

Sound production in neonate sperm whales (L)

P. T. Madsen^{a)}

The Whale Conservation Institute, Lincoln, Massachusetts and Department of Zoophysiology, University of Aarhus, 8000 Aarhus C, Denmark

D. A. Carder

Navy Marine Mammal Program, SSC SD, San Diego, California

W. W. L. Au and P. E. Nachtigall

Marine Mammal Research Program, Hawaii Institute of Marine Biology, Hawaii

B. Møhl

Department of Zoophysiology, University of Aarhus, 8000 Aarhus C, Denmark

S. H. Ridgway

Navy Marine Mammal Program, SSC SD, San Diego, California

(Received 30 August 2002; revised 21 January 2003; accepted 14 March 2003)

Acoustic data from two sperm whale neonates (*Physeter macrocephalus*) in rehabilitation are presented and implications for sound production and function are discussed. The clicks of neonate sperm whale are very different from usual clicks of adult specimens in that neonate clicks are of low directionality [SL anomaly (0° – 90°) < 8 dB], long duration (2–12 ms), and low frequency (centroid frequency between 300 and 1700 Hz) with estimated SLs between 140 and 162 dB/1 μ Pa (rms). Such neonate clicks are unsuited for biosonar, but can potentially convey homing information between calves and submerged conspecifics in open ocean waters at ranges of some 2 km. Moreover, it is demonstrated that sperm whale clicks are produced at the anterior placed monkey lips, thereby substantiating a key point in the modified Norris and Harvey theory and supporting the unifying theory of sound production in odontocetes. © 2003 Acoustical Society of America. [DOI: 10.1121/1.1572137]

PACS numbers: 43.80.Ka, 43.80.Gx [FD]

I. INTRODUCTION

Norris and Harvey (1972) proposed that the sperm whale nasal complex, homologous with the sound producing nasal complex of smaller odontocetes (Cranford *et al.*, 1996), is a giant generator of clicks to be used for echolocation and communication. Array recordings have shown that sperm whales produce usual clicks with the highest source levels ever recorded in the animal kingdom (Møhl *et al.*, 2000, 2003) and show properties of high directionality (Møhl *et al.*, 2000, 2003; Thode *et al.*, 2002). Ridgway and Carder (2001) found that clicks are produced at the foremost part of the nasal complex, and deployment of sound recording tags has demonstrated that sperm whales produce at least two click types, usual clicks suited for biosonar, and coda clicks more suited for communication (Madsen *et al.*, 2002b). The latter study also revealed that sperm whales can maintain and regulate the acoustic output down to at least 700 m of depth, and that the clicks show properties similar to clicks from smaller odontocetes (Madsen *et al.*, 2002b). Acoustic experiments on recently expired sperm whales have shown that the spermaceti compartments of the nasal complex can transmit sound (Møhl, 2001), and that the spermaceti organ and the junk form an acoustic continuum (Møhl *et al.*, 2002).

Here we present acoustic data opportunistically collected from two neonate sperm whales in rehabilitation and discuss implications for sound production and function.

II. MATERIALS AND METHODS

A. Galveston calf

A neonate (umbilicus not healed), male sperm whale with a body length of 341 cm and a body weight of 546 kg was found stranded at Sabine Pass, Texas in September 1989 and moved to Sea-Arama Marine World for rehabilitation. Seven recording sessions were carried out in a 1-m deep, 3×10 m² concrete pool with a Racal Store7 instrumentation recorder with Ampex 797 tapes operated at varying tape speeds (17/8–60 ips). Two calibrated B&K 8103 hydrophones were connected to two B&K 2635 charge amplifiers, relaying the signals to the instrumentation recorder. Clicks were digitized with a PC-sound card (flat frequency response between 0.01 and 17 kHz) and analyzed with Cool Edit 2000 (*Syntrillium*), and custom designed routines in Matlab (*Mathworks 6.0*).

The rms sound pressures were obtained by integrating the square of the pressure over the interval between the -3 -dB end points of the envelope of the signal and comparing it with calibration signals, recorded on the tapes. Source levels were estimated by back calculating (spherical spreading) from received sound pressure levels and from the distance between the whale and the hydrophones (noted on the tapes and documented by photographs). Durations of the clicks were defined as the time between the -10 -dB points of the envelope of the signal.

^{a)}Electronic mail: peter.teglberg@biology.au.dk

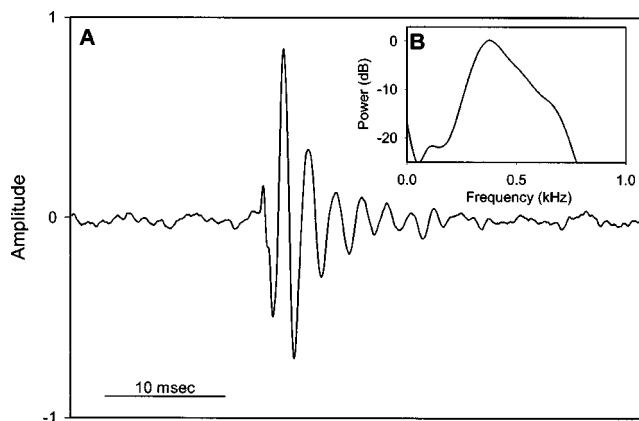


FIG. 1. (a) Waveform of a representative click from the Galveston neonate. SL of 160 dB//1 μ Pa rms. (b) Power spectrum of the click depicted in (a). Sample rate 48 kHz. FFT size 1024.

B. Kona calf

A neonate (umbilicus not healed), female sperm whale with a body length of 312 cm and an estimated weight of 400 kg was found stranded on the beach of Kona, Big Island, Hawaii on 14 August 2001. For rehabilitation, the animal was taken to a 1.2-m-deep, temporary pool (diameter of 6 m) at the Natural Energy Laboratory, Kona, Hawaii. The recording setup consisted of two calibrated B&K 8103 hydrophones connected to a custom built amplifier and a Sony TCD-D3 DAT recorder sampling at 48 kHz. During each recording session, the hydrophone placement was documented with a digital camera (courtesy of C. R. Kastak) and noted on the tapes. Time of arrival differences (TOADs) at the two hydrophones of the same click were determined by using cross-correlation routines written in Matlab (courtesy of M. Wahlberg). Post mortem, a dissection was conducted on the nasal complex, yielding data on the morphometrics of the structures involved in sound production and relative placement of the hydrophones.

III. RESULTS

A. Galveston calf

Preliminary results of acoustic recordings from this calf were presented in Ridgway and Carder (2001). Here a more detailed account is provided. A total of 253 clicks and 47 grunts were analyzed from seven recording sessions. The waveforms of the clicks have no apparent multipulse structure [Fig. 1(a)] and centroid frequencies between 300 and 1000 Hz [Fig. 1(b)] with -10 dB BW of 200–400 Hz (Table I). Duration of the clicks varied between 5 and 12 ms and may include some distortions due to the small tank size. Estimated click SLs (referred to 1 m from the anterior termi-

nation of the spermaceti organ) range from 150 to 162 dB//1 μ Pa rms. During one of the recording sessions, a hydrophone was suspended at one measured meter ahead of the animal and another hydrophone 1 m from the side of the animal, perpendicular to the eye as the calf was held in the water. Derived SLs were 4–8 dB higher when recorded with the hydrophone 1 m in front of the animal than when recorded lateral to the eye, thereby indicating a low, but present, directionality. Frequency content and duration of clicks recorded from these two aspects were alike. Grunts have messy waveforms with likely some distortions from pool walls and surface with durations of 50–150 ms and frequency emphasis around 500 Hz. Derived grunt SLs varied between 140 and 152 dB//1 μ Pa rms [also see grunt spectrograms published by Ridgway and Carder (2001)]. No consistent directionality effects pertaining to SL, frequency or duration were observed in the grunts.

B. Kona calf

A total of 58 clicks were recorded from this individual. Estimated SLs ranged from 150–161 dB// μ Pa rms. Estimated SLs from the two employed hydrophones differed by less than 6 dB, indicating a low directionality of the clicks. Frequency content and duration of the clicks were generally comparable to those of the Galveston calf (Table I). However, two clicks had a significantly different frequency content with peak frequencies around 8 kHz, but still no apparent multipulse structure. Four clicks contained two high frequency pulses (around 8 kHz), spaced 0.7 msec. No grunts were recorded from this individual.

34 of the 58 clicks were recorded from hydrophones, spaced 13 cm apart, held at the distal sac (hydrophone 1) and at the anterior part of the junk (hydrophone 2) (Fig. 2). A consistent TOAD was observed between the two hydrophones. The clicks recorded by the hydrophone placed at the anterior part of the junk were received with a delay of some 50 μ s relative to the hydrophone placed at the distal sac. Based on this TOAD and knowledge of the speed of sound in the tissues, the sound source location can be restricted to a hyperboloid surface in the nasal complex (*ad modum* Diercks *et al.*, 1971). However, it may be too simplistic to assume a fixed sound speed in the various tissue types of the head for which reason two hyperboloid surfaces were generated, one for a sound speed of 1300 m/s and one for 1500 m/s to cover the relevant range of sound speeds in biological tissues. The hyperbolic interceptions between these hyperboloid surfaces and the sagittal plane of the nasal complex are depicted in Fig. 2. It is seen that the hyperbolas are passing the location of the monkey lips. For further details on the morphology of this calf, see Møhl *et al.* (2002)

TABLE I. Characteristics of sound types from neonate sperm whales.

Sound type	SL (rms) (dB//1 μ Pa)	SL (pp) (dB//1 μ Pa)	Duration (ms)	Centroid frequency (Hz)	-10 dB BW (Hz)
Galveston Click	154–162	162–175	5–12	300–1000	200–350
Galveston Grunt	140–155	150–165	50–150	200–700	200–700
Kona Click	150–161	161–174	2–15	500–1700	200–450

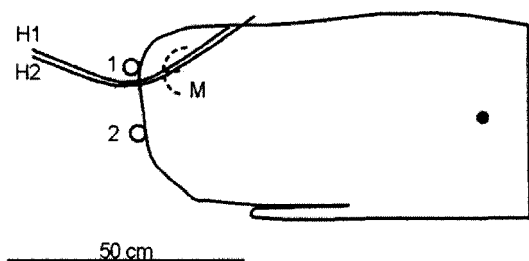


FIG. 2. Hydrophone placement (1,2) on the head of the Kona calf. H: Hyperbolas (1: sound speed of 1500 m/s, 2: sound speed of 1300 m/s) given by the interception between the sagittal plane of the neonate head and the hyperboloid surfaces derived from the consistent TOAD between hydrophone 1 and 2. M: Monkey lips. Location of the monkey lips is based on a photo-documented dissection of the animal.

IV. DISCUSSION

The present data should be evaluated in the light of the opportunistic nature of recordings in temporary holding tanks not suited for acoustic investigations, and considering that the rehabilitating neonates most likely were not in good health. Despite this situation, the difference in recording gear and the different reverberation patterns in two different pool types, the recorded clicks from the two neonates are generally alike in having -10 -dB bandwidths of 200 to 450 Hz, centroid frequencies around 500 Hz, SLs up to 162 dB//1 μ Pa rms, and durations of 2–15 ms (Table I). These source characteristics match the click properties of young sperm whale calves, reported by Watkins *et al.* (1988), and thus seem to be representative of the click repertoire of sperm whale neonates.

A few unusual higher frequency clicks from both calves, having pulses with frequency emphases at 8–16 kHz, did not fit the general picture. It is possible that these unusual higher frequency clicks are a beginning in the ontogeny of echolocation click that may be employed by the adult sperm whale (Møhl *et al.*, 2002). In the Kona calf, four clicks contained two such pulses with an interpulse interval (IPI) of 0.7 ms. It can be conjectured that the first pulse may represent the initial sound production event and the second pulse had traversed the spermaceti organ and junk of the nasal complex before entering the water. However, the lack of additional trailing pulses makes such a notion speculative. An IPI of 0.7 msec is intriguing, as it is comparable to an IPI of 0.8 ms found by projecting artificial pings into the nasal complex of the same, expired animal (Møhl *et al.*, 2002). In addition, an IPI of 0.7 ms is consistent with the two-way-travel time between the distal and the frontal air sac of the Kona neonate and the speed of sound in spermaceti oil (Møhl *et al.*, 2002). This finding is supportive of the view that the IPI of sperm whale usual clicks and coda clicks is given by the two-way-travel time of the spermaceti compartments (Norris and Harvey, 1972; Gordon, 1991), and that the spermaceti compartments are involved in sperm whale sound production. Due to the low-frequency nature and long duration of all other clicks produced, it is not possible to discuss the potential involvement of the spermaceti compartments in the production of these clicks.

Although the neonate clicks were generated in short trains, they do not show the repetitive, stereotyped click pat-

terns found in codas produced by juvenile and adult sperm whales for communicative purposes (Watkins and Schevill, 1977; Weilgart and Whitehead, 1993). Older calves produce repetitive trains of two to five clicks that may be viewed as coda-precursors (Watkins *et al.*, 1988), but the random number of clicks and irregular click rate of these phonating neonates rather indicate that the number of clicks is likely not yet fully controlled. Watkins *et al.* (1988) argue that the long duration and low-frequency emphasis of most calf clicks make them unsuited for echolocation, and that they consistently resemble the properties of clicks from adult sperm whales. We do not share the latter view as adult sperm whale usual clicks have a multipulse structure totally dominated by a single p1 pulse of short duration with very high SL (Møhl *et al.*, 2000, 2003), high directionality (Møhl *et al.*, 2000, 2003; Thode *et al.*, 2002), and a frequency emphasis between 5 and 32 kHz (Watkins, 1980; Madsen *et al.*, 2002a), and are therefore not comparable to calf clicks (Table I).

The properties of the calf clicks are, as noted by Watkins *et al.* (1988) and in contrast to usual adult clicks, indeed not favorable for echolocation. Biosonar-signals should be of a shorter duration, higher frequency and more directional to allow for adequate temporal and spatial resolution in a noisy and cluttered environment (Au, 1993). While the apparent need for biosonar signals is very small in calves that are entirely nourished from suckling the first year of their lives (Rice, 1989), the need for communicative signals to maintain contact with babysitting adults seems more likely. Sperm whale calves remain at the surface while their mothers undertake feeding dives apparently too deep and too long for the calves to follow. This has led to development of asynchronous dive behavior and allomaternal care in the form of babysitting where calves at the surface are accompanied and often suckled by a number of different females (Gordon, 1987; Whitehead, 1996). Thus, sperm whale calves are unaccompanied at the surface for up to 31% of the time, and female sperm whales take turns in babysitting between feeding dives (Whitehead, 1996).

Considering the reduced mobility of neonate calves compared to their babysitters, it would seem advantageous if the calves produced homing signals to facilitate maternal localization. A maximized communicative space is achieved by using long duration, omni-directional signals of low frequency. Sperm whale calf clicks have such properties and we propose that these rudimentary clicks may play a communicative role in the allomaternal behavior of asynchronous dives and babysitting in sperm whales. The passive sonar equation can be used to assess the possible detection range of calf clicks by adult, babysitting whales. Assuming that a sperm whale neonate calf can be modeled as an omnidirectional source with a SL of 160 dB//1 μ Pa rms, and using a spectral noise density of 60 dB//1 μ Pa²/Hz at 500 Hz (Urlick, 1983), an auditory filter bandwidth corresponding to the centralized RMS-BW (Au, 1993) of a representative calf click (250 Hz) and a S/N of 10 dB for detection, it can be estimated that sperm whale calf clicks can be detected by conspecifics at a range of some 2 km [transmission loss=160 dB//1 μ Pa rms-(10 dB+60 dB// μ Pa²/Hz+10 log(250 Hz))=66 dB, which corresponds to 2

km, assuming spherical spreading]. Such a range estimate may only be valid if the receiving whale is submerged in deep water away from the acoustic shadow zone.

The Galveston calf produced a large number of grunts, which are very different from clicks. This difference may relate to the structures involved in sound production as grunts appear to be produced near the frontal sac at the base of the skull [see Figs. 2–4 in Ridgway and Carder (2001)] and thus not at the monkey lips as is the case for clicks (see below). We have no clues as to the functional significance of grunts, but, considering that they generally have SLs some 10–15 dB lower than clicks, suggests that the potential communicative range would be reduced by a factor of 3–5.

Norris and Harvey (1972) surmised that the monkey lips, homologous with the phonic lips in delphinoids (Cranford *et al.*, 1996), are the sound source in sperm whales. That observation has gained support from palpative studies (Ellis, 1981) and palpative/stethoscope investigations (Ridgway and Carder, 2001), concluding that the sound source is located at the foremost part of the nasal complex of sperm whales, beneath the blowhole. From the consistent TOADs between the two hydrophones held at the anterior part of the nasal complex of the Kona calf, the location of the sound source could be restricted to a hyperboloid surface. When relating the hydrophone placement and the derived hyperboloid surfaces with the morphometrics of this calf (Fig. 2), it becomes evident that both hyperboloid surfaces are passing the location of the monkey lips. This finding is not only excluding a laryngeal sound source, but also demonstrating that the sound source for click generation in sperm whales is indeed the monkey lips. This demonstration substantiates a key point in the modified Norris and Harvey theory (Møhl, 2001), where the initial sound pulse of multipulsed usual clicks is to be generated at the monkey lips, before transmission through the acoustic continuum formed by the spermaceti organ and the junk.

With the vital sound source placed at the foremost part of the nasal complex, it would indeed be surprising if the primary use of the nasal complex of sperm whales is a ramming device in male-male interactions, as recently suggested by Carrier *et al.* (2002). Moreover, in their unifying theory of odontocete sound production, Cranford *et al.* (1996) proposed that clicks are produced in the same biomechanical way by homologous structures across the entire odontocete suborder. The present demonstration of sound production in the monkey lips is consistent with that notion.

ACKNOWLEDGMENTS

We thank a number of people for assistance during investigations and for valuable comments on the manuscript. Experiments were carried out under the authority of a permit afforded to S. H. Ridgway and all investigations were conducted in accordance with the conditions of that permit. The work on the Galveston calf was funded by ONR grants, issued to S. H. Ridgway and D. A. Carder by Dr. R. Gisiner. The Kona calf study was supported by the Edwin M. Pauley Foundation Summer Program of the Hawaii Institute of Ma-

rine Biology via a grant issued to P. E. Nachtigall. Additional support for equipment was available from ONR Grant No. N00014-98-1-0687 to P. E. Nachtigall and W. W. L. Au administered by Dr. R. Gisiner. Analysis was funded by the Danish National Research Foundation through Center for Sound Communication, USD.

- Au, W. W. L. (1993). *The Sonar of Dolphins* (Springer Verlag, New York).
- Carrier, D. R., Deban, S. M., and Otterstrom, J. (2002). "The face that sank the *Essex*: potential function of the spermaceti organ in aggression," *J. Exp. Biol.* **205**, 1755–1763.
- Cranford, T. W., Amundin, M., and Norris, K. S. (1996). "Functional Morphology and Homology in the Odontocete Nasal Complex: Implications for Sound Generation," *J. Morphol.* **228**, 223–285.
- Diercks, K. T., Trochta, R. T., Greenlaw, C. F., and Evans, W. E. (1971). "Recording and analysis of dolphin echolocation signals," *J. Acoust. Soc. Am.* **49**, 1729–1732.
- Ellis, R. (1981). "The whale that visited New York," *Bull. Am. Littoral Soc.* **13**, 5–12.
- Gordon, J. C. (1987). "The Behaviour and Ecology of Sperm Whales off Sri Lanka," Ph.D. thesis, Darwin College, Cambridge, UK.
- Gordon, J. C. (1991). "Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations," *J. Zool. Lond.* **224**, 301–314.
- Madsen, P. T., Wahlberg, M., and 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., Wahlberg, M., Kerr, I., and Møhl, B. (2002b). "Sperm whale sound production studied with ultrasound-time-depth-recording tags," *J. Exp. Biol.* **205**(13), 1899–1906.
- 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., Wahlberg, M., Madsen, P. T., Heerford, A., and Lund, A. (2003). "The monopolised nature of sperm whale sonar clicks," *J. Acoust. Soc. Am.* (in press).
- Møhl, B., Wahlberg, M., Madsen, P. T., Miller, L. A., and Surlykke, A. (2000). "Sperm whale clicks: Directionality and source level revisited," *J. Acoust. Soc. Am.* **107**, 638–648.
- Møhl, B., Madsen, P. T., Wahlberg, M., Au, W. W. L., Nachtigall, P., and Ridgway, S. (2002). "Sound transmission in the spermaceti complex of a recently expired sperm whale calf," *Acoust. Res. Lett. Online* **4**(1), 19–24.
- Norris, K. S., and Harvey, G. W. (1972). "A Theory for the Function of the Spermaceti Organ of the Sperm Whale," *NASA SP-262*, 397–417.
- Rice, D. W. (1989). "Sperm Whale (*Physeter macrocephalus* Linnaeus, 1758)," in *Handbook of Marine Mammals*, edited by S. H. Ridgway and R. Harrison (Academic, New York), Vol. 4.
- Ridgway, S. H., and Carder, D. (2001). "Assessing hearing and sound production in cetacean species not available for behavioral audiograms: experience with *Physeter*, *Kogia*, and *Eschrichtius*," *Aquat. Mammals* **27**, 267–276.
- Thode, A., Mellinger, D. K., Stienessen, S., Martinez, A., and 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.
- Urick, R. J. (1983). *Principles of Underwater Sound*, 3rd ed. (McGraw-Hill, New York).
- Watkins, W. A. (1980). "Acoustics and the behavior of sperm whales," in *Animal Sonar Systems*, edited by R. Busnel and F. Fish (Plenum, New York), pp. 283–289.
- Watkins, W. A., and Schevill, W. E. (1977). "Sperm whale codas," *J. Acoust. Soc. Am.* **62**, 1485–1490.
- Watkins, W. A., Moore, K. E., Clark, C. W., and Dahlheim, M. E. (1988). "The sounds of sperm whale calves," in *Animal Sonar, Processes and Performance*, edited by P. E. Nachtigall and P. W. B. Moore (Plenum, New York), pp. 99–107.
- Weilgart, L., and Whitehead, H. (1993). "Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands," *Can. J. Zool.* **71**, 744–752.
- Whitehead, H. (1996). "Babysitting, dive synchrony, and indications of alloparental care in sperm whales," *Behav. Ecol. Sociobiol.* **38**, 237–244.