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CLICK COMMUNICATION IN HARBOUR PORPOISES PHOCOENA PHOCOENA

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ABSTRACT

Sound plays an important role for toothed whales in foraging and communication. However, little is known about acoustic communication in the toothed whale species that only produce narrow band high frequency (NBHF) clicks, such as the harbour porpoise Phocoena phocoena. To study acoustic behaviour and to quantify the source parameters of porpoise communication signals, the acoustic and swimming behaviour of three adults and one calf were recorded using an array of hydrophones, acoustic tags and an overhead video camera. We tested the hypothesis that different behavioural interactions between porpoises involve specific click patterns for communication and measured the source characteristics of these click patterns to estimate the active space of porpoise click communication. Our results provide strong evidence that porpoises communicate acoustically using specific patterns of clicks with source properties comparable to normal echolocation clicks, and that they employ stereotyped aggressive click patterns, exposing conspecifics to received levels of up to 180 dB re 1 µPa (pp). The measured source properties render estimated active spaces of less than 1000 meters for porpoises' communication sounds. Compared to other cetaceans, porpoises must therefore remain much closer to be able to communicate acoustically.

Keywords: harbour porpoise, Phocoena phocoena, click communication, mother-calf pair, active space

INTRODUCTION

Marine mammals are adapted to the aquatic environment where light attenuates rapidly, but sound propagates well over long distances. Active and passive use of sound therefore plays an important

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role for cetaceans in foraging, predator avoidance, navigation and communication (Au 1993; Tyack & Clark 2000; Morisaka & Connor 2007). The ranges over which communication calls can be heard or the ranges at which prey targets can be echolocated are affected by the source properties of the emitted signals, the sensitivity of the receiver's auditory system, the ambient noise levels, and sound propagation in the habitat of the vocalising animal (Bradbury & Vehrencamp 1998).

Higher frequencies suffer more from absorption than lower frequencies do (Urick 1983) and will be more directional than low frequency sounds for the same transmitting aperture of the sound source. The sound beam of echolocation clicks from toothed whales is made directional in part by using high frequencies, resulting in signals of much higher on-axis source level (SL) that generate lower clutter levels compared to signals of the same power at lower frequencies. High frequency sounds of high directionality are necessary for sonar, whereas sounds of lower frequency content, and hence lower directionality, ensonify greater volumes of water and seem more useful for communication if the aim is to maximize active space (Tyack 1998).

Within these physical constraints and options, cetaceans have evolved the use of a broad variety of sounds for communication in forms of whistles (Ford 1989), pulsed calls (e.g. Payne & Webb 1971; Ford 1989), and repetitive patterns of clicks in the form of codas (Watkins & Schevill 1977). Whistles are generally of comparatively lower frequency and, hence, have low absorption and broad radiation patterns generating large active spaces (Janik 2000; Miller 2006). Echolocation clicks, on the other hand, are powerful directional signals, normally of high frequency (Au 1993), which in general have much smaller detection ranges for passive monitoring (Hansen *et al.* 2008).

Accordingly, many echolocating toothed whales produce dedicated signals with different source properties suited for communication and echolocation. For example, most dolphins produce lower frequency whistles of low directionality and/or pulsed calls for communication (e.g. Caldwell & Caldwell 1965 & 1968; Tyack 1986; Sayigh *et al.* 1990) and broadband, high frequency echolocation clicks of high directionality for navigation and foraging (Au 1993). Sperm whales, which only produce clicks, have dedicated click types with different source properties for echolocation and communication (Madsen *et al.* 2002 a,b).

However, the Phocoenidae family (Hatakeyama & Soeda 1990; Au et al. 1999, Jefferson et al. 2008), the dolphin genus Cephalorhynchus (Dawson 1988), the Hourglass Dolphin Lagenorhynchus cruciger (Kyhn et al. 2009) and the Pygmy Sperm Whale Kogia breviceps (Madsen et al. 2005) apparently only produce narrowband, high frequency clicks (NBHF). These NBHF signals have comparable durations around 100 µsec, high directionality, centre frequencies around 130 kHz, and source levels generally well below 200 dB re 1 µPa (Au 1993; Madsen *et al.* 2005; Villadsgaard *et al.* 2007; Kyhn *et al.* 2009).

These source properties render NBHF clicks unsuited for longrange communication, and it has been proposed that observed low frequency components in the NBHF clicks could serve the purpose of communication rather than the main sound pulse at around 130 kHz (Dubrovskii et al. 1971; Møhl & Andersen 1973; Verboom & Kastelein 1995). Recent experiments have shown that the low frequency component of NBHF clicks is so weak that it is unlikely to play a communicative role (Hansen et al. 2008). Thus, any acoustic communication by porpoises is apparently only mediated by stereotyped NBHF clicks with source properties suited for echolocation and little room for information encoding. Nevertheless, harbour porpoise do seem to make use of acoustic communication during social interactions (Nakamura et al. 1998, Amundin 1991), and it can be surmised that acoustic communication is of importance for mating and during mothercalf interactions as it is for many or all other odontocetes (e.g. Tyack 1998). That then begs the question of how porpoises communicate with these apparently stereotyped NBHF clicks with a small active space and little basis for information transfer.

In one of the very few studies attempting to address this problem, it was shown that Hector's Dolphins *Cephalorhynchus hectori* may convey information via the repetition rate patterns of their NBHF clicks, at least during aggressive behaviour where more high repetition rate click trains appear (Dawson 1991). Similar observations were made on harbour porpoises by Nakamura *et al.* (1998), who also noted that aggressive interactions were accompanied by high-repetitive click trains. In an unpublished thesis, Amundin (1991) defined stereotyped time-repetition-rate patterns of clicks and linked them to different behavioural interactions between animals, indicating that porpoises may use their echolocation clicks for communication by modulating the click repetition rates.

Here we test the hypothesis that different behavioural interactions between porpoises involve specific click repetition rate patterns as would be expected for a communication function of such signals. We measure the source characteristics of these click patterns and discuss implications for the active space of porpoise click communication.

MATERIALS AND METHODS

Animals

The acoustic and swimming behaviours of a female calf and three

adult harbour porpoises *Phocoena phocoena* (two females and one male) were recorded at the Fjord and Baelt, Denmark.

During experiments, the calf's age ranged from three to nine months and all adults were at least four years old. Experimental observations of acoustic and swimming behaviour were made in three settings: 1) interactions of a mother-calf pair; 2) aggressive interactions between a male porpoise and the mother-calf pair during the first four introductions of the male; and 3) aggressive behaviour of a female and male porpoise during food competition. In the first two experiments the sound recordings were obtained with a hydrophone array and filmed with overhead and underwater video cameras, and in the third study we used acoustic recording tags (Johnson & Tyack 2003; DeRuiter *et al.* 2009.) on the animals to measure the sound exposures of conspecifics during aggressive interactions.

Recording gear

The hydrophone arrays consisted of three or four calibrated Reson 4014 hydrophones with measured sensitivities of -187 dB re $1V/\mu$ Pa at 130 kHz. The signals were amplified by 40 dB by a custom built amplifier and filtered with a highpass filter at 1 kHz (1st order) and a lowpass filter at 150 kHz (4th order). The signals were digitised by two analogue to digital converters (National Instruments, USB-6251). Using a custom made program (written in Labviewtm 8.2), each channel was sampled continuously at 500 kHz (16 bits) and data was saved on a disk. The behaviour was recorded on video camera; a security-center-TV7043, 24 frames per second set at analogue TV was used during mother-calf interactions, an underwater camera (Profiline CTV7040) during isolation of the calf, and a Sony DCR-VX1000 during the introduction of the male. For synchronisation, a porpoise echolocation click detector (dual channel, 100 to 160 kHz, envelope detector) relayed acoustic data to the video camera via a video signal digitiser (Terratec, Grabster AV 400). The sound and behaviour recordings were subsequently acoustically synchronised off line to link the swimming and acoustic behaviour of the porpoises.

To relate any given behaviour to the sounds produced, we cut the videos into small clips (using honestech Easy Video Editor 2.0) to ensure that only the sound produced during the specific behaviour was analysed and that there was no interference with sound produced during different behaviours. Events were defined as a given behaviour only in cases where the specific behaviour was observed without interruption. Only sequences with the well-defined behaviours depicted in Figure 1 were included in the analysis.

The source locations of the clicks were determined by localising the porpoise using time of arrival differences (TOADS) (implemented in Matlab, *MathWorks Inc*, 6.1 according to equations in Madsen & Wahlberg (2007)), and by comparing the acoustic locations with visual locations derived from the video recordings. Clicks localised to positions outside the study pen were not analysed. The clicks were visually inspected to ensure that reflections were not analysed as direct path clicks. Further, we required that the full signal should be audible (when down-sampled 16 times) and have an amplitude at least 1dB below the clipping level of the recording chain to ensure that the recording was not overloaded.

Clicks produced during bottom grubbing could not be analysed as direct path clicks and were therefore not analysed. Clicks were only selected when the signal-to-noise ratio (SNR), given by the ratio between the rms power of the signal of interest and the ambient noise level measured in the same frequency band as the signal, was at least 10 dB. Also, the first and last clicks in a click train were identified if possible, to include as much of the entire click train as possible in the analysis. Due to the directionality, some click trains



Figure 1. Behavioural categories. Aggressive behaviour (A) is characterised by a sudden change in a porpoise's position accompanied by emission of a directed buzz toward another porpoise, which immediately and rapidly swims away ('sideward turn thread call', sensu Amundin 1991). Approach (B) is defined as two porpoises swimming towards each other. Contact calling (C) is defined by the calf being physically separated from the mother and clicking toward her. The calf was in one pen, the mother in another. Echelon (D) is when the calf is continuously swimming underneath her mother near the tail ('infant position', sensu Gubbins *et al.* 1999). During grooming (E) two or more porpoises are swimming closely together in the same direction with constant body contact; rubbing each other, twisting and turning ('echelon position', sensu Gubbins *et al.* 1999). Bottom grubbing (F) is when the mother (in this case) is searching for food near the bottom and the calf is swimming around nearby.

may have been incompletely sampled at the beginning or the end of a behavioural sequence.

Experiments

Mother and calf interactions

A) To test whether mother and calf porpoises might communicate through acoustic signalling, we logged and analysed the clicks produced by the mother and the calf during defined social interactions consisting of aggressive display, approach, echelon, grooming and contact calling (Figure 1).

To reduce observer influence on the porpoises' behaviour, the recordings were made during late afternoons and evenings (at which time there were no persons near the pen), and the hydrophone array was placed in the pen at least one and a half hours prior to recordings to reduce the porpoises' interest in the array. The sounds during normal interactions were recorded in a nursing net pen (8 \times 13m, 104m²) using a horizontal linear array (Perspex pipe) of four calibrated Reson 4014 hydrophones placed 1 metre apart, deployed 1 metre below the water surface along one of the shorter sides of the pen. The short sides of the pen were both limited by concrete walls, and the array was placed more than 1.5 m away from the wall to avoid interference from reflections from the wall. The long side of the pen consisted of nets connecting to the harbour on one side and to an additional porpoise pen on the other side. The behaviour and sounds produced during mother-calf interactions were documented in ten hours of recordings made over eight days during the period from October 2007 to February 2008.

B) Contact calls of isolated calf

To study possible contact calls, we separated the mother from the calf (Sayigh *et al.* 1999). The three adults were in a larger net-pen (270 m²) and the calf stayed in the adjacent nursing pen. The net walls of the pens allowed acoustic contact between mother and calf during separation. Sounds were recorded using a horizontal linear array of three or four calibrated Reson 4034 hydrophones placed 1 metre below the water surface in the larger pen. Recordings were also made with a star shaped array (Au 2004) consisting of four Reson 4014 hydrophones spaced 0.55 m apart, held from a pole in the smaller pen. For both array systems, a custom-built amplifier was used with the same digitising system outlined in section A.

Introduction of male porpoise

The acoustic and swimming behaviour of a harbour porpoise mother-

calf pair and an introduced adult male were recorded during the first introductions of the male. This was done to test how acoustic communication may be used during initial encounters between conspecifics. In January, 2008, three hours of observations and recordings of aggressive interactions between the introduced male porpoise and the mother-calf pair were conducted.

Interaction between female and male porpoise

The acoustic and swimming behaviour of a female and male harbour porpoise were recorded in the larger pen to test how acoustic communication may be used during food competition between conspecifics. The acoustic behaviour was recorded using two porpoise tags (modified version of the DTAG, Johnson & Tyack 2003), one on each animal. The behaviour of the animals was recorded with a handheld video camera (Sony DCR-VX1000) and an underwater camera (Profiline CTV7040). The tag data was sampled in stereo at a rate of 400 kHz per channel at 16-bit resolution and stored in onboard memory (3 GB) (see DeRuiter *et al.* 2009; Johnson & Tyack 2003 for tag details).

The tags were attached to the porpoises non-invasively with custom-made suction cups. They were placed on both animals immediately behind the blowhole, and the animals were allowed to swim around freely for 10-15 minutes. Fish were then thrown into the pen, and behaviour during the feeding interactions of the porpoises was recorded. A total of 65 minutes of data from the aggressive interactions between the female and male porpoises have been analysed.

Acoustic analysis

Prior to analysis, the sound files were filtered with a high-pass digital Butterworth filter (4th order, 100 kHz –3dB cut off frequency). Repetition rates were measured for the selected click trains in all experiments and the duration of click trains for each behavioural category was logged along with the duration of the class of behaviour. Click repetition rates were either measured using an automated click detection algorithm made in Matlab or, for long ICI click trains, by computing the pulse repetition spectrum (Watkins 1967). To reduce the interference of surface reflections in the repetition rate analysis single apparently high repetition rates of a single click was left out. Each of these events was examined to ensure that it was a reflection and not a click. This method can be further verified since it is known that a click interval depends on the previous click. The latter analysis was verified using artificial click trains of known repetition rate and carried out on the recorded data using the following steps: Click envelopes were calculated using the analytical signal. Subsequently the sequence was lowpass-filtered at 10 kHz and resampled by a factor of 16 to increase the speed of analysis. Spectrograms of the envelopes were generated with a 65536 point FFT on 512 sample (16 ms) long Hann-weighted windows with an 80% overlap (Figure 2). The time frequency contour of the fundamental, which corresponds to the repetition rate as a function of time, was then tracked using Matlab's "ginput" function.

The source level, estimated received level at the exposed animal (using the estimated source level and the range between the two animals), source energy flux density, click duration, peak and centroid frequency, and bandwidth (-10 dB, -3 dB and rms) were derived for the interactions between the mother and the calf. The source level (SL) can be calculated from the sonar equation (Au 1993) as the sum of the received level (RL) and the transmission loss (TL) when the clicks are recorded on the acoustic axis (Madsen & Wahlberg 2007). The energy flux density of a click was estimated by



Figure 2 Spectral analysis of the inter click intervals in a high repetition rate click train. A) The time series of a click train. B) Pulse repetition spectrum. Spectrogram (FFT size: 65536, window: 512, overlap 80%) of the normalised click train of A. The pulse repetition rate is given by the frequency in kHz between the harmonics appearing in the spectrogram (Watkins 1967).

subtracting 52 dB from the apparent peak-peak source level, using the conversion factor established by previous investigators (Kastelein *et al.* 1999a). Maximum received level (peak-peak) and sound expose level (SEL) were estimated for the interaction between the female and male porpoise. SEL is used as a measure of overall acoustic exposure and was calculated as the cumulative energy flux density for every click train to which the tagged animal was exposed to. SEL is thus given by the integrated click energy of the exposure period (Madsen 2005; Madsen *et al.* 2006).

Statistical analysis

The statistical analyses were all performed in Matlab 6.5.1 (MathWorks Inc). Due to our low sample size and non-normally distributed data, we used a Kruskal-Wallis test (Kruskal & Wallis 1952) to test whether there was a difference between the maximum, mean and median repetition rates of the click trains for each of the different behaviours. A multiple comparisons test (Dwass 1960) was used on the Kruskal-Wallis test output to determine whether click repetition rates produced during different behavioural events were different and whether maximum, mean or median click repetition rates could characterise a specific behaviour. A probability level (p) of 0.05 was used as the limit for statistical significance in all tests.

RESULTS

Mother and calf interactions

We conducted ten hours of acoustical and behavioural recordings during the mother-calf observations. Out of these it was possible to fully analyse seven events of each behavioural type (aggressive, approach, contact calling, echelon and grooming). The sound parameters of the most powerful click during each event were estimated and are reported in Table 1. The clicks produced had source parameters similar to those of normal porpoise echolocation clicks. We estimate that during aggressive interactions, the mother porpoise exposed the calf to received levels of up to 178 dB re 1 µPa pp (mean 163 ± 9.8 dB re 1 µPa pp).

Repetition rate pattern of click communication during mother and calf interactions

Repetition rates of the clicks emitted by the porpoises during the

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Behaviour	Aggressive $(n = 7)$	Approach $(n = 7)$	Contact calls $(n = 7)$	Echelon (n = 7)	$\begin{array}{c} Grooming\\ (n = 7) \end{array}$
SL (dB re 1µPapp)	155 (143-164)	160 (149–171)	169 (160–174)	170 (165–176)	168 (156–177)
SL energy (dB re μPa^2*sec)	103 (91 - 112)	108 (97–119)	117 (108–122)	118 (113–124)	116 (104–125)
Duration of click train (sec)	$1.3 \ (0.4 - 2.3)$	3.5 (0.6-6.4)	0.6 (0.3 - 0.8)	3.4(2.0-9.0)	$11.8 \ (5.2 - 16.0)$
Duration of click (µsec) DL	70 (40–110)	$62 \ (42-82)$	56 (42 - 90)	72 (52–82)	64 (50-72)
геак frequency (kHz)	127 (119–141)	$135 \ (122 - 147)$	129 (121 - 137)	$123 \ (121 - 130)$	125 (121–142)
Centrola frequency (kHz)	129 (125 - 134)	131 (127–143)	136 (134 - 143)	$129 \ (126-134)$	$129 \ (128 - 136)$
${ m bW}_{-10}$ dB (kHz)	25 (16 - 34)	27 (17 - 35)	$33 \ (25-39)$	$25 (17{-}27)$	27 (17–28)
${ m DW}_{-3}^{-3} { m dB}$ (kHz)	6 (4-27)	$19 \ (7-21)$	16 (5-28)	9 (5-20)	11 (6–20)
D W _{rms} (kHz)	11 (10 - 12)	10 (8–12)	18 (15-32)	8 (8–9)	9 (8–10)

defined behaviours were calculated. The click repetition rates from seven events of each behavioural category are shown in Figure 3. The repetition rates of the click trains (maximum, mean and median) emitted during the different behaviours differ significantly (Kruskal-Wallis, p < 0.05, d.f. = 4).

Aggressive behaviour and contact calls are characterised by upsweeping, high repetition rate click trains, differing in their maximum and minimum repetition rates (Figure 3A & C). During aggressive behaviour the overall minimum repetition rate of all events was around 200 clicks/s and the maximum of all events was approximately 1000 clicks/s (Figure 3A). The aggressive events were sometimes made up of one click train and other times consisted of three to four click trains. These were all emitted by the mother towards the calf at ranges of less than 1.5 meters. The mother would suddenly turn towards the calf to emit the high repetition rate click train, often performing a rapid scanning movement of her head. The calf always swam away rapidly after receiving this directed high repetition rate click train.

The maximum repetition rate during aggressive behaviour was significantly different from approach, echelon and grooming behaviour, whereas the mean repetition rates of aggressive behaviour could be distinguished from mean repetition rates of echelon and grooming behaviour (multiple comparison tests).

The overall minimum repetition rate during contact calls was some 20 clicks/s and the maximum repetition rate was approximately 800 clicks/s (Figure 3C). The contact calls are generally characterised by a low repetition rate followed by a sudden steep increase (Figure 3C). The maximum and mean repetition rates during contact calling were significantly different from echelon behaviour (multiple comparison test). All contact calls were produced by the calf and emitted in the direction of her mother and the two other adults in the other pool. During contact calls the calf was observed to perform a rapid vertical scanning movement of the head while emitting the call.

The aggressive and contact call events are generally of a shorter duration than the approach, echelon and grooming events (Table 1), and the median repetition rate of aggressive and contact calling were both significantly different from echelon and grooming behaviour, whereas approach behaviour could not be said to be different from the other behaviours (multiple comparison tests).

During approach behaviour the clicks were most often emitted by the calf, though the third and the last events were emitted by the mother. The click repetition rate varied considerably during approach behaviour (Figure 3B). Some of the click trains appeared to be normal echolocation click trains whereas others have both an up-sweep and down-sweep in repetition rate. However, the click rate never exceeded 650 clicks/s for those signals (Figure 3B).



Figure 3. Click repetition rate patterns for seven acoustic events of each behaviour. For more explanations see text.

The acoustic behaviour during echelon swimming was characterised by very low repetition rate click trains similar to normal echolocation click trains and never exceeding 100 clicks/s (Figure 3D). As the mother-calf pair was swimming very close (the calf underneath the tail of the mother) their sound would come from the same direction. However, the video recordings enabled us to determine which animal was emitting the clicks. At times, they pointed their heads in different directions, enabling us to identify the source by comparing relative click levels on the array hydrophones.

The grooming behaviour was also characterised by very low repetition rate click trains similar to normal echolocation click trains. However, in three of the seven events there were some (between one and three) incidences of up-sweeping, high repetition rate click trains between the low repetition rate click trains (Figure 3E). The duration of the grooming event and the duration of the click trains during the event were generally much longer than the click trains emitted during the other behaviours recorded (Table 1). In all the grooming events analysed, the mother emitted the clicks. The maximum click repetition rates during the up-sweeps were between about 700 and 800 clicks/s, whereas the other click trains never exceeded 100 clicks/s (Figure 3E).

Distribution of repetition rates during mother and calf interactions

Histograms of the click repetition rates for each behavioural category (including all clicks of all acoustic events of that behaviour) show that the distribution of clicks among repetition-rate bins varied between the different behaviours (Figure 4). Only high repetition rates were found during aggressive behaviour, where 25% of all clicks were emitted with a repetition rate of some 900 clicks/s. During approach, approximately 30% of all clicks were produced with a repetition rate of 100 clicks/s or less, but there was also a peak around 400 clicks/s. Contact call repetition rates were dispersed over a broad range with emphases around 50 clicks/s and between 450–700 clicks/s. Almost all clicks produced during echelon behaviour were produced at less than 100 clicks/s, with repetition rates below 50 clicks/s accounting for almost 90% of clicks. Grooming repetition rates are dispersed over a broad range, with the most pronounced peak at 0–100 clicks/s and minor peaks of about 10% at 400–450 and 650–750 clicks/s.

Introduction of male porpoise

The aggressive behaviour between an introduced male porpoise and



Figure 4. The distribution of click repetition rates during the different behaviours. The y-axis varies in order to increase the readability of the histograms; aggressive, approach and contact calls have the same y-axis, while echelon and grooming have different scales.

the mother-calf pair was recorded. During one hour of acoustic and behavioural recordings, we identified six aggressive events that met our acoustic and behavioural criteria. The calf often followed the introduced male porpoise, more so than the mother did. On three occasions the male emitted aggressive click train patterns towards the calf, and on three occasions the mother emitted a directed aggressive click train pattern at the male porpoise. The 'aggressive' porpoise would suddenly turn towards the subject of aggression (either the calf or the male) and emit a high repetition rate click pulse often while performing a rapid scanning movement of its head. The receiving porpoise always fled after receiving this directed high repetition rate click pattern. The duration of the click trains was short, between 0.3 and 3 seconds, and similar to the duration of the aggressive high repetition rate click pulses during the mother-calf interaction study (Table 1). The aggressive behaviour during the introduction of the male was also characterised by up-sweeping, high repetition rate click trains (Figure 5).

The first three events in Figure 5 were emitted by the mother towards the male porpoise (\bigcirc) and the last three events were aggressive high repetition rate clicks pulses emitted by the male towards the calf (\circlearrowleft) (Table 2). The aggressive sequences were sometimes made up of one click train and other times consisted of up to three click trains.

The maximum repetition rates of clicks emitted during aggressive behaviour were similar between the study of the mother-calf interaction and the introduction of the male (Figure 3 & 5) (ranging between about 670 to 1000 clicks/s and 750 to 1100 respectively).

Interactions between female and male porpoises studied with acoustic tags

We analysed 65 min of acoustic data recorded during interactions of a male and a female porpoise, both tagged with modified DTAGs. We found eight aggressive events that met our acoustic criteria: seven received by the female and one received by the male (Figure 6).

The aggressive behaviour was characterised by up-sweeping, high repetition rate click trains. During aggressive behaviour the overall minimum repetition rate of all events was 150 and the maximum was 1100 clicks/s. The aggressive events were sometimes made up of one click train and other times consisted of up to four click trains; on one occasion the event consisted of 11 click trains.

During the aggressive interactions the tagged porpoises were exposed to received levels of up to 180 dB re 1 μ Pa pp (mean 166 dB re 1 μ Pa pp). The total sound exposure level of the click trains ranged from 114 to 148 dB re 1 μ Pa²s (mean 131 dB re 1 μ Pa²s) (Figure 7).

DISCUSSION

Communication can be defined as a process where the behaviour of one individual affects the behaviour of another (Altmann 1967). Given that porpoises emit narrowband high frequency (NBHF) clicks highly suited for echolocation, the question is whether porpoises also are

TABLE 2

The overall range of minimum, maximum, mean and median repetition rates values are shown for aggressive behaviour of the male porpoise towards the calf and aggressive behaviour of the mother towards the male.

Aggressive behaviour	Minimum	Maximum	Mean	Median
	repetition	repetition	repetition	repetition
	rate	rate	rate	rate
	(clicks per	(clicks per	(clicks per	(clicks per
	second)	second)	second)	second)
Male towards calf	150-500	900-1100	$\begin{array}{c} 675\\728\end{array}$	743
Mother towards male	100-630	750-1050		825



Figure 5. Click repetition rate patterns during aggressive interactions between the introduced male porpoise and the mother-calfpair. The three first events show the repetition rate click pattern when the mother emitted aggressive buzzes towards the male (\mathfrak{P}) and the three last events (separated by the dotted line) are aggressive buzzes emitted by the male porpoise towards the calf (\mathcal{J}) .



Figure 6. Click repetition rate patterns during aggressive interactions between a female and male porpoise while feed-ing. The first seven events show the aggressive click repetition rate pattern received by the female (\mathfrak{P}) and the last event (separated by the dotted line) was received by the male (\mathfrak{I}).



Figure 7. A) An example of an aggressive buzz during competition for a fish. B) Cumulative sound exposure level experienced by the exposed porpoise during the buzz in A.

able to use these NBHF clicks for communication, and if so, what the implications are for information encoding and active space.

To our knowledge Amundin (1991) and Nakamura *et al.* (1998) have provided the only previous accounts on acoustic communication in porpoises. Of the two, Amundin (1991) is the more detailed. He defined acoustic communication signals by their repetition rate patterns. Amundin's studies were preliminary and focused primarily on the alleged low frequency components of porpoise clicks (Verboom & Kastelein 1995). These low frequency click components are very weak (or artefacts from the use of analogue tape recorders) and have recently been shown to have little if any relevance to porpoises communication (Hansen *et al.* 2008). However, as they are emitted/ recorded concomitantly with the high frequency component of the clicks, they probably still reflect click patterns associated with specific behaviours.

There are some physical limitations to the use of high frequency clicks for communication: 1) they suffer from high absorption and the active space will hence be small, 2) high frequency toothed whale sounds are inherently directional, so the receiver and the emitter must be close or face each other to successfully communicate acoustically, and 3) the stereotypy of NBHF clicks leaves little room for encoding information within a single signal, compared to frequency modulated whistles. Here we studied the click production of a) a mother and her calf in different behavioural contexts, b) during the first introductions of a male porpoise, and c) a male and a female porpoise during aggressive behaviour related to foraging. With the inherent limitations of studying a few animals in captivity in mind we find that harbour porpoises do use specific click patterns that can be linked to broad behaviour categories, strongly suggesting that porpoises do communicate with narrowband high frequency clicks (Figure 3 & 4) as inferred by Amundin (1991). Analyses of the source parameters show that the clicks produced in specific click patterns linked to specific behaviours are identical to the NBHF click used by porpoises during echolocation (Table 1), and our results thus strongly indicate that porpoises indeed use NBHF echolocation clicks for acoustic communication.

Context specific click repetition rate patterns

We found that a porpoise mother and calf produce different click patterns during specific behaviours. The click repetition rates of approach, echelon and grooming behaviour were similar to normal echolocation clicking activity (Figure 3) with generally low repetition rate click train patterns (Teilmann et al. 2002; Verfuß et al. 2005; Villadsgaard et al. 2007). The click repetition rate pattern during aggressive behaviour was similar to the repetition rate pattern of low frequency sounds recorded by Amundin (1991) in what he coined a "sideward turn threat call". The maximum repetition rates of clicks during aggressive behaviour are much higher than the click repetition rates recorded during feeding buzzes (e.g. DeRuiter et al. 2009). The third event of aggressive behaviour and the contact calls have similar appearances. They were, however, produced during two different behavioural categories by two different animals. Both aggressive and contact calling click trains were produced in absence of fish and during well-defined behaviours, and are therefore not echolocation buzzes.

The maximum repetition rates of click trains during approach behaviour were found to be statistically different from the aggressive maximum repetition rate but not different from the other behaviours. Occasional up-sweeps and down-sweeps in repetition rate of the click trains might have affected the statistical tests in such way that approach behaviour could not be statistical discriminated from the other behaviours.

The click train patterns within approach behaviour look quite different from one another, which might be expected since approach is not as stereotyped a behaviour as the others. The click trains emitted by the mother seem to be as variable as the click trains emitted by the calf. However, the sample size is too small to test whether there is an individual difference or a behaviour-related difference in the repetition rate click pattern during approach. While our tests were not able to distinguish all the behaviours on the basis of their distribution of click repetition rates (Figure 4) and their repetition rate development, we do show that at least aggressive behaviour, contact calling, echelon behaviour, and to some extent grooming can be defined by behaviour-specific repetition rate patterns. The repetition rate pattern of one of the high frequency distress calls (#12) of a young male porpoise recorded by Amundin (1991) looks similar to one of our contact call recordings. The distress call had a rapid, steady increase in repetition rate from 271 to 468 clicks/s, where our contact call had a repetition rate from about 240 to 640 clicks/s (Figure 3); both calls lasted about 100 msec. The distress call reported by Amundin (1991) may thus have been what we call a contact call.

Overall, the link between specific click patterns and behavioural categories for the four animals studied strongly suggest that repetition rates are used to encode information for porpoises to communicate acoustically. We analysed individual clicks from the mother and the calf and there was no indication that porpoises produce individual signature clicks. Hence, the information in their signals seems to be encoded within the click rate pattern rather than within the individual click structure. There may also be individual click train differences; however, our sample size is too low to test this assertion. Further there might be differences in the way that captive and wild porpoises communicate regarding to source levels and the repetition rate pattern. However, as the signature whistles of bottlenose dolphins during voluntary separations (Smolker et al. 1993) and involuntary separations in the wild (Sayigh et al. 1990) and during captivity (Caldwell et al. 1990) are very stereotype, these differences in wild- and captive porpoise communication are most likely minor. In future studies the compelling evidence mustered here for information encoding in click repetition rate patterns should be confirmed with playback experiments on both captive and wild animals, where both the exposure and behaviour should be logged concomitantly.

Aggressive stereotyped click repetition rate pattern

The aggressive behaviour we observed was similar to the 'sideward turn threat call' defined by Amundin (1991), where the porpoise emits a high repetition rate click pulse while performing a rapid scanning movement of its head. The repetition rate patterns during these aggressive behaviours are characterised by up-sweeping, high repetition rate click trains which are also characteristic of aggressive behaviour in Hector's Dolphins (Dawson 1991).

The repetition rate patterns during aggressive behaviour were similar across different individuals in three different aggressive

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contexts (the mother-calf interactions, the introduction of the male porpoise and the female-male aggressive behaviour during competition for fish). The maximum and minimum repetition rates were also similar to what we have observed during all aggressive behaviours (figure 3A, 5 & 6).

We found that during these aggressive interactions, the porpoises expose each other to very high received levels (up to 180 dB re 1 μ Pa pp) that seem to be very uncomfortable for the exposed animals, which always move away. The aggressive signals may thus serve as acoustic weapons akin to the burst pulses of bottlenose dolphins (Blomqvist & Amundin 2004).

Active space

We have now found strong indications that porpoises do use specific patterns of echolocation clicks to communicate acoustically, but have not addressed the ranges at which they may be able to hear each other. To do so, we must estimate the active space determining 1) the maximum separation at which animals can maintain acoustic contact and 2) the space where other animals can intercept the signal or eavesdrop on an interaction (Janik 2000). When estimating this range, both the porpoises' highly directional click production and their directional hearing sensitivity must be considered. If a form factor of 11 dB (Au et al. 1999) and the length of a porpoise click (~100µs) is taken into account, the energy flux density of a click can be estimated by subtracting 51 dB from the SL (peak-peak). The onaxis received echo level detection threshold for a porpoise has been found to be 44 dB re 1 μ Pa²s (Kastelein *et al.* 1999b). So overall the receiver's threshold for detecting a NBHF click would in this case be about 95 dB re 1 µPa (peak-peak). The maximum active space of a porpoise click is attained when the clicking and listening porpoises are facing each other and, according to the passive sonar equation, the transmission loss equals the difference between the click source level (peak-peak) and the detection threshold. In porpoise habitats, on average, NBHF clicks propagate following the inverse square law plus absorption (Villadsgaard et al. 2007; DeRuiter et al. in press). Using this model, active space can be estimated from: $TL = 20\log(r) + 1$ αr , r being the estimated range in meters and α being the frequency dependent absorption at 130 kHz at 15 degrees Celsius.

We estimated the active space for the measured source parameters of click patterns produced during the different behaviours (Table 1). As porpoises emit highly directional clicks and have directional hearing, both the maximum and the minimum active space (on the transmitting and receiving axes and off the transmitting and receiving axes, respectively) were estimated. The maximum detection range is when the two porpoises face each other. The receiving directionality index (DI) of a porpoise click has been estimated to be 11.7 dB at 100 kHz (Kastelein *et al.* 2005).The apparent source level (ASL) of the emitted click is greatest forward of the animal, where ASL=SL, and decreases dramatically towards the posterior part of the porpoise. The ASL measured at an angle of about 135° from on-axis is 44 dB lower than SL (Hansen *et al.* 2008) and is used here as a proxy for the ASL when the clicking animal is pointing away from the receiver. To estimate the shortest range at which a porpoise click can be detected, the receiving DI was added to the detection threshold for the receiver and a further 44 dB was subtracted from the SL (peak-peak) of the clicking animal to estimate the TL and hence the active space when the animals point away from each other (Hansen *et al.* 2008).

We found that the active space differs according to the click parameters of a given behaviour and the orientation of the porpoises (Figure 8). We estimated that there is up to approximately 500 meters difference in the range between both porpoises being on or off axis due to their directional transmitting and receiving systems. These large variations in the calculated active spaces within the different behaviours could to some extent be explained by some clicks being recorded more on axis then others underestimating the source levels. The active space of aggressive behaviour and approach is smaller (minimum ranges of some 1.5-4 m to maximum ranges of some 250-320 m) than the others (minimum ranges of some 7-11 m to maximum ranges of some 440-530 m). This may reflect the fact that aggressive and approach acoustic behaviours are directed to porpoises nearby, whereas contact calls may need to function over greater ranges to facilitate reunions of separated mothers and calves. In fact, the calf emitted the contact calls while moving its head in a rapid scanning motion, further increasing the calls' active space. The active space during echelon behaviour was large, which may be a byproduct of navigation and prey detection if the porpoises do in fact just echolocate when swimming in echelon.

Tursiops mother-calf pairs' separation distances are consistently smaller than the estimated active spaces of their whistles (Quintana-Rizzo *et al.* 2006). If the same is the case for porpoises, it can be inferred from Figure 8 that a mother-calf pair should stay within about 10 meters of each other to ensure acoustic contact. Separation beyond this range would significantly reduce the chance of detecting each other and hence potentially compromise calf survival during the year of nursing (Lockyer 2003).

If wild harbour porpoises produce communication signals of higher source levels than captive porpoises, as indicated for echolocation clicks (Villadsgaard *et al.* 2007), our estimated active spaces would be underestimated. Applying the same active space estimation method

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but assuming a maximum SL of 205 dB re 1µPa, porpoises in the wild (Villadsgaard *et al.* 2007) may detect each other's echolocation clicks at ranges of up to about 200 m if they were facing away from each other and 1200 m if they were facing each other.

When we compare the detection range for porpoises with that of e.g. bottlenose dolphins and killer whales, it becomes clear that there are significant differences in active space when communicating with NBHF clicks versus lower frequency whistles with comparable or lower peak pressures. We found the absolute maximum active space to be some 530 meters for click communication in porpoises, given the source properties measured here (extended to 1200 meters if using the highest reported SLs (Villadsgaard et al. 2007)), whereas Janik (2000) estimated the active space for Bottlenose Dolphins Tursiops truncatus to be between 1.5–25 km depending on whistle type and sea state. Quintana-Rizzo et al. (2006) estimated active spaces for different Tursiops whistle types in shallow water to be between 500 m and 20 km depending on whistle frequency and habitat. Miller (2006) estimated the active space for Killer Whales Orcinus orca calls to be between 5-9 km during social and resting behaviour and 10-16 km during travel and foraging behaviour. Active space estimation is prone to uncertainty, and apart from the source levels of the sounds other environmental factors such as ambient noise, temperature gradients,



Figure 8 The maximum and minimum active spaces (on and off transmitting and receiving axes) are shown. The estimated maximum range is for on-axis clicks and the estimated minimum range is for clicks in an off-axis aspect due to their highly directional clicks/sound production and hearing. Hence the active space differs according to the behaviour and the orientation of the porpoises.

obstacles in the sound path, seafloor properties and topography, water depth, sea state (ambient noise) and depth of the transmitting and receiving animal may affect sound transmission (DeRuiter *et al.* in press; Quintana-Rizzo *et al.* 2006). However, it is safe to conclude that the active space estimates for porpoises using NBHF clicks for communication are more than an order of magnitude smaller than normally estimated for whistling delphinids, and that porpoises will simply not be able to stay in acoustic contact at ranges beyond some 1000 meters.

The stereotyped NBHF clicks of porpoises, which may encode information only in the repetition rate, and their very limited active space, can lead to the impression that porpoises employ a very rudimentary communication system full of disadvantages. However, such a conclusion may be premature. First of all, porpoises are either solitary or found in relatively small groups, with a reduced need to identify group members from among a large number of candidates. Hence, they likely face a lower selective pressure for complex whistles with a large potential for signature information. Therefore, the need for information encoding can apparently be covered by changing the repetition rate of stereotyped NBHF clicks rather than using complex whistles with a larger potential for information encoding (Searby & Jouventin 2004). Secondly, the lack of whistling and sole use of weak, directional NBHF clicks may in fact be advantageous when trying to avoid predation and harassment. More specifically, the use of highly directional high frequency clicks rather than whistles for communication rather may be an adaptation to reduce the risk of acoustic detection by predators such as killer whales (Morisaka & Connor 2007). Marine mammal eating killer whales rely mainly on passive acoustic cues to find their prey (Barrett-Lennard et al. 1996), but their hearing sensitivity drops off rapidly above 100 kHz (Szymanski et al. 1999), and hence the 130 kHz clicks emitted by porpoises and other NBHF species could be an adaptation to avoid predators (Andersen & Amundin 1976; Madsen et al. 2005; Morisaka & Connor 2007). Furthermore, bottlenose dolphins may kill or harass porpoises (Patterson et al 1998), and while NBHF clicks are within the hearing range of young healthy dolphins, communication with low powered, directional NBHF clicks may reduce the risk of being detected significantly as found for other species using acoustic crypsis (e.g. Nakano et al. 2008; Tuttle & Ryan 1981).

CONCLUSION

The present data provide strong evidence to suggest that harbour porpoises communicate acoustically using narrowband high frequency clicks and that they convey information via repetition rate patterns of their clicks. Some click repetition rate patterns are linked to specific behaviours and it thus seems that acoustic recordings may have the potential to be used for identifying broadly defined behaviours of porpoises in the wild without using complimentary visual recordings. We have shown that the repetition rate patterns during aggressive behaviour are similar across different individuals in three different interactions between adults and a calf. The active space of NBHF click communication depends heavily on the orientation of the porpoises and their behaviour. Clicks produced during aggressive behaviour and approach have smaller active spaces than the others, which may reflect that these behaviours are directed to porpoises nearby, whereas the active space during contact calling is larger, likely to increase the range at which a mother would hear her calf. The active space during echelon behaviour was large, which may be a secondary consequence of the echolocating animal trying to facilitate navigation and prev detection. Overall, harbour porpoises have little room for signal encoding in their acoustic communication system, and they must stay in close contact to communicate acoustically which in turn may prove to increase fitness via reduced risks of detection by eavesdropping predators.

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REFERENCES

Altmann, S. A. (1967). The structure of primate social communication. In Social communication among primates (Ed. by S. A., Altmann), pp. 325-362 Chicago: University of Chicago Press.

- Amundin, M. (1991). Sound production in Odontocetes with emphasis on the harbour porpoise, (*Phocoena phocoena*). *Ph.D. dissertation*, University of Stockholm.
- Andersen, S. H. & Amundin, M. (1976). Possible predator-related adaption of sound production and hearing in the harbour porpoise (*Phocoena phocoena*). Aqua. Mam., 4, 56–57.
- Au, W. W. L. (Ed.) (1993). The Sonar of Dolphins. New York: Springer Verlag.
- Au, W. W. L. (2004). Echolocation Signals of Wild Dolphins. Acoust. Physics., 50, 454–462.
- Au, W. W. L., Kastelein, R. A., Rippe, T. & Schooneman, N. M. (1999). Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). J. Acoust. Soc. Am., **106**, 3699–3705.
- Barrett-Lennard, L. G., Ford, J. K. B. & Heise, K. A. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behav.*, 51, 553-665.
- Blomqvist, C. & Amundin, M. (2004). High-Frequency Burst-Pulse Sounds in Agonistic/ Aggressive Interactions in Bottlenose Dolphins, *Tursiops truncatus*. In *Echolocation* in Bats and Dolphins (Ed. by J. A. Thomas, C. Moss & M. Vater), pp. 425–431. Chicago: The University of Chicago Press.
- Bradbury, J. W. & Vehrencamp, S. L. (Eds.) (1998). *Principles of Animal Communication*. Sutherland: Sinauer Associates.
- Caldwell, M. C. & Caldwell, D. K. (1965). Individualized Whistle Contours in Bottlenosed Dolphins (*Tursiops truncatus*). Nature, 207, 434–435.
- Caldwell, M. C. & Caldwell, D. K. (1968). Vocalization of Naïve Dolphins in Small Groups. Science, New Series, 159, 1121–1123.
- Caldwell, M. C., Caldwell, D. K. & Tyack, P. L. (1990). Review of the signature-whistle hypothesis for the Atlantic Bottlenose Dolphin. In: The Bottlenose Dolphin (Ed. by S. Leatherwood & R. R. Reeves), pp. 199–234. New York: Academic Press.
- Dawson, S. M. (1988). The high-frequency sounds of Hector's dolphins Cephalorhynchus hectori. Rept. Int. Whal Commn. Spec. Issue, 9, 339–344.
- Dawson, S. M. (1991). Clicks and communication the behavioural and social contexts of Hector's dolphin vocalisations. *Ethology*, 88, 265–276.
- DeRuiter, S. L., Bahr, A., Blanchet, M.-A., Hansen, S. F., Kristensen, J. H., Madsen, P. T., Tyack, P. L., & Wahlberg, M. (2009). Acoustic behaviour of echolocating porpoises during prey capture. J. Exp. Biol., 212, 3100-3107.
- DeRuiter, S. L., Hansen, M., Koopman, H. N., Westgate, A. J., Tyack, P. L. & Madsen, P. T. (In press). Propagation of narrow-band-high-frequency clicks: Measured and modeled transmission loss of porpoise-like clicks in porpoise habitats. J. Acoust. Soc. Am.
- Dubrovskii, N. A., Krasnov, P. S. & Titov, A. A. (1971). On the emission of echolocation signals by the Azov sea harbor porpoise. *Soviet physics Acoust.*, 16, 444– 447.
- Dwass, M. (1960). Some k-sample rank-order tests. In Contributions to Probability and Statistics (Ed. by I. Olkin, S. G. Ghurye, H. Hoeffding, W. G. Madow & H. B. Mann), pp. 198–202. Stanford: University Press.
- Ford, J. K. B. (1989). Acoustic behaviour of *resident* killer whales (Orcinus orca) off Vancouver Island, British Columbia. Can. J. Zool., 67, 727–745.
- Gubbins, C., McCowan, B., Lynn, S. K., Hooper, S. & Reiss, D. (1999). Mother-infant spatial relations in captive bottlenose dolphins, *Tursiops truncatus. Mar. Mam. Sci.*, 15, 751–765.
- Hansen, M., Wahlberg, M. & Madsen, P. T. (2008). Low-frequency components in harbour porpoise (*Phocoena phocoena*) clicks: communication signal, by-product, or artifacts? Acoust. Soc. of Am, 124, 4059–4068.
- Hatakeyama, Y. & Soeda, H. (1990). Studies on echolocation of porpoises taken in salmon gillnet fisheries. *Sensory Abilities of Cetaceans* (Ed. by J. Thomas & R. Kastelein), pp. 269–281. New York; Plenum Press.

- Janik, V. M. (2000). Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. J. Comp. Physiol. A., 186, 673–680.
- Jefferson, T. A., Webber, M. A. & Pitman, R. L. (Eds.) (2008). Marine Mammals of the World: A Comprehensive Guide to their Identification. London: Academic Press.
- Johnson, M. P. & 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.
- Kastelein, R. A., Au., W. W. L., Rippe, H. T. & Schooneman, N. M. (1999a). Target detection by an echolocating harbor porpoise (*Phocoena phocoena*). J. Acoust. Soc. Am., 105, 2493–2498.
- Kastelein, R. A., Bunskoek, P., Hagedoorn, M., Au., W. W. L. & de Haan, D. (1999b). Audiogram of a harbor porpoise (*Phocoena phocoena*) measured with narrow-band frequency-modulated signals. J. Acoust. Soc. Am., **112**, 334–344.
- Kastelein, R. A., Janssen, M., Verboom, W. C. & de Haan, D. (2005). Receiving beam patterns in the horizontal plane of a harbor porpoise (*Phocoena phocoena*), J. Acoust. Soc. Am., 118, 1172–1179.
- Kruskal, W. H. & Wallis, A. (1952). Use of ranks in one-criterion variance analysis. J. Am. Stat. Ass., 47, 583–621.
- Kyhn, L. A., Tougaard, J., Jensen, F. H., Wahlberg, M., Stone, G., Yoshinaga, A., Beedholm, K. & Madsen, P. T. (2009). Feeding at a high pitch: Source parameters of narrow band, high frequency clicks from echolocating off-shore hourglass dolphins and coastal Hector's dolphins. J. Acoust. Soc. Am., 125, 1783–1791.
- Lockyer, C. (2003). Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Biological parameters. In *Harbour Porpoises in the North Atlantic*, vol. 5 (Ed. by T. Haug, G. Desportes, G. A. Vikingsson & L. Witting), pp. 71–89. North Atlantic Marine Mammal Commission Scientific Publications.
- Madsen, P. T., Wahlberg, M. & Møhl B. (2002a). Male sperm whale (*Physeter* macrocephalus) acoustics in a high-latitude habitat: implications for echolocation and communication. Behav. Ecol. Sociobiol., **53**, 31–41.
- Madsen, P. T., Payne, R., Kristiansen, N.U., Kerr, I., and Moehl, B. (2002b). Sperm whale sound production studied with ultrasound-time-depth-recording tags. J. Exp. Biol., 205, 1899–1906.
- Madsen, P. T. (2005). Marine mammals and noise: Problems with root mean square sound pressure levels for transients. J. Acoust. Soc. Am., 117, 3952–3957.
- Madsen, P. T., Carder, D. A., Beedholm, K. & Ridgway, S. H. (2005). Porpoise clicks from a sperm whale nose convergent evolution of 130 kHz pulses in toothed whale sonars? *Bioacoust.*, **15**, 195–206.
- Madsen, P. T., Johnson, M., Miller, P. J. O, Aguilar Soto, N., Lynch, J. & Tyack, P. (2006). Quantitative measures of air-gun pulses recorded on sperm whales (*Physter macrocephalus*) using acoustics tags during controlled exposure experiments. J. Acoust. Soc. Am., **120**, 2366–2379.
- Madsen, P. T. & Wahlberg, M. (2007). Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales. *Deep-Sea Res. I*, **54**, 1421–1444.
- Miller, P. J. O. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. J. Comp. Physiol. A., **192**, 449–459.
- Møhl, B. & Andersen, S. (1973). Echolocation high-frequency component in the click of the harbour porpoise (*Phocoena ph. L.*). J. Acoust. Soc. Am., 54, 1368–1372.
- Morisaka, T. & Connor, R. C. (2007). Predation by killer whales (Orcinus orca) and the evolution of whistle loss and narrow-band frequency clicks in odontocetes. J. Evol. Biol, 20, 1439–1458.
- Nakamura, K., Akamatsu, T., & Shimazaki, K. (1998). Threat clicks of captive harbor porpoises, Phocoena phocoena. Bulletin of the Faculty of Fisheries Hokkaido University, 49, 91–105.

- Nakano, R., Skals, N., Takanashi, T., Surlykke, A., Koike, T., Yoshida, K., Maruyama, H., Tatsuki, S. & Ishikawa, Y. (2008). Moths produce extremely quiet ultrasonic courtship songs by rubbing specialized scales. *PNAS*, **105**, 11812–11817.
- Patterson, I. A. P., Reid, R. J., Wilson, B., Grellier, K., Ross, H. M. & Thompson, P. M. (1998). Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? *Proc. R. Soc. Lond. B*, **265**, 1167–1170.
- Payne, R. & Webb, D. (1971). Orientation by means of long range acoustical signalling in baleen whales. Ann NY Acad Sci, 188, 110–141.
- Quintana-Rizzo, E., Mann, D. A., & Wells, R. S. (2006). Estimated communication range of social sounds used by bottlenose dolphins (*Tursiops truncatus*). J. Acoust. Soc. Am., 120, 1671–1683.
- Sayigh, L. S., Tyack, P. L., Wells, R. S. & Scott, M. D. (1990). Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. *Behav. Ecol. Sociobiol.*, 26, 247–260.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R. & Scott, M. D. (1999). Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Anim. Behav.*, 59, 41–50.
- Searby, A. & Jouventin, P. (2004). How to measure information carried by a modulated vocal signature? J. Acoust. Soc. Am., 116, 3192–3198.
- Smolker, R. A., Mann, J. & Smuts, B. B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behav. Ecol. Sociobiol.*, 33, 393–402.
- Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S. & Henry, R. (1999). Killer whale (Orcinus orca) hearing: auditory brainstem response and behavioural audiograms. J. Acoust. Soc. Am., 106, 1134–1141.
- Teilmann, J., Miller, L. A., Kirketerp, T., Kastelein, R. A., Madsen, P. T., Nielsen, B. K. & Au, W. W. L. (2002). Characteristics of echolocation signals used by a harbour porpoise (*Phocoena phocoena*) in a target detection experiment. Aqua. Mam., 28, 275–284.
- Tuttle, M. D. & Ryan, M. J. (1981). Bat Predation and the Evolution of Frog Vocalizations in the Neotropics. Science, 214, 677–678.
- Tyack, P. L. (1986). Population biology, social behavior, and communication in whales and dolphins. *Trends Ecol Evol*, 1, 144–150.
- Tyack, P. L. (1998). Acoustic communication under the sea. In Animal acoustic communication: Recent technical advances (Ed. by S. L. Hopp, M. J. Owren & C. S. Evans), pp. 163–220. Heidelberg: Springer-Verlag.
- Tyack, P. L. & Clark, C. W. (2000). Communication and Acoustic Behavior of Dolphins and Whales. In *Hearing by Whales and Dolphins* (Ed. by W. W. L. Au, A. N. Popper & R. R. Fay), pp. 156–224. New York; Springer-Verlag.
- Urick, R. J. (Eds.) (1983). Principles of Underwater Sound. Peninsula; Los Altos.
- Veerbom, W. C. & Kastelein, R. A. (1995). Acoustic signals by harbour porpoises (*Phocoena phocoena*). In *Harbour porpoises – laboratory studies to reduce bycatch* (Ed. by P. E. Nachtigall, J. Lien, W. W. L. Au & A. J. Read), pp. 1–39. De Spil Publishers, Woerden, Netherlands.
- Verfuß, U. K., Miller, L. A. & Schnitzler, H.-U. (2005). Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*). J. Exp. Biol., 208, 3385– 3394.
- Villadsgaard, A., Wahlberg, M. & Tougaard, J. (2007). Echolocation signals of wild harbour porpoises, *Phocoena phocoena*. J. Exp. Biol., **210**, 54–64.
- Watkins, W. A. (1967). The harmonic interval: fact or artefact in spectral analysis of pulse trains. In *Marine bioacoustics*, vol 2, (Ed. by W. N. Tavolga), pp. 15–43. Oxford: Pergamon.
- Watkins, W. A. & Schevill, W. E. (1977). Sperm whale codas. J. Acoust. Soc. Am., 62, 1485–1490.

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