so that our measured clicks were not recorded on the acoustic axis. This seems highly unlikely, as we recorded thousands of clicks from dolphins approaching the array so that one would think that at least a few of these should be recorded on axis. It is also possible that we simply did not record the animals as they were producing their highest outputs. Only measurements of clicks within a 40 m range of the array were analyzed in the field recordings, so the animals may not have been challenged to detect small objects at extreme ranges under these circumstances. In addition, although these two bottlenose dolphin species are morphologically similar to one another, *T. aduncus* is somewhat smaller than *T. truncatus* (Connor et al., 2000). Larger animals are assumed to produce higher source levels than smaller ones (Gillooly and Ophir, 2010). Thus, size differences between animals at the different recording sites and animals from the studies made in captivity may have affected the measured source levels. Also, the ambient noise level was at least 10 dB higher during the long-range target detection trials as compared to the ambient noise levels during the field measurements of *T. aduncus* (Au, 1993; Jensen et al., 2009a). A trained beluga whale (*Delphinapterus leucas*) that was moved to a facility with a higher ambient noise level increased its source level click output (Au et al., 1985). Bottlenose dolphins would most likely adjust their source level in a similar manner when encountering higher background noise levels, within the biophysical constraints of the sound generator. Thus, variations in the background noise levels at the various field sites and in the captive studies may have affected the source levels used by the recorded animals. Finally, the maximum ranges that the animals were trained to achieve in the long-range target detection trials may not be representative of the way dolphins normally make use of their sonar in the field. As animals are capable of adjusting the source level, the source parameters may be adjusted to their present foraging habitat and may even be influenced by the behavioral state of the animal. It is likely that the training and psychophysical trial situation enforces the dolphin to produce higher sound levels than it would normally produce in daily life. Although this provides us with valuable knowledge of the maximum capabilities of the animal, other ecological variables such as reverberation or clutter levels may constrain the biosonar detection in shallow waters. The actual use of echolocation by *Tursiops* to find food in the wild will probably have to await suitable miniaturization of onboard sound recording tags (e.g., Johnson et al., 2009).

The range at which *Tursiops* and other toothed whales may detect fish, gill nets, and other structures in the water

has been of keen interest in many biosonar studies (e.g. Kas-telein *et al.*, 2000; Au *et al.*, 2007; Larsen *et al.*, 2007). These studies are usually based on the performance of captive animals in psychophysical tasks and on target strength measurements of the targets of interest. However, as noted earlier, there are both acoustic and behavioral reasons why toothed whales may not use their maximum biosonar abilities under normal circumstances, and that possibility should be considered when modeling detection distances.

In contrast to the four different echolocation click types identified in some studies (Au, 1993; Au *et al.*, 1995; Houser *et al.*, 1999), the on-axis click structure and especially the spectral structure of the clicks recorded in all field sites of this study were quite stereotyped (Fig. 3). Emitting a stereotyped signal probably facilitates target discrimination as any changes in temporal and spectral features of the returning echo can be attributed to the acoustic properties of the target rather than to variations in the outgoing click. The alternative would be that the dolphin stores a memory template for each outgoing click and that each returning echo must be compared to the template of the click that gave rise to that particular echo before information could be extracted. This seems extremely complicated to achieve, especially at high click rates, where the neural processing of each click template and returning echo is very unlikely to happen over less than 10 ms. It has implications for discriminating between different dolphin species recorded with passive acoustic monitors. Classification of species using spectral notches (Soldevilla *et al.*, 2008) may be affected by the behavior of the animals around the recorder, including approach distance or investigative behaviors.

A click that has been transmitted from an aperture or through collimating tissue will have its wave shape and spectrum changed in a predictable manner when observed off the acoustic axis (Beedholm and Møhl, 2006). This is observed in Fig. 4, where the spectra of off-axis clicks are plotted. A clearly visible spectral notch is progressively moving toward lower frequencies, the further off-axis the signal is recorded. This distorts the frequency spectrum from a unimodal on-axis spectrum to a more bimodal off-axis spectrum (Fig. 4). The phenomenon is well explained by cancellation of certain frequencies due to edge contributions of the transmitting aperture: the further off-axis, the longer the longest canceled wavelength gets. Similar notches or indentions in the click spectra have been reported from presumably on-axis clicks of *Tursiops* and other species (e.g., Au *et al.*, 1995; Houser *et al.*, 1999; Madsen *et al.*, 2004a,b). The reason for very few bimodal clicks being found among the on-axis signals in this study, as compared to previous studies, may be either that this study did not fully sample the true clicking repertoire of bottlenose dolphins, or more likely that in previous recordings some off-axis clicks had incorrectly been classified as having been recorded on the acoustic axis.

The relationship between source level and frequency content of the clicks as shown in Fig. 5 has been well-established not only for *T. aduncus* and *Pseudorca*, but also for smaller pelagic dolphins of the genus *Stenella* (Au and Herzog, 2003), and the largest of all toothed whales, the sperm whale (*Physeter catodon*) (Møhl *et al.*, 2000; Madsen *et al.*,

2002). Thus, it appears to be a common trait across different species of toothed whales. The simplest explanation for this pattern seems to be found in the Odontocete sound production system: To produce sounds, toothed whales force air through a pair of phonic lips in the nasal passages (Cranford *et al.*, 1996). Higher source levels involve a higher driving air pressure to actuate the more tightly shut phonic lips leading them to vibrate under more tension, and therefore presumably to generate higher frequencies than during low-level sound production. The causal relationship behind the intensity and frequency emphasis leading up to the pattern observed for *T. aduncus* and *P. crassidens* in Fig. 5 is not known, but there are good reasons to believe that the animal increases the source level by which the frequency of the clicks is automatically increased.

Moore and Pawloski (1990) trained bottlenose dolphins to vary the amplitude and spectral content of their echolocation signals. However, during psychophysical target detection trials it seems that dolphins are *not* making any drastic changes to the temporal and spectral shape of their biosonar signals (Au, 1993), except for the slight changes in frequency content connected to variations in the source level of the signal as described previously. When comparing with previous data from another delphinid, *Pseudorca crassidens* (Au *et al.*, 1995), the frequency content of the *T. aduncus* clicks recorded here seems actually to vary much less as a function of the source level, as indicated by the significantly lower regression slope in Fig. 5. For *T. truncatus* there is no significant relationship between the two parameters at all. Thus, even though dolphins can be trained to modulate the frequency content of their signals they do not seem to necessarily do so to the same extent under natural conditions.

For *T. truncatus*, the click directionality measurements are similar to the ones previously measured in captivity, whereas the clicks recorded from *T. aduncus* seem noticeably more directional (however, note that all captive data are from *T. truncatus* so an intraspecies comparison between field and captivity for *T. aduncus* cannot be made). Due to our methods of quantifying composite directionality in this study, the resulting estimate of directionality is possibly an underestimate of the actual directionality of individual clicks (even though our beam pattern calibrations indicate that there is a very good fit between the estimated and real directionality of the signal). Therefore, it cannot be ruled out that *T. truncatus* signals may have been as directional as the ones from *T. aduncus* because of an unknown source of bias in the *T. truncatus* recordings or analysis. Also, in the field measurements we have no control over the size of the animal being recorded, and one may expect larger dolphins to emit more directional signals than smaller ones. Increased directionality from recordings in the field as compared with recordings in the laboratory has also been reported from bats (Surlykke *et al.*, 2009). The beam width for *T. aduncus* measured here is almost identical to previous field measurements of another delphinid, the white-beaked dolphin (Rasmussen *et al.*, 2004). There may be an adaptive value to decrease the beam width in situations where the sonar performance is restricted by clutter. This may explain the directionality differences between *T. aduncus* and *T. truncatus*, as

the Australian recordings were performed in a shallow area with presumably higher clutter levels than the open water site of the Tenerife recordings.

The most obvious way to regulate the directionality of a transmitting system is to increase the frequency of the signals used. From Table I and Fig. 2(c) it is clear that *T. aduncus* is using higher frequencies than *T. truncatus*, and this may in part explain their different directionalities. However, this effect could be counterbalanced by the fact that the slightly smaller *T. aduncus* would be expected to produce less directional signals than larger *T. truncatus* for the same frequency content of the signals. Even though we do not have any data on which sizes of animals were recorded in this study, if the recorded *T. aduncus* were smaller than the recorded *T. truncatus* individuals, the data indicate that *T. aduncus* may be using other means to increase the directionality of the clicks. The air sacs connected to the nasal passages and surrounding the sound production organ are important in shaping the directionality of outgoing biosonar pulses (Aroyan *et al.*, 1992; Cranford *et al.*, 1996). If the animals are capable of regulating the amount of air in the air sacs and the conformation of the soft structures of the melon, it seems plausible that they may change the directionality pattern of their outgoing signals (Moore *et al.*, 2008; Au *et al.*, 2010; Madsen *et al.*, 2010; Miller, 2010; Starkhammar *et al.*, 2011).

There is a striking parallel between the findings reported here on the dissimilarities between signals characterized in laboratory and field studies for the two species most used for echolocation research: the bottlenose dolphin for Cetacea and the big brown bat for Chiroptera (Surlykke and Moss, 2000). The fact that many detailed studies have been made on captive specimens, whereas data are almost completely lacking from animals in the field, is true for both species. This is not surprising from a technical and logistical point of view: even though there have recently been tremendous advances in the technical development of devices to study animals in the field, it is still often difficult to obtain high-quality observations. Keeping animals in captivity gives a much more controlled situation to perform carefully designed experiments to understand the mechanisms of biosonar operation. However, as we have documented here, field studies are critical to understand if the mechanisms reported from captive specimen are also valid for the challenges experienced by animals in the field. The fact that we find distinct differences in laboratory and field studies of the biosonar signals of both the big brown bat and the bottlenose dolphin strongly implies that the differences in echolocation performance between animals in captive situations and in the field may also apply to other species of bats and toothed whales. It is therefore very instructive to complement studies made in captivity with field recordings of wild conspecifics before elaborate ecophysiological and evolutionary conclusions are drawn for their biosonar performances in the wild.

Studies of Risso's dolphins provide a good example of parallel research in captivity and in the field. A specimen kept in a captive facility was reported to have a hearing range of up to ~70 kHz (Nachtigall *et al.*, 1995). Later on, field recordings showed that the biosonar signals of free-

ranging animals had peak energies well beyond 100 kHz (Madsen *et al.*, 2004a). Thus there seemed to be a mismatch in the hearing and biosonar data from this species. A recent hearing study on a second captive specimen showed that this individual was capable of hearing well above 100 kHz, indicating that the first captive individual had a hearing deficiency (Nachtigall *et al.*, 2005). We believe there are likely many such examples where studies on animals in the field and in captivity can work hand in hand to give us a better understanding of the biosonar performance of both dolphins and bats.

The source parameters estimated from wild bottlenose dolphins are not only relevant for assessing the performance of the biosonar of this species in the wild. Field measurements are also crucial for identifying the right input parameters in passive acoustic monitoring and detection. There is currently a rapid development in such methods as a tool for studying, e.g., the effects on marine animals of human-induced sounds in the underwater environment, or to understand the habitat use of certain species when establishing mitigation rules such as marine reserves, fishery regulations, etc. Passive acoustic monitoring has also become a widely used complement to visual surveys to get distribution and abundance data of many species of marine mammals. These methods rely on an adequate set of input data, applicable to situations in the wild, to provide accurate and relevant results. Used appropriately, such techniques will not only help us to better understand the biology of bottlenose dolphins and other species, but also help to protect and conserve them in their natural habitats.

V. CONCLUSION

Here we show that the echolocation signals from Atlantic and Indian Ocean bottlenose dolphins are similar in frequency content to the signals of trained conspecifics echolocating in open waters. However, none of the on-axis signals measured here have the bimodal frequency pattern reported in, e.g., Au *et al.* (1995) and Houser *et al.* (1999), which could be due to off-axis recordings being included in these studies. Free-ranging dolphins produce considerably higher level clicks than a dolphin in a tank (Norris, 1967). In contrast, the source levels measured in the field are in some cases lower than and in other cases similar to the levels from trained animals performing long-range target detection tasks. This may be due to free-ranging animals being seldomly forced to use the maximum source level clicks, whereas trained animals can be pushed to use maximum levels when solving long-range echolocation tasks. Click directionality is higher in specimens of *T. aduncus* than in *T. truncatus*. These discrepancies between the characteristics of biosonar signals produced by two closely related species, and for the same species when comparing its performance in the field and in the laboratory, may be important adaptations to the sonar of dolphins working in an environment restricted by clutter and ambient noise. The results suggest that field recordings are a crucial complement to studies made in captivity to understand the biosonar performance in bottlenose

dolphins and probably also for all other species of toothed whales.

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