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Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication

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Abstract Sperm whales (*Physeter macrocephalus*) are deep-diving predators foraging in meso- and bathypelagic ecosystems off the continental shelves. To investigate the ecophysiological and communicative function of various click types from male sperm whales in a high-latitude habitat, we deployed a large-aperture array of calibrated hydrophones off northern Norway (N69, E15). Data show that sperm whales in this habitat produce three click types: usual clicks, creak clicks and, occasionally, slow clicks. Usual clicks and creak clicks exhibit short duration, profound directionality and a frequency content suited for echolocation on meso- and bathypelagic fish and squids. The acoustic properties and low repetition rate of usual clicks are suited for long-range echolocation, whereas creak clicks have properties equivalent to signals in buzzes, the terminating pulse trains known from echolocating bats during prey capture. From these source parameters and the high acoustic activity during foraging dives, it is concluded that echolocation is an important sensory cue in prey location. Sound pressure levels of creak clicks and usual clicks measured off the acoustic axis suggest that sperm whales may be subjected to eavesdropping by conspecifics, thereby conveying information about food aggregations at estimated ranges of 6 km for creak clicks and 16 km for usual clicks. Slow clicks exhibit low directionality, low-frequency emphasis and a reduced repetition rate, suggesting that this click type is more suited for communication than for echolocation. Slow clicks can be detected by submerged conspecifics at ranges up to 60 km. Thus, sperm whales producing slow clicks may represent an odontocete species that utilizes long-range sound communication.

Keywords Sperm whale · Echolocation · Communication · Clicks

Introduction

Toothed whales (Cetacea: Odontoceti) produce clicks and tonal sounds for communication and echolocation (Au 1993). In delphinoids, both sound types are produced pneumatically in the nasal complex (Amundin and Andersen 1983; Ridgway and Carder 1988; Cranford 2000). A similar sound-producing function has been ascribed to the enormous nasal complex of the largest odontocete species, the sperm whale (Norris and Harvey 1972). Recent anatomical (Cranford et al. 1996; Cranford 1999) and physiological (Møhl 2001; Ridgway and Carder 2001) investigations have corroborated the Norris and Harvey theory. Hence, considering that the nasal complex takes up between one-quarter and one-third of the total body length (Nishiwaki et al. 1963), it can be expected that sound plays an important role for sperm whales (Norris and Møhl 1983; Cranford 1999).

Although whalers have reported sounds emanating from sperm whales for centuries, they were not scientifically described until 1957, when Worthington and Schevill noted that sperm whales produce clicks (Worthington and Schevill 1957). In a more thorough investigation, Backus and Schevill (1966) reported that sperm-whale clicks are multipulsed and broadbanded in the frequency range from 0.2 to 32 kHz. Backus and Schevill (1966) proposed that the clicks could be used both for echolocation and as a unique marker in communication, due to the multipulse structure within the clicks. Sperm whales undertake deep and long dives (Watkins et al. 1993, 2002) in the quest for a food mass amounting to approximately 3% of their body weight a day (Lockyer 1981). For a 30-ton specimen, this corresponds to some 1,000 medium-sized squid and fish (Clarke et al. 1993). It is not understood how a large, slow-moving predator, like a sperm whale, performs such a task nor have the sensory modalities involved in

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the location of the prey been established (Fristrup and Harbison 2001).

The association between deep foraging dives and so-called usual clicks (*sensu* Whitehead and Weilgart 1991) has led a number of researchers to suggest that prey items are located by biosonar (Norris and Harvey 1972; Gordon 1987; Goold and Jones 1995; Jaquet et al. 2001). However, Watkins (1980) argued that sperm-whale usual clicks are more suited for communication than echolocation, as he found that usual clicks are seldom produced out of acoustic range of conspecifics, and are too low in frequency, of too long duration and of too low directionality to be used for echolocation. The last objection has been rejected by recent data showing that sperm whale usual clicks show properties of high directionality (Møhl et al. 2000; Thode et al. 2002).

More consensus is found regarding the possible function of stereotyped, repetitive patterns of clicks, called codas (Watkins and Schevill 1977). Investigations on sperm whale behaviour in tropical waters have shown that codas are exchanged between individual whales socializing at the surface (Gordon 1987; Whitehead and Weilgart 1991). Codas do not appear to be used for individual identification, but more likely to maintain social cohesion within clusters of whales (Weilgart and Whitehead 1993). Different coda dialects have been identified among different groups (Weilgart and Whitehead 1997), and the dialects appears to be linked with similarity in mtDNA, suggesting that codas are maternally transmitted through generations (Whitehead et al. 1998). However, much research is still needed to understand how the complex social structure of sperm whales in tropical waters can apparently be maintained by click patterns (Weilgart et al. 1996).

Mature male sperm whales spend most of the time foraging at high latitudes (Rice 1989). Here, the whales are solitary and perform little if any social interactions (Weilgart and Whitehead 1988). Their acoustic repertoire differs from that of socializing groups of whales in the tropics by the lack of coda exchanges (Weilgart and Whitehead 1988; Madsen and Møhl 2000). Shared acoustic signals between socializing groups in the tropics and males in high-latitude habitats include usual clicks, sequences of clicks with high repetition rate, called creaks, and slow clicks (called clangs by Gordon 1987). Creaks are suggested to be equivalent to buzzes, terminating trains of echolocation signals in bats (Gordon 1987), and slow clicks are believed to be used for acoustic display in male-female and male-male interactions (Gordon 1987; Weilgart and Whitehead 1988) and/or echolocation (Goold 1999; Tyack and Clark 2000).

In order to substantiate or reject conjectures about the possible communicative and ecophysiological function of various signal types, it is essential to know the source parameters of the signals of interest. To shed light on the possible function of male sperm whale sounds in a high-latitude habitat, a calibrated, large-aperture hydrophone array was deployed off northern Norway in the summers of 1998 and 2000. Here we present data on the source parameters of various sperm whale signal types and dis-

cuss their implications for the echolocation and communication hypotheses.

Methods

Study site and subjects

Recordings were made between 8 and 24 July 1998 and between 12 and 21 July 2000 in Bleik canyon 20 km northwest of Andenes, northern Norway, (69°30N, 15°50E). Solitary, adult male sperm whales are found in this canyon year round (Ciano and Huerle 2001). The whales are several kilometres apart and are most likely foraging.

Recordings

1998 setup

Recordings in 1998 were performed with an array of five hydrophones (B&K 8101 and HS-150, Sonar Products) deployed from three vessels 0.5–1 km apart. Three hydrophones, lowered to depths of 30, 100 and 400 m, were deployed from the main vessel and one hydrophone was deployed from each of two satellite vessels. Radio links (UHF) relayed the signals from the hydrophones of the satellite platforms to an instrumentation recorder (Racal Store-7D, 7.5 ips) at the main platform. In addition, signals from the hydrophones on the satellite vessels were recorded on one of the channels of a DAT-recorder. The recording chains had a flat frequency response from 0.1 to 22 (DAT) and 0.1–35 kHz (Racal). All recording chains were high pass filtered at 100 Hz to reduce flow noise. To establish the geographical coordinates of each of the platforms, the output from Garmin 45 GPS receivers was converted to an FSK (frequency shift keying) signal that was recorded on the second channel of the DAT recorders and on one of the channels of the instrumentation recorder. This system had an rms (root mean square) precision of 90 m for the geographical coordinates. For further details, see Møhl et al. (2000) and Wahlberg et al. (2001).

2000 setup

Recordings in 2000 were performed with a large-aperture array of six to eight non-linked recording platforms spaced 0.5–2 km apart. The principles of this array are described in Møhl et al. (2001). In short, telemetry links were dispensed with synchronization between vessels obtained from the GPS system. The positional precision was enhanced (rms-error <2 m) through the use of differential GPS-technique. Each platform was equipped with one to three calibrated hydrophones (B&K 8101; 8105, HS-150 or Reson TC-4032) which, via an anti-alias filter (–12 dB/oct, $f_0=11$ kHz; for further details see Møhl et al. 2000), relayed the signals to one of the channels of a DAT stereo-recorder (Sony TCD-D3,7,8 and 10), sampling at 48 kHz. The anti-alias filters were compensated for during analysis, giving a flat frequency response from 0.1 to 22 kHz of the DAT recording systems. A –40 dB attenuator could be inserted in the recording chain to avoid overload. In addition, one of the platforms was equipped with a B&K 7006 instrumentation recorder. This system had a flat frequency response between 0.1 and 100 kHz. Most of the hydrophones were lowered to depths between 5 and 30 m, but two hydrophones were lowered to 100 and 485 m.

Calibration

During both expeditions, calibration signals from a B&K 4223 pistonphone-calibrator were sent through each of the recording chains and stored on tape.

Table 1 Estimated source parameters of various male sperm whale click types recorded off northern Norway (*CF* centroid frequency, *BW* –10 dB bandwidth)

Click type	ASL (dB/1 μ Pa rms)	ASL (energy dB/ μ Pa ² s)	Directionality	CF (kHz)	BW (kHz)	Duration τ (μ s)
Usual click (<i>N</i> ^a =20)	220–236 ^b	191–198 ^b	High ^b	15	15	120 ^c
Creak click (<i>N</i> =5)	179–205	145–161	High	15	13	100
Slow click (<i>N</i> =6)	175–190	156–166	Low	3	4	500–10,000

^a Number of sequences that allowed for source parameter estimation

^b Data from Møhl et al. (2002)

^c Duration of the p1 pulse

Source localization

For analysis, the contents of the DAT-tapes were digitally transferred to CD-ROM files. Sound analysis was performed with commercially available software (Cool Edit, Syntrillium). The whales were localized from time of arrival differences of the same click at the various receiver platforms, using custom software (A. Heerford and M. Wahlberg) and algorithms as outlined in Wahlberg et al. (2001). A sound velocity profile (SVP) was calculated from the Leroy-equation (Urick 1983), based on temperature and salinity measured down to 500 m depth using a Star Oddi DST 200 tag. Additional temperature and salinity data to 1,000 m depth were obtained from the Institute of Marine Research, Bergen. Based on the SVP, ray-tracings were generated, showing that transmission losses could be modelled by spherical spreading. This was largely confirmed experimentally, using detonators and imploding light bulbs at depth.

Analysis

Energy and duration calculations were made with Matlab 5.3 (Math. works). We defined the duration τ as the interval restricted by the –10 dB end points relative to the peak of the corresponding envelope function (sensu Møhl et al. 1990). Received sound pressure level (RL) was calculated as dB/1 μ Pa rms by integration over the –3 dB duration of the envelope, and by comparison with the calibration signal recorded on all tapes. Source levels (SL) were calculated: SL=RL (received level)+TL (transmission loss), where TL was calculated from the range (R) between the source and the receivers, assuming spherical spreading: TL=20log(R)+ α R (α =1.5 dB/km at 15 kHz). Energy was derived by integrating the square of the pressure over –3 dB duration around the maximum value of the envelope function.

The spectral content of the clicks was described by the centroid frequency (the frequency dividing the spectrum in two halves of equal energy), and by the –10 dB BW. Range-dependent absorption of high frequencies was compensated for during analysis (Urick 1983). Repetition rate (rep. rate) normally describes the number of clicks per second. Here the instantaneous rep. rate (1/ICI) is used to describe the changes between productions of usual clicks and creak clicks.

Results

Acoustic behaviour

Acoustic data are derived from analysis of 20 h of recordings on 3–10 hydrophone channels (i.e. more than 100 h in total). Usual clicks are the dominating click type of sperm whales in this habitat. When initiating a deep dive, the whales start to produce usual clicks after 30–60 s at a depth of 50–250 m. The repetition rate varies between 0.7 clicks/s and 4 clicks/s, i.e. inter-click intervals (ICI) of

0.25 and 1.4 s. Trains of usual clicks are regularly disrupted by apparent silence or by a creak. After a pause of 5–20 s, the production of usual clicks is resumed; 30–40 min into the dive, the whales stop clicking during the last few 100 m of ascent back to the surface. No sounds, with the possible exception of slow clicks, have been associated with surfaced specimens. Both usual clicks and creaks have been recorded from single whales with no conspecifics observed in the canyon area visually or acoustically. No codas or tonal sounds (Perkins et al. 1966; Goold 1999) were detected in our recordings.

Usual clicks

Multi-hydrophone recordings have revealed that the amplitude, waveform and frequency content of usual clicks depend greatly on the whale-receiver aspect. The derived SL of the same click may differ more than 40 dB between what is believed to be on the acoustic axis (Møhl et al. 2000) and a few degrees off-axis. Due to these directional properties of usual clicks and the lack of knowledge on how the animal is oriented relative to the various recording platforms, we cannot be sure that the derived properties are true source parameters of the signals on the acoustic axis. Accordingly, we have adapted the term Apparent Source Level (ASL) from Møhl et al. (2000). The highest ASLs were measured in the range 220–236 dB/1 μ Pa rms (Table 1). Figure 1a depicts the waveform of a usual click selected to illustrate a signal close to or on the acoustic axis (ASL of 230 dB/1 μ Pa rms). The click is multi-pulsed, but the p1 pulse (sensu Møhl 2001) totally dominates the click in having an amplitude 40 dB above the preceding and trailing pulses within the click (Fig. 1a). The p1 pulse has a simple waveform, dominated by 1–2 cycles with a duration of some 120 μ s (Fig. 1b). The power spectrum of the p1 pulse seen in Fig. 1b is broadband with –10 dB spectral endpoints at 5 and 24 kHz (Fig. 1c). The centroid frequency is found around 15 kHz (Table 1). This is in contrast to the same clicks recorded from a different aspect, off-axis. Here the ASL of the p1 is reduced by some 45 dB to around 185 dB/1 μ Pa rms; the decay rate between pulses within the click is low, and the centroid frequency is found below 10 kHz. In wideband recordings, there is no significant energy (–20 dB) above 40 kHz in any on-axis clicks. More detailed properties of usual clicks are reported in Møhl et al. (2002).

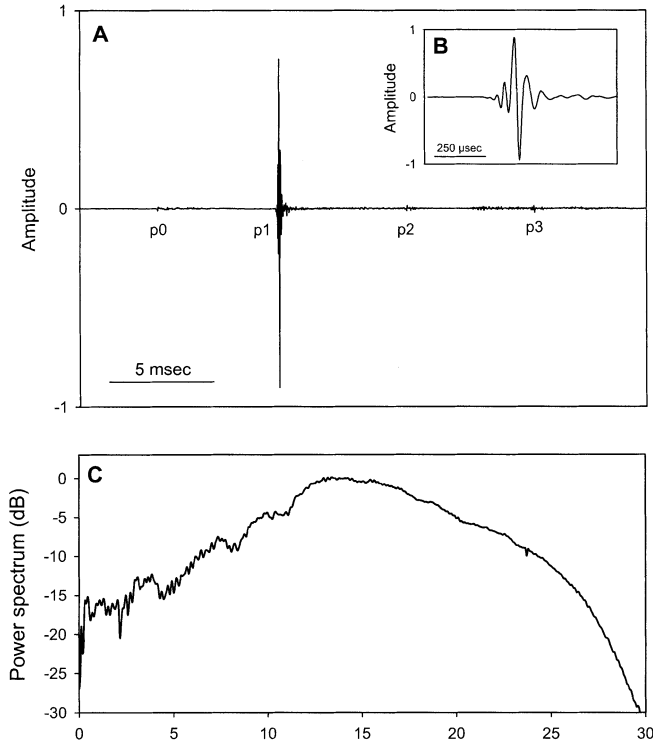


Fig. 1 **A** Waveform of an on-axis version of a usual click; $p0$ – $p3$ mark the multipulses of the click (sensu Møhl 2001). Note that $p1$ dominates by far the energy content of the click. The inter-pulse interval (IPI) is 6.5 msec. **B** Waveform of the $p1$ pulse depicted in **A**. Note the simple pulse structure and short duration. **C** Power spectrum of the $p1$ pulse shown in **A**. Sample rate 200 kHz. FFT-size 512. High pass filtered at 100 Hz

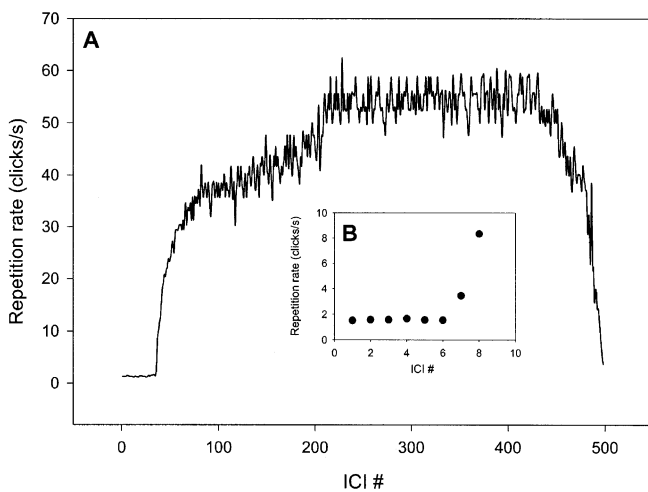


Fig. 2 **A** Instantaneous rep. rate ($1/ICI$) development during the transition from usual clicks to creak clicks. **B** Enlarged version of the transition zone between usual clicks and creak clicks. Note how the instantaneous rep. rate is doubled in two consecutive ICIs when the creak is initiated

Creak clicks

A creak denotes a train of a special type of sperm-whale clicks with very short ICIs (Gordon 1987). The name refers to the creaking sound of clicks with a fast repetition

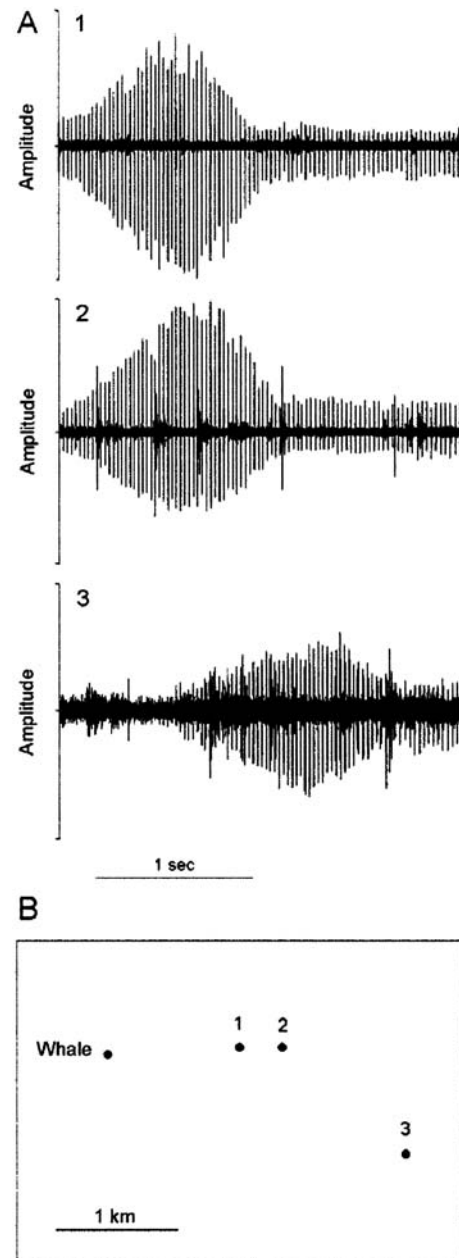


Fig. 3 **A** Creak recorded on three different platforms. The same click is aligned in time on the three tracks. Full ASL-amplitudes on the y -axes correspond to a tone of 205 dB/1 μ Pa rms. Note how the ASL anomaly shifts between platforms. **B** Whale-receiver geometry of the recordings shown in **A**. The whale was localized with the aid of two additional recording stations

rate. We extracted 20 creaks with good S/N (signal to noise ratio) for detailed analysis. Five of these sequences allowed for ASL estimates. Creaks normally terminate a train of usual clicks and can be identified by an abrupt increase in instantaneous repetition rate ($1/ICI$) (Fig. 2a). The shift between usual clicks and creak clicks is characterized by a doubling of rep. rates in two consecutive ICIs (Fig. 2b), followed by a steady increase in instantaneous rep. rate to about 50 clicks/s (Fig. 2a). Creaks may last from 10 to 30 s and are normally terminated by

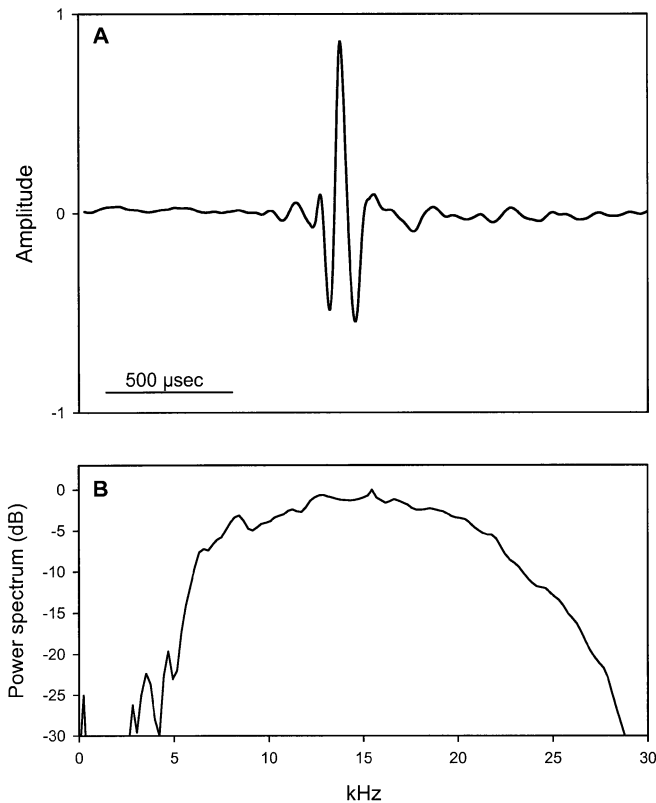


Fig. 4 **A** Waveform of an on-axis creak click. Note the simple pulse structure and short duration. **B** Power spectrum of the creak-click depicted in **A**. Sample rate 200 kHz. FFT-size 512. High pass filtered at 100 Hz

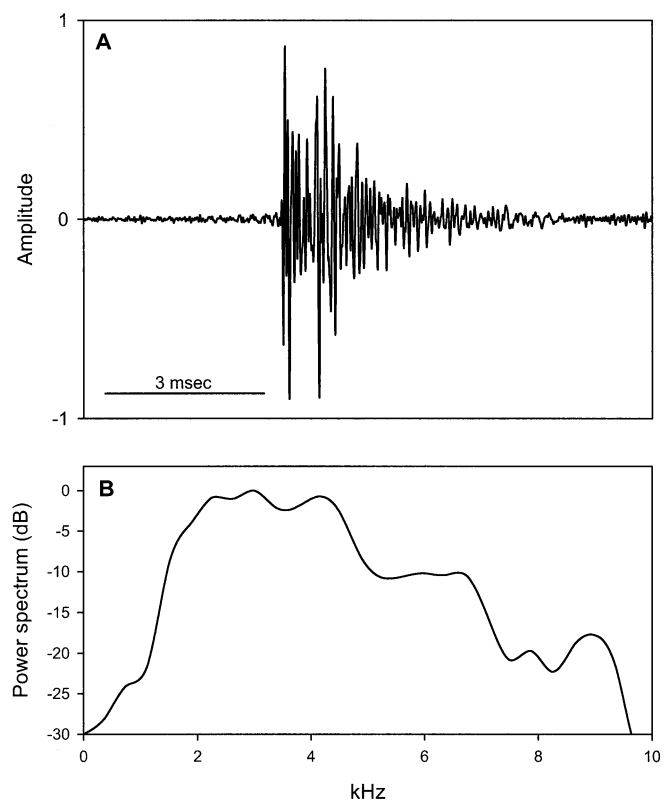


Fig. 5 **A** Waveform of slow click. **B** Power spectrum of the slow click depicted in **A**. Sample rate 48 kHz. FFT-size 256. High pass filtered at 100 Hz

clicks with longer ICIs and then silence for 5–20 s. At times, the production of usual clicks is resumed directly from a creak. Figure 3a shows the same creak recorded on three different platforms. The whale-receiver geometry is depicted in Fig. 3b. It appears that the derived ASL of the same click differs by more than 20 dB between the platforms, and that the ASL differences are changing in time. The aligned platforms 1 and 2 are illuminated first with estimated ASL upwards 205 dB//1 uPs rms, and then the inferred sound beam sweeps towards platform 3. The alternating illumination of platforms indicates a directional source with changing heading. Hence for description, the waveform and frequency content are obtained from creak clicks with high ASLs. The waveform is dominated by 1–2 cycles with a duration of 100 μs and has no traces of the multipulse structure found in usual clicks (Fig. 4a). The power spectrum of the creak click depicted in Fig. 4a is broadband with –10 dB BW spectral endpoints at 6 and 23 kHz (Fig. 4b). The centroid frequency is found around 15 kHz (Table 1).

Slow clicks

Slow clicks are very rare in this habitat. This signal type has been detected in less than 1% of the 20 h spent re-

ording (5-min bins). We extracted ten sequences of slow clicks for detailed analysis. Six of these sequences allowed for ASL estimates. Slow clicks occur either alone or as trains with ICIs of 4–7 s. On one occasion, we recorded two different whales (based on different TOADs) producing two different slow clicks simultaneously. One of the whales produced a train of clicks with ICIs of 5 s, whereas the other whale produced four slow clicks with long and irregular ICIs. The centroid frequencies differed by some 700 Hz between the slow clicks produced by each of the whales. Trains of slow clicks may last for more than a minute, containing 10–15 clicks or more. The waveforms of slow clicks have variable durations of 0.5–10 ms (Fig. 5a). In some of the less reverberant clicks, a multipulse structure with IPis similar to usual clicks can be recognized. The power spectra of the slow clicks are narrow banded with spectral endpoints at 1 and 5 kHz (Fig. 5b). The centroid frequency is generally found around 3 kHz (Table 1). The waveforms and frequency contents of the same slow click recorded from different aspects (with approximately the same range between whale and receivers) are generally alike, as opposed to the situation in usual clicks. A special feature of slow clicks is an ever-present environmental reverberation from the bottom, surface and steep slopes of the underwater canyon.

Discussion

Usual clicks

Usual clicks dominate the acoustic repertoire of sperm whales in this habitat, and they are only produced during deep foraging dives. We have recorded this click type in the presence of up to five whales phonating simultaneously, producing a cacophony of clicks. However, on several occasions solitary specimens have produced this click type as well. This has been reported in several other studies (Gordon 1987; Mullins et al. 1988; Møhl and Amundin 1991), which in turn questions the view that solitary whales seldom phonate (Watkins 1980).

Due to the high directionality of usual clicks, it seldom happens that the sound beam illuminates one of the hydrophones of the array. We have identified some 20 high-level events with derived ASLs between 220 and 236 dB/1 μ Pa rms. It should be noted that sperm whales can alter the acoustic output with at least 20 dB (fixed recording aspect, Madsen et al. 2002) which, together with the unknown orientation of the animals, can create situations where on-axis signals of usual clicks may have higher or lower ASLs than reported here. On-axis versions of usual clicks are very different in frequency and time characteristics (Table 1) from clicks recorded off-axis. The time-frequency characteristics of usual clicks recorded off-axis in our studies are of the same duration and frequency content as normally reported for usual clicks in the literature (e.g. Backus and Schevill 1966; Goold and Jones 1995).

The frequency content of usual clicks is reportedly dominated by energy at 2 kHz (Goold and Jones 1995), 5–7 kHz (Levenson 1974; Møhl and Amundin 1991) and 2–32 kHz (Backus and Schevill 1966; Watkins 1980). These discrepancies can in part be explained by lack of reporting standard, varying bandpasses of the recording chains and the fact that one should discern between the frequency content of coda clicks and usual clicks (Madsen et al. 2002). However, the spectra of sperm-whale usual clicks differ not only between click types and animals (Backus and Schevill 1966) but also in time. It has been shown that sperm whales can alter the spectral content of their clicks (Madsen et al. 2002), but this phenomenon cannot account for different spectra of the same click seen from different aspects. Instead, we regard the aspect-dependent differences in waveform and frequency content to be the result of directionality (Whitney 1968; Møhl et al. 2000; Madsen et al. 2002).

As seen from Fig. 1c, the centroid frequencies of on-axis clicks are found around 15 kHz and the lower and upper –10 dB spectral endpoints are located around 5 and 24 kHz (Table 1). Spectral endpoints at 5 and 24 kHz are in close agreement with the reported best hearing sensitivity of a neonate sperm whale calf (Ridgway and Carder 2001). This ABR (acoustic brainstem response) study revealed that sperm whales have a best hearing sensitivity from 5 to 20 kHz, and a better sensitivity at 40 kHz than at 2.5 kHz (Ridgway and Carder 2001).

It should be stressed that the frequency emphases of usual clicks are positively correlated with the acoustic output (Madsen et al. 2002) and that the centroid frequency of on-axis clicks accordingly may differ from the 15-kHz region if the whale reduces or increases the sound pressure levels. However, for evaluation of the biosonar potential, we regard the on-axis properties listed in Table 1 as being representative of sperm-whale usual clicks.

Sperm whales feed mainly on medium-sized squid and fish (Clarke et al. 1993) with total mantle lengths between 0.2 and 1 m (Kawakami 1980). A rigid sonar target (i.e. with no resonating air bubbles) should have a ka -product (where k is the wave number and a is the radius of the target) equal to or larger than 1, to reflect sound efficiently, so-called geometric scatter (Clay and Medwin 1977). Hence, with a centroid frequency around 15 kHz, sperm-whale usual clicks are suited to detect targets with a volume corresponding to a sphere with a radius larger than 2.5 cm. If the targets contain air bubbles, the effective radius may decrease by almost an order of magnitude. Therefore, mesopelagic fish species with a swim-bladder radius smaller than 2.5 cm should also provide efficient backscatter. The point recently made (Fristrup and Harbison 2001) that sperm-whale usual clicks would be most suitable for detecting targets of a dimension larger than 1 m seems accordingly to be off by more than an order of magnitude.

Sperm whales usually forage in and below the deep scattering layer (Watkins et al. 1985; Gordon 1987; Papastavrou et al. 1989; Wahlberg 2002). Hersey and Bachus (1962) employed a long-range sonar at the surface to measure the frequency-dependent reflections from the deep scattering layer. It appeared that the maximum acoustic backscatter from organisms at these depths is obtained in the frequency band from 2.5 to 25 kHz (Hersey and Bachus 1962). When comparing these backscatter data with the spectrum of an on-axis p1-pulse (Fig. 1C, Table 1), it is tempting to suggest that usual clicks are matched to long-range biosonar detection of targets in the mesopelagic prey community. The high source level, high directionality and short duration of the p1 pulse in sperm-whale usual clicks do not refute that hypothesis.

In that light, it can be speculated that the hypertrophied nasal complex of the sperm whale may have evolved to maximize directionality and source levels of 15-kHz pulses with low absorption (1–2 dB/km) and sufficient resolution (geometric scatter for target radius larger than 2.5 cm) to be used for long-range biosonar detection of mesopelagic cephalopod prey with low target strength.

Creak clicks

A creak is produced at depth during foraging dives and is normally preceded by a train of usual clicks. This has led a number of researchers (Gordon 1987; Goold and Jones

1995; Jaquet et al. 2001) to speculate that creaks serve the same function as buzzes in the terminal part/catch phase of signal trains from echolocating bats. Weilgart and Whitehead (1993) proposed that creaks might serve a communicative purpose rather than echolocation. In the present study, no creaks were produced at the surface or in the context of possible social interactions. Rather, they were interleaved with series of usual clicks. Hence, we conclude that creaks in this habitat are associated with foraging.

If indeed creaks are equivalent to buzzes in echolocating bats, creak clicks should show the same fundamental features as the signals of microchiropteran buzzes: directionality, high repetition rate, reduced output, short duration and a frequency content suited for the size of the potential targets (Simmons et al. 1979). Regarding the directionality, it is seen from Fig. 3a that there is a >20 dB ASL anomaly between platforms and that the anomaly shifts between them. Moreover, single hydrophone recordings reveal similar shifts between the direct and surface-reflected paths. These observations strongly suggest that creak clicks are directional (*sensu* Watkins and Schevill 1974).

The directional nature and the reduced ASL on-axis, compared with usual clicks, of 185–205 dB//1 μ Pa rms also make creak clicks hard to detect on a sufficient number of hydrophones to allow for localization of the source and subsequent derivation of source parameters. This explains the limited numbers of ASL estimates for this click type (Table 1). Our ASL estimates fall in the same range as reported for a presumed creak (rep. rate 20/s) where the derived SLs were 180–205 dB//1 μ Pa (Frankel 2001). A reduced output concomitant with high rep. rates has also been seen in buzzes from narwhals (Miller et al. 1995) and harbour porpoises (Verfuss et al. 2000). We propose that this is an inherent feature of high repetition rates in odontocetes.

The waveform of creak clicks consists of 1–2 cycles with a duration of some 100 μ s, which is similar to the p1 pulse duration of usual clicks (Fig. 1a, Table 1) and consistent with the temporal properties of signals from odontocetes with biosonar (Au 1993). We have, in accordance with Backus and Schevill (1966) and Gordon (1987), not been able to detect a multipulse structure in creak clicks. On the contrary, Jaquet et al. (2001) reported that creak clicks are multipulsed and that the IPI is considerably shorter than in usual clicks. The latter observation, however, questions that the multipulses observed are source generated, as accumulating evidence suggests that the IPI is almost constant (Madsen et al. 2002), representing the two-way travel time of the sperm-whale nasal complex (Norris and Harvey 1972; Gordon 1991; Møhl 2001). The discrepancy between the multipulsed clicks in the Jaquet et al. study and the present study may be explained by the fact that the high-repetition clicks trains in the Jaquet study could have been chirrups (Gordon 1987), which are also produced with high repetition rates, but exhibit a distinct multipulse structure (Madsen 2002). We know from tag de-

ployments that sperm whales can change the mode of sound transmission in the spermaceti compartments when producing usual clicks and coda clicks (Madsen et al. 2002). That a different sound production mode is involved in creak-click generation has been implicated by the abrupt shift in ICI from usual clicks to creak clicks (Fig. 2b) (Gordon 1987). However, testing of this conjecture and the possible difference between creak clicks and chirrup clicks call for further deployments of sound-recording tags.

The frequency content of an on-axis creak click resembles that of a p1 pulse of on-axis usual clicks, which validates the same speculations for a match between the frequency content and backscatter of prey items in the meso- and bathypelagic ecosystem. Hence, creak clicks are just as suited for echolocation as are usual clicks, but the reduced output and high repetition rate suggest a shorter sonar range. The conjectured involvement of creaks in prey collection has gained support from observations with an onboard tag that allows for sound recording concomitant with logging of 3-D movements of the animal (Johnson et al. 2001). These novel investigations have shown that creaks are associated with fast 3-D movements of the tagged animal, implying that the whale is pursuing moving prey. The source parameter estimates presented here and the recent behavioural observations substantiate the contention that sperm-whale creaks serve the same function as buzzes from smaller odontocetes and echolocating bats.

Since biosonar intrinsically conveys information to conspecifics about foraging activity (Barclay 1982), usual clicks and creaks in particular are likely to be vehicles of such information. It can accordingly be instructive to evaluate the range of potential eavesdropping by conspecifics. Considering the highly directional nature of both usual and creak clicks, sperm whales are most likely to hear phonating conspecifics from an off-axis aspect. Assuming off-axis levels of 185 dB//1 μ Pa rms for usual clicks and 165 dB//1 μ Pa rms for creak clicks, possible detection ranges can be estimated from the passive sonar equation (Urick 1983). In the deep sea, the background noise level around 10 kHz at sea state 1 is 36 dB/1 μ Pa²/Hz (Urick 1983). Assuming a detection threshold (DT) 10 dB above background noise levels and a filter bandwidth corresponding to the cRMS BW (Au 1993) of the p1 spectrum (6 kHz), the DT will be 35 dB+10 \times log(6000)+10=84 dB. Assuming spherical spreading and a frequency-dependent absorption of 1 dB/km at 10 kHz, transmission losses of (185–84) 101 dB and (165–83) 82 dB yield detection ranges of 16 km for usual clicks and 6 km for creak clicks. Such estimated ranges are only valid if both the transmitter and the receiver are submerged in deep water away from the shadow zones of the surface (Urick 1983). If conspecifics are illuminated by on-axis versions of these click types, the potential range of eavesdropping may be increased by almost an order of magnitude. Considering that the males in this habitat are usually spaced 1–5 km apart and show no coordinated feeding behaviour, it be-

comes evident that eavesdropping of phonating conspecifics potentially plays an important role in location of food aggregations.

Buzzes terminating signal trains in echolocating bats usually imply that the animal has located and possibly caught one prey item (Schnitzler et al. 1985). It seems therefore problematic from an energetic point of view if a creak is mandatory for collection of all prey types and that collection of one prey item requires one creak. Clarke et al. (1993) estimated that large male sperm whales locate and catch approximately 1,000 prey items a day. If creaks are an inherent part of the collection of all prey types, this implies that sperm whales should produce at least 1,000 creaks a day. Considering that male sperm whales in this habitat undertake 15–25 foraging dives during 24 h, this would imply that each dive should involve more than 40 creaks. We do not observe creaks nearly that often. Part of this may be explained by the fact that creaks are difficult to detect due to their reduced output and pronounced directionality. Careful filtering and amplification of sequences of apparent silence between series of usual clicks reveal at times that creaks are present, but that the signal to noise ratio is too poor for immediate detection. Nevertheless, failing detection cannot account for the “lack” of creaks and some pauses between usual clicks simply do not contain creaks. We hypothesize that the production of a creak is associated with collection of several prey items, and that not all prey items (perhaps large and/or slow moving species; Clarke et al. 1993, e.g. spawning squid) require a creak to be collected.

Slow clicks

Slow clicks are rare off northern Norway, implying that this sound type is not a crucial part of the foraging behaviour. Our data are consistent with those of Gordon (1987), Weilgart and Whitehead (1988) and Goold (1999) showing that slow clicks have a long duration (1–10 ms), a reverberant waveform and low frequency emphasis (2–4 kHz). Such properties make slow clicks poor signals for echolocation of prey. Moreover, the largest source-level anomalies for slow clicks are in the order of 10 dB and no illuminations of single hydrophones have been observed. This suggests a low directionality in slow clicks, which speaks against biosonar as a possible function. It should be stressed, however, that it is practically impossible to demonstrate low or omnidirectionality for a free-ranging, biological sound source. Modest source-level anomalies between receivers either imply that the source is of low directionality or that none of the receivers are illuminated by the putative beam of the source. To rule out the latter for a free-ranging source of unknown orientation requires, in principle, an infinite number of receivers surrounding the source.

There are, however, other cues that may assist in testing the possible low directionality of slow clicks. With dominating wavelengths in the order of 0.5 m (centroid

frequencies between 2 and 4 kHz), a low directionality can be predicted from the ratio between the wavelength and the possible aperture (approx. 1 m) of the foremost part of the male sperm-whale nasal complex. In addition, we observe that reverberations from the seafloor, surface and slopes of the canyon are inherent features of slow clicks. Similar reverberations are seen when firing small detonators in the canyon area for calibration of the array (Madsen and Møhl 2000). Detonators are by nature omnidirectional (Urick 1983), and that similar reverberation patterns are seen in slow clicks demonstrate that they are of low directionality. Several investigators (Goold 1999; Tyack and Clark 2000) have proposed that slow click-generated echoes from large subsurface structures may provide information about water depth and underwater topography. That hypothesis cannot be tested from present data, but it would indeed be surprising if the whales did not utilize the information from the inherent reverberation of slow clicks when navigating. However, the scarcity and the fact that apparently only male sperm whales produce these sounds suggest that echolocation off large underwater structures is not the primary purpose of slow clicks.

While it seems doubtful that slow clicks have a biosonar function, they may have a role in communication. Gordon (1987) and Weilgart and Whitehead (1988) proposed that slow clicks are used for acoustic display between males when competing for females on the breeding grounds. Our observations and those of others (Mullins et al. 1988; Goold 1999) of slow clicks in male-only habitats suggest that slow clicks are not entirely produced as a part of an acoustic courtship in the competition for females. In contrast to females and juveniles (Gordon 1987), male sperm whales in this habitat have no coordinated dive behaviour, which points towards a solitary and thus potentially competitive foraging behaviour. In a male-only, high-latitude habitat, slow clicks could thus be used for acoustic display in competition for food aggregations. Tyack and Clark (2000) proposed that differences in the frequency spectrum may be related to the size of structures within the sound-producing apparatus and, thereby, the overall size of the two phonating whales. We have observed a difference of 700 Hz in centroid frequencies from two males producing slow clicks simultaneously, but the conjecture of Tyack and Clark (2000) cannot be evaluated from the present data, as the sizes of the two whales are unknown.

The apparently low directionality and the relatively high SL of slow clicks call for an evaluation of the potential communicative space of slow clicks. In the deep sea, the background noise level around 3 kHz at sea state 1 is 43 dB/1 $\mu\text{Pa}^2/\text{Hz}$ (Urick 1983). Assuming a DT 10 dB above background noise levels and a filter bandwidth corresponding to the cRMS BW of the signal spectrum (2.5 kHz), the DT will amount to 87 dB [10 dB+43 dB+10 log (2500)]. An omnidirectional source with an SL of 190 dB/1 μPa rms (Table 1) producing slow clicks would therefore theoretically allow for detection after a transmission loss of 190 dB–87 dB=

103 dB. Taking frequency-dependent absorption into account (0.13 dB/km at 3 kHz) and provided that the sound energy is distributed according to the inverse square law (spherical spreading), 103 dB of transmission loss corresponds to a distance of 60 km. Such a value may only be valid if both the transmitter and the receiver are submerged in deep water away from the shadow zones of surface. However, if both the transmitter and receiver dive to the SOFAR channel (Urick 1983), the range may be longer. In the light of the limited number of derived ASLs of slow clicks in the present study, we may have underestimated the maximum acoustic output in slow-click production, and thereby also the size of the communicative space. Assuming that the same acoustic power is available for production of slow clicks of low directionality as for production of the highly directional usual clicks, slow-click ASLs of some 200 dB/1 μ Pa rms would be predicted. Future studies should test this hypothesis.

The potential role of slow clicks in long-range communication is not only supported by theoretical considerations, but also by empirical data from Barlow and Taylor (1997). This study showed that slow clicks can be detected by towed hydrophones at ranges up to 20 nm (37 km) which, together with detection ranges of 14 nm (26 km) from a similar towed hydrophone array system (J. Jones/Ocean Alliance, personal communication), signifies the potential of slow clicks for long-range acoustic communication.

The advantage of long-range communication in a male foraging habitat is not obvious, but may serve as a useful tool in maintaining the apparent cohesion among males during migrations (Goold 1999). On the breeding grounds, the large communicative space of slow clicks seems advantageous when sexually mature males wish to announce their presence to competitors and females. Sexually mature male sperm whales rove between groups of females searching for receptive partners (Whitehead 1993) and, provided that the communicative range of 60 km is valid, a roving male that makes slow clicks may announce its presence to submerged conspecifics in an area covering more than 11,000 km². Sperm whales producing slow clicks may thus represent an odontocete species that utilizes long-range sound communication. However, with a frequency emphasis two decades higher than blue- and fin-whale calls, slow clicks do not have the ocean-traversing potential of these signals (Payne and Webb 1971).

Conclusions

The present data from a large-aperture hydrophone array have shown that male sperm whales in a high-latitude habitat off northern Norway produce three distinct click types: usual clicks, creak clicks and, at times, slow clicks. Slow clicks exhibit low directionality, low frequency emphasis and a reduced repetition rate, suggesting that this click type is more suited for communication than for

echolocation. We propose that slow clicks serve a communicative purpose, perhaps in conjunction with competition for food aggregations in this habitat. The communicative space of sperm whales producing slow clicks potentially covers a range of 60 km, which may play a significant role for male sperm whales during migrations and for male-male and male-female interactions on the breeding grounds. The short duration, high directionality and frequency content of usual clicks and creak clicks make them strong candidates for signals involved in active echolocation on the meso- and bathypelagic prey community. The high ASL and low repetition rate of usual clicks support the view that this click type is used for long-range echolocation, whereas the high repetition rate and lower ASL of creak clicks infer that this click type is equivalent to signals in buzzes produced by echolocating bats, harbour porpoises and narwhals during prey capture. The high phonation rate of foraging sperm whales and the estimated source parameters of usual clicks and creak clicks presented here lend weight to the view that echolocation is an important sensory cue for detection of mesopelagic prey. It is speculated that the hypertrophied nasal complex of the sperm whale may have evolved to maximize directionality and source levels of 15-kHz pulses with low absorption and sufficient resolution to be used for long-range biosonar detection of mesopelagic cephalopods with low target strength. We hope that these new acoustic observations will nourish deployment of crittercams (Marshall 1996; Davis et al. 1999) which can link acoustic recordings with observable behaviour of sperm-whale foraging at great depths.

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References

- Amundin M, Andersen SH (1983) Bony nares air pressure and nasal plug muscle activity during click production in the harbour porpoise, *Phocoena phocoena*, and the bottlenosed dolphin, *Tursiops truncatus*. *J Exp Biol* 105:275–282
- Au WWL (1993) *Sonar of dolphins*. Springer, Berlin Heidelberg New York
- Backus RH, Schevill WE (1966) Physeter clicks. In: Norris KS (ed) *Whales, dolphins, and porpoises*. University of California Press, Berkeley, pp 510–528
- Barclay RMR (1982) Interindividual use of echolocation calls, eavesdropping by bats. *Behav Ecol Sociobiol* 10:271–275

- Barlow J, Taylor B (1997) Acoustic sensus of sperm whales in the eastern temperate North Pacific. *J Acoust Soc Am* 102:3213
- Ciano JN, Huerle R (2001) Photo-identification of sperm whales at the Bleik Canyon, Norway. *Mar Mammal Sci* 17:175–180
- Clarke MR, Martins HR, Pascoe P (1993) The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philos Trans R Soc Lond B* 339:67–82
- Clay CS, Medwin H (1977) *Acoustical oceanography*. Wiley, Chichester
- Cranford TW (1999) The sperm whale's nose: sexual selection on a grand scale? *Mar Mammal Sci* 15:1133–1157
- Cranford TW (2000) In search of impulse sound sources in Odontocetes. In: Au WWL, Popper AN, Fay RR (eds) *Hearing in whales and dolphins. Handbook on Auditory Research*. Springer, Berlin Heidelberg New York, pp 109–155
- Cranford TW, Amundin M, Norris KS (1996) Functional morphology and homology in the odontocete nasal complex: implications for sound generation. *J Morphol* 228:223–285
- Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning M (1999) Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 282:993–996
- Frankel AS (2001) Dive patterns and source levels of sperm whales off New Zealand. *J Acoust Soc Am* 110:2771
- Fristrup KM, Harbison GR (2001) How do sperm whales catch squids? *Mar Mammal Sci* 18:42–54
- Goold JC (1999) Behavioural and acoustic observations of sperm whales in Scapa Flow, Orkney Islands. *J Mar Biol Assoc UK* 79:541–550
- Goold JC, Jones SE (1995) Time and frequency domain characteristics of sperm whale clicks. *J Acoust Soc Am* 98:1279–1291
- Gordon JC (1987) The behaviour and ecology of sperm whales off Sri Lanka. PhD Thesis, Darwin College, Cambridge
- Gordon JC (1991) Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. *J Zool Lond* 224:301–314
- Hersey JB, Bachus RH (1962) Sound scattering by marine organisms. In: Hill MN (ed) *The sea*, vol 1. Interscience, New York, pp 498–539
- Jaquet N, Dawson S, Douglas L (2001) Vocal behavior of male sperm whales: why do they click? *J Acoust Soc Am* 109:2254–2259
- Johnson MP, Tyack PL, Zimmer WMX, Miller PJO, D'Amico A (2001) Acoustic vocalizations and movement patterns of a tagged sperm whale (*Physeter macrocephalus*) during foraging dives. Abstracts of the 14th Biennial Conference of the Biology of Marine Mammals, Vancouver
- Kawakami T (1980) A review of sperm whale food. *Sci Rep Whales Res Inst* 32:199–218
- Levenson C (1974) Source level and bistatic target strength of the sperm whale (*Physeter catodon*) measured from an oceanographic aircraft. *J Acoust Soc Am* 55:1100–1103
- Lockyer C (1981) Estimates of growth and energy budget for the sperm whale, *Physeter catodon*. *Mammals in the seas*, vol III. FAO series no 5. FAO, Rome
- Madsen PT (2002) Sperm whale sound production. PhD Thesis, University of Aarhus
- Madsen PT, Møhl B (2000) Sperm whales (*Physeter catodon* L. 1758) do not react to sounds from detonators. *J Acoust Soc Am* 107:668–671
- Madsen PT, Payne R, Kristiansen NU, Wahlberg M, Kerr I, Møhl B (2002) Sperm whale sound production studied with ultrasound time/depth-recording tags. *J Exp Biol* 205:1899–1906
- Marshall GJ (1996) Crittercam: an animal-borne imaging and data logging system. *Mar Technol Ser* 32:11–17
- Miller LA, Pristed J, Møhl B, Surlykke A (1995) The click sounds of narwhals (*Monodon monoceros*) in Inglefield Bay, Northwest Greenland. *Mar Mammal Sci* 11:491–502
- Møhl B (2001) Sound transmission in the nose of the sperm whale, *Physeter catodon*. A post mortem study. *J Comp Physiol A* 187:335–340
- Møhl B, Amundin M (1991) Sperm whale clicks: pulse interval in clicks from a 21 m specimen. PhD Thesis, University of Stockholm
- Møhl B, Surlykke A, Miller LA (1990) High intensity narwhal clicks. In: Thomas J, Kastelein R (eds) *Sensory abilities of cetaceans*. Plenum Press, New York
- Møhl B, Wahlberg M, Madsen PT, Miller LA, Surlykke A (2000) Sperm whale clicks: directionality and source level revisited. *J Acoust Soc Am* 107:638–648
- Møhl B, Wahlberg M, Heerfordt A (2001) A large-aperture array of nonlinked receivers for acoustic positioning of biological sound sources. *J Acoust Soc Am* 109:434–437
- Møhl B, Wahlberg M, Madsen PT, Herford A, Lund A (2002) The mono-pulsed nature of sperm whale clicks. *J Acoust Soc Am* (in press)
- Mullins J, Whitehead H, Weilgart L (1988) Behavior and vocalizations of two sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Can J Fish Aquat Sci* 45:1736–1743
- Nishiwaki N, Oshumi S, Maeda Y (1963) Changes in form of the sperm whale accompanied with growth. *Sci Rep Whal Res Inst Tokyo* 17:1–13
- Norris KS, Harvey GW (1972) A theory for the function of the spermaceti organ of the sperm whale. NASA SP-262:397–417
- Norris KS, Møhl B (1983) Can odontocetes debilitate prey with sound? *Am Nat* 122:85–103
- Papastavrou V, Smith SC, Whitehead H (1989) Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Can J Zool* 67:839–846
- Payne R, Webb D (1971) Orientation by means of long range acoustic signaling in baleen whales. *Ann NY Acad Sci* 188:110–141
- Perkins PJ, Fish MP, Mowbray WH (1966) Underwater communication sounds of the sperm whale (*Physeter catodon*). *Norw Whal Gaz* 55:224–228
- Rice DW (1989) Sperm whale (*Physeter macrocephalus* Linnaeus, 1758). In: Ridgway SH, Harrison R (eds) *Handbook of marine mammals*, vol 4. Academic Press, New York
- Ridgway SH, Carder DA (1988) Nasal pressure and sound production in an echolocating white whale, *Delphinapterus leucas*. In: Nachtigall PE, Moore PWB (eds) *Animal sonar systems: processes and performance*. Plenum Press, New York, pp 53–60
- Ridgway SH, Carder DA (2001) Assessing hearing and sound production in cetacean species not available for behavioral audiograms: experience with *Physeter*, *Kogia*, and *Eschrichtius*. *Aquat Mammal* 27:267–276
- Schnitzler H-U, Hackbarth H, Heilmann U, Herbert H (1985) Echolocation behavior of rufous horseshoe bats hunting for insects in the flycatcher-style. *J Comp Physiol A* 157:39–46
- Simmons JA, Fenton BM, O'Farrell MJ (1979) Echolocation and pursuit of prey by bats. *Science* 203:16–21
- Thode A, Mellinger DK, Stienessen S, Martinez A, Mullin K (2002) Depth-dependent acoustic features of diving sperm whales (*Physeter macrocephalus*) in the Gulf of Mexico. *J Acoust Soc Am* 112:308–321
- Tyack P, Clark CW (2000) Communication and acoustic behavior of whales and dolphins. In: Au WWL, Popper AN, Fay RR (eds) *Hearing in whales and dolphins. Handbook on Auditory Research*. Springer, Berlin Heidelberg New York, pp 156–224
- Urick RJ (1983) *Principles of underwater sound*, 3rd edn. McGraw-Hill, New York
- Verfuss U, Miller LA, Schnitzler HU (2000) Fish catch and echolocation behavior of the harbour porpoise (*Phocoena phocoena*). Proceedings of the fourteenth annual conference of the European Cetacean Society
- Wahlberg M (2002) The acoustic behavior of diving sperm whales observed with a hydrophone array. *J Exp Mar Biol Ecol* 281:53–62
- Wahlberg M, Møhl B, Madsen PT (2001) Estimating source position accuracy of a large aperture hydrophone array for bioacoustics. *J Acoust Soc Am* 109:397–406

- Watkins WA (1980) Acoustics and the behavior of sperm whales. In: Busnel R, Fish FJ (eds) Animal sonar systems. Plenum Press, New York, pp 283–289
- Watkins WA, Schevill WE (1974) Listening to Hawaiian spinner porpoises, *Stenella cf. longirostris*, with a three-dimensional hydrophone array. *J Mammal* 55:319–328
- Watkins WA, Schevill WE (1977) Sperm whale codas. *J Acoust Soc Am* 62:1485–1490
- Watkins WA, Moore KE, Tyack P (1985) Sperm whale acoustic behaviors in the southeast caribbean. *Cetology* 49:1–15
- Watkins WA, Daher MA, Fristrup KM, Howald TJ (1993) Sperm whales tagged with transponders and tracked underwater by sonar. *Mar Mammal Sci* 9:55–67
- Watkins WA, Daher MA, DiMarzio NA, Samuels A, Wartzok D, Fristrup KM, Howey PW, Maiefski RR (2002) Sperm whale dives tracked by radio tag telemetry. *Mar Mammal Sci* 18:42–54
- Weilgart L, Whitehead H (1988) Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). *Can J Zool* 66:1931–1937
- Weilgart L, Whitehead H (1993) Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Can J Zool* 71:744–752
- Weilgart L, Whitehead H (1997) Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav Ecol Sociobiol* 40:277–285
- Weilgart L, Whitehead H, Payne K (1996) A colossal convergence. *Am Sci* 84:278–287
- Whitehead H (1993) The behavior of mature male sperm whales on the Galapagos breeding grounds. *Can J Zool* 71:744–752
- Whitehead H, Weilgart L (1991) Patterns of visually observable behavior and vocalizations in groups of female sperm whales. *Behavior* 118:275–296
- Whitehead H, Dillon M, Dufault S, Weilgart L, Wright J (1998) Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. *J Anim Ecol* 67:253–262
- Whitney W (1968) MPL-U-11/68. Marine Physical Laboratory, Scripps Institution of Oceanography
- Worthington LV, Schevill WE (1957) Underwater sounds heard from sperm whales. *Nature* 10:291