Feeding at a high pitch: Source parameters of narrow band, high-frequency clicks from echolocating off-shore hourglass dolphins and coastal Hector's dolphins

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Toothed whales depend on echolocation for orientation and prey localization, and source parameters of echolocation clicks from free-ranging animals therefore convey valuable information about the acoustic physiology and behavioral ecology of the recorded species. Recordings of wild hourglass (*Lagenorhynchus cruciger*) and Hector's dolphins (*Cephalorhynchus hectori*) were made in the Drake Passage (between Tierra del Fuego and the Antarctic Peninsular) and Banks Peninsular (Akaroa Harbour, New Zealand) with a four element hydrophone array. Analysis of source parameters shows that both species produce narrow band high-frequency (NBHF) echolocation clicks. Coastal Hector's dolphins produce clicks with a mean peak frequency of 129 kHz, 3 dB bandwidth of 20 kHz, 57 μs, 10 dB duration, and mean apparent source level (ASL) of 177 dB re 1 $\mu Pa_{p.-p.}$. The oceanic hourglass dolphins produce clicks with mean peak frequency of 126 kHz, 3 dB bandwidth of 8 kHz, 116 μs, 10 dB duration, and a mean estimated ASL of 197 dB re 1 $\mu Pa_{p.-p.}$. Thus, hourglass dolphins apparently produce clicks of higher source level, which should allow them to detect prey at more than twice the distance compared to Hector's dolphins. The observed source parameter differences within these two NBHF species may be an adaptation to a coastal cluttered environment versus a deep water, pelagic habitat.
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I. INTRODUCTION

Toothed whales echolocate to navigate and find prey by processing echoes generated from emission of ultrasonic short clicks of high directionality and source level (Au, 1993). The performance of a toothed whale biosonar system depends on the source parameters of the transmitted echolocation clicks, and analysis of click properties can thus convey valuable information about the acoustic physiology and behavioral ecology of recorded toothed whale species (e.g., Au, 1993; Madsen and Wahlberg, 2007). The variation in habitat and prey type from ice filled fjords, muddy rivers, and deep open oceans provides diverse acoustic environments that may have contributed to the evolutionary shaping of different click types, but little is known about how click

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source parameters may be linked to the physical environment of the different echolocating toothed whale species (Wood and Evans, 1980).

A biosonar is ultimately limited in detection range by either noise or clutter (Urich, 1983). By clutter is meant echoes from irrelevant objects ensonified by the sonar that masks target echo reception when there is temporal overlap in the arrival of target and clutter echoes (Au and Benoit-Bird, 2008). Increasing the source level of the sonar potentially leads to significant ensonification of more unwanted objects in the water meaning that the received echo-to-clutter ratio remains constant or even deteriorates with increasing source level. Instead an improved echo-to-clutter ratio can be achieved by increasing the directionality of the sonar signal as objects outside the sound beam do not add significantly to the clutter, but this gain is at the expense of search width of the sonar beam.

A noise-limited biosonar, on the other hand, is limited by either the ambient noise or the self-noise of the auditory system. For most young and healthy toothed whales (Kastelein et al., 1999; Johnson, 1967) the hearing threshold seems to be close to or below normal ambient noise level in the relevant frequency band, if the current interpretations of how toothed whales integrate noise are correct. Accordingly, an increase in source level increases the echo-to-noise ratio and hence the performance of the biosonar. The echo-to-noise ratio can also be raised by increasing the receiving directionality, which serves to reduce reception of anisotropic noise. Finally, echolocation signals may be shifted to higher frequencies where the ambient noise levels are lower (Møhl and Andersen, 1973; Urich, 1983; Au, 1993) but at the cost of increased sound absorption (Urich, 1983). Thus, different toothed whale species likely have optimized their echolocation capabilities to the specific habitat they have evolved in as seen for bats (Neuweiler and Fenton, 1988), as a trade-off between click source parameters matched to prey properties, sound absorption, ambient noise levels, clutter, and the functional constraints imposed by the morphology and size of their sound generators (Madsen and Wahlberg, 2007; Madsen et al., 2005).

For example, the large sperm whale operates a powerful long range biosonar system to locate mesopelagic prey patches at long ranges by using clicks with high source levels and centroid frequencies between 15 and 20 kHz where absorption is low (Madsen et al., 2002; Møhl et al., 2000, 2003). At the other extreme, several smaller toothed whales have been shown to produce narrow band high-frequency (NBHF) clicks around 130 kHz (Møhl and Andersen, 1973; Dawson, 1988; Madsen et al., 2005; Li et al., 2007). These signals suffer from range-dependent absorption about 40 times higher than sperm whale clicks, so the sonar can only operate at short ranges. The species producing NBHF clicks are found in three different odontocete families and they all produce echolocation clicks at peak frequencies of more than 120 kHz, 3 dB bandwidth of 6–26 kHz and Q-values between 8 and 20 [e.g., *Phocoena phocoena*, *Neophocaena phocaenoides*, *Kogia breviceps*, and *Cephalorhynchus hectori* (Møhl and Andersen, 1973; Au, 1993; Dawson, 1988; Madsen et al., 2005; Li et al., 2007)].

The NBHF clicks are apparently very similar, yet it is not clear what factors may have driven the seemingly convergent evolution of NBHF clicks in species that live in very different habitats. Morisaka and Connor (2007) suggested that the NBHF signal evolved for acoustic camouflage as an anti-predator strategy against killer whales (*Orcinus orca*) whose hearing sensitivity decreases sharply at frequencies above 60 kHz and is practically zero above 100 kHz (Szymanski et al., 1999). For this anti-predator strategy to be effective all energies of the NBHF signal must be emitted at frequencies over 100 kHz, above the upper hearing limit of the killer whale. Since absorption at the same time increases considerable with frequency above 100 kHz, the NBHF species have a small frequency band at their disposal to adapt to their environment. Yet, it seems that the very different habitats from deep water of *Kogia* to the coastal environment of porpoises would face these animals with different echolocation tasks in terms of prey, predation, noise, and clutter levels. Examples of such NBHF species living in different habitats are Hector's dolphin (*Cephalorhynchus hectori*) and the hourglass dolphin (*Lagenorhynchus cruciger*).

Hector's dolphins are coastal and have a body length of about 1.5 m and weigh around 50 kg (Reeves et al., 2002). They are only found in New Zealand and are most often found within 1 km from land (Slooten et al., 1993; Bräger et al., 2002). They feed opportunistically on smaller fish and squid caught at the bottom and at the surface (Slooten and Dawson, 1988). The hourglass dolphins are oceanic and slightly larger than Hector's dolphins, measuring ~1.4–1.9 m and weighing 74–88 kg (Godall et al., 1997). Molecular phylogenies (May-Collado and Agnarsson, 2006) suggest close taxonomic affinity to the *Cephalorhynchus* genus. With its oceanic circumpolar sub-Antarctic distribution knowledge about this species is primarily circumstantial (Godall et al., 1997). The few collected stomachs of hourglass dolphins contained remains of small fish (*Mycophidae*) and squid (*Onychoteuthidae* and *Enoloteuthidae* families) (Godall et al., 1997). So, while NBHF species seemingly produce almost identical clicks, it is possible from their differences in habitat and morphology that they do display differences in source parameters within the NBHF click class, in particular, with respect to source level.

Here we show that echolocation clicks of Hector's and hourglass dolphins have different source levels, duration, and bandwidth, possibly due to the different acoustic conditions posed by their respective habitats.

II. MATERIALS AND METHODS

A. Recording chain and field sites

Recordings were made with a linear, vertical array of four Reson TC 4034 spherical hydrophones (Reson A/S, Slangerup, Denmark) with 20 m cable and a measured sensitivity of −222 dB re 1 V/μPa between 100 and 150 kHz. Hydrophones were mounted horizontally in the same direction along a vertical Perspex rod with 1 m hydrophone spacing. The entire array was suspended either 1 m (Hector's) or 2 m (hourglass) below a buoy in the surface and with a 0.5 kg lead weight attached to the other end of the array (*sensu*

Madsen *et al.*, 2004a). Signals were bandpass filtered [100 Hz (one pole) to 200 kHz (four poles)], amplified in a custom-built four-channel amplifier, and digitized [500 kHz, 12 bit NuDAQ pci9812, AdLink, Los Angeles, CA]. The measured frequency response of the entire recording chain was flat (± 2 dB) from 200 Hz to 180 kHz and allowed for continuous streaming of data to disk. Clip level of the recording chain was 189 dB re μPa (peak) with 50 dB gain for hourglass dolphins, and either 169 or 189 dB re μPa (peak) for Hector's dolphins (70 or 50 dB gain) set by the max input voltage of ± 5 V peak in the analog-to-digital converter.

Recordings were obtained at two field sites. Hector's dolphins were recorded in the coastal habitat around Akaroa Harbour, New Zealand (43°52′9″S; 172°56′16″E) on January 7 and 9, 2007. When dolphins approached the large rigid-hulled inflatable boat (RHIB) to bow ride, the engine was turned off and the recording array lowered in the water. No other marine mammals were in sight or detected acoustically. Recordings were made under very calm weather conditions (low winds, sea state 0–1 Beaufort, sea temperature of 14 °C, and salinity of 34.5‰).

Hourglass dolphins were recorded on January 30, 2007, in the Drake Strait (58°17′50″S; 61°29′39″W) at open sea between Tierra del Fuego and the Antarctic Peninsular. A group of about 20 hourglass dolphins was sighted from the naval vessel HDMS "Vædderen" and identified by their characteristic hourglass-shaped white markings on the flanks and prominent dorsal fin. No other marine mammals were in sight or detected acoustically. The dolphins were approached in a RHIB and when animals were encountered within 100 m of the RHIB the recording array was deployed. Recordings were made under calm weather conditions (low winds, sea state 2 Beaufort, moderate swell, sea temperature of 5.1 °C, and salinity of 33.9‰).

B. Click analysis

Dolphin clicks are very directional and it is thus essential to ensure that clicks used for analysis are recorded as close to on-axis as possible (Au, 1993; Madsen and Wahlberg, 2007). Off-axis clicks are distorted and with much lower apparent source level (ASL) (Au *et al.*, 1986), and the click parameters may be different than on-axis (Au, 1993). For click analysis we applied a set of criteria for on-axis properties following Villadsgaard *et al.* (2007) to ensure that only clicks recorded close to on-axis were used. However, since we did not know whether focal animals were actually pointing their acoustic axis at the array, we used the definition of Møhl *et al.* (2000) of ASL, i.e., the back calculated sound intensity at a distance of 1 m from a directional source recorded in an unknown aspect, for the clicks complying with the following on-axis criteria: (i) recorded on all four channels; (ii) part of a scan, i.e., a series of clicks closely spaced in time normally first increasing then decreasing in amplitude (*sensu* Møhl *et al.*, 2003); (iii) of maximum amplitude on one of the two middle hydrophone channels; and (iv) the direct path of the click had to be stronger than any trailing bottom or surface reflections. Further, we determined that the localization error (see below) could not give rise to a

transmission error of more than 2 dB in the source level calculations. Additionally, we visually inspected all on-axis clicks and removed clicks that contained double or triple pulses, since these likely arise from surface reflections and are not source generated (Li *et al.*, 2005).

The source properties were quantified using a series of parameters *sensu* Au (1993) and Madsen and Wahlberg (2007) for each click accepted as on-axis: Duration (defined as between -10 dB points on the envelope, calculated as the absolute value of the analytical waveform. From here on stated as 10 dB duration); peak frequency, centroid frequency (i.e., the frequency dividing the spectrum in two halves of equal energy on a linear scale), 10 dB bandwidth, (i.e., bandwidth at -10 dB points below the spectrum peak), 3 dB bandwidth (i.e., bandwidth at -3 dB points below the spectrum peak), rms bandwidth (i.e., spectral standard deviation around the centroid frequency on a linear scale), and Q-value (centroid frequency divided by the rms bandwidth).

Interclick intervals (ICIs) were found as the interval between the on-axis click and the click preceding the on-axis click in the same click scan. ICI is given in milliseconds. A few clicks were too closely spaced with echoes and clicks from several scans to objectively derive the ICI and these clicks were thus not included in the ICI analysis

The recordings were browsed using ADOBE AUDITION 1.5 (Syntrillium, Adobe, Mountain View, CA) and all analysis and signal processing were performed with custom written scripts in MATLAB (Mathworks).

### C. Calibration of localization routines

The array performance was evaluated in Aarhus Harbour, Denmark, by playing out calibrated tone pips with source parameters similar to NBHF clicks at known ranges from the array. The four-hydrophone-array was suspended from a buoy with the top hydrophone 1 m below the surface. The sound source (at 3 m depth) was moved gradually away from the array at measured ranges in 10 m steps. Tone pips (130 kHz sinus pulses of 15 cycles and a 100 μs duration) were transmitted with an omni-directional hydrophone (B&K8105) connected to a sound generator (Agilent, model 33220A). The same recording chain and settings as used for the dolphin recordings were used to record signals transmitted in a range interval from 10 to 80 m from the array. Speed of sound was estimated from the Leroy equation (Urich, 1983) from measured temperature and salinity. A precise localization range was defined as a range within which the rms error (Villadsgaard *et al.*, 2007) with respect to the actual range was within a range jitter corresponding to a variation in transmission loss (TL) (spherical spreading) of <2 dB.

D. Estimation of source level

Synchronized recordings of the same click on four channels allow localization of the clicking dolphin with three hyperbolas calculated from time of arrival differences of the click pair wise among the four hydrophones. Localizations were performed using MATLAB implementing the localization routines of Wahlberg *et al.* (2001) and Madsen and Wahlberg (2007). It proved essential to use a robust measure of the
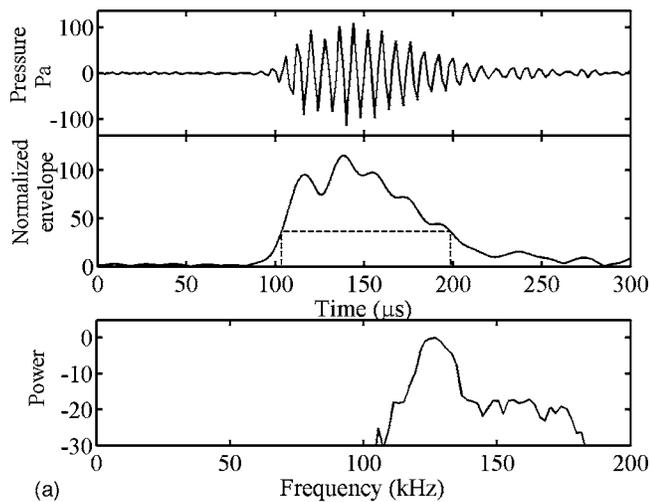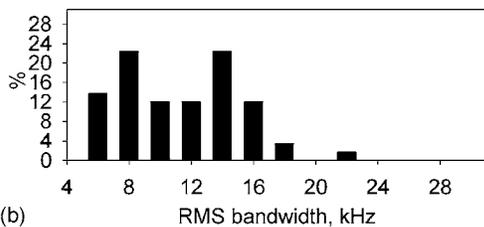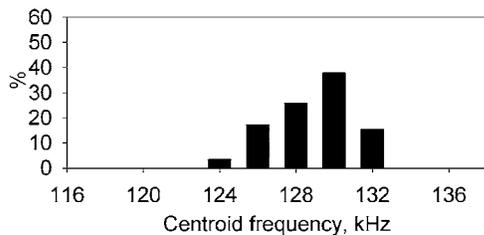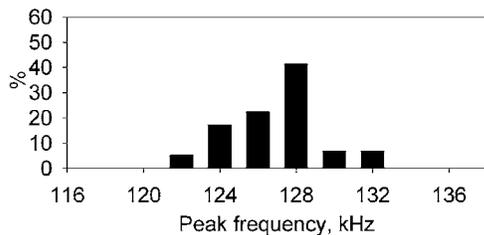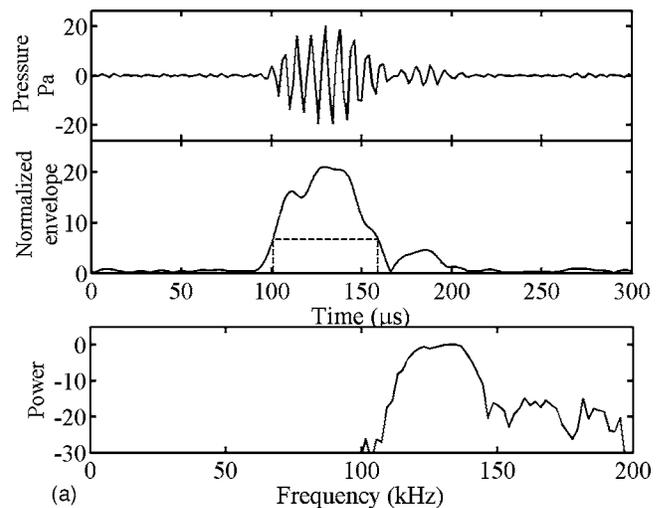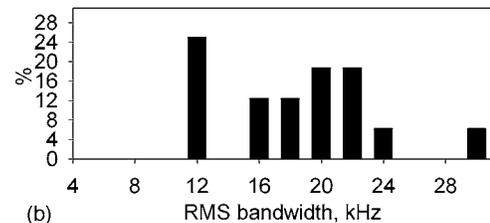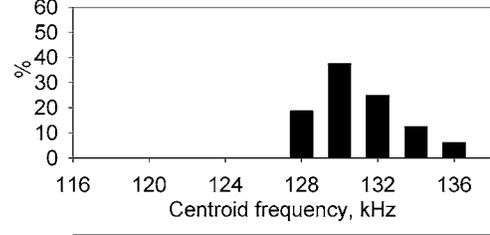
FIG. 1. (a) Time domain, envelope, and power spectrum of a representative hourglass dolphin signal. The dashed square in the envelope denotes the 10 dB duration. [Fast Fourier transform (FFT) size of 256, spectrum interpolated with a factor 100, sampling rate of 500 kHz, and rectangular window.] (b) Histograms of 58 on-axis hourglass dolphins' clicks with peak frequency, centroid frequency, and rms bandwidth. Binwidth is 2 kHz.
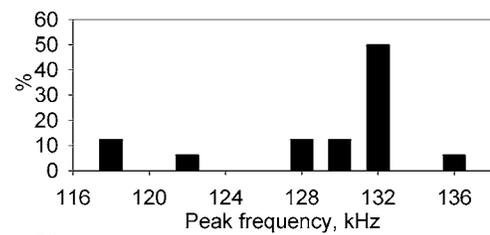

FIG. 2. (a) Time domain, envelope, and power spectrum of a representative Hector's dolphin signal. The dashed square in the envelope denotes the 10 dB duration. (FFT size of 256, spectrum interpolated with a factor 100, sampling rate of 500 kHz, and rectangular window.) (b) Histograms of 16 on-axis Hector's dolphins' clicks with peak frequency, centroid frequency, and rms bandwidth. Binwidth is 2 kHz.

time of arrival differences for the same signal recorded on the four channels. We determined the timing of a click from the first sample exceeding −10 dB of the peak of the click envelope [Figs. 1(a) and 2(a)].

Once the range to the animal has been estimated, TL can be calculated and added to the received level (RL) of a click. Villadsgaard et al. (2007) found that propagation loss of 130 kHz porpoise clicks in a shallow water habitat was well approximated by spherical spreading plus the frequency dependent absorption. Given the short distances and good mixing of the water column in the two habitats in the present study, we also assumed that TL could be approximated by spherical spreading plus absorption. ASL of echolocation clicks was thus calculated using the equation

$$ASL = RL + TL(=20 \log r + \alpha r) \quad (Urich, \ 1983),$$

where α is the absorption coefficient in dB/m and r is range in m. For the present field sites of 14 and 5.1 °C for Akaroa and the Drake Passage, α was calculated following expressions from Fisher and Simmons (1977) using the centroid frequency of the clicks (α is 0.037 for Hector's dolphin and 0.029 or hourglass dolphin). ASLs are given as peak-peak pressure, rms pressure, and energy flux density (EFD) and were computed as follows. $RL_{p.-p.}$ (dB re 1 $\mu Pa_{p.-p.}$) was measured directly from the maximum and minimum peak pressures of the waveform. RL_{rms} (dB//1 μPa rms) is the rms pressure calculated over the 10 dB duration of the signal. RL_{EFD} (dB//1 μPa^2 s) is the signal energy integrated over the 10 dB duration (Madsen, 2005).

1786   J. Acoust. Soc. Am., Vol. 125, No. 3, March 2009

Kyhn et al.: Sounds of hourglass and Hector's dolphins

TABLE I. Mean ($\pm$standard deviation) and range of echolocation click source parameters of hourglass dolphins (*Lagenorhynchus cruciger*) and Hector's dolphins (*Cephalorhynchus hectori*).

Parameters	Hector's dolphin *Cephalorhynchus hectori*		Hourglass dolphin *Lagenorhynchus cruciger*	
	Mean values (stdev)	Range	Mean values (stdev)	Range
10 dB duration (μs)	57($\pm$6)	41–65	115($\pm$24)	79–176
$RL_{p.-p.}$, dB re 1 $\mu Pa_{p.-p.}$	156($\pm$6)	145–166	162($\pm$4)	155–168
$ASL_{p.-p.}$, dB re 1 $\mu Pa_{p.-p.}$ [a]	177($\pm$6)	161–187	197($\pm$4)[a]	190–203[a]
$RL_{-10\ dB}$, dB re 1 μPa rms	145($\pm$6)	133–154	151($\pm$4)	144–158
$ASL_{-10\ dB}$, dB re 1 μPa rms[a]	166($\pm$6)	152–175	186($\pm$4)[a]	179–193[a]
$EFD_{-10\ dB}$, dB re 1 μPa^2 s [a]	121($\pm$4)	110–126	146($\pm$3)[a]	140–152[a]
Peak frequency (kHz)	129($\pm$5)	117–135	126($\pm$2)	122–131
Centroid frequency (kHz)	128($\pm$3)	125–132	128($\pm$2)	124–132
3 dB bandwidth (kHz)	20($\pm$3)	12–26	8($\pm$2)	5–11
10 dB bandwidth (kHz)	30($\pm$10)	24–66	13($\pm$2)	9–18
rms bandwidth (kHz)	18($\pm$5)	11–29	11($\pm$4)	5–22
$Q_{-3\ dB}$	6($\pm$1)	5–11	17($\pm$4)	12–25
Q_{rms}	8($\pm$2)	4–12	13($\pm$5)	6–26
Mean range from array (m)	11($\pm$4)	4–19	50[b]	50[b]
n	16		58	

[a]ASL for hourglass dolphins is calculated from an estimated range.
[b]Estimated minimum range of 50 m, corresponding to a transmission loss of 35 dB.

III. RESULTS

Several hundred Hector's dolphin clicks were recorded over 2 days from 12 groups of between two and eight animals approaching to within 1 m from the hydrophone array. Due to the fission-fusion structure of Hector's dolphins groups (Slooten and Dawson, 1988; Slooten *et al.*, 1993) and their small home range (Bräger *et al.*, 2002) some animals have likely been recorded more than once. The dolphins approached the boat to bow ride.

Around 200 hourglass dolphin clicks were recorded on one occasion from a group of around 20 animals. The clustering of the dolphins and lack of directional movement suggested that they were engaged in feeding activities. Fifty-eight hourglass dolphins' clicks were judged to have been recorded on-axis; however, all were recorded at too great a range (>40 m) from the hydrophone array to allow for accurate localization. We thus based ASL calculations on estimated range. In order to ensure a conservative ASL estimate we used a range of 50 m to calculate TL (see equation above) between the clicking dolphin and the hydrophone array. A TL of 35 dB was therefore added to each RL for this species. No dolphins were recorded closer to the array than 40 m, and we therefore assume that the derived source levels are minimal estimates with the possibility of the estimated source levels to be higher, but very unlikely to be lower.

Source signal parameters of both species are summarized in Table I. Hourglass dolphins and Hector's dolphins both produced clicks with a centroid frequency of 128 kHz with little intraspecific variation and identical maximum values of 132 kHz. Bandwidths were much narrower for hourglass dolphins meaning that the click energy was contained in a smaller frequency band giving a higher Q-value. The RLs of hourglass dolphins ranged from 155 to 168 dB re 1 $\mu Pa_{p.-p.}$ and Hector's dolphins RL ranged from 145 to 166 dB re 1 $\mu Pa_{p.-p.}$. The peak-to-peak source level of hourglass

dolphin was thus estimated to be about 20 dB higher than Hector's dolphin clicks, since they were at least 50 m away whereas Hector's dolphins were localized to be <20 m from the array. Hourglass dolphin clicks were on average more than twice as long as Hector's dolphin clicks and appeared to have an EFD at least 25 dB higher due to the higher source level and longer duration. Representative clicks and histograms of click parameters are shown in Figs. 1(a), 1(b), 2(a), and 2(b). We found no correlation for click duration or bandwidth with ICI, for either species (Fig. 5).

For the array calibration 2451 clicks were included in the analysis of the localization routines. 130 kHz clicks could be localized precisely (with a rms error up to 2 dB) out to 40 m from the hydrophone array (Fig. 3). At greater distances the routines underestimated the actual distances to the sound source, giving rise to errors larger than 3 dB in TL.

IV. DISCUSSION

NBHF clicks of porpoises and the *Cephalorhynchus* genus have been described as stereotypical (Au, 1993; Madsen *et al.*, 2005). The source parameters of Hector's and hourglass dolphins recorded in this study, however, displayed some apparent differences. Both species produced NBHF clicks with a centroid frequency of 128 kHz, but clicks of hourglass dolphins were about twice as long, with a narrower bandwidth and therefore higher Q-value, than those of Hector's dolphins. Hourglass dolphins consequently concentrated their energy in a narrower frequency band while the peak frequency and centroid frequency were similar for the two species.

Hourglass dolphins had higher estimated source levels than Hector's dolphin, and the fact that even the highest of the Hector's source levels found in this study did not exceed the lowest of the estimated hourglass dolphin source levels suggests that there is a genuine source level difference be-
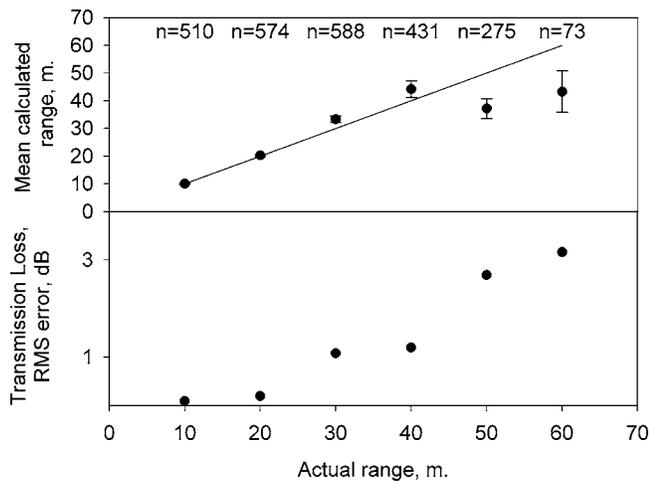
FIG. 3. Calibration of localization precision using a 3 m aperture four element hydrophone array. (a) Mean calculated ranges with standard deviation plotted against actual range. The line denotes the expected localization range from each of the actual ranges. (b) Effect of localization error on TL expressed in rms error, dB. With a 3 m aperture array NBHF species may be localized out to 40 m with ±2 dB precision on source level calculations.

tween the two species. Despite the apparent on-axis approach used in this study we can, however, only ensure that the clicks used for analysis were those recorded closest to on-axis of the clicks in a given scan. Since the ASL decreases with increasing angle to the acoustic axis (Au, 1993), source levels may be underestimated in our analysis compared to true on-axis clicks. Furthermore, the ASL of hourglass dolphins is a rough (but most likely conservative) estimate since the dolphins were too far away to be localized. The estimated range of 50 m for the calculation of TL was based on a visual estimation made at the time of recording and on the fact that 130 kHz clicks can be located accurately out to 40 m from the array. We could not see the animals under water, but the fact that we could not locate any of the recorded clicks leads us to suspect that all dolphins were at greater ranges than 40 m from the array during recording. Further, the hourglass dolphins had a mean RL of 162 dB re 1 $\mu Pa_{p.-p.}$ and was ~50 m away, whereas Hector's dolphins were <20 m away and had a mean RL of 156 dB re 1 $\mu Pa_{p.-p.}$. A mean ASL of 197 ± 4 dB re 1 $\mu Pa_{p.-p.}$ at 1 m and unknown aspect is thus a conservative best estimate for the hourglass dolphin (a range increase from 50 to 100 m would increase mean SL to 204 dB re 1 $\mu Pa_{p.-p.}$), whereas the estimate of ASL for Hector's dolphins was 177 ± 6 dB re 1 $\mu Pa_{p.-p.}$ at 1 m (Table I).

Hector's dolphins came to bow ride, and as they were very close to the boat and the hydrophone array at the time of recording their source levels may likely have been lower than during natural foraging, which the hourglass dolphins were engaged in. However, Dawson and Thorpe (1990) also found low ASLs of ~150 dB re 1 $\mu Pa_{p.-p.}$ for Hector's dolphins foraging at the surface within 5 m from their boat. They also recorded clicks of up to 163 dB re 1 $\mu Pa_{p.-p.}$, but could not discern the vocalizing animal and thus estimate distance to the hydrophone.

If the source parameters measured in this study are representative for the two species, the ASLs of hourglass dolphins are an order of magnitude higher than those of Hec-

tor's dolphins. Hourglass dolphins have been found up to around 40 cm longer and 40 kg heavier than Hector's dolphin and it is possible that the higher ASL of hourglass dolphins can be ascribed to this size difference. However, Villadsgaard et al. (2007) reported that ASLs clicks of wild harbor porpoises, similar in size to Hector's dolphins, vary considerable between different recording sites (178–205 dB re 1 $\mu Pa_{p.-p.}$), possibly depending on background noise level and behavioral states of the animals. The variation in ASL of harbor porpoises thus spans both Hector's and hourglass dolphins, also spanning the size differences between the two. Hector's and hourglass dolphins likely also have a large dynamic range within which they produce clicks since we cannot ascertain that the full source level repertoire was sampled during these recordings.

Source level influences heavily on the range at which a dolphin can detect prey and the source level differences found here may thus provide a hint to the ranges at which the dolphins have adapted their sonars to search for prey. Detection range can only be estimated knowing the echo level threshold (DT) of a dolphin for a prey object with known target strength (TS). Kastelein et al. (1999) measured the psychophysical target detection threshold (expressed as echo energy flux density, EE) for a captive harbor porpoise echolocating at two water-filled stain-less steel spheres to be ~27 dB re 1 $\mu Pa^2 s$ (between 22.4 and 27.4 dB re 1 $\mu Pa^2 s$); however, these calculations were based on too low source level (Au et al., 2007) and the present best estimate of harbor porpoise detection threshold is 44–45 dB re 1 $\mu Pa^2 s$ (Au, personal communication). To calculate detection range Kastelein et al. (1999) used the active sonar equation (EE=SE$-2 \times$TL+TS$_E$=DT) solved for EE at maximum range of detection, where SE is source EFD, TL is transmission loss, and TS$_E$ is target strength energy. The non-noise-limited form of the sonar equation was used due to the low background noise usually found around 130 kHz (Kastelein et al., 1999; Au et al., 2007). Au et al. (2007) found that a 30 cm cod has a broadside target strength of -25 dB emitting artificial NBHF clicks with a centroid frequency of 130 kHz. Assuming that Hector's dolphin and hourglass dolphin have detection thresholds comparable to that of the harbor porpoise of 45 dB re 1 $\mu Pa^2 s$ and using the porpoise as a model we can thus estimate detection ranges of these two species. Under the assumption that both species were recorded with representative maximum source levels, Hector's dolphin is predicted to be able to detect a 25 cm cod broadside up to 10–24 m away, while hourglass dolphins are predicted to detect the same fish out to about 52–96 m, using minimum and maximum EFD source levels of 110 and 126 dB re 1 $\mu Pa^2 s$ and 140 and 152 dB re 1 $\mu Pa^2 s$ and respective absorption values (α, see above) (Fig. 4). Using the same assumptions wild harbor porpoises are predicted to detect the same cod 20–84 m away using minimum and maximum EFDs of 123 and 150 dB re 1 $\mu Pa^2 s$ and α of 0.04 (Villadsgaard et al., 2007). The 25 dB lower EFD of Hector's dolphin clicks thus more than halves the detection range compared to the hourglass dolphin.

Hector's dolphins live within the coastal zone. Shallow coastal areas generally have a higher productivity and thus
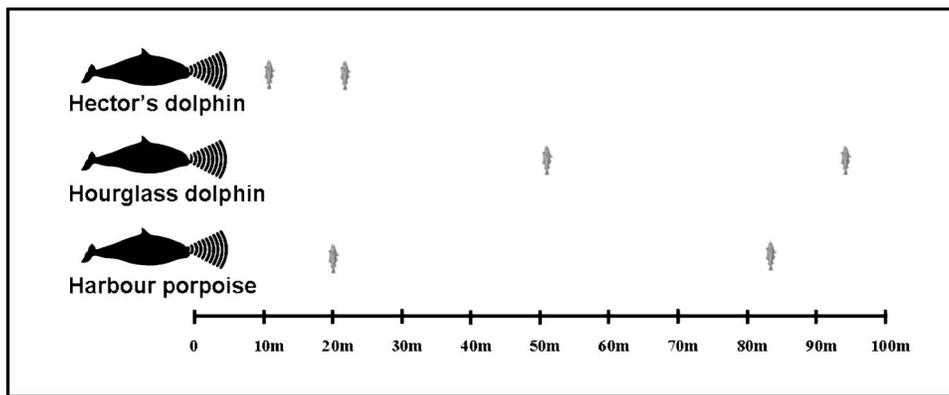
FIG. 4. Estimated detection ranges of hourglass dolphin and Hector's dolphin calculated for minimum and maximum EFD source levels using the harbor porpoise as model (Kastelein *et al.*, 1999, see text for further explanation) and target strength of a 25 cm cod measured broad side (Au *et al.*, 2007). Minimum and maximum detection ranges of harbor porpoise are shown for comparison, build on data from Villadsgaard *et al.* (2007) and Au (personal communication).

greater prey availability, but clutter and reverberation levels are also higher. Since an increase in source level also increases clutter this may explain why Hector's dolphins use a comparatively low source level. Increased transmission and receiving directivity will increase detection range in a cluttered environment since a more directional beam or sound reception will result in fewer unwanted echoes. Transmission directivity depends on size of the sound transducer relative to the emitted wavelength. If the sound production apparatus scales with head diameter of the animal (Au *et al.*, 1999), transmission directivity likely compares among the similar sized Hector's and hourglass dolphins presenting no special adaptation of Hector's dolphin to a cluttered environment. However, if prey density is also higher in the coastal environment, Hector's dolphin may not need high source levels to locate prey there. Future studies may uncover whether Hector's dolphins are capable of producing higher source levels at other behavioral states as observed for harbor porpoises (Villadsgaard *et al.*, 2007).

The higher source levels of hourglass dolphins oppositely suggest that they forage in an environment with lower prey density or with longer distances between prey patches. Since their click duration is also about twice that of Hector's dolphins, the energy content is increased two-ways compared to Hector's dolphin: higher source level (20 dB) and longer duration (doubling of energy content, 3 dB). If there is a size restricted maximum output for NBHF species, as suggested by Au (1993), the longer click duration suggests that hourglass dolphins may be noise limited and that they maximize energy content by making longer clicks to facilitate a longer detection range. The source parameters of hourglass' clicks may be the result of selection for increased target range in a noise-limited sonar situation.

For odontocete clicks, duration and bandwidth are inversely related (Wiersma, 1988; Au, 1993; Beedholm, 2008) so that a change in one parameter will change the other as well. It is therefore not surprising to find that bandwidth of hourglass dolphin clicks is about half that of Hector's clicks. However, it is interesting to note that despite differences in bandwidth both species have all click energy above 100 kHz [Figs. 1(a) and 2(a)] and the differences in source parameters observed between these two NBHF species are thus not in disagreement with the NBHF anti-predator hypothesis of Morisaka and Connor (2007).

The duration of Hector's dolphins' clicks of ∼60 µs found in this study is lower than in previous published studies of 80–800 µs (Dawson, 1988; Dawson and Thorpe, 1990; Dawson, 1991; Thorpe *et al.*, 1991; Thorpe and Dawson, 1991). These differences in duration likely arise from the fact that previous studies included so-called double, triple, and quadruple pulsed clicks in their analysis, which we omitted here as they are most likely the result of surface and bottom reflections (Li *et al.*, 2005) and possibly off-axis distortions. In addition, previous studies measured duration by hand, whereas we used a definition of −10 dB from maximum amplitude of the signal envelope. The durations of Hector's clicks measured here correspond to that of another NBHF species the finless porpoise (*Neophocaena phocaenoides*) of ∼30–60 µs (unknown recording aspect and definition of duration) (Akamatsu *et al.*, 1998) and are among the shortest of NBHF clicks. Villadsgaard *et al.* (2007), however, reported a range in 10 dB duration of harbor porpoise clicks from 44 to 113 µs thus spanning the range of both Hector's and hourglass dolphin clicks. It is possible that some click source parameters change with behavior and thus that the variation in duration between Hector's and hourglass' clicks could be caused by differences in behavior at the time of recording. Since ICIs change during, e.g., approach and capture phases of prey in other toothed whales (Johnson *et al.*, 2007), we used ICI as a proxy for behavior, and to test whether Hector's dolphins and hourglass dolphins changed their click duration and/or bandwidth with ICI we thus plotted each ICI preceding an on-axis click against its 10 dB duration and rms bandwidth for both species in Fig. 5. ICIs were generally longer for hourglass dolphins, but where the two species overlapped in ICI, the click duration and bandwidth were distinctly different (Fig. 5). Although it is possible that more recordings of the species measured here engaged in different behaviors may show a greater dynamic range in click duration resulting from changes in the context of sonar use, and not only from differences in habitat, this study suggests a genuine difference in click duration between Hector's dolphin and hourglass dolphin.

So far ASLs have only been measured for three free-ranging NBHF species: the harbor porpoise (Villadsgaard *et al.*, 2007) and the two present species (this study and Dawson and Thorpe, 1990). The highest levels were found for hourglass dolphins with a range 190–203 dB re 1 $\mu Pa_{p.-p.}$
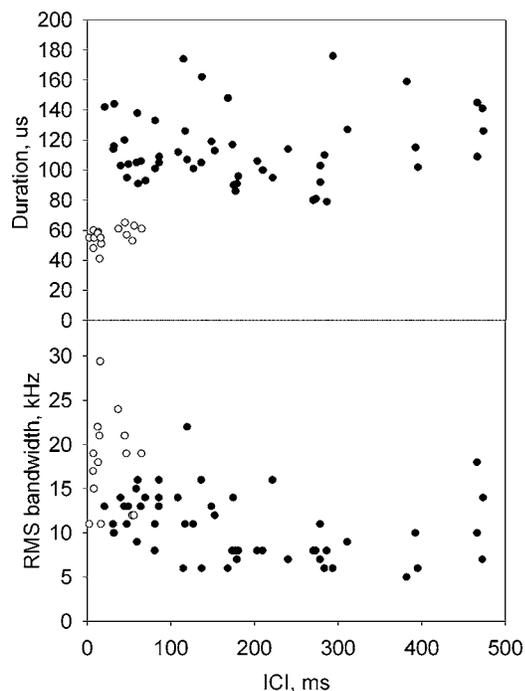
FIG. 5. rms bandwidth and 10 dB duration as a function of ICI. ICI is the one preceding the on-axis click for which bandwidth and duration was measured. Closed circles are hourglass dolphins and open circles are Hector's dolphins.

(Table I) and harbor porpoises with a range from 178 to 205 dB re 1 $\mu Pa_{p.-p.}$ (Villadsgaard *et al.*, 2007) and Hector's dolphins with a range 161–187 dB re 1 $\mu Pa_{p.-p.}$ (Table I). These levels are 10–30 times lower than in general for broadband dolphin clicks that have source levels of up to ∼220 dB re 1 $\mu Pa_{p.-p.}$ (Au, 1993; Rasmussen *et al.*, 2002; Madsen *et al.*, 2004b), which again is reflected in the much longer detection range. It is precarious to generalize from only two species, especially with a very limited sample size in terms of behavior; but at least for *Cephalorhynchus* dolphins and the hourglass dolphin, offshore NBHF dolphins seem to produce clicks with higher source level than coastal dolphins do. To gain a better insight into the evolution and plasticity of the NBHF clicks this hypothesis should be tested by recording clicks from other *Cephalorhynchus* and porpoise species engaged in different behaviors. On the basis of the present findings we hypothesize that the oceanic Dall's porpoise will have a greater source level than coastal-offshore species such as the harbor porpoise and that riverine and very coastal species will have the lowest source levels.

ACKNOWLEDGMENTS

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