Echolocation in sympatric Peale's dolphins (*Lagenorhynchus australis*) and Commerson's dolphins (*Cephalorhynchus commersonii*) producing narrow-band high-frequency clicks

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SUMMARY

An increasing number of smaller odontocetes have recently been shown to produce stereotyped narrow-band high-frequency (NBHF) echolocation clicks. Click source parameters of NBHF clicks are very similar, and it is unclear whether the sonars of individual NBHF species are adapted to specific habitats or the presence of other NBHF species. Here, we test whether sympatric NBHF species sharing the same habitat show similar adaptations in their echolocation clicks and whether their clicks display signs of character displacement. Wide-band sound recordings were obtained with a six-element hydrophone array from wild Peale's (*Lagenorhynchus australis*) and Commerson's (*Cephalorhynchus commersonii*) dolphins off the Falkland Islands. The centroid frequency was different between Commerson's (133±2 kHz) and Peale's (129±3 kHz) dolphins. The r.m.s. bandwidth was 12±3 kHz for both species. The source level was higher for Peale's dolphin (185±6 dB re 1 μPa p.–p.) than for Commerson's (177±5 dB re 1 μPa p.–p.). The mean directivity indexes were 25 dB for both species. The relatively low source levels in combination with the high directivity index may be an adaptation to reduce clutter when foraging in a coastal environment. We conclude that the small species-specific shifts in distribution of centroid frequencies around 130 kHz may reflect character displacement in otherwise-stereotyped NBHF clicks.

Key words: acoustic species separation, acoustics, character displacement, clutter adaptation, static acoustic monitoring, sympatric species.

INTRODUCTION

Toothed whales, with more than 70 species, cover a large range of sizes and habitats, from shallow rivers to deep mesopelagic ocean water. They presumably all use echolocation to find and capture prey, but little is known about the evolutionary forces shaping the speciation and biosonar source parameters of toothed whales (Wood et al., 1980). In three phylogenetically different groups of toothed whales [Phoconoidea, *Cephalorhynchid* dolphins and the pygmy sperm whale (*Kogia breviceps*)], the same narrow-band high-frequency (NBHF) echolocation signal has evolved, likely as an adaptation to avoid predation from killer whales (*Orcinus orca*) (Andersen and Amundin, 1976; Morisaka and Connor, 2007). However, it is unclear whether these different species have special adaptations within the NBHF signal and, if so, which selective pressures have affected their acoustic signal and foraging strategy within each specific habitat.

Target strength, background noise and clutter are all properties of the acoustic environment of echolocating species, and this means that, regardless of animal adaptations, a sonar will ultimately be limited by either noise or clutter (Au, 1993). For all sonar systems, the limiting factor deciding whether a returning echo is detected is either the echo-to-noise ratio (ENR) of the returning echo or the echo-to-clutter level. The ENR is given by the emitted source level (SL) plus the target strength, minus the two-way transmission loss (absorption and spreading) and the received noise (Urick, 1983). We may thus expect the source parameters of a given animal sonar to be adapted either to maximize range under noise-limited conditions or to reduce clutter, depending on the habitat to which the species has adapted.

Besides noise, clutter in the form of unwanted echoes may also interfere with detection of the returning echo. The influence of clutter is reduced by the directionality of the transmitter: the greater the directionality, the smaller the area ensonified by the animal, and a greater directionality will thus reduce the number of unwanted echoes. By contrast, an increased receiving directionality will decrease amount of received noise. An animal may thus adapt to echo detection in noise by increasing the source level and/or the receiving directionality, whereas an increased transmitting directivity will facilitate echo detection in clutter and increase the SL for the same output power.

Examples of such sonar adaptation are found among bats. The terrestrial environment of echolocating bats offers a range of different types of foraging niches and habitats, facing the animals with different prey types, clutter and noise levels. Accordingly, the sonar signals of different Microchiropteran bats show adaptations to different clutter and noise levels, and several eco-types of bat sonar have been proposed based on how close the bats forage to reflective surfaces such as the foliage, the ground or water surfaces, which all create clutter (Neuweiler, 1989; Neuweiler, 2000; Denzinger et al., 2004; Jung et al., 2007). Open-space foragers have, for example, adapted to noise by making their echolocation signals and cry patterns suitable to long-range navigation by producing high source level, narrow-band signals of lower centroid frequency and with shallow frequency modulation emitted with relatively large inter-pulse intervals, whereas bats foraging in dense forest use clicks of lower SL to avoid clutter (Neuweiler, 1989; Neuweiler, 2000; Denzinger et al., 2004; Jung et al., 2007).

The same type of links between habitat and sonar properties has not been established for toothed whales, despite an increasing number of studies of animals in the wild as well as in captivity. Based on data from only a few odontocetes, there is a tendency for smaller animals to have lower directionality and source level than larger animals without regard to habitat (Au, 1993; Au et al., 1995; Au et al., 1999). That raises the question whether inter-specific differences can be explained by the size of the species alone or whether more-biological shaping factors such as habitat, prey and predation also play important roles in shaping the signals of toothed whale biosonar systems.

As introduced above, three phylogenetically distinct groups of small (<2.5 m) odontocetes have evolved the same type of sonar signal: an NBHF click with a peak frequency around 130 kHz and a half-power bandwidth around 15 kHz. The groups producing these strikingly similar NBHF clicks include the *Phocoenidea* family (Møhl and Andersen, 1973; Akamatsu et al., 1998; Villadsgaard et al., 2007), the *Cephalorhynchus* genus (Kamminga and Wiersma, 1982; Dawson and Thorpe, 1990; Kyhn et al., 2009) within the dolphin family [including the hourglass dolphin (*Lagenorhynchus cruciger*)] and the pygmy sperm whale (Madsen et al., 2005). Furthermore, the Francicana river dolphin (*Pontoporia blainvillei*) (von Fersen et al., 2000) is proposed to use NBHF clicks, but only the peak frequency and –3 dB bandwidth was stated by the investigators (von Fersen et al., 2000).

Peale's dolphin (*Lagenorhynchus australis*) is expected to use the NBHF signal as its sister species, the hourglass dolphin, uses NBHF signals, and both species are here considered to be part of a phylogenetic group consisting of these two species and the *Cephalorhynchus* genus (May-Collado and Agnarsson, 2006; Tougaard and Kyhn, 2010). All together, at least 14 species produce NBHF echolocation clicks, and they mostly inhabit shallow water, but with a few oceanic (such as the hourglass dolphin) and even deep-diving (the pygmy sperm whale) species.

All these species likely use the NBHF signal as a result of evolutionary convergence under the possibly shared selection forces of a small body size and predation from killer whales (Andersen and Amundin, 1976; Madsen et al., 2005; Morisaka and Connor, 2007) that hear frequencies above 100 kHz very poorly (Szymanski et al., 1999). Not all small toothed whales, however, are NBHF species, and, as discussed by Morisaka and Connor (Morisaka and Connor, 2007), there are general differences in both behaviour and group size between NBHF species and non-NBHF species. Although the risk of predation may have driven the evolution of the four phylogenetically different types of NBHF sonar systems to be narrow band and with a peak frequency around 130 kHz to keep all energy above 100 kHz (Andersen and Amundin, 1976; Morisaka and Connor, 2007), the increased absorption and masking noise with increasing frequency have likely restrained the peak frequency upwards to around 130 kHz (Madsen et al., 2005). Within those constraints, however, it is unclear to what degree each species has adapted to its specific habitat in relation to noise and clutter as well as to competition from sympatric NBHF species.

Similar habitats may provide similar selective forces on biosonar systems to favour the same signals, but complete overlap in signal structure may pose disadvantages for sympatric species exploiting the same foraging niche as it may confound communication and possibly interfere with echolocation if echoes from other individuals/species cannot be separated from own echoes – so-called jamming. Some families of sympatric Microchiropteran bats overlap in size, range and foraging niche and have shown inter-specific acoustic specializations. For example, ten sympatric species of Emballonurid bats display inter-specific variation in echolocation signal parameters such as peak frequency, call duration, pulse interval and direction of modulation of the frequency sweep, which cannot readily be explained by habitat specialization (Jung et al., 2007). Such species-specific differences may instead serve to avoid jamming of echolocation signals and/or serve communication in order to provide a basis for species recognition, as it is suggested that the same type of sonar signals may serve both communication and echolocation (Fenton, 1986), depending on the situation. Such specializations have not been examined in toothed whales.

In an attempt to address this deficiency, we recorded two NBHF species in the wild – Peale's dolphin and the smaller Commerson's dolphin (*Cephalorhynchus commersonii*) that are closely related and live sympatrically off the Falkland Islands (Islas Malvinas). As such, they offer a suitable experimental platform for elucidating whether similar trade-offs are at play among the toothed whales between meeting biophysical demands for a given body size, food niche and predation scheme versus the negative effects of not being able to tell each other apart acoustically. The two species overlap in distribution at the Falklands Islands and are both associated with kelp beds. However, whereas Commerson's dolphins are found strictly within 10 km from land, Peale's dolphins range over the continental shelf and may thus be found all the way between the Falklands Islands and Argentina (White et al., 2002).

Based on the knowledge from Microchiropteran bats, we wanted to test the hypotheses that these sympatric NBHF dolphins: (i) may show similar adaptations in source parameters owing to their shared habitat, or (ii) demonstrate scaling with size or character displacement that has led to different distributions of source parameters in these sympatric species.

MATERIALS AND METHODS
Recording chain and field sites

Recordings were made with a linear array of six Reson TC 4034 spherical hydrophones (Reson A/S, Slangerup, Denmark) with a 20 m cable and a measured sensitivity of –222 dB re 1 V/µPa between 100 and 150 kHz. The hydrophones were calibrated in an anechoic tank both prior to and following the field recordings. Hydrophones were mounted horizontally in the same direction along a vertical Perspex rod with 0.75 m hydrophone spacing, except between the two topmost hydrophones that were spaced 1.5 m apart. The 41 mm diameter Perspex rod was hollow and water filled when submersed and very stiff to avoid bending of the array during deployment. The hydrophones were mounted in fixed holes spaced with sub-millimetre accuracy in all dimensions. This is crucial as time-of-arrival differences of the same click between the different hydrophones are used to compute the distance to the animal, which again is a prerequisite for the source level and beam pattern estimations.

The array was suspended vertically below a buoy, with the top hydrophone 2 m below the surface and the bottom hydrophone 6.50 m below the surface. A 0.5 kg weight in the bottom kept the array vertical in the water. Signals were bandpass filtered at 1 kHz (1 pole) to 180 kHz (4 poles) and amplified either 50 or 60 dB by custom-made amplifiers. Signals were digitized in three synchronized National Instruments A/D converters (USB-6251) at a sampling rate of 500 kHz per channel and a resolution of 16 bits. The measured frequency response of the entire recording chain was within ±2 dB in the range from 2 kHz to 180 kHz. The clip level of the recording chain was 186 dB re µPa (peak) for Peale's dolphins (*Lagenorhynchus australis*, Peale 1848), and either 186 or 176 dB re µPa (peak) for Commerson's dolphins (*Cephalorhynchus commersonii*, Lacépède 1804), depending on gain settings.

Recordings were obtained at two different field sites at the Falkland Islands (Fig. 1) on six occasions in the period 25 February to 11 March 2008. Peale's dolphins were recorded outside Stanley Harbour (51°39′29.31″S, 57°48′10.04″W) at Gypsy Cove and Tussac Point, and Commerson's dolphins were recorded at Mare Harbour (51°54′39.30″S, 58°25′45.54″W). Both field sites were close to shore, with an estimated water depth of 10–20 m. The dolphins were recorded from six different vessels (four different RHIBs, an engine-going sailing yacht and a military landing craft). When the dolphin groups approached the boat to bow ride, the engine was turned off and the hydrophone array lowered into the water. Only one species was observed at a time, and no other marine mammals were observed or detected acoustically. Recordings were made under very calm weather conditions (low winds, sea state 1), and the surface behaviour and whereabouts of the dolphins were noted.

Click analysis

To minimize the risk of including distorted off-axis clicks in the analysis (Madsen and Wahlberg, 2007) we applied a set of criteria to determine clicks as being on-axis by following the methods of Villadsgaard and colleagues (Villadsgaard et al., 2007) and Kyhn et al. (Kyhn et al., 2009): On-axis clicks should be: (i) recorded on all six channels; (ii) part of a scan – that is, a series of clicks closely spaced in time, normally first increasing then decreasing in amplitude (*sensu* Møhl et al., 2003); (iii) of maximum amplitude in the scan; (iv) of maximum amplitude on one of the four middle hydrophone channels; and (iv) such that the direct path of the click had to be stronger than any trailing bottom or surface reflections. Furthermore, the localization error (Villadsgaard et al., 2007) could not give rise to an r.m.s. transmission error of more than 3 dB in the source-level calculations. Additionally, we visually inspected all on-axis clicks and removed clicks that contained double or triple pulses, as these likely arise from surface reflections and are not source generated (Li et al., 2005). Owing to the one-dimensional vertical configuration of the array, the on-axis definition pertains only to the vertical plane, and we have assumed that the clicks are on-axis in the horizontal plane as well.

The source properties were quantified using a series of parameters *sensu* Au (Au, 1993) and Madsen and Wahlberg (Madsen and Wahlberg, 2007) for each click accepted as on-axis: duration$_{-10 dB}$ given by the −10 dB points of the signal envelope (the absolute value of the analytical waveform); peak frequency (F_{Peak}), centroid frequency (F_C) defined as the frequency dividing the spectrum in two halves of equal energy, −10 dB bandwidth defined as the bandwidth at −10 dB points below the spectrum peak, −3 dB bandwidth defined as the bandwidth at −3 dB points below the spectrum peak), r.m.s. bandwidth defined as the spectral standard deviation around the centroid frequency on a linear scale, $Q_{r.m.s.}$ defined as the centroid frequency divided by the r.m.s. bandwidth, and $Q_{-3 dB}$ defined as the peak frequency divided by the −3 dB bandwidth.

Inter-click intervals (ICIs) were defined as the pause between an on-axis click and the previous click. If click trains overlapped, ICIs were found for several preceding pauses to find the correct interval to include in the analysis. All analysis and signal processing were performed with custom-written scripts in Matlab 6.5 (Mathworks).

Calibration of localization routines

The array localization performance was evaluated in Aarhus Harbour, Denmark, by playing out calibrated tone pips with duration and spectral properties similar to NBHF clicks at known ranges from

Fig. 1. Field sites for making recordings of Peale's and Commerson's dolphins. Red cross: recordings of Peale's dolphins at the Stanley Harbour area (51°39′29.31″S, 57°48′10.04″W). Red circle: recordings of Commerson's dolphins at Mare's Harbour (51°54′39.30″S, 58°25′45.54″W).

the array. The six-element hydrophone array was suspended from a buoy, with the top hydrophone 1 m below the surface. Tone pips (130 kHz sinus pulses of 15 cycles and a 100 µsec duration) were transmitted with an omni-directional hydrophone (B&K8105, depth 3 m below surface) connected to a sound generator (Agilent, model 33220A). The same recording chain and settings used for the field recordings were used to record signals transmitted in a range interval from 10 to 80 m from the array. The speed of sound was estimated from the Leroy equation (Urick, 1983) from the measured temperature and salinity.

Estimation of source level

To obtain the range to the vocalising animal, we used the linear array of six hydrophones to generate an over-determined localization setup whereby the localization error can be assessed for each click (Wahlberg et al., 2001; Madsen and Wahlberg, 2007). The six hydrophones yield a localization calculated from time-of-arrival differences of the click pair-wise among the six hydrophones. Localisations were performed using Matlab implementing the localization routines of Wahlberg and colleagues (Wahlberg et al., 2001) and Madsen and Wahlberg (Madsen and Wahlberg, 2007). It proved essential to use a robust measure of the time-of-arrival differences for the same signal recorded on the six channels. We determined the timing of a click from the first sample (using an interpolation factor of 10) exceeding −10 dB of the peak of the click envelope. All localizations were evaluated visually, and, based on results from the array calibration, all localizations giving rise to an r.m.s. error (translated to transmission loss) larger than 3 dB were omitted from the data set. Furthermore, only clicks recorded at a distance of less than 65 m were included in the analysis.

Once the range to the animal has been estimated, transmission loss (TL) can be estimated and added to the received level (RL) of a click. Villadsgaard and colleagues (Villadsgaard et al., 2007) found that the 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 shallow water column in the two habitats in the present study, we also assumed that transmission loss could be approximated well by spherical spreading plus absorption. The apparent source level (ASL) of echolocation clicks was thus calculated using the equation (Urick, 1983):

$$\text{ASL} = \text{RL} + \text{TL} \ (\text{TL} = 20 \log r + \alpha r) , \qquad (1)$$

where α is the absorption coefficient in dB/m and r is the range in meters. A value of α of 0.039 dB/m was used, based on the equations of Fisher and Simmons (Fisher and Simmons, 1977) for 130 kHz and a water temperature of 9°C. SL is given as peak–peak (p.–p.) pressure, r.m.s. pressure and energy flux density (EFD) computed as follows: $\text{SL}_{\text{p.–p.}}$ (dB//1 µPa p.–p.) was measured from the maximum and minimum peak pressure of the waveform. $\text{SL}_{\text{r.m.s.}}$ (dB//1 µPa r.m.s.) is the r.m.s. pressure calculated over the duration$_{-10\text{dB}}$ of the signal. SL_{EFD} (dB//1 µPa^{2}s) is the signal energy over the duration$_{-10\text{dB}}$ (Madsen, 2005; Madsen and Wahlberg, 2007). We used the term apparent source level (ASL) to denote the sound pressure back-calculated to one meter off the acoustic axis.

Estimation of beam pattern

The apparent source level as a function of the angle to the acoustic axis – the source beam pattern – can be estimated when it can be assured that the same click has been recorded simultaneously both on and off the acoustic axis at known angles (Au, 1993). A linear array does not provide any information on animal orientation relative to the array, and the beam pattern must therefore be assumed to be rotationally symmetrical around the acoustic axis – that is, assuming that the beam pattern in the horizontal plane is the same as in the vertical plane (Madsen and Wahlberg, 2007).

Radiation plots were created by plotting the apparent source-level values against the angle relative to the assumed on-axis at which they were recorded. The peak amplitude and zero angle were subsequently adjusted in order to approach on-axis by interpolating between the highest recorded source level and the values from the two neighbouring hydrophones using a Lagrange interpolation polynomial. Unfortunately, for NBHF clicks, it is not always possible to tell whether a click was indeed recorded on-axis, and the actual aspect angle may therefore be underestimated when making such a plot. To address that problem and compare with the present data, we therefore carried out a Monte Carlo simulation of the process to estimate the theoretical distribution as it would have looked if the whales were indeed theoretical piston transducers with a 4 cm diameter [as is found using values from Au and colleagues (Au et al., 1999) and the circular piston model of Au et al. (Au et al., 1987)]. In the Monte Carlo simulation, a theoretical 4 cm diameter piston transducer transmitted clicks at angles up to 50 degrees off the acoustic beam and at ranges of 2–15 meters from the array, matching the distances to the recorded animals. Using the same on-axis criteria and algorithms as for our recorded data, we then fitted the resulting collection of click power versus estimated angle to the piston model by means of a non-linear least-squares method. Only in extreme cases with angles up to 30 degrees off the array did the model fail and consistently underestimate the parametric piston diameter.

Having asserted that the Lagrange approach was indeed sound, we then proceeded to fit the collection of real data points from the two dolphins in the same way to arrive at the least-square fit of the diameter of the piston that matched the data of each species best.

The use of the flat piston model over other geometries has mostly consequences for the side lobes. Side lobes are much more pronounced for tonal signals, which is not the situation for the more broad-band echolocation clicks. For describing the echolocating performance of dolphins, the side lobes are therefore less relevant, and, as argued by Morse (Morse, 1948), we therefore used the piston model to describe the beam pattern of the two target species.

Species separation

To test whether the two species could be separated based on the observed differences in mean centroid frequency, we made a Monte Carlo simulation with a classification criterion of 130.5 kHz. The criterion of 130.5 kHz was the centroid frequency resulting in the highest number of correct classifications for both species. Clicks with a centroid frequency below this value were classified as Peale's dolphin and clicks with a centroid frequency at or above 130.5 kHz were classified as Commerson's dolphin. For each species, clicks were drawn at random from clicks recorded from the species and the proportion of clicks correctly classified was noted. The random clicks drawn consisted of the on-axis clicks from the analysis above as well as the corresponding off-axis clicks for the same recordings – that is, a 1:5 on-axis to off-axis values. One hundred clicks were drawn 10 times for each species, and the mean percentage correct as well as standard deviation of the mean were calculated. The entire procedure was then repeated with sets of clicks, such that the mean centroid frequency of 2, 4, 8, 16 and 32 random clicks was compared with the threshold criterion.

RESULTS

130 kHz clicks could be localized with a precision corresponding to an r.m.s. error on source level of less than 3 dB out to 65 m from the six-element hydrophone array (Fig. 2). At greater distances, the routines underestimated the actual distances to the sound source, giving rise to combined errors larger than 3 dB in transmission loss.

Signals from Commerson's dolphins were recorded on two occasions at the same field site in the harbour of the Falkland Royal Air Force (RAF), Mare's Harbour (Fig. 1). According to the military personnel at the RAF base, Commerson's dolphins are always present in the area and, on the days of recording, approximately 30–40 dolphins were present in the area. On both occasions, the dolphins were engaged in foraging in a kelp bed before coming to bow ride. Some dolphins remained foraging while 10–15 dolphins came to bow ride in front of the boat. The dolphins stayed around the boat some time after the engine was turned off, ensonifying the hydrophone array. However, they quickly lost interest and returned to the kelp bed. Only Commerson's dolphins were seen at the time of recording. More than 1000 clicks were recorded, and, of these, 94 met the on-axis criteria, and had source ranges within 65 m from the hydrophone array. The waveform and power spectrum of a representative click are shown in Fig. 3. The source parameters of Commerson's clicks are summarized in Table 1.

Signals from Peale's dolphins were recorded on four occasions, and no other odontocetes were observed during the recordings (Fig. 1). Recordings were made of several different groups, ranging in size from three to more than ten animals, likely up to 20. We did not observe the dolphins until they were fast approaching to bow ride, but, when they left, we saw them forage in near-shore kelp beds. On one occasion, a group containing two calves was observed,
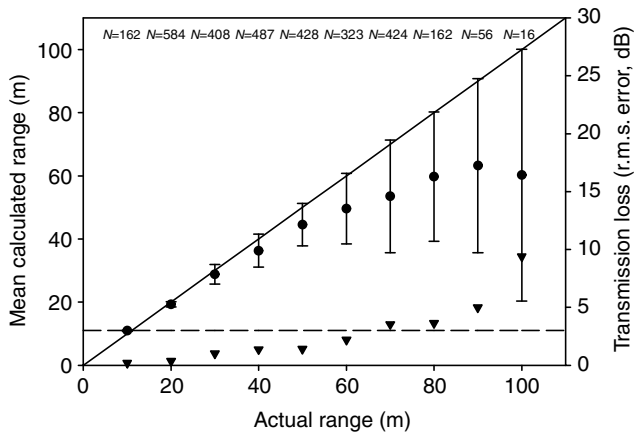
Fig. 2. Localization performance of a 4.5 m aperture six-element hydrophone array. Closed circles are mean calculated ranges (with standard deviation) plotted against the actual range. The solid line denotes the expected localization range from each of the actual ranges. The effect of localization error on transmission loss is expressed in r.m.s. error dB, and plotted as triangles while utilizing the separate right *y*-axis. The broken line signifies that, with a 4.5 m aperture array, NBHF species may be localized out to 65 m with less than 3 dB r.m.s. error on source-level calculations. The number of measurements (*N*) made at each range is shown along the top of the graph.
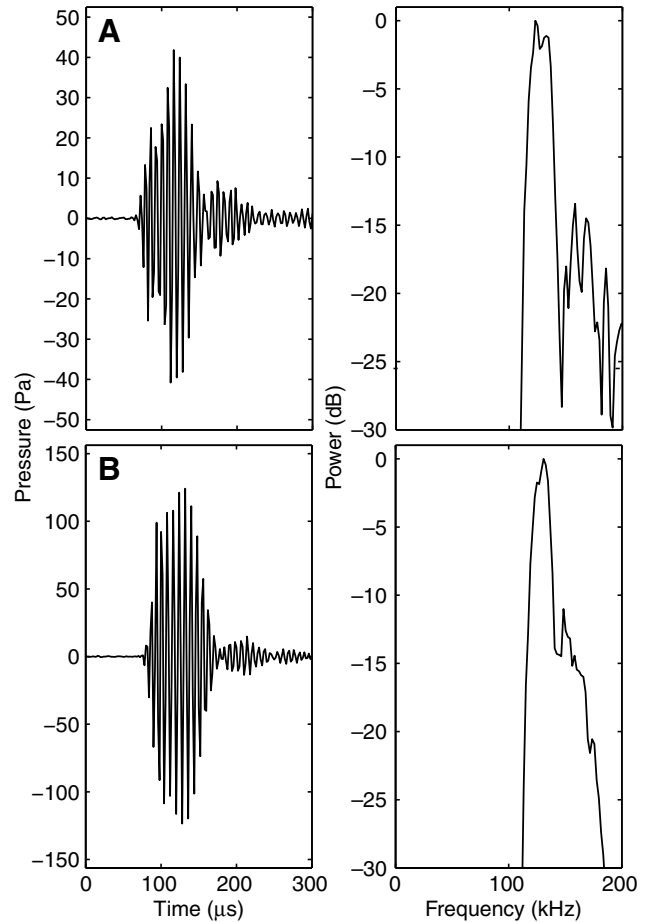

Fig. 3. Time domain signal and power spectrum of a representative click of (A) Commerson's dolphin and (B) Peale's dolphin. (Fast Fourier transform size of 256, spectrum interpolated with a factor 10, sampling rate 500 kHz, rectangular window.) The difference in pressure on the *y*-axis is caused by different received levels.

but data from this group were omitted from the analysis. Of more than 1000 clicks recorded, 87 clicks were defined as on-axis according to the listed criteria and subsequently included in the analysis. All these clicks were recorded at ranges of less than 65 m. The waveform and power spectrum of a representative click are shown in Fig. 3. The source signal parameters of both species are summarized in Table 1. ICIs for both species are plotted against range in Fig. 4.

Fig. 5 depicts the results of the non-linear least-squares method used to validate the use of the method for estimating the directionality of the two species. Directional characteristics generated by the piston model together with the real data for both species are shown in Fig. 6. The piston diameter for which the directional characteristics fitted the data best was 6.5 cm for Commerson's dolphins and 7 cm for Peale's dolphin.

The centroid frequencies of both species had a normal distribution [Kolmogorov–Smirnov (two-tailed): $P=0.00$, $N=87$ (Peale's), $N=94$ (Commerson's)]. Source levels of Peale's dolphins were significantly higher than source levels of Commerson's dolphins (Mann–Whitney *U*-test = 8178, $\chi^2=134.8$, $P<0.001$, $N=181$) (Tables 1 and 2; Fig. 4). Centroid frequency was significantly higher for Peale's dolphin ($U=7034.5$, $\chi^2=69.95$, $P<0.001$, $N=181$) (Table 1).

Commerson's dolphin could be classified with higher certainty and using fewer clicks than Peale's dolphins could (Fig. 7). Based on the mean centroid frequency of 16 clicks, almost all click series were classified correctly. Clicks from Peale's dolphin, by contrast, proved more difficult, and, even with a click series of 32 clicks, the percentage of misclassifications was 10.2%.

DISCUSSION

We present the first wide-band recordings of Peale's dolphins and show that they produce NBHF clicks, with the main energy centred around 130 kHz. No tonal sounds or clicks of lower frequency were heard or recorded from Peale's or from Commerson's dolphins. The NBHF properties are in contrast to the only previously published recordings from Peale's dolphins; Schevill and Watkins (Schevill

and Watkins, 1971) recorded sounds from Peale's dolphins with dominant frequencies below 5 kHz. However, their analog recording apparatus was band-limited at around 30 kHz and would thus not have picked up the NBHF sounds. In line with what has been shown for harbour porpoise signals (Hansen et al., 2008), it is very likely that most of the low-frequency sounds recorded by Schevill and Watkins (Schevill and Watkins, 1971) were in fact distortion products of the NBHF signals, created by clipping the analog tape recorder/amplifier. The present results are consistent with the recent finding that the sister species of the Peale's dolphin, the hourglass dolphin, also produces NBHF signals (Kyhn et al., 2009), supporting the suggested close phylogenetic affinity of these two species to the dolphin genus *Cephalorhynchus* (May-Collado and Agnarsson, 2006; Tougaard and Kyhn, 2010).

The source parameters of Peale's and Commerson's clicks are very similar (Table 1). However, there are small, but consistent, differences with relevance for the two stated hypotheses: Peale's dolphins produce clicks of lower centroid frequency than Commerson's dolphins. Furthermore, Peale's dolphins produce clicks of higher source level than Commerson's dolphins. However, the source levels of both species were lower than for offshore species of similar size.
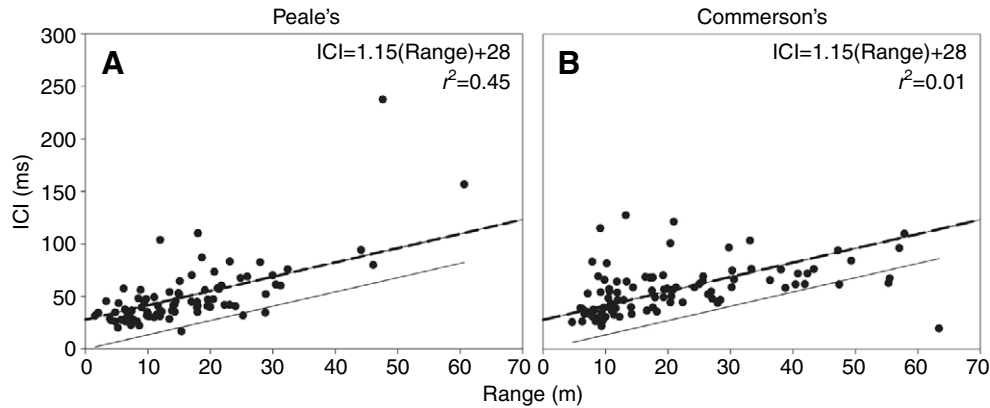
Fig. 4. Relationship between inter-click intervals (ICIs) and recording range. Plots show Peale's (A) and Commerson's (B) dolphin ICIs as a function of range from array. The thin solid line is the expected two-way travel time (TWT) if the dolphins were focusing at the array. The bold regression line was plotted with a fixed slope given by: 2*TWT*(speed of sound in water)$^{-1}$ (1470 ms^{-1})=1.15 ms. The interception of the regression line with the y-axis may thus be interpreted as the lag time of the dolphins – that is, the time between reception of an echo and emission of a new click.

The scaling hypothesis predicts that the larger Peale's dolphins would produce the lowest frequencies if normal scaling of sound production was the primary evolutionary driving force (Bradbury and Vehrencamp, 1998). We found that the mean centroid frequency of clicks of Peale's dolphins was 4 kHz lower than that of Commerson's, and this was significant (Table 1). However, their distributions of centroid frequencies are overlapping, and, with a mean difference of only 3%, it seems that such a small difference is less than that implied by the size difference of the two species. Second, Morisaka and Connor (Morisaka and Connor, 2007) did not find a correlation between body size and frequency for NBHF species. The small shift in centroid frequency between Peale's and Commerson's dolphins (Table 1) may instead be an adaptation to the sympatric living around the Falkland Islands. We hypothesized that these two sympatric NBHF dolphins would show some degree of character displacements in their frequency content to allow species recognition. For the two species to tease apart their clicks with mean differences of only 4 kHz demands high-frequency resolution and

sampling of several clicks to get a sufficiently large sample to identify a click source as conspecific. We found, however, that the significant difference in mean centroid frequencies alone is sufficiently large to form the basis for species classification in, for example, static acoustic monitoring (SAM) (Fig. 7). We based the discrimination on a random mix of on- and off-axis clicks recorded at various angles and from various animals, thus with some variation in centroid frequency. An animal itself, by contrast, will evaluate incoming clicks over entire click trains, with less variation in centroid frequency over the click train. It is highly likely, therefore, that the found mean difference in centroid frequency is big enough for the animals to do the same. To base species recognition accurately on centroid frequency in SAM, however, requires that the SAM data logger has a frequency resolution sufficiently high to resolve the small difference in centroid frequency between the species. Furthermore, the centroid frequency threshold should be evaluated carefully, and it may prove useful to use several thresholds to find the highest percentage of correctly classified clicks for entire click

Table 1. Mean (±s.d.) and range of echolocation click source parameters of Peale's (*Lagenorhynchus australis*) and Commerson's (*Cephalorhynchus commersonii*) dolphins

	Commerson's dolphin *Cephalorhynchus commersonii*		Peale's dolphin *Lagenorhynchus australis*	
	Mean ± s.d.	Range	Mean ± s.d.	Range
10 dB duration (µs)	78±1	52–138	92±2	65–153
Source level (dB re 1 µPa p.–p.)	177±5	165–190	185±6	169–196
Source level$_{-10dB}$ (dB re 1 µPa r.m.s.)	166±5	153–180	173±6	156–185
Energy flux density$_{-10 dB}$ (dB re 1 µPa2 s)	125±5	111–137	133±6	117–144
Peak frequency (kHz)	132±6	119–139	126±3	120–133
Centroid frequency (kHz)	133±2	123–137	129±3	123–138
3 dB bandwidth (kHz)	21±3	16–31	15±4	9–34
r.m.s. bandwidth (kHz)	12±3	7–19	12±3	5–23
$Q_{-3 dB}$	6±1	4–8	9±2	4–14
$Q_{r.m.s.}$	12±3	7–18	12±3	6–23
Directivity index (dB)*	25		25	
Equivalent aperture diameter (cm)*	6.4		7.0	
Sample size, N	94		87	

*Only 45 clicks from Commerson's and 49 clicks from Peale's dolphins were recorded at a range of less than 15 m and included in the beam pattern and directivity calculations.
p.–p., peak–peak; r.m.s., root mean square.

Table 2. Body sizes and source levels of five NBHF dolphin species

	Source level (dB re 1 µPa p.–p.)		Body length (m)	
	Range	Mean ± s.d.	Mean	Max.
Hector's dolphin *Cephalorhynchus hectori*	161–187	177±6	n.a.	145
Commerson's dolphin *Cephalorhynchus commersonii*	165–190	177±5	n.a.	146
Harbour porpoise *Phocoena phocoena*	178–205	191	145–160	168 (>200)
Hourglass dolphin *Lagenorhynchus cruciger*	190–203	197±4	142–187	187
Peale's dolphin *Lagenorhynchus australis*	169–196	186±6	193	218

Tabulated data derived from various sources (see Godall et al., 1997a; Godall et al., 1997b; Reeves et al., 2002; Villadsgaard et al., 2007; Kyhn et al., 2008). p.–p., peak–peak.

trains. Additionally, a combination of several criteria – for example both centroid frequency and r.m.s. bandwidth – may improve the probability of species identification.

The hypothesis of acoustic character displacement is thus supported here and could be tested further by recording the same species where there is no overlap with other NBHF species. Character displacement is 'the situation in which, when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone' (Brown and Wilson, 1956). Therefore, the possibility that Peale's and Commerson's dolphins are subject to character displacements in their echolocation clicks may be investigated further by performing wideband sound recordings of Commerson's dolphins at the Kerguelen Islands, where the species do not overlap with other NBHF species. The existing recordings from Kerguelen (Dziedzic and Buffrenil, 1989), however, do not allow for such detailed analysis.

Along the same line, it is interesting that, within the porpoise family and the *Cephalorhynchus* genus, for species overlapping with other NBHF species, there is a tendency for greater diversity in coloration than for species with no overlap with other NBHF species. Noteworthy is, for example, the striking difference in coloration between sympatric Dall's and harbour porpoises, between sympatric Commerson's and Peale's dolphins and between sympatric Commerson's and Chilean dolphins, contrary to the inconspicuous colour patterns of the isolated NBHF Vaquita and finless porpoise. Colour patterns may thus be an important short-range cue for species recognition in these acoustically very similar species if other evolutionary selection forces limit the acoustic differences in NBHF clicks across species.

Kyhn and colleagues (Kyhn et al., 2009) showed that offshore hourglass dolphins produce clicks of higher source levels than the coastal Hector's dolphins. Hourglass dolphins are oceanic and may thus have evolved to generate a higher source level than coastal NBHF species as prey patches are more widely distributed in the open sea as opposed to shallow coastal habitats where the inter-prey distances are smaller, and where clutter levels likely are higher. For the present study, with the differences in overall habitat between Peale's and Commerson's dolphins (White et al., 2002), we thus hypothesized that Peale's dolphins would have the highest source level of the two species and that the source levels of both species would be lower than the source levels of the offshore hourglass dolphin. The collected data do indeed show that source levels of the shelf-living Peale's dolphins are significantly higher than the source levels of the coastal Commerson's dolphins (Table 1 and Fig. 4). The higher source level of Peale's dolphin could also be caused by the larger size of this species; however, among all the five NBHF species recorded to date, there is no apparent relationship between body size and source levels (source levels and body sizes are listed in Table 2) (Villadsgaard et al., 2007; Kyhn et al., 2009) (this study). Many factors may influence the measured source levels of biosonar systems (Madsen and Wahlberg, 2007), but here we recorded the two species in the same habitat in the same behavioural states with the same recording system, which should reduce many of the factors that can be attributed to other things than actual species differences. In Fig. 4,
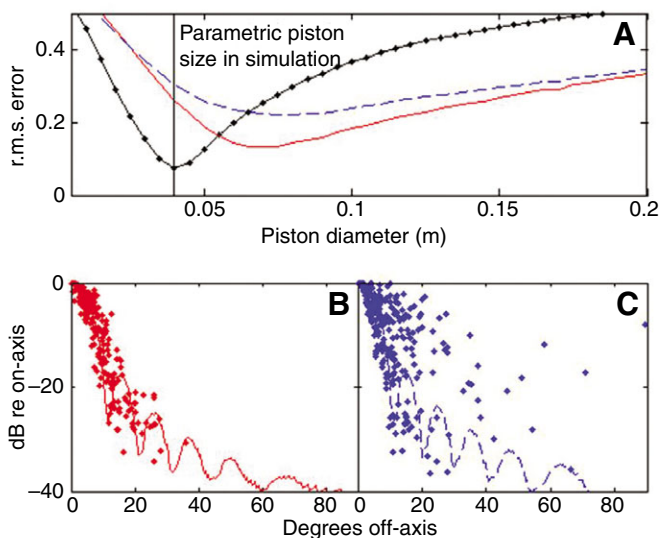

Fig. 5. Fits to the piston model (A) and transmission beam patterns of Commerson's dolphin (B) and Peale's dolphin (C). In (A), the dash-dot black line shows the r.m.s. error of a fit to simulated data from a piston of 4 cm aperture transmitting a Commerson's dolphin click as a function of piston diameter. The vertical line is at the correct 4 cm diameter. The real data from the two species (Commerson's solid red, and Peale's broken blue line) were likewise fitted to piston models of varying diameters to find the best match. The diameter giving the best fit – that is, with the least r.m.s. error for each species – was taken to be the best estimate of the diameter of the transmitting aperture. The radiation patterns for the piston diameter with the least r.m.s. error for each animal found in (A) are plotted in (B) and (C) as lines on top of the data points. The points are field data: on-axis clicks (45 Commerson's and 49 Peale's clicks), each with five off-axis versions recorded on the other hydrophones simultaneously. All used clicks were recorded within 15 m of the array.
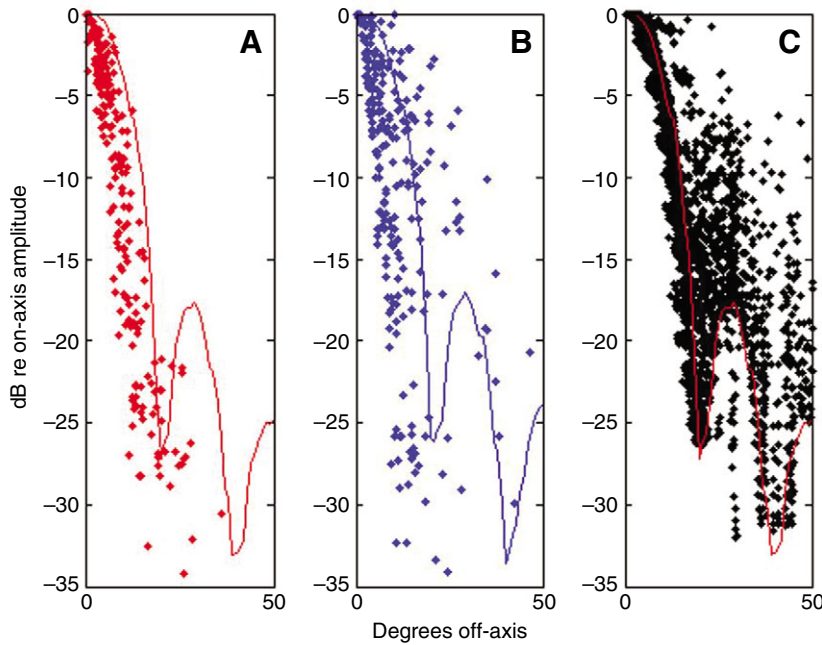
Fig. 6. Transmission beam pattern data from Commerson's (A) and Peale's dolphin (B) together with theoretical 4 cm piston data (C). Lines denote the beam pattern of a 4 cm piston transmitting a click of the respective species (Commerson's dolphin in C). Black dots in (C) show the theoretical 4 cm diameter piston transmitting a Commerson's dolphin click and recorded at varying degrees off angle in a Monte Carlo simulation to test the applicability of the piston model.

ICIs are plotted as a function of range, showing a positive relationship with a constant lag-time, suggesting that, in this study, both dolphin species were focusing at the array (*sensu* Au, 1993) at the time of recording. As the array calibration showed that only ranges of less than 65 m would render source-level estimates with errors of less than 3 dB (Fig. 2), we only included clicks recorded within this range. Within these 65 m, Commerson's dolphins were recorded at a mean and median range of 20.7 m and 16.9 m, and Peale's were recorded somewhat closer, with a mean of 16.2 m and median of 14.1 m, thus a rather small difference in range. This means that the observed source-level differences cannot relate to differences in recording range. We thus consider the observed higher source levels of Peale's dolphin to be genuine.

For the five NBHF species detailed in Table 2, the oceanic and shelf-living species (harbour porpoise, Peale's and hourglass dolphins) produce the highest source levels (Table 2). Close to shore, prey ranges may decrease, but the clutter level likely increases owing to echoes from the nearby sea floor and kelp beds. We observed both species foraging in kelp beds, and the few scientific records available on both species report that among other species closely associated with the kelp (Schiavini et al., 1997; Viddi and Lescrauwaet, 2005) they prey on cephalopods (Clarke and Goodall, 1994; Schiavini et al., 1997). This means that they forage in an environment expected to be highly cluttered. Bats living in cluttered environments have evolved different strategies to reduce the problems of clutter. One general adaptation is that bat species in cluttered habitats use lower source levels than open-space foragers (Neuweiler, 2000) because a higher source level will not improve the performance of a clutter-limited sonar. The low source levels found for our two studied NBHF species may reflect a similar adaptation among odontocetes to operate a biosonar system in a highly cluttered habitat: a high source level will not improve biosonar performance in shallow water. The lower source level of the Commerson's dolphins may in that light reflect their closer affiliation with very shallow water compared with that of the Peale's dolphins. If this hypothesis is correct, we predict that Kogias that forage on mesopelagic prey produce higher source levels than observed for any of the coastal NBHF species.

If high clutter levels of shallow water are a primary driving force for those of the NBHF species that inhabit them, it is also relevant to address other means by which biosonars can reduce clutter. As the problem of clutter is the reception of unwanted echoes interfering with target signals, another way to reduce clutter would be to increase transmission directionality to reduce the width of the sound cone emitted from the animal and thus reducing the ensonified area
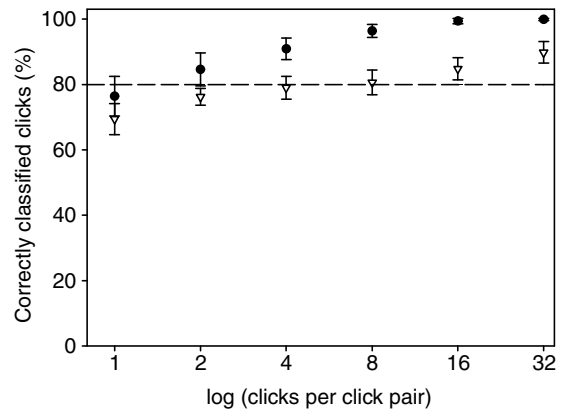

Fig. 7. Acoustic species discrimination. Peale's and Commerson's dolphins may be separated by means of differences in centroid frequency using a criterion of 130.5 kHz, even using off-axis values. Commerson's dolphins (circles) can be determined with higher certainty than Peale's dolphins (triangles); however, the more clicks included in a click pair, the better the discrimination. The dashed line indicates 80% correctly classified clicks. Dolphins will have entire click trains available arriving from more-or-less fixed angles, thus with lower variation between clicks, and it therefore seems very likely that the mean difference in centroid frequency is sufficient for accurate species recognition by the dolphins. Such species recognition may prove useful in static acoustic monitoring, provided there is fine-scale frequency resolution in the recordings. The percentage correct (y-axis) for each click pair is the mean of ten rounds of randomly drawing 100 click pairs consisting of *N* clicks per pair (x-axis), and the values are shown with the standard error of the mean. The clicks included are 1:5 on-axis to off-axis clicks.

ahead of the animal. In line with Au and colleagues (Au et al., 1999), we hypothesized that the larger Peale's dolphin would have a more directional sound beam owing to a larger aperture transmitting clicks of almost the same centroid frequency as Commerson's clicks (Table 1).

The radiation diagrams shown in Figs 5 and 6 indicate that both Commerson's and Peale's dolphins are more directional than what has been reported for porpoises. The piston for which the radiation diagram fitted the data best had a diameter of 6.5 and 7 cm for Commerson's and Peale's dolphins, respectively, and the corresponding transmitting directionality indices (DIs) were 25 dB for both species. These estimated DIs are less prone to the type of errors typically relevant when estimating the beam pattern from recordings of wild odontocetes (Møhl et al., 2003; Rasmussen et al., 2004). The most important error in the previous studies is that the supposed on-axis clicks may in fact not be recorded on-axis despite the conservative on-axis selection regime. Here, we used a novel method interpolating between the channel deemed on-axis and its two neighbour channels to find the acoustic axis, and the method was further verified using a Monte Carlo simulation (Fig. 6). We used a one-dimensional vertical hydrophone array and have thus assumed rotational symmetry around the acoustic axis, which may not be the case for these species, even though it has been found for harbour porpoises, bottlenose and white-beaked dolphins as well as the beluga (Au et al., 1999; Rasmussen et al., 2004). Both species were more directional than found for the similar-sized harbour porpoise (DI=22 dB) and match the larger bottlenose dolphin better (DI=25.8 dB) (Au et al., 1999). Despite the controlled setup of Au and colleagues (Au et al., 1999), the array for those measurements was also one-dimensional, and the clicks were not corrected for slight off-axis values, as done here with the Lagrange method. Accordingly, it may be that the DI of porpoises is indeed higher than 22 dB and is thus comparable to the values found here and for bottlenose dolphins. The effect of a higher directionality is a reduced ensonified area in front of the animal. This high directionality will in combination with the low source levels reduce the number of returning echoes for each click emitted. The high directionality may thus be the result of similar adaptations by the two species to solve the biosonar challenges faced in a coastal cluttered environment.

The exact number of animals, and their body sizes, sampled in this study is not known as the dolphins were free ranging and not filmed under water. Although this is a shortcoming when quantifying and comparing the acoustic source parameters of two species, NBHF species in general are known to produce very stereotyped clicks within the same species (Au, 1993; Madsen et al., 2005; Villadsgaard et al., 2007; Akamatsu et al., 1998). The centroid frequency of both species was normally distributed. This implies that either these species produce stereotyped clicks or that a large number of animals were recorded. If only a low number of animals with non-stereotyped clicks were recorded, the distribution of centroid frequencies would not likely have been normal. Also BW_{-3dB}, $BW_{r.m.s.}$ and Q_{-3dB} were normally distributed for both species. As these different source parameters show normal distributions, we argue that the present data set actually represents the two species.

In conclusion, Peale's and Commerson's dolphins both use very similar NBHF clicks, and no other types of sounds were recorded, suggesting that these closely related dolphins evolved to operate their sonars under similar selection pressures. The two species have overlapping distributions of centroid frequency around 130 kHz, but with means that differ by 4 kHz. That difference may be caused by character displacement to allow species recognition among these sympatric NBHF dolphins within the constraints of operating an NBHF sonar above the hearing range of killer whales and at the same time avoiding too high absorption at higher frequencies. As the two species are observed to forage predominantly in non-overlapping groups and, as they use very narrow beams, there may not have been strong selection for further acoustic specialization to avoid jamming, and there is no indication of strong acoustic niche segregation, as is observed for sympatric Microchiropteran bats. Peale's dolphins produced clicks of higher source levels than Commerson's dolphins, but the levels of both species were lower than observed in general for both NBHF and non-NBHF off-shore dolphins. Both species produced clicks of higher directionality than previously found for similar-sized species. In combination, the relatively low source levels and high directionality of these two small NBHF species may be adaptations to echolocate for prey in a cluttered coastal environment.

LIST OF ABBREVIATIONS

ASL	apparent source level
BBT	broad-band transient
BW_{-3dB}	bandwidth measured at –3dB from the peak
BW_{rms}	r.m.s. bandwidth
DI	directivity index
EFD	energy flux density
ENR	echo-to-noise ratio
F_C	centroid frequency
FM	frequency modulation
F_{Peak}	peak frequency
ICI	inter-click interval
n.a.	not available
NBHF	narrow-band high-frequency
p.–p.	peak–peak level
Q_{-3dB}	peak frequency / –3dB bandwidth
Q_{rms}	centroid frequency / r.m.s. bandwidth
r	range
r.m.s.	root mean square
RAF	Royal Air Force
RL	received level
s.d.	standard deviation
SL	source level
TL	transmission loss
TWT	two-way travel time
α	absorption coefficient

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