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ORIGINAL PAPER

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Sound transmission in the nose of the sperm whale *Physeter catodon*. A post mortem study

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Abstract During a sperm whale stranding at Rømø, the Wadden Sea, Denmark, on 4 December 1997, we were notified in time to start acoustic transmission measurements in the spermaceti complex 1 h after the specimen was seen alive. Frequency-modulated sound pulses, sweeping from 30 kHz to 10 kHz in 25 ms, were injected at the frontal surface at two positions: at the distal sac, and at the center of the junk (a compartmentalized structure below the spermaceti organ). A hydrophone next to the projector served as receiver. The analyses of the recordings show a repetitive, decaying reflection pattern at both projection sites, reminiscent of the multi-pulse click peculiar to sperm whales, although with minor differences in the duration of the intra-click intervals. This experimental evidence supports the Norris and Harvey (1972) theory of click generation in the spermaceti organ. Accordingly, the click is composed of a primary event, followed by a train of reflected pulses, spaced by the time required for the event to travel back and forth between air sacs (reflectors) at each end of the organ. The results also show that the junk readily transmits sound and probably is in acoustic contact with the spermaceti organ.

Keywords Norris/Harvey theory · Bent horn model · Spermaceti organ · Multi-pulse click · Sound generator

Abbreviations *ACR* autocorrelation function · *FM* frequency-modulated sound · *IPI* inter-pulse interval · *peRMS* peak equivalent root-mean-square · *TBL* total body length · *TWT* two-way transit time

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Introduction

The sperm whale owes its peculiar appearance to the grossly enlarged forehead. This structure, accounting for up to one-third of the total body length or body weight, is distinctly different from homologous structures in the smaller odontocete species (Cranford et al. 1996). In these odontocetes, the tissues involved in sound production are situated above the bony nares and below the blowhole, immediately in front of the brain case and behind an impedance matching structure, the fatty melon. In the sperm whale (Fig. 1), the sound-generating structures with their associated nasal ducts and blowhole have migrated forward and above the homologous structure of the melon during fetal development. A small, fatty structure, the right posterior bursae of other odontocetes, has expanded enormously to become the spermaceti organ, a bag of fluid wax (the spermaceti) extending from the frontal air-sac, which lines the trough of the skull, to the museau du singe (monkey muzzle, a set of lips of tough connective tissue) beneath the blowhole (Cranford 1999). In front of the museau is another air sac, called the distal sac. The spermaceti organ attains a length of about 5 m and has a tapering, round cross-section (Amundin 1991, Fig. VII.4). The underlying, melon derived tissue is broken up in some 20 compartments or lenses, containing spermaceti. This structure was called the 'junk' by whalers, a name still in use. Surrounding this complex is a layer of long tendons and muscles, pulling from the skull and inserting into the general area of the distal sac and the museau.

The most common sound of this odontocete is as peculiar as its anatomy: clicks, composed of a train of regularly spaced, decaying pulses (Fig. 2), first reported by Backus and Schevill (1966). Norris and Harvey (1972) proposed that this pattern was the result of a single acoustic pulse being reflected multiple times between two acoustic mirrors (frontal sac, A, and distal sac, E, in Fig. 1) within the nasal structure of the whale, and that the inter-pulse interval (IPI) represented the

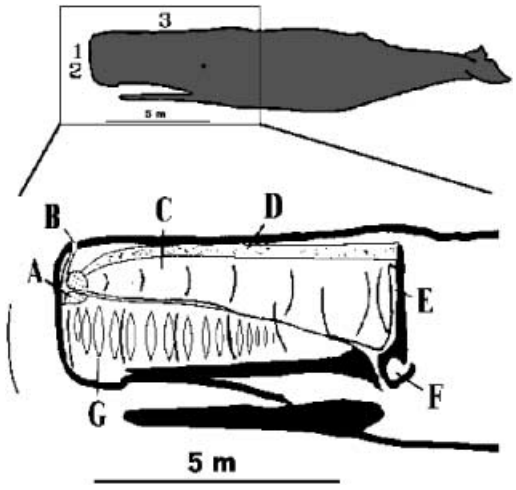

Fig. 1 Sketch of proposed sound generation mechanism in the sperm whale (bent horn model). *Numerals* indicate stimulation sites (redrawn from Møhl 1992). *A* monkey muzzle; sound-generating site. Covered anteriorly by the distal sac; *B* duct to blow-hole; *C* spermaceti case. Filled with liquid wax, sound velocity about 1.3 m ms^{-1}; *D* muscle layer. Pulling power about 10 tonnes; *E* frontal airsac, slightly concave; *F* brain case; *G* bodies of spermaceti in the 'junk'

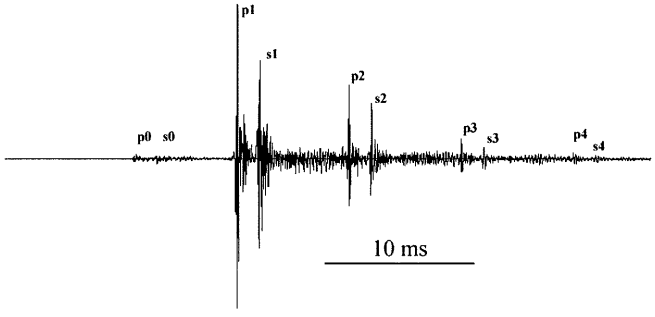

Fig. 2 Sperm whale click wave form, selected to show the regular spaced multi-pulse pattern. Individual pulses are labeled according to the convention of Møhl and Amundin (1991), s-pulses signifying surface reflected pulses

two-way transit time (TWT) between the mirrors. Mackay (1972, 1980), proposed a slightly modified mechanism, in which the reflected pulse triggered the release of energy, generating the next pulse (the bugle model). In both schemes, the most intense pulse is considered to be the primary event (p1), radiated directly into the water. Møhl and Amundin (1991) and Møhl et al. (2000) described a low amplitude pulse (p0) preceding the p1 pulse and proposed that p0 is the primary event that is radiated directly and possibly omni-directionally, while the p1 has traveled from the generation site (the museau) back to the frontal sac, reflected forward and then radiated from the flat, frontal surface of the junk (Fig. 2). In this scheme, the trailing pulses are derived from a small fraction of the reflected pulse returning via the spermaceti organ to the distal sac, where it is re-reflected and starting another round trip.

The hypotheses mentioned, as well as a number of quite different ideas about the possible function of the spermaceti complex, are primarily based on anatomical observations (which now includes a wealth of quantitative details from CT-scanning of a sperm whale head (Cranford 1999). However, physiological measurements are lacking since the idea of a captive, cooperative sperm whale is unrealistic at present. Also, since whaling has been banned for about 25 years, there is little opportunity to experiment with fresh preparations. What is left are stranded whales, mostly in a state of decomposition that makes physiological-acoustic experiments futile.

On 4 December 1997, a pod of 13 male sperm whales stranded at Rømø in the Wadden Sea (Jensen 1999). We received an early warning and arrived at the scene of a stranded, semi-submerged and subsequently drowned specimen, about an hour after it was observed to be alive. In the following, we report observations from injecting sounds into the spermaceti complex and recording the reverberation pattern within the nose of this whale. The main findings are: (1) that a single excitation at the distal sac produced a multi-pulse pattern much like that reported from live sperm whales, (2) that such a pattern was also produced by injecting pulses into the junk, suggesting that the compartmentalized junk and the spermaceti bag form an acoustic continuum; and (3) that pulses injected dorsally about 3 m behind the tip of the snout did not generate a multi-pulse pattern.

Material and methods

The whale, a bull of 15.1 m total body length (TBL), trapped in a shallow lead during ebb, was lying on its left side and had probably drowned, being unable to raise the blow hole out of the water. At arrival of the recording team, only the part of the head from a little forward of the right eye and rearwards was above the water. Water depth was 2 m.

Sounds were transmitted from a custom made electro-dynamic projector. Hand-triggered pulses, sweeping from 30 kHz to 10 kHz in 25 ms were fed to the projector. The maximum level was 162 dB re 1 μPa peak equivalent root-mean-square (peRMS) at 1 m in water. The frequency response of the projector varied ±8 dB in the frequency range below 22 kHz. A Brüel and Kjaer 8100 hydrophone served as the receiver, followed by an Etec HA01A amplifier, set at 26 dB gain. The recorder was a Sony TCD-3 DAT recorder, operated at a clock-rate of 48 kHz. This limited the frequency response of the recording system to a nominal 22 kHz and caused aliasing from energy above 24 kHz. Both transducers were hand-held against the surface of the whale by two skin divers. The recording session lasted 8 min.

Points of sound application were at the distal sac (marker 1 in Fig. 3), at the center of the front of the junk (marker 2), and at the top of the head, 3 m behind the front. All positions were below the water surface. The receiver was placed next to the transmitter in the two first cases (monostatic configuration), and at the distal sac in the last case (bistatic). Seventeen pings were produced at the distal sac, 12 at the junk, and 2 at the top of the head. The latter produced no reflection patterns above noise; only the direct signal (p0) could be detected. The returns at the two former places were quite similar within each set, so just one example for each is described below.

For analysis, the tape was first converted to wav-file format by a Zefiro-II card and then imported into a sound editing program (CoolEdit 96). Auto-correlation was carried out by custom-made software (A. Heerfordt).

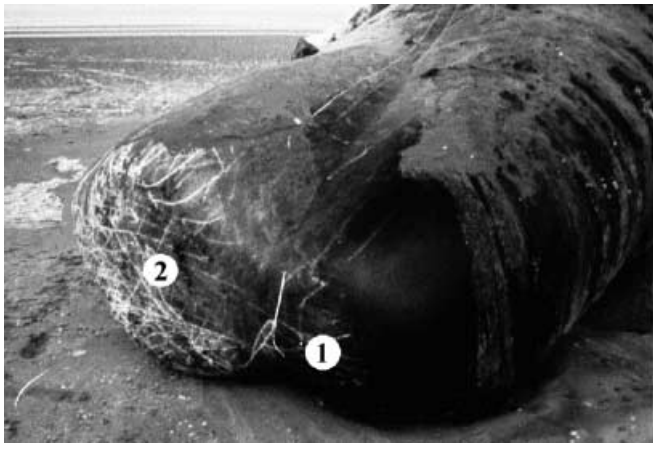

Fig. 3 Frontal aspect of a stranded sperm whale bull, lying on its left side. *Marker 1* indicates sound injection and recording site at the distal air sac; *marker 2* indicates the site at the frontal surface of the junk compartment. Note the 'over-and-under barrel'-organization of the spermaceti-complex with lateral groves separating the spermaceti bag from the junk. Note also the flat and abrupt termination of the latter, and its dense pattern of white scars, believed to be acquired during fights with other bulls (The photo is of a different member of the same pod of similar sized whales)

The choice of the stimulating signal was dictated by availability of equipment. However, a frequency-modulated (FM) pulse with a high bandwidth-time product has good timing properties, as well as high energy in peak-limited equipment.

Results

The excitation pulse has a duration of 25 ms, which is long in relation to the TWT within the complex (about 7.5 ms). Consequently, the high-amplitude, direct signal and the first reflections are overlapping and cannot readily be separated in an oscillogram. However, in a sonagram format (Fig. 4), the characteristic, regularly spaced repetition of the down-sweeping signal is fairly obvious. The emphasis at the highest and lowest frequencies is caused by the transmitter response. The broadband transients at 1 ms and 26 ms mark the on- and off-time of the stimulus.

To quantify the intervals between the set of pulses in Fig. 4, the envelope of the one-sided autocorrelation function (ACR) of the waveform was computed and its envelope obtained via Hilbert transformation. A low-pass filtration to 4 kHz was used to smooth the ACR. To emphasize the low-amplitude late returns, a semi-logarithmic presentation format has been adopted (Fig. 5). Here, the same symbols are used to label the peaks as in Fig. 2 although their nature is quite different. The delays between the peaks are, however, controlled by the same phenomenon.

Intervals between the four peaks in Fig. 5 are 7.7 ms, 6.9 ms, and 7.7 ms, respectively. An 'out-of-order'-reflection is seen trailing p1 in Fig. 4, but is not clearly discernible in the ACR (Fig. 5). For comparison, the sperm whale click of Fig. 2 was treated in the same way. Here, all three intervals in the range p1–p4 came out as 7.5 ms. Note that p2 in Fig. 5 is broader than the other pulses. Such a broadening is not seen in the analogous sperm whale click function.

With both transducers placed at the junk, the general picture (Fig. 6) is similar but the signal to noise ratio is somewhat lower. A distinct extra reflection is apparent between p0 and p1. No reflection later than p2 is detectable. The envelope of the ACR of the junk-ping is given in Fig. 7. The intervals in this function are: p0–p1: 8.1 ms, p1–p2: 6.6 ms. A small peak is trailing p2 by 1.1 ms. Delay between p0 and the extra reflection before p1 is 4.5 ms. A broadening of the p2 peak similar to that in Fig. 5 is seen.

Sound injection at the dorsal side of the nose resulted in only one, detectable sweep, interpreted to be the directly transmitted signal (p0), propagated through the water.

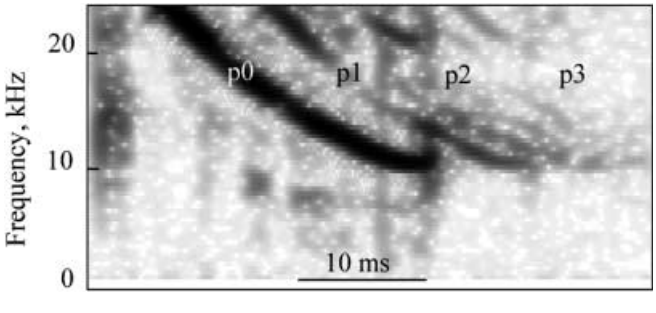

Fig. 4 Sonagram description of recording obtained with the transducers held against the distal sac (marker 1 in Fig. 3). Resolution 375 Hz, Blackman weighted; dynamic range 80 dB. The primary event, labeled *p0* is the direct transmission between the transmitter and the receiver. Reflections p1, p2 and p3 are marked. Additional, weaker reflections can be identified. A broad-band click at the onset and termination of excitation is seen. Aliasing effects are seen at the beginning of p0 and p1

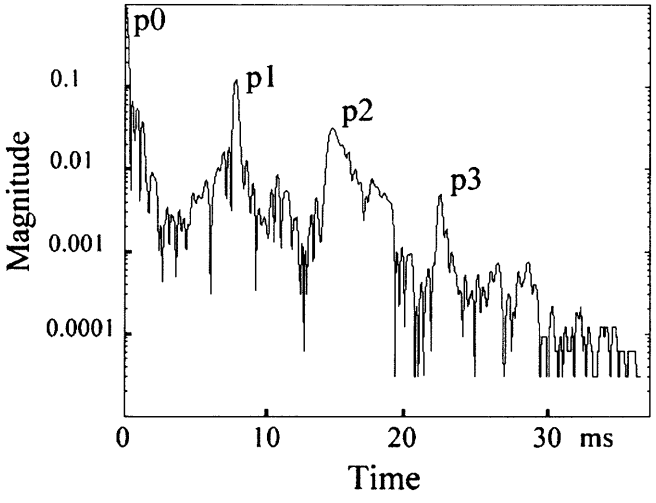

Fig. 5 Envelope of the one-sided autocorrelation function of the signal in Fig. 4. Semi-logarithmic plot. Peaks labeled as in Fig. 4

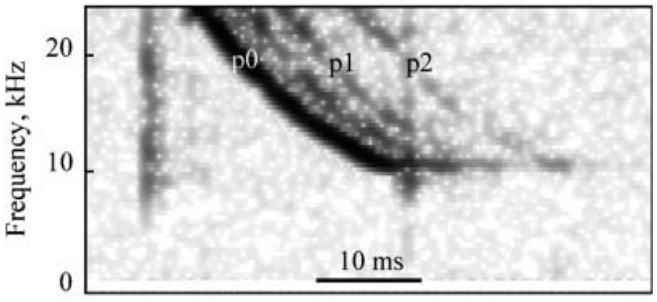

Fig. 6 Sonagram description of recording obtained with the transducers held against the junk (marker 2 in Fig. 3). See legend for Fig. 4 for other details

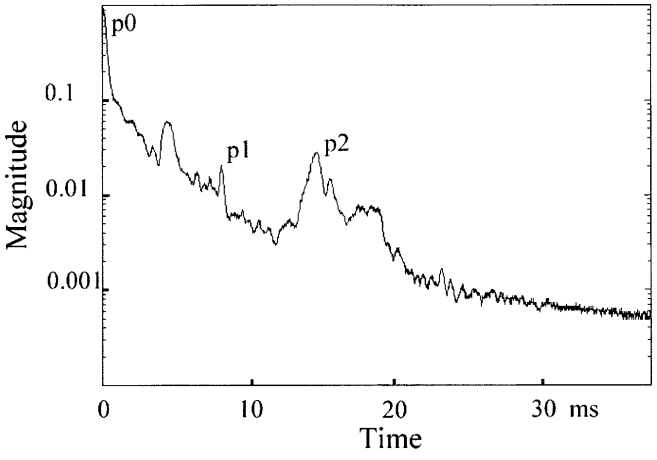

Fig. 7 Envelope of the one-sided autocorrelation function of the signal in Fig. 6 (junk). Semi-logarithmic plot. Peaks labeled as in Fig. 6

Discussion

Findings

The sound reflection patterns in Figs. 4 and 5 come close to the predictions of the Norris and Harvey theory for click generation in the nose of the sperm whale. Notably, the data shows that a single event will generate the hallmark of sperm whale clicks: a train of pulses of decaying amplitude with a fixed interval. No other odontocete produces clicks with this pattern, and no other odontocete has a structure comparable in size and organization with the spermaceti complex. It should be noted, however, that this pattern is best seen in off-axis, low-level sperm whale recordings. In high intensity, near axis recordings only p1 may be seen, the trailing pulses being of such low amplitude (relatively) that they usually are masked by system noise (Møhl and Amundin 1991; B. Møhl et al., unpublished observations). Therefore, even though the trailing pulses constitute a hallmark of clicks from this species, we regard them as a byproduct of the generation process and of no obvious significance for sonar or other functions. This view on the trailing pulses is influenced by the recognition of the sperm whale click generator being by far the largest and most intense of all biological sound generating mechanisms, specialized to emit the on-axis p1-pulse (Møhl et al. 2000; B. Møhl et al., unpublished observations). The fact that the trailing pulses are readily observed in the present measurements is possibly the result of the system being excited in an unnatural location.

As explained in the introduction, the two reflectors are believed to be the frontal and the distal air sac (Fig. 1A, E). The aerial film in these sacs is assumed to reflect a high percentage of the sound. There are a number of problems with this concept. First, in this experiment sound was injected in front of the distal sac. The p1 pulse should then be traveling across the aerial space of the distal sac, passing the upper lip of the museau, proceeding into the spermaceti sac, then being reflected at the frontal sac and reaching the receiver by reversing this route. The p2 pulse is assumed to be a part of p1 that is reflected at its return to the distal sac, and subsequently making another return trip. The p3 should have a history similar to p2. However, in this scheme the distal sac has conflicting functions: it is a sound path, and at the same time a reflector. This could be explained by assuming only partial reflection by the distal sac, e.g., if it was partially filled with water, or partially collapsed, but such an explanation has the weakness common to all auxiliary hypotheses.

An apparent problem of a different nature is that the mechanism should be operational across a wide range of hydrostatic pressures. Sperm whales dive to depths in the order of 1000 m (Watkins et al. 1993). At such depths, the volume of air in the respiratory tracts and aerial sacs will have its volume reduced 100 times relative to surface volume with a corresponding increase in density, and this would tend to reduce the reflectivity of the aerial sacs. However, the ratio of acoustic impedances of the compressed air to that of tissue/water is still about 50, indicating that the reflective properties of the sacs will remain largely intact over this range of hydrostatic pressures (Mackay 1980) provided a film of air is present. A potentially more difficult problem is that the sound generator is believed to be pneumatically driven (Cranford et al. 1996). It is at present not understood how a limited and highly compressed volume of air can be administered to provide the continuous series of clicks, produced from deep diving sperm whales (Whitney 1968).

When studying the intervals in Fig. 5, it is seen that the p0-p1 interval is longer than the p1–p2 interval. This can be explained by noting that the p1 pulse has to travel the excess path from the projector to the monkey lips, the hypothesized organ of sound generation in the live whale (Cranford et al. 1996; Cranford 1999). However, this leads to the prediction that the p1–p2 and the p2–p3 intervals should be equal, which is not the case. This implies that the simple model of two parallel mirrors, connected by a tube with a sound transparent medium

of constant velocity of sound, is too simple. The broadening of the p2 peak in Fig. 5 indicates the presence of different transmission modes and/or differences in the sound velocity profile. Importantly, such broadening is not seen in similar functions from sperm whale clicks. We have at present no interpretation of the source of the extra reflections seen in Figs. 4 and 6. Similar, 'in-between' pulses are often observed in recordings of sperm whale clicks, particularly between p1 and p2 (P.T. Madsen, personal communication).

The time separation between pulses in Fig. 5 is in the right ballpark for a whale of 15.1 m TBL. Gordon (1991) published an algorithm for the derivation of TBL of sperm whales from IPIs, based on the Norris and Harvey (1972) theory of sperm whale click generation, the velocity of sound in spermaceti, and the ratio of length of head to TBL. This algorithm is of practical importance since it allows for remote estimation of the size and hence age of the whale [an earlier algorithm by Møhl et al. (1976), based on the same principles, is now acknowledged to be in error (Møhl et al. 2000)]. From the average of 7.3 ms for the p0–p1 and p1–p2 intervals, Gordon's equation predicts TBL to be 15.3 m. It is therefore concluded that the reflection patterns observed mimic the situation in the live whale quite well. The significance of this is that it is the first physiological demonstration of the Norris and Harvey concept of sound generation in the sperm whale.

The use of artificial sounds on a fresh cadaver would seem to rule out the mechanism proposed by Mackay (1972, 1980), in which each pulse is source-generated de novo and actively, albeit still governed by the two-way travel time for sound within the spermaceti organ.

As an addition to the original Norris and Harvey theory, the junk is now implicated in the sound path following the demonstration that it transmits sounds, and that it has a multi-pulse reflection pattern with largely the same properties (delays, broadening of p2) as that obtained at the 'upper barrel' of the spermaceti complex. The p0–p1 interval of 8.1 ms for the lower barrel (the junk) is so close to the value found for the upper barrel (7.7 ms) that it is reasonable to assume that the same structure, the frontal sac, is responsible for the forward reflection. This leads to the conclusion that the two barrels are acoustically connected, and to the concept of the bent horn (Fig. 1). This is in accordance with Cranford's (1999) view that is based on CT data.

The observation that the spermaceti complex could not be similarly excited by sound injected at the dorsal surface over the middle of the spermaceti bag (the connective tissue case) supports a concept of this bag as a kind of wave guide, not allowing sound to leak out laterally. This concept is contrary to the proposal of Mackay (1980): '.., with sound being released in all directions from the forward sac (as is observed) and the monopole pattern being slightly modified toward a dipole pattern from the two sacs. The layered ''junk'' might help couple sound forward'.

Discussion of methods

Over the years, we have tried five times to obtain sound transmission measurements on sperm whale cadavers, but found them to be non-transmissive. However, in all these cases the specimen had been dead for 8–22 h before our arrival. This time, speed of arrival at the scene was given priority over time to assemble equipment. Consequently, the methods and equipment used were not ideal for the task. Particularly, the signal generator and the DAT recorder were not matched in frequency, resulting in aliasing effects and sparse sampling at high frequencies. This precludes averaging of the series of stimulations. Also, while matching the spectrum of sperm whale clicks quite well (Madsen and Møhl 2000), the use of a long-duration FM sweep has some drawbacks in a structure as complicated as the nose of a sperm whale, as evidenced by the broadening in time of some of the returns. Further, it makes it difficult to monitor the quality of the recordings at the site. In fact, not until the subsequent sonagram analysis was done in the lab the existence of the reflection pattern became known.

The latter effect led to the decision to terminate the measurements since apparently nothing was recorded. It is regrettable that no bistatic experiments were made with excitation at the distal sac and recording at the junk. Also, receivers could have been introduced into the spermaceti sac and the junk. Finally, the change in transmission properties with time could possibly have been followed if proper logistic considerations were made. Notwithstanding, prioritizing to get to the scene quickly rather than well equipped is not regretted since it secured the results reported.

Conclusions

The reflection patterns from the FM sound pulses injected into the nose of a fresh cadaver of a sperm whale conform closely with predictions of the basic principles of the Norris and Harvey (1972) theory of sound generation in this species. This occurred even though the pulses used have properties quite different from the short duration, broad- band clicks of this whale. The Gordon equation for estimating TBL from pulse intervals predicted the measured length quite well.

The observation of sound transparency in the junk, the similarity in reflection interval magnitudes in the junk and the spermaceti organ, and the similar broadening of the p2 peak for both conditions indicate that the junk is an integral part of the sound path in the sperm whale. Cranford (1999) reached the same conclusion, based on his CT-scanning. This constitutes an amendment to the Norris and Harvey (1972) theory, as does the concept of p0 being the primary event.

Finally, the finding that no reflection patterns were observed for sound injection at the dorsal side of the spermaceti organ indicates that sound is contained in the

spermaceti complex and primarily coupled to the medium at the front.

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References

Amundin M (1991) Sound production in Odontocetes, with emphasis on the harbour porpoise, *Phocoena phocoena*. Ph.D dissertation, University of Stockholm

Backus R, Schevill WE (1966) Physeter clicks. In: Norris KS (ed) Whales, porpoises and dolphins. University of California Press, pp 510–528

Cranford TW (1999) The sperm whale's nose: sexual selection on a grand scale? Mar Mammal Sci 15:1133–1157

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

Gordon JCD (1991) Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. J Zool Lond 224**:**301–314

Jensen T (1999) The 1996 and 1997 mass stranding on Rømø. Biological Papers, No 1. Fisheries and Maritime Museum, Esbjerg, Denmark, pp 9–12

Mackay RS (1972) Discussion in Norris KS, Harvey GW (1972) A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L). In: Galler SR (ed) Animal orientation and navigation. NASA SP-262, pp 397–417

Mackay RS (1980) A theory of the spermaceti organ in sperm whale sound production. In: Busnel RG, Fish JF (eds) Animal sonar systems. Plenum Press, pp 937–940

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

Møhl B (1992) Narhvaler og den akustiske Big-Bang hypotese. Carlsbergfondets Årsskrift, pp 18–24

Møhl B, Amundin M (1991) Sperm whale clicks: Pulse interval in clicks from a 21-m specimen. In: Amundin M op. cit., pp 115–125

Møhl B, Larsen E, Amundin M (1976) Sperm whale size determination: outlines of an acoustic approach. FAO Fisheries Series No. 5, vol 3, pp 327–332

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

Norris KS, Harvey GW (1972) A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L). In: Galler SR (ed) Animal orientation and navigation. NASA SP-262, pp 397–417

Watkins WA, Daher MA, Fristrup KM, Howald TJ, Sciara GND (1993) Sperm whales tagged with transponders and tracked underwater by sonar. Mar Mammal Sci 9:55–67

Whitney W (1968) Observations of sperm whale sounds from Great Depths. MPL-U-11/68, Marine Physical Laboratory, Scripps Institution of Oceanography (unpublished report)