Marine Mammal Science

Memories

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Bertel Møhl[1]
1936–2017

Honorary member of the Marine Mammal Society, Bertel Møhl, died peacefully in his bed on 19 September 2017 after a long and interesting life in science. An adventure is often defined as a journey that, due to a series of unexpected mishaps, brings the traveler into peril from which he/she miraculously comes out on top to tell the tale. Bertel did not look at adventures that way; rather he actively pursued them through life, and always coined his field trips "expeditions" perhaps subconsciously to reflect his well-developed skills for ending up in semiprecarious situations during data collection matched by equally well-developed skills for getting out of them again. Being the oldest son of curator and taxidermist Ulrich Møhl at the Zoological Museum in Copenhagen, Bertel grew up in a home full of scientific

[1]Bertel Møhl on R/V *Narhvalen* in northeast Greenland in the summer of 2006. (Photo by L. A. Kyhn).

wonder where he received very early training as a zoologist. On Sundays, Bertel and his brothers would often be tasked with classification of animal bone fragments that his father brought home from archeological excavations of Neolithic kitchen middens. Skills that later won him a student job with Mary and Louis Leakey during hominid excavations in Olduvai Gorge, Kenya, in 1961–1962. Before starting as a biology student at Copenhagen University in 1959, Bertel managed to fulfill a childhood dream by joining the weather station in Danmarkshavn, northeast Greenland, as research assistant for 2 yr between 1955 and 1957. The many adventures driving sledge dogs in winter darkness and relying partly on subsistence hunting of marine mammals for survival installed in Bertel a deep and lifelong affection for Greenland and kindled his interests in the physiology of pinnipeds.

For his graduate degree Bertel decided to address the fundamental problem of how pinnipeds as amphibious mammals can hear well both in air and in water. Lightly supervised by Professor Torkel Weis-Fogh, Bertel trained seals to participate in psychophysical experiments to generate the first information on harbor seal hearing in air and water (Møhl 1964). After graduating in 1965, he spent 2 yr at the NATO funded marine mammal research station in Strib, Denmark, where he continued a series of seminal studies on seal hearing, showing that seals can hear well both in air and water (Møhl 1967*b*, 1968*a, b*). He also showed that pinnipeds can hear at very high frequencies in water, proposing that the upper functional hearing limit should be defined by the frequency at which frequency discrimination can no longer take place (Møhl 1967*a*). After that, he went to Guelph in Canada as a postdoctoral fellow with Keith Ronald for 2 yr, studying the auditory pathways to the inner ear in air and water by recording cochlear microphonics from implants in harp seals (Møhl and Ronald 1975), as well as reporting on the vocal repertoires of several ice seals, in collaboration with his first graduate student, Jack Terhune (Møhl *et al.* 1975). He returned to Denmark to assume a position as associate professor in sensory physiology at the Department of Bioscience, Aarhus University. One of the first problems he tackled upon his return was the stark contrast between the reports that harbor porpoises echolocate at 2 kHz (Busnel *et al.* 1963, Schevill *et al.* 1969) and the observations at the Strib research center that blindfolded porpoises could navigate in a maze of very thin wires that should not produce any detectable echoes of a 2 kHz sonar pulse with a 75 cm wavelength (Busnel *et al.* 1965). In a close collaboration with his life-long colleague and friend Søren Andersen, Bertel proceeded to show that harbor porpoises in fact echolocate at 130 kHz, reconciling the sonar outputs of the porpoises with physical predictions of detectable backscatter from the wires (Møhl and Andersen 1973).

Concurrently, Bertel and a newly hired young scholar at University of Southern Denmark, Lee Miller, also initiated a long-lasting research program on the acoustic interactions between echolocating bats and their ultrasound hearing and sound producing insect prey (Møhl and Miller 1976). However, when a large sperm whale was reported to be stuck in a fjord with a shallow entrance on the Faroe Islands in 1975, Bertel immediately rushed to the airport with as many hydrophones and tape recorders as he could carry. Prompted by the then recent paper by Norris and Harvey (1972) proposing that the sperm whale nose is a gigantic sound generator, Bertel was keen to make recordings of the multipulsed click of sperm whales in known aspects to the whale. When Bertel returned to Denmark with several tapes of high quality recordings of sperm whale clicks, he quickly identified a weak p0 pulse preceding the primary p1 pulse by 7 ms. Based on this and detailed anatomical investigations of sperm whale heads at Icelandic whaling stations, Bertel proposed that the Norris and Harvey (1972) theory be modified so that most of the sound energy produced at the monkey lips is not directed into the water. Instead, he hypothesized that sound is projected back into the nose, where the combination of the spermaceti organ, air sacs, and wafers of the junk complex collimate it into a highly directional p1 pulse emitted from the junk surface. However, each manuscript submission of the new findings invariably got rejected, perhaps because the notion at the time was that sperm whale clicks were not directional and only used for communication.

In the late 1970s, Bertel engaged in some of the earliest assessment of noise impact on cetaceans by being one of the experts tasked with investigating the consequences of having icebreaking LNG carriers sail through the Northwest Passage and down Baffin Bay, named the Arctic Pilot Project (APP). He went on several trips with Lars Thiele and Charles Green to measure levels and propagation of icebreaker noise in the Arctic, and from those experiments, he introduced the concept of "range reduction factor" to evaluate the loss of active space from masking noise (Møhl 1980, 1981). This concept has recently been reintroduced under different names (*e.g.*, Clark *et al.* 2009), and is gaining wider use as a metric in noise impact assessment (*e.g.*, Jensen *et al.* 2012, Hermannsen *et al.* 2014).

During a guest professorship in 1980, Ken Norris spent a year at Aarhus University with Bertel to write a seminal paper in *American Naturalist* elaborating on the biological big bang theory (Belkovich and Yablokov 1963, in Berzin 1972) by proposing that sperm whales can produce source levels so high that their cephalopod prey are debilitated thereby facilitating capture (Norris and Møhl 1983). Subsequently, Bertel and his students and postdoctoral fellows carried out a series of experiments involving either blasting caps or high voltage spark generators to show that at least fish prey could be debilitated by low frequency, high pressure transients (Zageisky 1987). Later research using more realistic high frequency clicks failed to demonstrate acoustic debilitation at relevant exposure levels (Benoit-Bird *et al.* 2006, Schack *et al.* 2008, Wilson *et al.* 2007) and today we know from tag studies that sperm whales do not debilitate prey with sound (Fais *et al.* 2016). However, that was not known in the mid-1980s, and neither was it known if sperm whales or other large toothed whales in the wild could generate the very high source levels needed to debilitate prey. Bertel therefore returned to his beloved Greenland in the late 1980s to make hydrophone array recordings of echolocating narwhals in Inglefield sound, Thule. He went on to show for the first time that wild toothed whales can produce source levels up to 227 dB re 1 μPa (pp) (Møhl *et al.* 1990), and together with Lee Miller and Annemarie Surlykke, he reported the first feeding buzzes for a wild toothed whale as well (Miller *et al.* 1995). Recognizing that it would be very insightful to know how wild toothed whale employ their biosonars over long time periods, he went on, together with his skilled technician Niels Kristiansen, to develop a sound logging device that mounted on the tusk of male narwhals should relay summary statistics of click outputs levels back *via* the Argos system. For various technical reasons, the tags did not work, but now 30 yr later the same idea is reappearing so we can hopefully learn about the vocal behavior of whales for long time periods.

In the mid-1990s, Bertel returned to the issue of whether sperm whales can produce source level that match the size of their sound producing nose. He realized that he needed a vessel of his own to be able to make the needed, 1,300 nmi field trips to northern Norway where male sperm whales feed in the Bleik canyon. He proceeded to buy his beloved R/V *Narhvalen*, a 40 ft steel ketch that Bertel extended by 5 ft to allow for storage of up to 1,000 m of hydrophone cables. During a succession of field trips to northern Norway between 1996 and 2005 employing increasingly deep and complex multihydrophone large aperture arrays (Møhl *et al.* 2001, Heerfordt *et al.* 2007), he went to show that sperm whales produce by a large margin the loudest biological sounds in the animal kingdom with source levels up to 240 dB re 1 μPa (pp) (Møhl *et al.* 2000, 2003*a*). When a sperm whale calf stranded during a whale hearing workshop in Hawaii organized by Paul Nachtigall, Bertel also seized the opportunity to show that sound was indeed produced by the hypertrophied nose, and that the multipulsed sperm whale click was the result of a single pulse being reflected back and forth between air sacs in the nose (Møhl 2001, Madsen *et al*. 2003, Møhl *et al*. 2003*b*). In concert, these measurements by Bertel and others have shown that the hypertrophied nose of the sperm whale is indeed a gigantic generator of highly directional, powerful clicks for long range echolocation of deep sea prey (Møhl *et al*. 2003*a*, Madsen *et al*. 2007, Fais *et al*. 2015).

In 2006, at the age of 70, he decided to commemorate the 100 yr anniversary for the Denmark Expedition, a polar expedition launched in 1906 to map the last unknown section of northeast Greenland, by returning to the icefields of his youth. He therefore invited friends and family on a 3-mo-long, and 2,000 nmi roundtrip expedition to the deserted East Greenland on his beloved vessel *Narhvalen*. After an adventurous trip where he also made the first recordings of bottlenose whale echolocation clicks (Wahlberg *et al.* 2011), he returned to Aarhus a happy man. In 2007 he retired after teaching physiology at Aarhus University for almost 40 yr. He was both loved and feared by biology students for his demanding teaching style, having no patience for ill-thought questions and laziness, but a big heart for teaching science to curious students. He fought many battles with university administration to defend Humboldt's ideas of what a university is, and he was politically engaged in a lifelong activism to keep the Nordic countries free of nuclear weapons during the cold war. After a trip to the Canary Islands with *Narhvalen* in 2008, he went on his last field expedition to the Azores in 2010, as part of a large-scale endeavor to measure the details of the sperm whale echolocation sound beam. After returning to Denmark in the autumn of 2010, he fully retired from science to spend more time with his wife, Lotte, and his three sons and grandchildren.

Bertel supervised approximately 40 graduate students during his career and wrote a similar number of scientific papers. That is not much by today's standards, but every single paper and project he was engaged in was based on a carefully identified important scientific problem. He would much rather face what he coined "an intelligent failure" than engaging in descriptive stamp collection that is haunting many disciplines of science today, marine mammal science included. He championed hypothesis driven research in a biophysical framework, and fought many battles over scientific problems including disproval of the coherent receiver theory for bat echolocation (Møhl 1986, Troest and Møhl 1986). Conversely, he also accepted being proven wrong on some of his own ideas, including the big bang theory for sperm whales. He did not believe in life after extinction of the last membrane potential, but his way of thinking and conducting science have nevertheless left a permanent mark in the research field of sensory ecology of marine mammals that many of us benefit from every day. As one of few researchers, Bertel made significant contributions to the understanding of echolocation both in bats and toothed whales. In a premeeting to one of the biosonar conferences, one colleague was puzzled by the fact that Bertel both worked on bats and toothed whales and asked why. Before

Bertel could answer, Ken Norris quipped "Bertel has his head in the air, his feet in water, but he keeps his ass dry." We can think of no better way to describe him and his life in science.

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Inuulluarit [Yours sincerely],

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