

# Echolocation clicks of two free-ranging, oceanic delphinids with different food preferences: false killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*

P. T. Madsen<sup>1,2,\*</sup>, I. Kerr<sup>1</sup> and R. Payne<sup>1</sup>

<sup>1</sup>Ocean Alliance, 191 Western Road, Lincoln, MA 01773, USA and <sup>2</sup>Department of Zoophysiology, Institute of Biological Sciences, University of Aarhus, Denmark

\*Author for correspondence at present address: Woods Hole Oceanographic Institution, Wood Hole, MA 02543, USA  
(e-mail: pmadsen@whoi.edu)

Accepted 8 March 2004

## Summary

Toothed whales (*Odontoceti*, *Cetacea*) navigate and locate prey by means of active echolocation. Studies on captive animals have accumulated a large body of knowledge concerning the production, reception and processing of sound in odontocete biosonars, but there is little information about the properties and use of biosonar clicks of free-ranging animals in offshore habitats. This study presents the first source parameter estimates of biosonar clicks from two free-ranging oceanic delphinids, the opportunistically foraging *Pseudorca crassidens* and the cephalopod eating *Grampus griseus*. *Pseudorca* produces short duration (30  $\mu$ s), broadband ( $Q=2-3$ ) signals with peak frequencies around 40 kHz, centroid frequencies of 30–70 kHz, and source levels between 201–225 dB re. 1  $\mu$ Pa (peak to peak, pp). *Grampus* also produces short (40  $\mu$ s), broadband ( $Q=2-3$ ) signals with peak frequencies around 50 kHz, centroid frequencies of 60–90 kHz, and source levels between 202 and 222 dB re. 1  $\mu$ Pa (pp). On-axis clicks from both species

had centroid frequencies in the frequency range of most sensitive hearing, and lower peak frequencies and higher source levels than reported from captive animals. It is demonstrated that sound production in these two free-ranging echolocators is dynamic, and that free-ranging animals may not always employ biosonar signals comparable to the extreme signal properties reported from captive animals in long-range detection tasks. Similarities in source parameters suggest that evolutionary factors other than prey type determine the properties of biosonar signals of the two species. Modelling shows that interspecific detection ranges of prey types differ from 80 to 300 m for *Grampus* and *Pseudorca*, respectively.

Key words: false killer whale, *Pseudorca crassidens*, Risso's dolphin, *Grampus griseus*, biosonar, echolocation, target detection, sound production, source level, click.

## Introduction

Toothed whales (*Odontoceti*) use biosonar for orientation and echolocation of prey by emission of short sound pulses, and subsequent reception and processing of returning echoes. The last 30 years of research have provided a wealth of information about the production, transmission and reception of sound in dolphin sonar systems along with insights in their detection and discrimination capabilities (for a review, see Au, 1993).

These studies have not only demonstrated that the production and transmission of toothed whale sonar clicks show considerable interspecific variation, but also that conspecifics may produce very different signals, depending on the detection task and the acoustic Umwelt (Au, 1993). The latter is exemplified by the fact that signals from echolocating bottlenose dolphins *Tursiops truncatus* increased by 40 dB in source level (SL) and one octave in frequency emphasis when their signals were measured in open pens (Au et al., 1974) as

compared to measurements of animals in concrete tanks (Evans, 1973). Target detection experiments in pens have subsequently provided a multitude of physiological data about the maximum sonar system capabilities of a limited number of delphinid species so that comparison with bats (Au, 1997) and ideal receivers (Au and Pawloski, 1989) can be made.

While such controlled experiments with trained animals are vital for understanding the basic properties and performance of odontocete sonar systems, they may not provide data that fully reflect the properties and use of biosonar signals in natural habitats with conspecifics, predators and prey (Au, 1993). This reservation has been confirmed in a terrestrial echolocator, the big brown bat *Eptesicus fuscus*. Sonar signals recorded in the field were significantly longer, with longer interpulse intervals and greater variability in bandwidth than signals recorded in the laboratory (Surlykke and Moss, 2000). Therefore, data from controlled experiments with trained animals should be

complemented by field data from wild animals to understand the ecophysiological, behavioral and evolutionary significance of odontocete biosonar systems.

Collection of relevant acoustic data from free-ranging odontocetes has inherent logistical and practical problems (Watkins and Daher, 1992). In recent years, sound recording tags, attached to the clicking animal, have provided promising data pertaining to sound production, acoustic behaviour and biosonar involvement in orientation and prey location (Madsen et al., 2002; Johnson and Tyack, 2003). While sound recording tags have their advantages in terms of monitoring the acoustic behaviour and changes in sound production of the tagged animal, they cannot provide information about the source properties of highly directional biosonar signals. The latter calls for deployment of calibrated wideband recording gear with hydrophones in the far field in front of the phonating animals. Because the spectral content and amplitudes of odontocete clicks change with aspect (Au et al., 1986) and acoustic output (Au et al., 1995), it is essential that source parameters of biosonar signals are derived from the acoustic axis, and that they include reliable estimates of source level (Au and Herzing, 2003).

Estimation of source levels requires, among other things, knowledge about the range between the receiving hydrophones and the clicking animals, along with information about the transmission properties of the medium. Range estimates can be derived from time-of-arrival differences of the same signal at synchronized receivers with sufficient spacing (Watkins and Schevill, 1972; Spiesberger and Fristrup, 1990; Wahlberg et al., 2001). The study by Møhl et al. (1990) on narwhals was the first to report that click source levels from a free-ranging odontocete in some cases are comparable to the highest source levels measured from trained dolphins, and thereby to show that maximum source parameters can be quantified for free-ranging odontocetes.

For large species such as sperm whales, which can be detected acoustically at ranges in the order of kilometres, large aperture arrays of independent receivers have proved useful in estimating source parameters (Møhl et al., 2003). In the case of inquisitive delphinids repeatedly making close approaches towards the recording gear in calm coastal waters, a star-shaped array of four hydrophones with a video camera can be used. This has recently been done successfully with Atlantic spotted dolphins (Au and Herzing, 2003), spinner dolphins and pantropical spotted dolphins (Schotten et al., 2003), killer whales (Au et al., 2004) and white beaked dolphins (Rasmussen et al., 2002). However, large offshore delphinids seldom approach deployed recording gear, and they travel too fast in heaving seas to allow for small aperture arrays with video cameras to work optimally.

False killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus* are examples of such species. Both species are pelagic, social odontocetes living in tropical and temperate seas. *Pseudorcas* are opportunistic predators feeding on a variety of squid and large fish, including tuna (Odell and McClune, 1999), and may in some cases target other marine

mammals (Odell and McClune, 1999). The biosonar capabilities of captive *Pseudorcas* have been studied in terms of hearing threshold (Thomas et al., 1988a), masking (Thomas et al., 1990), discrimination (Brill et al., 1992), target detection (Thomas and Turl, 1990) and sound transmission (Au et al., 1995), but the echolocation clicks and the acoustic performance of free-ranging animals have not been investigated. *Grampus* differ from *Pseudorcas* in that they feed almost entirely on cephalopod prey during nocturnal foraging bouts (Kruse et al., 1999). Only a few preliminary studies have been undertaken on the sound production (Au, 1993), hearing (Nachtigall et al., 1995) and biosonar (Philips et al., 2003) capabilities of *Grampus*, but no data has been published about the biosonar signals of free-ranging specimens.

Estimation of source parameters of biosonar signals from such pelagic species calls for a multi-hydrophone, wide bandwidth array that can be rapidly deployed and with an aperture large enough to allow for localization at ranges up to at least 100 m. In an attempt to meet such requirements we designed a vertical array of three hydrophones connected to a wideband digital recording system that was deployed during research in the offshore waters of the Maldives and Sri Lanka in the spring of 2003.

Here we present acoustic field data from a free-ranging, opportunistically foraging, pelagic delphinid, the false killer whale *Pseudorca crassidens* (Owen 1846), which has been studied extensively in captivity, and data from a less studied, free-ranging, cephalopod-eating, pelagic delphinid, Risso's dolphin *Grampus griseus* (Cuvier 1812). We quantify estimated source parameters of biosonar signals from these two species, and we outline and discuss interspecific differences and similarities in acoustic performance, ecophysiology and prey localization potential in the light of data from captive animals.

## Materials and methods

### *Study area and platform*

The recordings were conducted in oceanic deep water in the waters of the Republic of the Maldives and Sri Lanka from February through May 2003. The recording platform was a 28 m steel ketch, R/V *Odyssey*, research vessel of the Ocean Alliance, fitted for long periods of offshore cetacean research. In daylight hours a visual lookout was maintained from a platform 5 m above sea level. When a group of animals were located visually, the research vessel was maneuvered to a parallel course. If the animals got within range, the boat was turned into the wind with the engine off, and the recording gear was deployed within 2 min on the windward side of the boat. Recordings were performed in sea state 2 or below, and only used in instances in which no other species were detected.

### *Hydrophone array*

The array consisted of three modified hydrophones (Reson TC4032, Slangerup, Denmark) with 20 m low-noise, two-pair shielded cable. The hydrophones had a nominal sensitivity

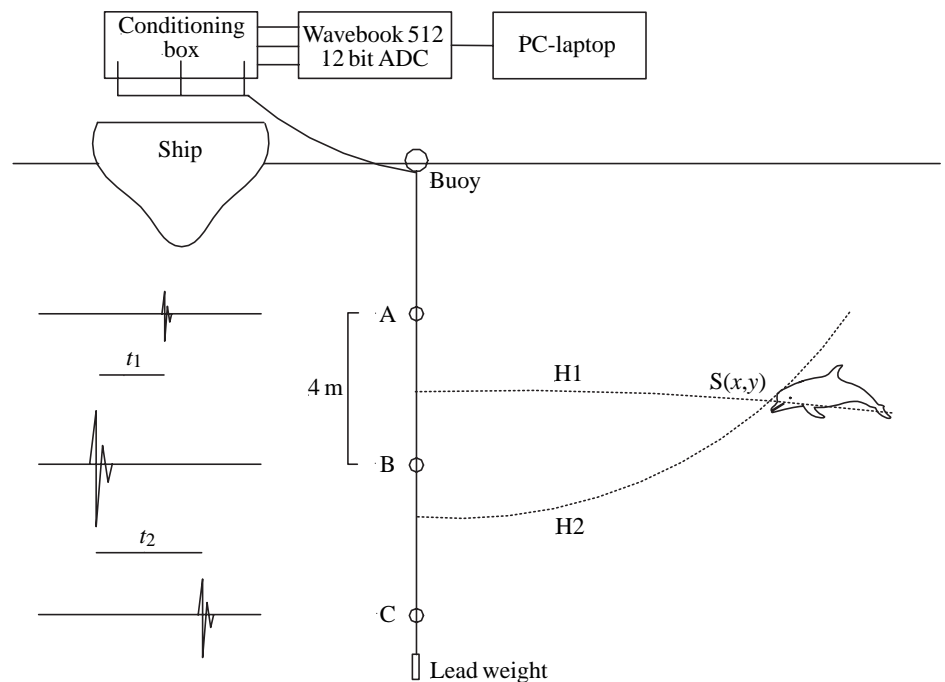


Fig. 1. The experimental set up consists of a linear array of three hydrophones (A, B, C) suspended from a buoy and a lead weight. The distance between the hydrophones is 4 m, and the first hydrophone is at a depth of 4 m. The clicking animal is localized from the time-of-arrival differences ( $t_1$ ,  $t_2$ ) of the same signal at the three receivers. The rotationally symmetric position of the sound source  $S(x,y)$  is given by the interception of the two hyperboloid surfaces (H1, H2). Analogue signals are amplified and band-pass filtered in the conditioning box before digitisation in the Wavebook 512, writing to the memory of a laptop.

(calibrated before and after the research period) of  $-220$  dBV re.  $1 \mu\text{Pa}$ , a flat frequency response ( $\pm 2$  dB) from 0.01 to 250 kHz, and omni-directional receiving characteristics (spherical element) from 0.01 to 180 kHz ( $\pm 2$  dB). To minimize flow and surface noise, the 8 m aperture array with 4 m between the hydrophones was suspended vertically between a buoy and a 10 kg lead weight (Fig. 1). The hydrophones were connected to a custom-built band pass and amplifier unit with a low impedance output. The gain and filter settings of this unit were clamped at 40 dB gain, high pass (HP) at 1 kHz ( $-24$  dB/octave) and low pass (LP) at 100 kHz ( $-24$  dB/octave). The latter LP cut-off was chosen well before the Nyquist frequency (160 kHz) in order to have a gently sloping anti-alias filter before the digitising system. The increasing LP-filter attenuation in the band from 100 to 160 kHz was compensated for during analysis, leaving an overall flat frequency response ( $\pm 2$  dB) of the recording system in the frequency range from 1 to 160 kHz.

#### Digitisation

The analogue signals from the amplifier unit were fed to a Wavebook 512 (IOtech, Cleveland, OH, USA) recorder for digitisation. The Wavebook 512 is an 8-channel digital recorder with a 12-bit analog to digital converter (ADC), sampling at 1 MHz. For this application, three channels were each sampling at 320 kHz, thus yielding a Nyquist frequency of 160 kHz. Digitization of the three channels was multiplexed into a single file with a maximal 3  $\mu\text{s}$  off-set between channels. The Wavebook was controlled by a laptop PC using *Waveview* software (IOtech). The software allows the operator to adjust sampling rate, clipping and pre-trigger levels in between recording sessions. Clipping levels were set at received sound pressures between 180 and 200 dB re.  $1 \mu\text{Pa}$  (peak to peak),

Each recording session lasted 20 s (with 6.4 mega samples acquired for each channel) and was triggered when the received level (RL) at one of the hydrophones exceeded 160 dB re.  $1 \mu\text{Pa}$  (pp) with a 5 s pre-triggering window. Due to an additional off-load time of 5 s from the Wavebook WBK30 memory buffer to the laptop, the maximum duty cycle during continuous triggering was 80%. The recordings were subsequently stored on CDs along with information about settings, animal behaviour and general comments.

#### Localization

Acoustic localization techniques use time of arrival differences (TOAD) of the same signal at receivers in known positions. Subsequently, source parameters such as source level can be estimated on the assumption of a set of propagation criteria. In the present study, a sound speed of  $1543 \text{ m s}^{-1}$  was calculated from the Leroy equation (Urlick, 1983) using a salinity value of 35 p.p.m. and an average measured temperature of  $29.5^\circ\text{C}$ . The range (R) between the phonating animal and the receiving hydrophones was estimated from TOADs at the three receivers. The TOADs between the receivers were measured as the time difference between the well defined peaks of the clicks (*sensu* Au and Herzing, 2003). Acoustic ranging with receivers in a two-dimensional system can be done with trigonometric methods (Watkins and Schevill, 1972; Spiesberger and Fristrup, 1991; Wahlberg et al., 2001). The range between the source and the receivers was calculated from the Pythagorean theorem, and the angles between the different receivers were derived from the cosine rule, assuming that the line between the clicking animal and the ensonified hydrophone was  $0^\circ$  relative the acoustic axis of the sound beam. Because of the linear receiver configuration the calculated location of the sound sources was

rotationally symmetric around the axis of the array. Source levels (SL) were calculated from the following equation:  $SL=RL+TL$ . Transmission loss (TL) was estimated by  $TL=20\log(R)+R\alpha$ , with  $\alpha$  being the frequency dependent absorption at the centroid frequency of the received click.

#### *On- or off-axis?*

All odontocete sonar clicks investigated show a pronounced directionality of amplitude, duration and frequency (Au, 1993). While the off-axis part of sonar clicks may play an important role in eavesdropping by conspecifics, predators and prey, it has probably little relevance to the performance of the sonar. According to Au (1993), because directionality of the hearing system is forward-oriented, only the source properties derived on or close to the acoustic axis are significant for the dolphin's sonar system.

In experiments with trained animals resting on a bite plate or in a hoop while echolocating, it can be ensured that signals are recorded from the beam of the sound generator. In free-ranging animals, however, it is more complicated to ensure that the clicks are recorded on-axis due to the combined effects of a directional, but dynamic, sound generator and rapid changes in the heading of the animals. At present, this analytical problem precludes derivation of stringent criteria for a signal being on- or off- the acoustic axis.

The term 'apparent source level' (ASL) has been adopted to emphasize that  $RL+TL$  equals the back-calculated sound pressure level at a distance of 1 m from a directional source of unknown orientation. The term source level (SL) can only be used where the recording aspect equals the axis of the sound beam. It is seen from Fig. 2 that ASL of the same clicks recorded with different hydrophones from different aspects varies considerably with time. This changing ensonification of hydrophones is presumably the result of scanning movements of the sound beam as it passes different parts of the array. In such click trains, the clicks with the highest ASL values are likely to represent the properties of sonar signals close to or on the acoustic axis of the phonating animal. Accordingly, we went through all recordings by hand, and classified signals that had maximal, relative amplitude in ensonifications as being close to or on the acoustic axis. This is a rather conservative approach as only a small fraction of the recorded clicks are being considered to be on-axis. However, in our view, there is no practical alternative at present.

#### *Signal analysis*

Analysis was performed with Cool Edit Pro (Syntrillium, Adobe) and custom written routines in Matlab 6.0 (Mathworks, Natick, MA, USA). Signal duration ( $\tau$ ,  $\mu s$ ) was determined from the relative signal energy derived by integrating the squared pressure over an interpolated (10 steps) 64 point window, symmetrical around the peak of the signal envelope. Onset of the signal was defined as the point at which 1.5% of the relative signal energy was reached, and the termination of the signal was defined as the point at which 98.5% of the relative signal energy was reached. Received levels at the

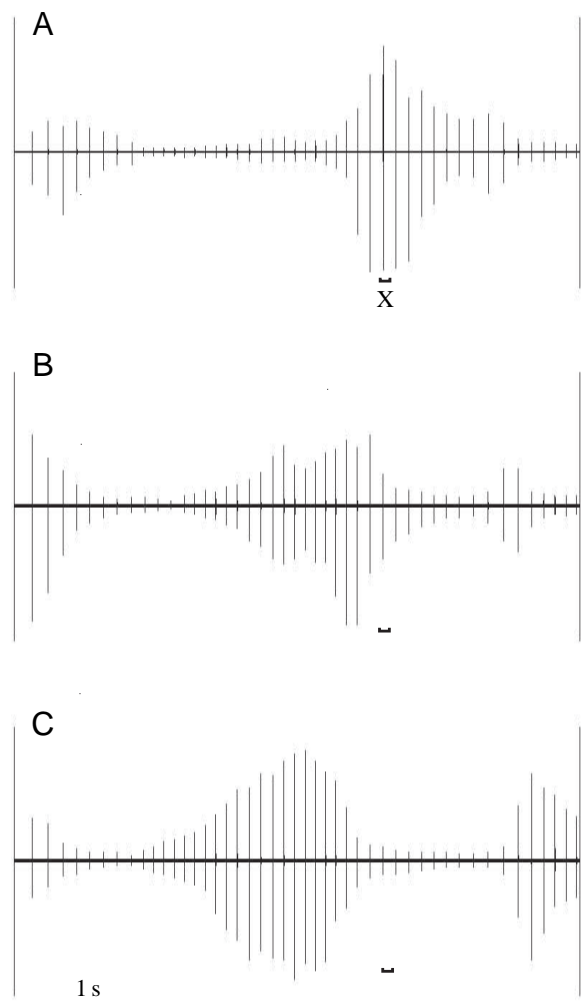


Fig. 2. Example of an ensonification event, during which an echolocating *Grampus* scans each of the three receivers (A,B,C). Note how the ensonification moves from hydrophone C to B to A. Full amplitude of the y-axes corresponds to an apparent source level (ASL) of 222 dB re. 1  $\mu Pa$  (pp). Local maxima on each of the three channels are likely to represent signals on or close to the acoustic axis of the sound beam. X marks a single click displayed in detail in Fig. 3.

hydrophones were calculated relative to a recorded calibration signal with a known RMS level. Peak-peak (pp) sound pressure level (dB re. 1  $\mu Pa$ , pp) was given by the pp amplitude difference between the signal and the pp value of the calibration signal +9 dB. The RMS sound pressure level (dB re. 1  $\mu Pa$ , rms) was calculated by integrating the square of the instantaneous pressure as a function of time over the time window  $\tau$  relative to the same integral over the same time  $\tau$  of the calibration signal. Energy flux density (dB re. 1  $\mu Pa^2 s$ ) was defined as the RMS sound pressure level (in dB)+10log( $\tau$ ) (*sensu* Au, 1993).

The spectral characteristics of the signals were quantified from a 256-point Fast Fourier Transform (FFT) on Hanning windowed data symmetrical around the peak of the envelopes.

The peak frequency ( $f_p$ , kHz) was defined as the center frequency of the band with the highest amplitude of the interpolated (10 step) spectrum. Interpolation was performed using the Matlab 6.0 low-pass interpolation routine with a symmetric filter. The centroid frequency ( $f_0$ , kHz) was defined as the point dividing the interpolated spectrum in halves of equal energy (Au, 1993). The bandwidth (BW) of the signals was described by the  $-3$  dB BW (kHz) and  $-10$  dB BW (kHz) and by the centralized root mean square bandwidth (RMS-BW, kHz) (Au, 1993), describing the spectral standard deviation around the centroid frequency ( $f_0$ ) of the spectrum. The resonant properties of clicks were expressed by the  $Q$ -value given by the centroid frequency divided by the centralized RMS-BW. Interclick interval (ICI, ms) was defined as the interval between successive clicks in a click train. Repetition rate (clicks  $s^{-1}$ ) was defined as the inverse of the ICI at any given time, and thereby used as a measure of the instantaneous repetition rate instead of the actual number of clicks per second in a given click train.

## Results

### Grampus

Recordings of *Grampus* were obtained on two occasions. On March 31, 2003, a group of slowly travelling *Grampus* were encountered SW of Sri Lanka at the position N5°56'/E81°30' (water depth 1200 m). The second recording of *Grampus* took place on April 25, off Sri Lanka at the position N6°20'/E81°40' (water depth 800 m). The two recording sessions yielded a total number of more than 3000 clicks on each of the three recording channels. Click trains were selected for detailed analysis in the sessions in which one or more of the hydrophones were illuminated by the sound beam of the animals (Fig. 2). Nineteen of such illuminating click trains provided un-clipped data with sufficient signal-to-noise ratio where the animal could be localized from TOADs at the three hydrophones.

*Grampus* clicks were predominantly part of long click trains that rose out of, and faded back into, the noise floor of the recordings. Repetition rates of the click trains were generally between 5 and 40 clicks  $s^{-1}$ , but during click bursts, the repetition rates rose to values approaching 400 clicks  $s^{-1}$ . A total of 11 well-defined, short click trains were also recorded containing 5–8 clicks with quite stable ICI values of 20 ms.

The importance of selecting on-axis clicks for analysis is demonstrated in Fig. 3, where the waveforms and spectra of the same click recorded from different aspects are displayed. It is seen that the click with the highest ASL of 220 dB re. 1  $\mu$ Pa (pp) has a waveform and spectral content quite different from the same click recorded in an aspect 6° off-axis (Fig. 3B), and markedly different from the same click recorded at an aspect 16° off-axis (Fig. 3C). The click with the highest ASL is considered to be recorded close to or on the acoustic axis. It consists of a few cycles with a sharp rise and fall time and a duration of 30  $\mu$ s. This putative on-axis click is broadband with a  $-3$  dB BW/ $-10$  dB BW of 30 kHz/60 kHz,  $Q=2.5$ , and a centroid frequency of 78 kHz (Fig. 3A). In the

clicks recorded off the acoustic axis, it is seen that there is a low-pass filter effect as a function of increasing azimuth in that the centroid frequency ( $f_0$ ) of the  $-6^\circ$  click is reduced to 53 kHz, and the  $f_0$  of the  $-16^\circ$  click is further reduced (to 50 kHz). While the peak frequency ( $f_p$ ) is constant around 45 kHz irrespective of aspect, it is seen that the spectrum of the off-axis clicks is distorted by an increasing number of notches in the spectrum (Fig. 3B,C). Distortion is also seen in the time domain of the off-axis clicks that are longer with more cycles compared to the on-axis signal.

This off-axis distortion in the spectral and time domains is seen in all click trains analysed irrespective of the source level of the assumed on-axis clicks. On top of the effects of off-axis distortion, there is also an effect of reduced source levels in that the  $f_0$  and RMS-BW of on-axis clicks decrease with source level. Analyses of clicks selected from ensonification events as seen in Fig. 2 support the general picture of the source parameters of on-axis *Grampus* clicks summarized in Table 1. An on-axis click has a SL of about 200–222 dB re. 1  $\mu$ Pa (pp) with an RMS sound pressure some 13 dB lower, and energy flux densities between 145 and 163 dB re. 1  $\mu$ Pa<sup>2</sup>s. The duration is 30–50  $\mu$ s and the spectral properties are broadband ( $Q=2-3$ ), RMS-BW around 25 kHz,  $f_p$  around 50 kHz and  $f_0$  around 75 kHz. No whistles were detected in the recordings.

### Pseudorca

Recordings of *Pseudorca* were obtained on two occasions. The first recording session commenced SW of the Maldivian archipelago (N2°24'/E71°53') on February 20, 2003, at a location that had a water depth of 3700 m. A mixed group of approximately 14 animals circled the boat for 20 min. The second recording session commenced in the vicinity of a group of 7–8 animals south west of Sri Lanka (N6°04'/E79°53') on April 3, 2003, at a location with a water depth of 1500 m.

The vast majority of clicks from this species were recorded from long click trains that rose from the noise floor of the recording during ensonification of the array until the amplitudes of the clicks faded back into the noise again. A total of more than 4000 clicks from such click trains were recorded on each of the three channels. The repetition rate varied between 5 and 40 clicks  $s^{-1}$  in most of the click trains, but during bursts or buzzes, click rates of more than 300 clicks  $s^{-1}$  were observed. A few of the recordings contained very short click trains of 5–8 clicks similar to the ones in *Grampus* recordings. In those short click trains the ICI was more constant at around 25 ms, i.e. an instantaneous repetition rate of around 40 click  $s^{-1}$ . Equivalent to the situation with the *Grampus* datasets, only clicks with relative maxima during ensonifications were considered to be recordings from or close to the acoustic axis. Twenty-two of the ensonification events provided non-clipped clicks with sufficient S/N that could be localized using TOAD at the three receivers. Such clicks are dominated by a single cycle followed by minor oscillations, having durations of around 30  $\mu$ s and estimated source levels between 201 and 225 dB re. 1  $\mu$ Pa (pp). The clicks are broadband with an RMS-BW around 20 kHz,  $-3$  dB BW/ $-10$  dB BW of 30/60 kHz,  $Q=2-3$ , and with peak

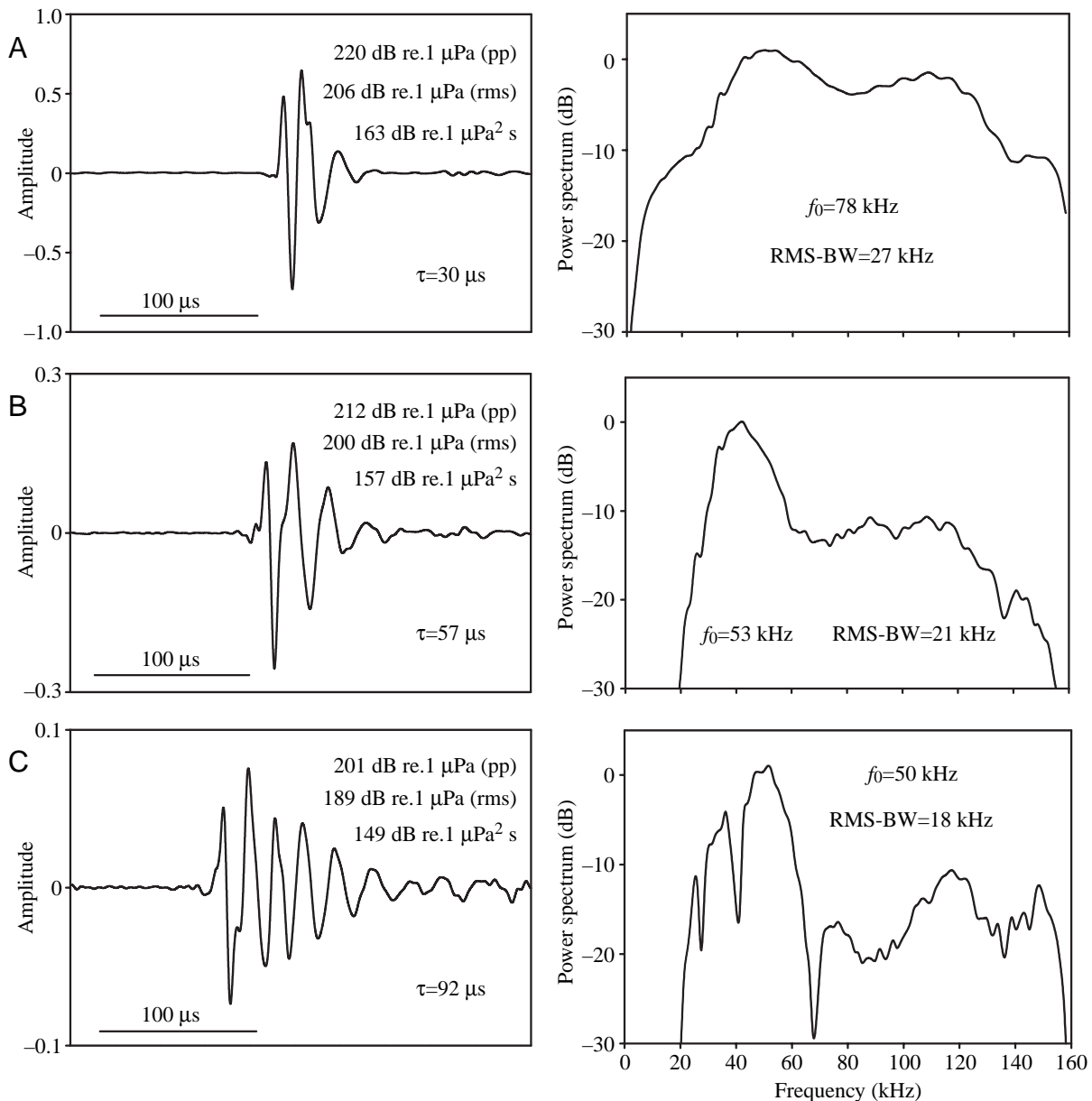


Fig. 3. Three versions of the same *Grampus* click X from Fig. 2 are displayed. (A) The presumed on-axis version of the click with a high apparent source level (ASL), short duration (left) and a smooth, broadband spectrum (right). (B) The same click recorded  $5^\circ$  off the recording aspect of A. The duration is longer, the ASL is lower, and the bandwidth and  $f_0$  are reduced compared to A. (C) The same click recorded in an aspect of  $10^\circ$  compared to A. The duration has increased, ASL,  $f_0$  and bandwidth have decreased compared to A and B, and a number of notches are seen in the spectrum.

frequencies around 40 kHz and centroid frequencies in the range 33–68 kHz. When analysing the off-axis versions of the same clicks, a pattern similar to the one for *Grampus* clicks emerges. ASL,  $f_0$  and bandwidths drop as a function of increasing azimuth, and the off-axis spectra show deep notches.

Presumed on-axis clicks not only differ in SL, but also with respect to their spectral properties. Fig. 4 gives three examples of on-axis clicks with different source levels from 200 to 225 dB re. 1  $\mu\text{Pa}$  (pp). It is seen that there is a low-pass filter effect with decreasing source level, even though  $f_p$  is more variable. This effect is also demonstrated in a reduced

bandwidth and  $f_0$  with decreasing source level. However, the spectra of the on-axis clicks are smooth and lack the notches seen in off-axis clicks with similar ASL values. Representative properties of on-axis *Pseudorca* clicks are summarized in Table 1. A large number of frequency modulated whistles were also recorded, but analysis of these is beyond the scope of this study.

### Discussion

Philips et al. (2003) conducted an echolocation experiment

Table 1. Source parameters from wild and trained *Grampus* and *Pseudorca* with maximum values from trained *Tursiops* for comparison

Parameters	<i>Grampus</i>		<i>Pseudorca</i>		<i>Tursiops</i>
	Wild	Trained	Wild	Trained	Trained
SL <sub>pp</sub> (dB re. 1 $\mu$ Pa, pp)	220 (202–222)	200 (170–216)	220 (201–225)	220 (155–225)	225
SL <sub>rms</sub> (dB re. 1 $\mu$ Pa, rms)	207 (190–210)	NA	208 (190–215)	NA	210
SL <sub>E</sub> (dB re. 1 $\mu$ Pa <sup>2</sup> s)	164 (147–166)	NA	163 (145–168)	NA	167
$\tau$ ( $\mu$ )	40 (30–75)	50 (40–70)	30 (18–55)	30–50	50
$f_0$ (kHz)	75 (58–91)	57 (53–83)	49 (33–68)	NA	100
$f_p$ (kHz)	49 (42–110)	48 (27–104)	40 (26–79)	30–125	115
RMS-BW (kHz)	25 (19–31)	25	20 (12–29)	NA	25
–3 dB BW (kHz)	27 (15–84)	40 (30–84)	35 (15–76)	5–80	50
–10 dB BW (kHz)	66 (20–124)	100	63 (39–89)	NA	60

Values give range. NA, not available.

SL, source level; pp, peak to peak; rms, root mean square; E, energy flux density;  $\tau$ , signal duration;  $f_0$ , centroid frequency;  $f_p$ , peak frequency; RMS-BW, rms bandwidth.

Data for the trained *Grampus* are from Philips et al. (2003).

Data for the trained *Pseudorc*as are from Thomas et al. (1988a), Thomas and Turl (1990), Brill et al. (1992) and Au et al. (1995).

Data for *Tursiops* are from Au (1993).

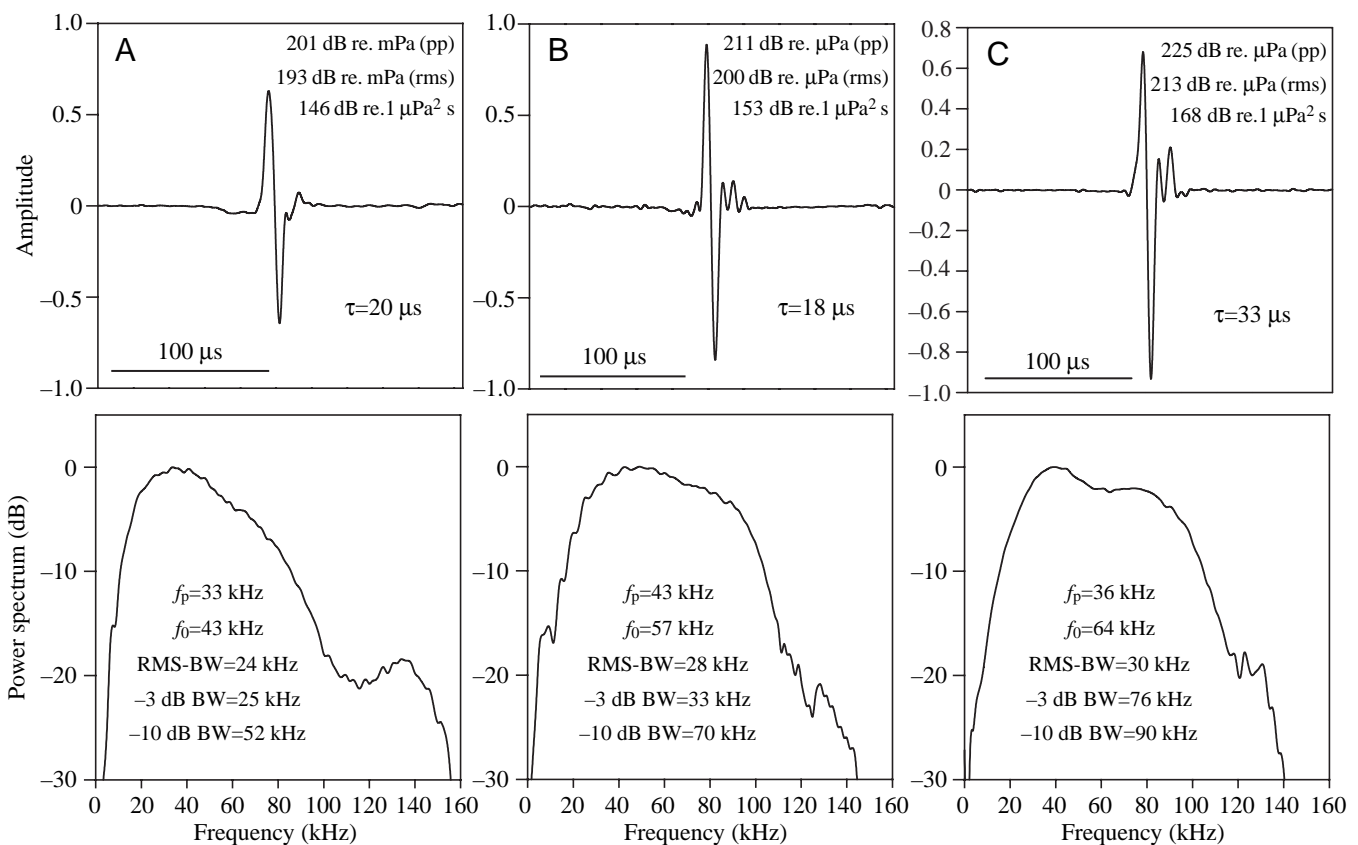


Fig. 4. Dynamics of the sound generator. Three examples (A–C) of on-axis clicks from *Pseudorca* are displayed (top) along with their spectra (bottom). All three clicks consist of one cycle with a short duration. While the  $f_p$  values are rather constant, it is seen that the  $f_0$  values and the bandwidth are positively correlated with the source level.

with a blindfolded *Grampus* that was trained to discriminate between two different sonar targets at ranges of 2–6 m. Sonar clicks believed to be recorded close to the acoustic axis of this animal showed estimated source levels as high as

216 dB re. 1  $\mu$ Pa (pp), durations between 40–70  $\mu$ s and bimodal spectra with peak frequencies around 50 kHz and  $f_0$  around 60 kHz (see Table 1). Such properties closely resemble the source properties derived from free-ranging specimens in

this study, except for lower SL values and longer click durations in the study by Philips et al. (2003).

The lower estimated source levels in the captive animal might be explained by the fact that the ranges between the animal and the target were small compared to the situation with the free-ranging *Grampus*. This is supported by the fact that the repetition rate of the captive animal was 20–100 clicks  $s^{-1}$  compared to 5–50 clicks  $s^{-1}$  in the present study, suggesting a longer target range for the free-ranging animals, and thereby also a potential need for higher SL values. This is corroborated by a recent study demonstrating that several free-ranging odontocetes adjust their SL to the target range when echolocating on deployed recording gear (Au and Benoit-Bird, 2003).

Philips et al. (2003) observed only a few high peak frequencies of more than 100 kHz, which is different from the consistently high peak frequencies in clicks obtained from other similar sized delphinids such as *Tursiops* and beluga when echolocating in pens in the same environment (Au, 1993). Philips et al. surmised that this lack of high peak frequencies may relate to the lower source levels from the *Grampus* during the short-range echolocation task, and that a *Grampus* producing higher source levels will have high peak frequencies comparable to clicks from *Tursiops* and *Beluga*. Although a single click with an  $f_p$  of 105 kHz was recorded from the free-ranging *Grampus*, we generally recorded  $f_p$  in the same frequency range between 40 and 50 kHz, despite the fact that the source levels of some clicks were twice as high (Table 1) as the maximum SL reported from the captive *Grampus*.

However, in bimodal spectra with low  $Q$  values, the peak frequency is not a very good measure of the spectral emphasis since very small shifts in the spectral energy distribution will lead to peak frequencies differing by more than an octave (see Fig. 3A). The centroid frequency is a much more robust measure of spectral emphasis than  $f_p$ , and it appears that the centroid frequencies of the captive and the free-ranging animals are generally alike in that they range from 50 to 70 kHz, despite their source level differences. It is therefore evident that free-ranging *Grampus* use biosonar clicks with source levels similar to trained *Tursiops* and *Belugas* during long range echolocation tasks, but with centroid frequencies almost one octave lower.

Centroid frequencies in the range 50–70 kHz match the frequency of best hearing from a trained *Grampus* involved in a psychophysical experiment (Fig. 5) (Nachtigall et al., 1995). Thus, free-ranging *Grampus* produce and hear biosonar pulses with a lower frequency emphasis than clicks from trained *Tursiops* and *Beluga*. It should be noted, however, that the most powerful clicks from the free-ranging *Grampus* have  $f_0$  close to 80 kHz, which is right at the high frequency cut-off in the only available audiogram for *Grampus* (see Fig. 5). If the returning echo has the same spectral distribution as the emitted pulse, the consequence will be that the animal cannot detect half of the energy in the returning sonar pulse. High frequency components are the byproduct of high acoustic outputs in

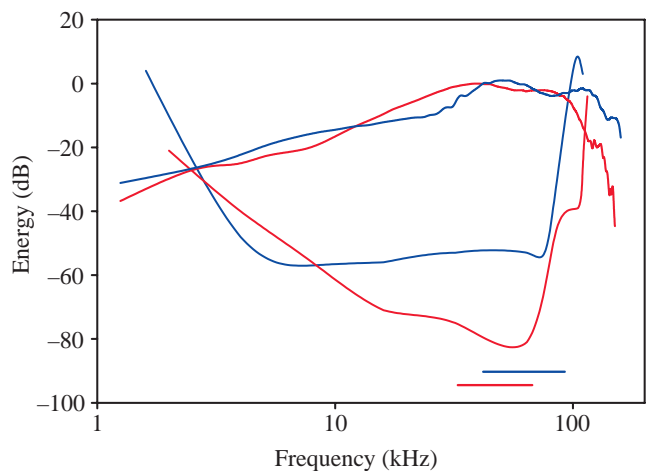


Fig. 5. Audiograms of *Grampus* (blue line) and *Pseudorca* (red line) along with representative spectra of on-axis clicks from each species on a relative dB scale. Note that high ambient noise levels masked the maximum sensitivity of the *Grampus* audiogram, which explains the large difference in threshold between the two species (Nachtigall et al., 1995). Coloured bars signify frequency range of the centroid frequencies of on-axis clicks from the two species recorded in the wild. The *Grampus* audiogram is from Nachtigall et al. (1995) and the *Pseudorca* audiogram from Thomas et al. (1988a).

odontocete sound production (Au et al., 1995), but the apparent 50% energy loss in the case of *Grampus* clicks with high SL values may be explained by the fact that the old *Grampus* used for the psychophysical experiment may have suffered from a hearing disability at higher frequencies, as seen in some old *Tursiops* (Ridgway and Carder, 1997). If so, the super-audial energy fraction in high-powered clicks may be considerably lower in young animals that have normal high frequency hearing.

Much data exists concerning properties of clicks produced by captive *Pseudorcas* in various setups. Thomas et al. (1988b) made the first study on echolocation in *Pseudorca*, when they trained a blindfolded animal to look for a spherical target at a short range of 4 m. The echolocation clicks from this animal had source levels around 150 dB re. 1  $\mu Pa$  (pp) and peak frequencies between 17 and 56 kHz. To test the maximum detection range, Thomas and Turl (1990) performed another study with a *Pseudorca* that was trained to echolocate a target at ranges between 40 and 120 m. Clicks recorded from this animal had high SL values of 200–225 dB re. 1  $\mu Pa$  (pp), short durations of 50–70  $\mu s$ , and spectra with peak frequencies between 95 and 125 kHz and little energy below 50 kHz.

Brill et al. (1992) conducted a discrimination test at short range, in which a young *Pseudorca* was trained to discriminate between a spherical and a cylindrical target. Signals produced during this activity had source levels around 175 dB re. 1  $\mu Pa$  (pp), peak frequencies around 38 kHz and  $-3$  dB BW around 40 kHz. Peak frequencies around 100 kHz were observed in those cases in which the animal produced clicks with source levels above 185 dB re. 1  $\mu Pa$  (pp). Au et al. (1995) recorded



signals from an echolocating *Pseudorca* with an array of hydrophones to quantify the directional properties of the sound beam. They classified the recorded signals in four groups, based on source level and spectra. This ranged from group 1 signals with a single, low-frequency peak around 40 kHz and source levels around 200 dB re. 1  $\mu$ Pa (pp) to group 4 signals with a single high-frequency peak around 100 kHz and source levels around 215 dB re. 1  $\mu$ Pa (pp). The two intermediate click groups had source levels that lay between these values and included bimodal spectra dominated by a low spectral peak (group 2) and a high spectral peak (group 3), respectively. Au et al. (1995) found a forward directed beam with a directionality index (DI) varying from 22 to 29 dB, depending on the centroid frequencies of the signals.

Thus, estimated source properties from trained *Pseudorcas* in various contexts show considerable differences in source level (50 dB) and spectral dominance (1–2 octaves). The source properties from free-ranging *Pseudorcas* also show some plasticity, but certain features are much more stable than is the case for signals from the various captive animal settings. The source levels of clicks from free-ranging *Pseudorcas* vary between 200 and 225 dB re. 1  $\mu$ Pa (pp), and the centroid frequencies are positively correlated with the source level, and range from 40 to 60 kHz. With a single exception of 78 kHz, the peak frequencies are quite stable around 35 kHz.

Hence, free-ranging *Pseudorcas* produce SLs in the same range of 200–225 dB re. 1  $\mu$ Pa (pp) as observed for a trained *Pseudorca* during a long-range target detection experiment, but the peak frequencies of the clicks from the free-ranging animals are 2 octaves lower than those made by a captive animal that was echolocating for a steel sphere at long range. Instead, the free-ranging animals produce clicks with spectral properties similar to the clicks in the discrimination study by Brill et al. (1992) and the type 2 clicks in the Au et al. (1995) study. However, as is the case with the broadband *Grampus* clicks, peak frequencies are not a very good measure of the spectral emphasis, and when using the more appropriate centroid frequency as a measure (Au et al., 1995) it becomes evident that  $f_0$  for free-ranging *Pseudorcas* lies between 40 and 60 kHz. This frequency range fits the frequency range of best hearing (Fig. 5) measured from a young animal in a psychophysical experiment (Thomas et al., 1988a).

It is seen from Fig. 5 that a powerful *Pseudorca* click with a centroid frequency of 60 kHz has a –10 dB BW that matches the –10 dB BW of highest sensitivity in an audiogram from a young, healthy *Pseudorca*. However, in the long-range, target-detection experiment by Thomas et al. (1990), the animal consistently produced clicks that had peak frequencies around 100 kHz, beyond the upper limit of best hearing. Available physiological data suggest that the audiometric system of odontocetes is characterized by a low-pass (LP) filter with a very high cut-off of more than 100 dB/octave. If the audiogram of the young *Pseudorca* is representative for the species, it is surprising at first glance to find that the spectral peaks of some clicks are found well above the upper hearing limit. However, when employing a sharp LP filter (100 dB/octave) at 85 kHz

of an on-axis *Pseudorca* click with an  $f_p$  at 78 kHz, it appears that the overall amplitude of the click is reduced by only 1.5 dB, whereby 85% of the click energy is retained and available for detection in the returning echo. Reductions of the same small order of magnitude can be expected from clicks with higher peak frequencies, but with the same approximate centroid frequency.

Thus, the present data lend weight to the contention by Au et al. (1995) that spectral energy at high frequencies is the byproduct of high source levels, and that the overall gain in audible energy from the returning echo is large compared to the non-detectable energy at high frequencies produced as a byproduct of high SL values. The important thing is that the centroid frequencies of the clicks are within the frequency range of best hearing (Fig. 5). This is consistently the case for the free-ranging *Pseudorcas*, and apparently also for captive conspecifics.

A remarkable feature of the source properties of odontocete sonar signals both in captivity and in the present study is the variable centroid frequencies. A physical consequence of this phenomenon is that the transmitting and receiving beam widths are affected (Au et al., 1995), so that a doubling in centroid frequency will double the directionality. It means that generation of low amplitude clicks with low centroid frequencies leads to a broader beam, i.e. a larger cone in front of the animal will be ensonified by the half-power beam. On the other hand, when high SL clicks are generated with higher centroid frequencies, the transmission beam will be narrower and the half power sound beam will cover a smaller cone in front of the animal. So the sonar beam will perform in a fashion similar to a flashlight with a variable light cone.

The results from the present study leave no doubt that free-ranging *Pseudorca* and *Grampus* do have a dynamic sound generator with variable SL and centroid frequencies. Transmitting and receiving beams estimated from clicks with high SL values and centroid frequencies represent the maximum properties of the sonar system. The present study shows that the biosonar of free-ranging animals is evidently not implemented by a static high-powered system with fixed beams, and what the functional consequences of this plastic modus operandi are in the wild remains to be investigated.

It appears that the source parameters of clicks from *Pseudorca* and *Grampus* are quite similar in terms of duration and source level range. The waveform of *Pseudorca* clicks is slightly shorter and simpler than the waveform of *Grampus* clicks, whereas the centroid frequencies of *Grampus* are some 25 kHz higher than those of *Pseudorca*. The higher centroid frequencies may relate to the fact that *Grampus* are smaller than *Pseudorca* with smaller sound producing structures, and that higher frequencies are needed to achieve the same directionality as found in *Pseudorca* clicks. It has been suggested that the sharp and unique indentation of the *Grampus* melon may affect its transmitting properties (Nachtigall et al., 1995; Philips et al., 2003), but there are at present no data to test this conjecture.

The source properties reported here for *Grampus* and *Pseudorca* are generally consistent with the sonar signal

properties of a very large group of delphinid odontocetes that produce short ( $<100 \mu\text{s}$ ) broadband ( $Q=1-3$ ) transients with source levels up to around 225 dB re.  $1 \mu\text{Pa}$  (pp) (Au, 1993). Both species in this study produce signals with amplitudes, energy flux densities, and durations that are comparable to *Tursiops* (see Table 1 for comparison). It is striking, though, that both the audiograms from the captive animals and the analysis of spectra from free-ranging specimens suggest that *Pseudorca* and *Grampus* produce and detect sonar signals with centroid frequencies almost one octave below those of the powerful clicks made by *Tursiops* and beluga (*Delphinapterus leucas*). Watkins (1980) has proposed that there is a link between the size of the animal, and thereby the size of the sound producing structures, and frequency emphasis of the clicks. While this holds true when comparing *Pseudorca* and *Grampus* with the slightly smaller *Tursiops*, size differences cannot account for the spectral differences if the comparison is made to the similar sized beluga. Additional data on signals, habitats, prey and behavior of other free-ranging odontocetes is needed before the shaping factors of odontocete sonar signals can be fully uncovered.

Analysis of click trains from a trained beluga in target detection experiments has shown that this animal, contrary to *Tursiops* and *Pseudorca*, emits packets of 4–5 clicks with ICI values (40 ms) that are shorter than the two-way-travel times between animal and target (Turl and Penner, 1989). Au (1993) speculated that this might relate to unknown adaptations to a life in a highly reverberant ice-covered habitat, or that the animal simply had a unique and peculiar echolocation pattern. In two of the recording sessions with the free-ranging *Pseudorca* and *Grampus*, similar short click trains of 5–8 clicks with ICI values of 20 ms were observed. There are no clues to determine whether they serve the same function and are produced in the same behavioral context as the packets of clicks from the captive beluga. We can only note their existence and point out that free-ranging species other than the single, captive beluga do produce short packets of clicks with constant ICI values. Hopefully, future studies will be able to uncover the functional significance of this type of apparent echolocation pattern, given that it is so very different from normal, longer trains of clicks.

From the above discussion it is evident that the signals used for echolocation are identical in *Grampus* and *Pseudorca*, despite their preferences for different prey. This suggests in turn that differences in size, foraging behaviour and use of habitat may play a more dominant role in shaping the properties of odontocete sonar signals than the size, distribution and acoustic properties of prey items. It should be recognized that the source parameters presented in this study are from animals echolocating on deployed recording gear rather than prey items, and we cannot be sure that the source properties would be the same when these same animals use their biosonar for foraging. We nevertheless feel confident that the properties reported here reflect the minimum capabilities of the sound production system of these two species, and that models for detection of prey can be made on this basis.

Evans (1973) advanced the idea that there is an inverse relationship between  $f_p$  and prey size, as detection of smaller prey requires higher frequencies for adequate resolution. To yield efficient backscatter, a sonar target must be in the geometric scatter zone where the effective circumference of the target is larger than the dominating wavelengths of the sonar pulse (Medwin and Clay, 1998). With minimum centroid frequencies of 40–50 kHz in *Pseudorca* and *Grampus* clicks, sonar targets with radii larger than 0.7 cm will thus provide geometric backscatter. Hence, all biologically relevant prey items, whether cephalopods or fish, will be in the geometric scatter zone. But the target strength changes with the size and properties of the target. Fish with swim bladders have a much higher target strength than similar-sized animals such as cephalopods, which have no air cavities. It is therefore relevant to evaluate the detection potential of the sonar clicks collected from free-ranging specimens in the light of the properties of representative prey items.

In a range detection experiment in the noisy environment of Kaneohe Bay in Hawaii, a female false killer whale was trained to echolocate a 7.62 cm spherical target with a target strength (TS) of  $-30$  dB. The distance to the target was increased until detection fell to chance. Using an average SL of 221 dB re.  $1 \mu\text{Pa}$  (pp) the animal had a 75% correct detection of the sphere at a range of some 98 m (Thomas and Turl, 1988). The ambient spectral noise level in Kaneohe Bay in the frequency range of the centroid frequency of *Pseudorca* clicks is around 50 dB re.  $1 \mu\text{Pa}^2 \text{Hz}^{-1}$  (Thomas et al., 1988a). Hence using the sonar equation (Urlick, 1983), and assuming that all variables are equal except for SL, ambient noise level and target strength, the detection range of biological targets by free-ranging *Pseudorcas* can be estimated. Using a SL value from this study of 220 dB re.  $1 \mu\text{Pa}$  (pp) (Table 1) and a spectral noise density in the open ocean away from the surface at sea state 3 of 35 dB re.  $1 \mu\text{Pa}^2 \text{Hz}^{-1}$  at 50 kHz (Urlick, 1983), the echo to noise ratio has been improved by 14 dB compared to the situation for the trained animal in Kaneohe Bay.

In the following, it is assumed that detection is limited by ambient noise. On that basis, we have tabulated the detection ranges at 75% level of prey items with different TS in Table 2. It is seen that *Pseudorcas* should be able to detect a medium-sized (1 m) yellowfin tuna *Thunnus albacares* at 75% level at ranges up to 200 m if both prey and predator are away from the noisy surface. This range is increased if the SL is increased, and it is decreased if the noise levels rise due to near-surface foraging, or deteriorating weather including rain and increased wave action. Prey items such as larger fish and other delphinids may be detected at even greater ranges (up to 300 m). However in the latter case, hunting tactics may involve a stealthy approach as has been indicated in transient killer whales (Barret-Lennard et al., 1996). In contrast, when hunting for squid, it is seen that *Pseudorca*'s estimated detection range drops to ranges comparable to those of *Grampus* when it is searching the same prey (Table 2). Recently, Au et al. (2004) made a foraging model for echolocating killer whales *Orcinus orca*, based on psychophysical data from captive specimens

Table 2. Estimated detection ranges of different prey items based on detection capabilities of a captive *Pseudorca*, and the source parameters derived in the present study

Predator	SL (dB re. 1 $\mu$ Pa, pp)	$f_0$ (kHz)	Noise (dB re. 1 $\mu$ Pa <sup>2</sup> Hz <sup>-1</sup> )	Prey	TS (dB)	Detection range (m)
<i>Pseudorca</i>	220	50	35	Tuna (1 m)	-30 <sup>1</sup>	210
<i>Pseudorca</i>	220	50	35	Dolphin ( <i>Tursiops</i> )	-20 <sup>2</sup>	320
<i>Pseudorca</i>	220	50	35	Small squid (20 cm)	-50 <sup>3</sup>	80
<i>Grampus</i>	220	75	32	Small squid (20 cm)	-50 <sup>3</sup>	85
<i>Grampus</i>	220	75	32	Large squid (80 cm)	-40 <sup>3</sup>	130

SL, source level;  $f_0$ , centroid frequency; TS, target strength.

It is assumed that detection is limited by ambient noise, and that the receiving system of a *Grampus* performs like that of a *Pseudorca*.

TS for a *Tursiops* may not represent TS for smaller delphinids preyed upon by *Pseudorca*, but it is the only available TS for a dolphin.

<sup>1</sup>Bertrand et al. (1999); <sup>2</sup>Au (1996); <sup>3</sup>Medwin and Clay (1998).

and source properties of clicks from free ranging specimens, and modelled scatter properties of moving salmonid prey. They estimated that foraging *Orcas* should be able to detect a salmon at a range of 100 m in sea state 4 noise conditions with a recognition differential of more than 9 dB. Thus, the estimated detection ranges of tunas by *Pseudorcas* in the present study are larger than estimated for *Orcas* foraging on chinook salmon (Au et al., 2004). The difference is likely to relate to the estimated recognition differential for the *Orcas* compared to the measured values for the *Pseudorca*, and the lower target strength estimates for the salmon compared to a 1 m tuna.

Although echolocation has been demonstrated in *Grampus* (Philips et al., 2003) there is no information about the maximum detection capabilities for this species. Making the crude assumption that the performance of the detection system matches that of *Pseudorca*, the detection ranges of cephalopod prey by *Grampus* can be evaluated. A spectral noise level of 32 dB re. 1  $\mu$ Pa<sup>2</sup> Hz<sup>-1</sup> at 75 kHz, being slightly lower than that used for *Pseudorca*, has been adopted because of the higher centroid frequencies of the *Grampus* clicks. Main prey items of *Grampus* include medium-sized squid with mantle lengths on the order of 30 cm (Clarke and Pascoe, 1985). The target strength of squids of this size is approximately -50 dB (Medwin and Clay, 1998). Under the outlined set of assumptions, it can be estimated that an echolocating *Grampus* can detect a single medium-sized squid at a range of some 80 m if both the source and the target are at the same depth. This is considerably less than the estimated maximal detection range for the primary prey of *Pseudorca*, and it relates primarily to the scatter properties of the prey targets and not to differences in the biosonar signals of the two odontocetes.

The behaviour and movements of the different prey types may in part compensate for the discrepancy between the ranges at which *Grampus* and *Pseudorca* can detect their primary prey. While larger fish may hold a distance in a school that maintains them as individual sonar targets, the schooling behaviour of mesopelagic squids may yield better scatter, because they are close enough to act as a single sonar target having a higher target strength than individual squid (Benoit-

Bird and Au, 2001), and thereby increase the potential detection range.

While the listed estimates of detection ranges for different prey types are indeed based on a number of unknowns, they are robust enough to suggest that free-ranging *Grampus* and *Pseudorcas* in a natural habitat can detect their primary prey at ranges of 100 m or more, and thereby at ranges similar to those at which trained animals can detect steel spheres in a noisy shallow water environment. Thus, source properties derived from free-ranging animals suggest that both odontocete species have evolved a sonar system that allows them to derive information about their habitat and prey at considerable ranges. *Pseudorca* is expected to detect large fish at ranges twice as far away as *Grampus* can searching for medium sized squids, which relates to different target properties rather than to different source properties. Neither of these species has the potential for long range biosonar that has been indicated for the sperm whale, which under equivalent noise conditions should be able to detect similar sized cephalopod prey at ranges of more than 500 m (Møhl et al., 2003). This is due to the fact that the sperm whale emits directional biosonar clicks with little attenuation at centroid frequencies 1–2 octaves lower than the centroid frequencies in the delphinid clicks. Also, the large and specialized sound generating mechanism in the nose of the sperm whale generates source levels that are five times higher than measured for smaller odontocetes (Møhl et al., 2003).

The capture of a wild, well-nourished, but deaf and mute dolphin (Ridgway and Carder, 1997) is a sobering reminder that biosonar may indeed not be the only sensory modality used by odontocetes for locating and capturing food. So although biosonar undoubtedly plays an important role in foraging, and in the successful evolutionary radiation of the entire odontocete suborder (Norris, 1968), there is a great need to understand the extent by which biosonar is assisted by other cues, and what the behavioral contexts of different sensory modalities are. Biosonar detection of a prey item at a certain range does not necessarily mean that the animal will pursue, if cost-benefit analyses render such engagement as futile.

One of the next challenges in this area of experimental field biology is to shed light on how and when biosonar signals of free-ranging odontocetes are used to locate prey, and how predators and prey interact acoustically. A relevant path in such research would be to combine knowledge of the source parameters of biosonar clicks from free-ranging species with information about 3-D movement patterns derived from onboard multisensor tags (Johnson and Tyack, 2003). This would make it possible to put the sound production dynamics in biosonar-based foraging systems into a relevant behavioral context.

In conclusion, this study has shown that source parameters can be estimated from free-ranging delphinids in oceanic waters. The source properties of *Grampus* and *Pseudorca* are generally in line with source properties from trained animals, but show less variation, higher source levels and lower centroid and peak frequencies. Click characteristics for both species are much alike, but *Grampus* clicks have centroid frequencies 25 kHz above those of *Pseudorca*. Both species exhibit dynamic sound production in terms of source level and spectral content, supporting the view that maximum source properties from trained animals are not fully representative of the production of biosonar signals in free-ranging conspecifics. The dynamics of the source parameters, linking centroid frequency and source levels, will affect the transmitting and receiving beams of these animals, but it is not clear at present what the biological implications are.

We have presented foraging models that utilize the synergistic effect of integrating psychophysical data from captive animals with source parameters of free-ranging animals. We estimate that *Grampus* can detect its primary prey, cephalopods, at ranges on the order of 100 m, and that *Pseudorca* can detect large fish at twice that range. The differences in detection ranges of prey for the two species relate to the acoustic properties of the prey rather than to the source parameters of the biosonar systems. The present results lend weight to the view that the physics of sound production, and foraging behaviour rather than acoustic prey properties have been the primary factors shaping the evolution of biosonar signals in these two delphinid species.

#### List of abbreviations

ADC	analogue-to-digital converter
ASL	apparent source level
BW	band width
DI	directionality index
E	energy flux density
$f_0$	centroid frequency
FFT	fast Fourier Transform
$f_p$	peak frequency
HP	high pass
ICI	interclick interval
LP	low pass
pp	peak to peak
R	range

RL	received level
RMS	root mean square
SL	source level
TL	transmission loss
TOAD	time-of-arrival difference
TS	target strength
$\alpha$	frequency dependent absorption
$\tau$	signal duration

We thank M. Preedy, R/V *Odyssey* crew, and the Lincoln staff for their help throughout. We thank A. Surlykke, S. B. Pedersen and B. Møhl for technical support, and M. Wahlberg, B. Dahl, K. Beedholm, W. M. X. Zimmer, B. Møhl and two referees for analytical and editorial suggestions. The amplifier unit was designed by N. U. Kristiansen, M. Bjørn built support for the array, and M. Wahlberg wrote the localization routine. P.T.M. was funded by postdoctoral grants from Ocean Alliance and the Danish Natural Science Research Council. The donors of the Ocean Alliance funded ship time, and recording gear was funded by the Oticon Foundation and the Novo Nordisk Science Foundation by grants issued to P.T.M. This work was carried out under NFMS permit no. 751-1641, research permit no. FA-A/33/2003/01 from Fisheries Research in the Maldives and research permit no. WL/3/2/1/18 from National Aquatic Resources Agency/The Wildlife Conservation Office of Sri Lanka. The research was in compliance with all US and local legislations.

#### References

- Au, W. W. L. (1993). *Sonar of Dolphins*. New York: Springer-Verlag.
- Au, W. W. (1996). Acoustic reflectivity of a dolphin. *J. Acoust. Soc. Am.* **99**, 3844-3848.
- Au, W. W. L. (1997). Echolocation in dolphins with a dolphin-bat comparison. *Bioacoustics* **8**, 162.
- Au, W. W. and Benoit-Bird, K. J. (2003). Automatic gain control in the echolocation system of dolphins. *Nature* **423**, 861-863.
- Au, W. W. L., Floyd, R. W., Penner, R. H. and Murchison, A. E. (1974). Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. *J. Acoust. Soc. Am.* **56**, 1280-1290.
- Au, W. W. L., Ford, J. K. B., Horne, J. K. and Allman K. A. N. (2004). Echolocation signals of free-ranging killer whales (*Orcinus orca*) and modelling of foraging for chinook salmon (*Oncorhynchus tshawytscha*). *J. Acoust. Soc. Am.* **115**, 901-909.
- Au, W. W. L., Moore, P. W. and Pawloski, D. (1986). Echolocation transmitting beam of the Atlantic bottlenose dolphin. *J. Acoust. Soc. Am.* **80**, 688-691.
- Au, W. W. L., Pawloski, J. L., Nachtigall, P. E., Blonz, M. and Gisner, R. C. (1995). Echolocation signals and transmission beam pattern of a false killer whale (*Pseudorca crassidens*). *J. Acoust. Soc. Am.* **98**, 51-59.
- Au, W. W. L. and Herzing, D. L. (2003). Echolocation signals of wild Atlantic spotted dolphin (*Stenella frontalis*). *J. Acoust. Soc. Am.* **113**, 598-604.
- Au, W. W. L. and Pawloski, D. A. (1989). A comparison of signal detection between an echolocating dolphin and an optimal receiver. *J. Comp. Physiol.* **A 164**, 451-458.
- Barret-Lennard, L. G., Ford, J. K. B. and Heise, K. A. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Anim. Behav.* **51**, 553-665.
- Benoit-Bird, K. J. and Au, W. W. L. (2001). Target strength measurements of Hawaiian mesopelagic boundary community animals. *J. Acoust. Soc. Am.* **110**, 812-819.
- Bertrand, A., Josse, E. and Masse, J. (1999). In situ acoustic target-strength

- measurement of bigeye (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) by coupling split-beam echosounder observations and sonic tracking. *ICES J. Mar. Sci.* **56**, 51-60.
- Brill, R., Pawloski, J. L., Helweg, D., Au, W. W. L. and Moore, P. W.** (1992). Target detection, shape discrimination and signal characteristics of an echolocating false killer whale (*Pseudorca crassidens*). *J. Acoust. Soc. Am.* **92**, 1324-1330.
- Clarke, M. and Pascoe, P.** (1985). The stomach contents of a Risso's dolphin (*Grampus griseus*) stranded at Thurleston, South Devon. *J. Mar. Biol. Assn. UK* **65**, 663-665.
- Evans, W. E.** (1973). Echolocation by marine delphinids and one species of freshwater dolphin. *J. Acoust. Soc. Am.* **54**, 191-199.
- Johnson, M. P. and Tyack, P. L.** (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Ocean. Eng.* **28**, 3-12.
- Kruse, S., Caldwell, D. K. and Caldwell, M. C.** (1999). Risso's dolphin. In *Handbook of Marine Mammals*, vol. 5 (ed. S. H. Ridgway and R. Harrison), pp. 183-211. Cambridge: Academic Press.
- Madsen, P. T., Payne, R., Kristiansen, N. U., Kerr, I. and Moehl, B.** (2002). Sperm whale sound production studied with ultrasound-time-depth-recording tags. *J. Exp. Biol.* **205**, 1899-1906.
- Medwin, H. and Clay, C. S.** (1998). *Acoustical Oceanography*. Boston: Academic Press.
- Møhl, B., Surlykke, A. and Miller, L. A.** (1990). High intensity narwhal click. In *Sensory Abilities of Cetaceans* (ed. J. Thomas and R. Kastelein), pp. 295-304. New York: Plenum Press.
- Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A. and Lund, A.** (2003). The monopulsed nature of sperm whale clicks. *J. Acoust. Soc. Am.* **114**, 1143-1154.
- Nachtigall, P. E. Au, W. W. L., Pawloski, J. and Moore, P.** (1995). Risso's Dolphin (*Grampus griseus*) hearing threshold in Kaneohe Bay, Hawaii. In *Sensory Systems of Aquatic Mammals* (ed. R. Kastelein, J. Thomas and P. E. Nachtigall), pp. 49-53. Worden: De Spil Publishers.
- Norris, K. S.** (1968). The evolution of acoustic mechanisms in odontocete cetaceans. In *Evolution and Environment* (ed. E. T. Drake), pp. 297-324. New Haven: Yale University Press.
- Odell, D. K. and McClune, K. M.** (1999). False Killer Whale. In *Handbook of Marine Mammals*, vol. 4 (ed. S. Ridgway and R. J. Harrison), pp. 213-243. Cambridge: Academic Press.
- Philips, J. D., Nachtigall, P. E., Au, W. W. L., Pawloski, J. L. and Roitblat, H. L.** (2003). Echolocation in the Risso's dolphin, *Grampus griseus*. *J. Acoust. Soc. Am.* **113**, 605-616.
- Rasmussen, M. H., Miller, L. A. and Au, W. W. L.** (2002). Source levels of clicks from free-ranging white-beaked dolphins (*Lagenorhynchus albirostris* Gray 1846) recorded in Icelandic waters. *J. Acoust. Soc. Am.* **111**, 1122-1125.
- Ridgway, S. H. and Carder, D. A.** (1997). Hearing deficits measured in some *Tursiops truncatus*, and discovery of a deaf/mute dolphin. *J. Acoust. Soc. Am.* **101**, 590-594.
- Schotten, M., Au, W. W. L., Lammers, M. O. and Aubauer, R.** (2003). Echolocation recordings and localizations of wild spinner dolphins (*Stenella longirostris*) and pantropical spotted dolphins (*Stenella attenuata*) using a four hydrophone array. In *Echolocation in Bats and Dolphins* (ed. J. Thomas, C. F. Moss and M. Vater), pp. 393-400. Chicago: University of Chicago Press.
- Spiesberger, J. L. and Fristrup, K. M.** (1990). Passive localization of calling animals and sensing of their acoustic environment using acoustic tomography. *Am. Nat.* **135**, 107-153.
- Surlykke, A. and Moss, C. F.** (2000). Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory. *J. Acoust. Soc. Am.* **108**, 2419-2429.
- Thomas, J., Chun, N., Au, W. W. L. and Pugh, K.** (1988a). Underwater audiogram of a false killer whale (*Pseudorca crassidens*). *J. Acoust. Soc. Am.* **84**, 936-940.
- Thomas, J., Pawloski, J. and Au, W. W. L.** (1990). Masked hearing abilities in a False Killer Whale (*Pseudorca Crassidens*). In *Sensory Abilities of Cetaceans* (ed. J. Thomas and R. Kastelein), pp. 395-403. New York: Plenum Press.
- Thomas, J., Stoermer, M., Bowers, C., Anderson, L. and Garver, A.** (1988b). Detection abilities and signal characteristics of echolocating False Killer Whales (*Pseudorca crassidens*). In *Animal Sonar* (ed. P. E. Nachtigall and P. W. Moore), pp. 323-328. New York: Plenum Press.
- Thomas, J. and Turl, C. W.** (1990). Echolocation characteristics and range detection threshold of a False Killer Whale (*Pseudorca crassidens*). In *Sensory Abilities of Cetaceans* (ed. J. Thomas and R. Kastelein), pp. 321-333. New York: De Spil Publishers.
- Turl, C. W. and Penner, R. H.** (1989). Differences in echolocation click patterns of the beluga (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **86**, 497-502.
- Urlick, R. J.** (1983). *Principles of Underwater Sound*. Los Altos: Peninsula Publishing.
- Wahlberg, M., Møhl, B. and Madsen, P. T.** (2001). Estimating source position accuracy of a larger-aperture hydrophone array for bioacoustics. *J. Acoust. Soc. Am.* **109**, 397-406.
- Watkins, W. A.** (1980). Click sounds from animals at sea. In *Animal Sonar Systems* (ed. R. G. Busnel and J. F. Fish), pp. 291-298. New York: Plenum Press.
- Watkins, W. A. and Daher, M. A.** (1992). Underwater sound recording of animals. *Bioacoustics* **4**, 195-209.
- Watkins, W. A. and Schevill, W. E.** (1972). Sound source location by arrival-times on a non-rigid three-dimensional hydrophone array. *Deep-Sea Res.* **19**, 691-706.