History of Dolphin Biosonar Research

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Research into the most sophisticated short range sonar.

Discovery of Biosonar in Animals

Research in biosonar can be traced back to the work of the Italian scientist Lazzaro Spallanzani who, in the 1770s, observed that bats could fly freely in a dark room. However, it was not until Pierce and Griffin (1938) detected, using an ultrasonic detector and a superheterodyne receiver, biosonar signals of the little brown bat (*Myotis lucifugus*) and big brown bat (*Eptesicus fuscus*), confirming the notion that ultrasonic signals were involved in echolocation.

In 1947, Arthur McBride, the first curator of Marine Studios (later Marineland, Florida) noted that bottlenose dolphins (*Tursiops truncatus*)[1] were able to avoid nets and find openings in enclosing nets at night and in murky waters, leading him to suspect that bottlenose dolphins had a biosonar capability (McBride, 1956). Other investigators such as Winston Kellogg, Forrest Wood, and the husband-and-wife team of William Schevill and Barbara Lawrence conducted the preliminary investigations on dolphin biosonar (Schevill and Lawrence, 1953).

Kenneth Norris and colleagues provided the first conclusive demonstration of bottlenose dolphin echolocation by placing rubber suction cups over the eyes of a bottlenose dolphin and found that it continued to swim normally through a maze of vertically hanging pipes and other obstacles while emitting clicks (Norris et al., 1961). They also speculated that the sonar sounds were directional and were projected from the top of its forehead (melon). Norris next showed that a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) also possessed a biosonar capability. In 1967, two French scientists trained a blindfolded harbor porpoise (*Phocoena phocoena*) to swim through a maze of vertically hanging wires (Busnel and Dziedzic, 1967).

Most of the early biosonar experiments were conducted by scientists in the US Navy Marine Mammal Program. C. Scott Johnson was the first to apply a rigorous psychophysical procedure to study hearing in *Tursiops* (Johnson, 1966). He found that *Tursiops* could hear sounds from 100 Hz to 150 kHz (**Figure 1**), the widest frequency range for any mammal. He also performed a masked hearing study to determine the critical ratio at different frequencies and demonstrated that the bottlenose dolphin integrated acoustic energy in a manner similar to most mammals. Forrest Wood and William Evans used suction-cup blindfolds to demonstrate echolocation in a Pacific pilot and killer whales (Wood and Evans, 1980). It soon become accepted that odontocetes (toothed whales) that emitted clicks were echolocating. The early history of the Navy program was summarized in the book *The Dolphin Doctor* by Sam H. Ridgway, the primary veterinarian in the Navy Marine Mammal Program (Ridgeway, 1987).

[1] *Note about the use of animal names. The term "dolphin" refers to all members of the family Delphinidae, a group within the odontocete (toothed whales). When a specific species of dolphin is referred to, a full common name (e.g., bottlenose dolphin) is used.*
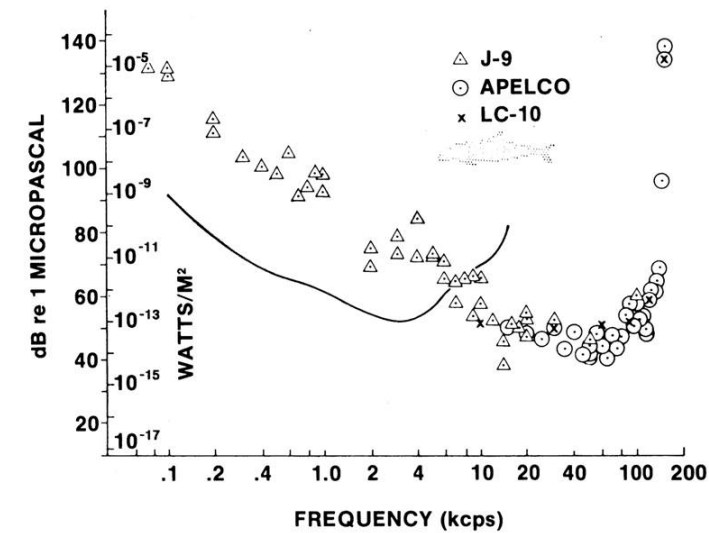

*Figure 1. First behavioral audiogram of an Atlantic bottlenose dolphin (*Tursiops truncates*; the "Johnson curve") along with a human audiogram (solid line). Symbols are different types of sound projectors used in the study. Adapted from Johnson (1966).*
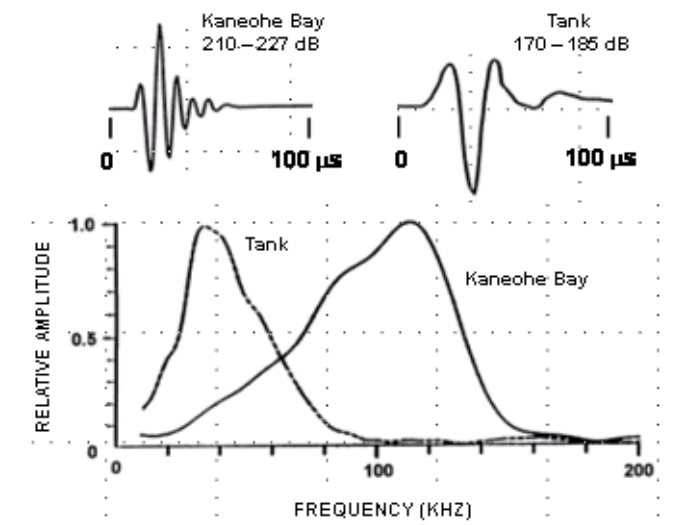

Figure 2. Example of representative biosonar signals used by bottlenose dolphins in concrete tanks and in open waters (Kaneohe Bay). The waveforms are shown in the top panels and the frequency spectra and peak-to-peak sound pressure levels (in dB re 1 µPa) are shown in the bottom panel. From Au and Hastings (2008), with permission from Springer-Verlag.

Two Decades of Biosonar Research (1973–1993)

In 1968, the Naval Ocean System Center (NOSC) opened a field station in Hawai'i on the Kaneohe Marine Corps Air Station that extended into Kaneohe Bay. The mere fact that bottlenose dolphins could project their signals into a large bay without tank walls to reflect their signals made a tremendous difference in how they used their biosonar. Teaming up with Robert Floyd, Ralph Penner, and Arthur "Earl" Murchison, we were the first to measure biosonar clicks that had peak frequencies as high as 120 kHz, which was an octave higher than signals measured in concrete tanks (Au, 1993). We also measured peak-to-peak source levels as high as around 227 dB re 1 µPa, which was over 40 dB (100 to 1,000 times) higher than previously in-tank measurements (**Figure 2**).

In the 1970s and 1980s, we found that bottlenose dolphins use a pulse system in which they adjusted the repetition rate of outgoing clicks so that the echoes were received before the next click was emitted. We also conducted experiments to determine the biosonar detection range of *Tursiops*. The distance a bottlenose dolphin could be to detect a target at a 50% correct threshold was 113 m for a 7.62-cm-diameter water-filled stainless steel sphere and 93 m for a 2.54-cm-diameter solid steel sphere. These two results with different sized spheres agreed within 1.5 dB when the difference in target strength was considered (Au, 1993). Experiments were also conducted with the 7.62-cm sphere at different fixed ranges in the presence of a broadband masking noise between a bottlenose dolphin stationed in a hoop and the

target. Again, the results from the noise-masking experiments were consistent with range detection experiments.

Another important experiment measured the discrimination acuity of an echolocating dolphin. Cylinders of the same height (17.8 cm) and outer diameter (3.81 cm) but with varying wall thicknesses were used. The standard cylinder had a wall thickness of 6.35 mm. Two targets (one standard and one nonstandard) separated by 22° in azimuth at a range of 8 m were presented to a bottlenose dolphin stationed in a hoop. The bottlenose dolphin was required to locate the standard target. The cylinders had the same target strength, with the only difference being the wall thickness of the cylinders. The results of the experiment are shown in **Figure 3**. At the 75% correct performance threshold, the bottlenose dolphin was able to discriminate a difference of -0.23 mm and 0.27 mm. We also measured the biosonar beam in both the horizontal and vertical planes for several bottlenose dolphins and obtained broadband 3-dB beam widths between 10 and 11° in both planes.

The receiving beam was also measured at 120, 60, and 30 kHz in the vertical and horizontal planes by Patrick Moore and myself. The frequency of 120 kHz matched the peak frequency of typical biosonar signals used by our bottlenose dolphins. The receiving beam pattern at 120 kHz was slightly larger than the transmitting beam pattern (**Figure 4**). The received beam got larger as the frequency decreased in a manner similar to a standard planar hydrophone.
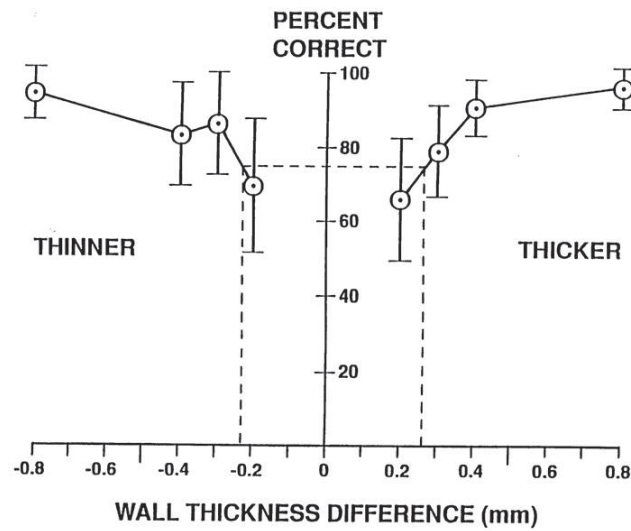
Figure 3. *Bottlenose dolphin wall thickness discrimination performance as a function of wall thickness difference. Thinner and Thicker are relative to the standard wall thickness. From Au (1993), with permission from Springer-Verlag.*

Figure 4. *Transmitting and receiving beam patterns of a bottlenose dolphin in the vertical (left) and horizontal (right) planes. The darker pattern represents the transmitting beam. From Au (1993).*

Moore and I also measured the critical bandwidth of a bottlenose dolphin and found that the ratio of the critical bandwidth to critical ratio was ~2.5 times larger than the same ratio for humans. Another important finding was that the integration time for broadband click signals was different (264 µs) than the ~2 ms for a narrowband tone with the same peak frequency (Au, 1993).

During this time period, Renaud and Popper (1975) performed experiments to measure the minimum audible angle (MAA) of a bottlenose dolphin. One stimulus was a broadband click with a peak frequency of 64 kHz, simulating a biosonar signal. The MAA in the horizontal plane was almost half that of a pure-tone signal with the same peaked frequency, thus demonstrating that the horizontal acuity of the animal was about two times better with a biosonar-like signal than a tonal signal in the horizontal plane and about three times better in the vertical plane.

Norris and Harvey (1974) dissected the melon of a bottlenose dolphin, measured the sound velocity and density distribution of the melon tissues, and found that a low-velocity core extended almost longitudinally from the nasal region to the surface of the animal's head with a velocity gradient that increased from the melon core to the surface of the head. They suggested that the melon acted as a "waveguide" to channel the acoustic energy produced in the nasal area into the water with a minor focusing role. Norris also hypothesized that sounds were received through the thin pan-bone
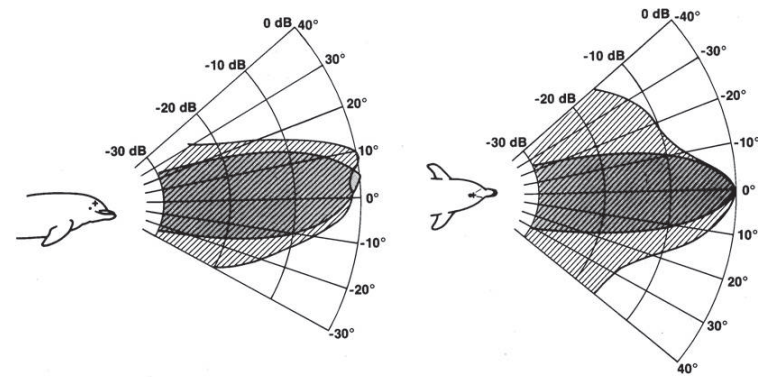
area of the lower jaw.

Ted Cranford pioneered the use of X-ray computer tomography (CT) and magnetic resonance imaging (MRI) scanners to examine the acoustic structures in a dolphin head (Cranford et al., 1996). He showed where the low-velocity core of the melon was situated geometrically. He also found a small pair of fatty bursae (monkey lips-dorsal bursae complex) "embedded in a pair of connective tissue lips, a cartilaginous blade, a stout ligament, and an array of soft tissue air sacs" within the nasal structures of many odontocetes (toothed whales such as dolphins) and hypothesized that the homologous relationships of structures "suggests that all odontocetes may be making their biosonar signals by a similar mechanism" (Cranford et al., 1997). At about the same time, Darlene Ketten pioneered the use of CT and MRI scans to study the ears and acoustic pathways of cetaceans (Ketten, 2014). Her studies on the cochlear and basilar membranes of cetaceans have been instrumental in providing deeper knowledge of how the ears of echolocating animals function.

James Aroyan performed simulation on sound propagation in the head of a bottlenose dolphin by applying the wave equation to a grid overlaying the head of a common dolphin and solving the wave equation using a finite difference technique. Aroyan's results suggested that the skull and air sacs were the dominant structures influencing the formation of the outgoing beam and that the melon played a minor role (Aroyan et al., 1992).

New Marine Mammal Research Program at the University of Hawai'i
When the NOSC Hawai'i Laboratory closed in 1993, Paul Nachtigall and I joined the Hawai'i Institute of Marine Biology (HIMB) located on Coconut Island in the same bay about 1.4 km from the defunct Hawai'i laboratory. My postdoctoral fellow Roland Aubauer and I were able to demonstrate that we could mimic different types of targets electronically

by digitizing the animal's outgoing biosonar signal, convolving each click with the previously collected transfer function of different targets, and playing the simulated echoes back to the dolphin. This technique provided us with another tool by which "targets" could be manipulated and used to investigate biosonar processing by echolocating bottlenose dolphins. My student Stuart Ibsen then used the phantom echo technique and bandlimited echoes to determine what part of target echoes were used by bottlenose dolphins in discrimination between water-filled steel and brass spheres. Using a bottlenose dolphin that emitted clicks with a center frequency close to 35 kHz, he found that a discrimination threshold occurred when the phantom echoes were band-passed by 13 kHz (Ibsen et al., 2009), which agreed with the 10-dB bandwidth of the dolphin auditory filter that we measured later (Lemond et al., 2012).

Another important project was the auditory pathway measurements conducted with Bertel Møhl (University of Aarhus, Denmark). A bottlenose dolphin was trained to beach on a mat and we measured the auditory brainstem response (ABR) of the animal as we played clicks through a piezo-electric crystal embedded in a suction cup that was placed at different positions on the animal's lower jaw. Our results showed that the maximum sensitivity was slightly forward of the pan-bone of the jaw and that the animal's head should be considered as a shaded receiver (Møhl et al., 1999) (**Figure 5**).

Alexander Supin of the Institute of Ecology and Evolution, Moscow, Russia, began a period of collaboration with Nachtigall in 2000. Supin and Nachtigall used a pulse frequency-modulated (FM) tone-burst stimulus (a modification of the continuous-wave FM signal used by Dolphin et al. [1995]) to measure the ABR of trained bottlenose dolphins. They also developed a way to measure the ABR on echolocating animals (Supin et al., 2004). The evoked response from an echolocating animal was averaged over many trials to see the ABR emerge out of the noise.

In later experiments, Nachtigall and Supin (2013) found that the ABR evoked by the target echoes in a false killer whale (*Pseudorca crassidens*) remained essentially the same as the target distance changed from 1 to 6 m with targets of varying reflectivity. The outgoing biosonar pulse produced a forward masking effect that affected the hearing sensitivity of the animal. They also conducted various types of automatic gain control or time-varying gain experiments with echolocating dolphins and hearing while echolocating and found that a
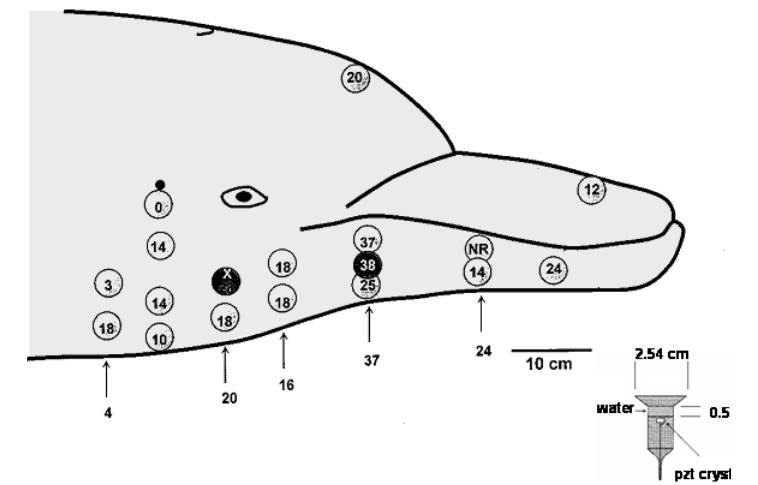

Figure 5. *Circles with numbers are relative decibel values of points of stimulation. The larger the number in each circle, the higher the sensitivity. The point marked "38" in white is the point of maximum sensitivity. The point marked NR had no response and X is the point of the minimum delay. The arrows refer to the sensitivity values on the midline under the jaw. The suction cup with the lead zirconate titanate (pzt) crystal is shown in the lower right panel. From Møhl et al. (1999).*

false killer whale was able to decrease its hearing sensitivity when a loud sound was preceded by a precursor (Nachtigall and Supin, 2013).

Nachtigall et al. (2005) also measured the ABR audiogram of a stranded neonate Risso's dolphin (*Grampus griseus*) and found that the high-frequency threshold extended to 100 kHz and the sensitivity was similar to that of the bottlenose dolphin.

Pacini et al. (2011) developed a portable ABR system and measured the audiogram of a stranded Blainville's beaked whale (*Mesoplodon densirostris*). The upper limit of hearing was found to be ~70 kHz and the frequency of best hearing was between 40 and 50 kHz, corresponding well with the FM biosonar signals used by this species. These results were also consistent with ABR measurements done on stranded Gervis beaked whales (*Mesoplodon europaeus*) in two other studies.

More recently, my research expanded to consider bottlenose dolphin biosonar from an ecological perspective and particularly to measure the biosonar signals of wild animals with a planar array of hydrophones. We were able to show that bottlenose dolphins possess a form of time-varying gain or automatic gain control by lowering their click amplitude as they approached a target (Au and Benoit-Bird, 2003). As the click amplitude was lowered, the frequency spectra of the clicks were also lowered, causing the transmit beam to widen.
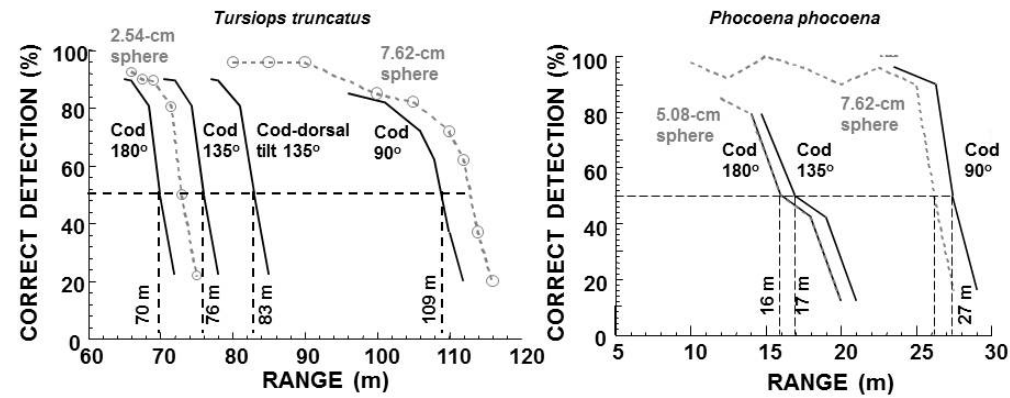
Figure 6. Predicted correct detection performance for a bottlenose dolphin (left) and a harbor porpoise (right) echolocating on a 30-cm-long Atlantic cod in a noise-limited environment. Dashed gray lines, actual animal performance curves with real water-filled spheres. The 50% correct detection threshold ranges are shown for different aspects of the fish. From Au et al. (2007).

I also collaborated for several years with Ronald Kastelein in The Netherlands and performed a number of experiments with harbor porpoises (*Phocoena phocoena*), including measuring the sonar detection range, the transmission beam pattern, the critical ratio, and the acoustic patterns on the heads of two harbor porpoises with suction-cup hydrophones. In 2006, we measured the echoes of four fish species in a holding tank using simulated bottlenose dolphin biosonar clicks and used the results to estimate the detection range of an Atlantic cod (*Gadus morhua*) by both bottlenose dolphins and harbor porpoises. The estimated detection ranges (**Figure 6**) are for Atlantic cod at a different orientation (Au et al., 2010). The differences in the echo structure of the fish species strongly suggested that both species should be able discriminate species by their echoes.

We also used high-amplitude simulated biosonar signals in an attempt stun the fish. We could not induce stunning or disorientation in the fish (Benoit-Bird et al., 2006). Kastelein et al. (2005) also made a major contribution in understanding the biosonar process by measuring the receiving beam pattern of a harbor porpoise.

The Navy Dolphin Program San Diego

In the many years of research not only on biosonar but also on audition, masking effects, temporary threshold shift, and the effects of anthropogenic activities, many important findings have been obtained. However, I will only address some of the biosonar research results. A team from this laboratory was able to monitor the movement of the phonic lips of a bottlenose dolphin with a high-speed video-endoscope system while the animal was producing clicks and whistles (Cranford et al., 1997). Ridgeway and Donald Carder showed that the hearing of a beluga whale (*Delphinapterus leucas*) was

essentially the same at the surface and at a depth of 300 m, suggesting that that this species' biosonar capability is not be affected by depth. Recently, Ridgway et al. (2014) found a likely connection between reward expectation, pleasure, and brain dopamine activation with the emission of burst pulses related to "terminal buzzes."

Stephen Martin built a biosonar measurement tool attached to a bite plate that a bottlenose dolphin could carry while performing a biosonar search for mines on the bottom. A hydrophone was connected on a rod extending in front of an animal to measure the on-axis clicks (Martin et al., 2005), and most of the acoustic data were analyzed by Houser et al. (2005). One animal produced many hundreds of clicks and was relatively slow in searching for the targets, whereas the other animal was much faster in performing a search and emitted considerably fewer clicks. Experience in performing such a search-and-detect task probably had an influence on how the two bottlenose dolphins utilized their biosonar. Patrick Moore and colleagues conducted an experiment in which an animal stationed on a bite plate had to detect targets that were up to ±20° off axis. The animal controlled both the direction and width of its outgoing beam. Finneran et al. (2013) examined the automatic gain control mechanism of an echolocating bottlenose dolphin and found that the ABR amplitude induced by a phantom target echo remained relative constant until the target range exceeded 14 m, after which it decreased as the target range increased. In another phantom target detection experiment, the animal emitted multiple pulses as the target range exceeded ~100 m.

I collaborated with Finneran's team at the naval facility and used suction-cup hydrophones to determine the location on the head of a bottlenose dolphin (**Figure 7**) where the biosonar signal exited (Au et al., 2010). In a second study, we measured of the biosonar beam pattern almost completely around a bottlenose dolphin in both the vertical and horizontal planes. We found that the signal levels dropped ~40 to 50 dB at angles greater than ±90° from the beam axis. At angles greater than about ±45°, a second signal appears that is due to internal reflection in the head of the dolphin and not from two phonic lips operating synchronously.
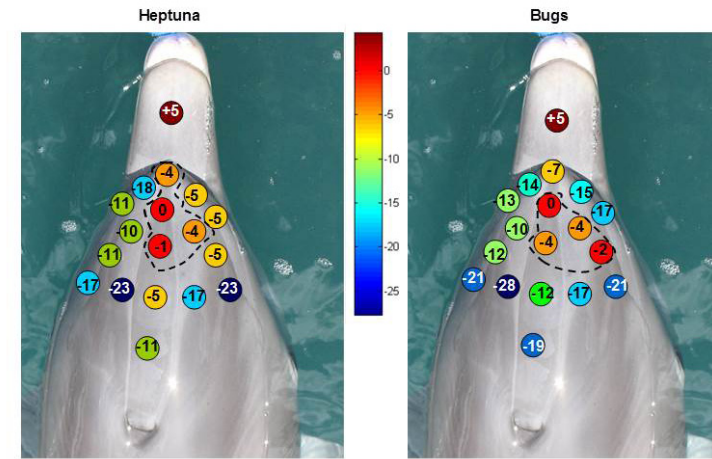

Figure 7. The relative distribution of acoustic pressure of the biosonar beam as emitted on the surface of the head of two bottlenose dolphins. The red circles with a "0" are where the beam axis emerges out of the head of the dolphins. The dashed lines surround the areas where the signal is close to its maximum value. From Au et al. (2010).

The Danish Contributions

Bertel Møhl and former students Peter Madsen, Magnus Wahlberg, and Kristian Beedholm did a number of studies on the biosonar of sperm whales (*Physeter macrocephalus*) using a variety of portable vertical line arrays. They used multiple observers on different boats with a hydrophone connected to one channel of a portable DAT recorder and a GPS sync signal into the other channel creating a "free-floating" horizontal array. Møhl and colleagues including Lee Miller and the late Annemarie Surlykke[2] were able to estimate the source levels of large male sperm whales foraging in the waters of Norway to be as high as 230-243 dB peak-to-peak and with a directivity index of ~27 dB (Møhl et al., 2003), both being the highest for any odontocete species. They were also able to confirm the hypothesis of Norris and Harvey (**Figure 8**) that a single pulse is produced by the museau du singe close to the blowhole at the anterior of the forehead that propagates through the spermaceti organ and is reflected and focused by the parabolic-shaped frontal air sac at the back of the skull. The reflected signal then travels through the "junk" area in the forward direction and eventually enters the water. The Danish team have also used vertical hydrophone arrays to measure the biosonar signals of at least 10 different dolphin species in the wild. The characteristics of the signals are given in a book chapter by Wahlberg and Surlykke (2014).

A variety of biosonar experiments with harbor porpoises were conducted at the Fjord & Bælt Center in Kerteminde,
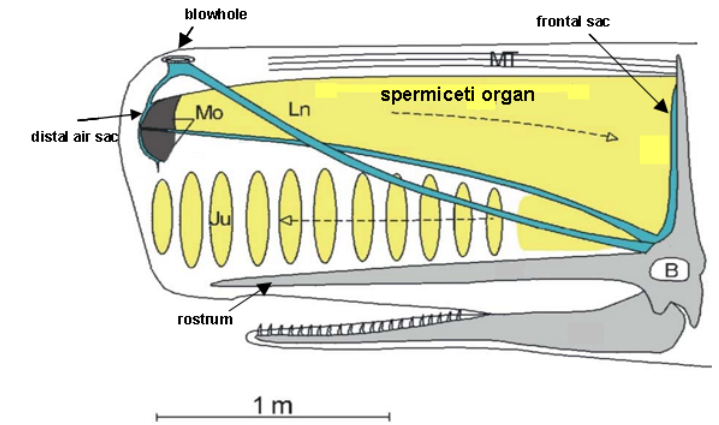

Figure 8. Diagram of anatomical structures in the sperm whale nose. **Mo**, monkey lips that are just posterior of the distal air sacs; **MT**, muscle tissues; **Ln**, left naris. Spermaceti oil is contained in the spermaceti organ and in the spermaceti bodies of the junk (**Ju**). Dotted arrows indicate the assumed sound path from the generating site. See text for further explanation. From Madsen et al. (2002).

Denmark. Wisniewska et al. (2012) demonstrated that automatic gain control occurred with this species as the animal reduced its signal level as the target range became shorter in free swimming biosonar experiments with live fish. Using simultaneous video and acoustic recordings, the investigators were able to discover a dynamic beam formation process while the animals approached a swimming fish prey and they also detected terminal buzz signals in the final phase of prey capture.

Knowledge from Acoustic Tags

Almost all of our information on the use biosonar for foraging by deep-diving odontocetes has come from suction cup-mounted digital acoustic tags. Madsen et al. (2002, 2005) performed the initial experiments on sperm and beaked whales (*Mesoplodon densirostris*). These animals typically dove to a depth between 600 and 1,200 meters to forage for squids and did not emit clicks until they descended several hundred meters below the surface. They also obtained data from sperm whales that suggested that the highly directional and intense clicks used for foraging and the omnidirectional and much less intense coda clicks used for communication were generated by the same process. They found that beaked whales emitted FM biosonar clicks, the only odontocetes to do so, and they also emitted a terminal buzz when capturing prey. Dives lasted up to an hour and tens of prey were captured.

Akamatsu et al. (2005) used a tag that measured the peak amplitude of biosonar clicks to study foraging by the Yangtze finless porpoise (*Neophocaena phocaenoides*). The porpoise

hunted for prey in a range up to ~70 m and would swim on average no more than 20 m without emitting any clicks. On detecting a prey, the porpoise would adjust its click rate so that echoes were received before the next click was emitted. Like the deep-diving species, the porpoises often rotated their bodies and captured the prey in a bottom-up position.

Recent Developments

A lively controversy argued in the literature arose in 2008 on whether or not dolphins use both phonic lips to produce biosonar signals. Finally, Madsen et al. (2013), using data from suction cup hydrophones on a false killer whale and four bottlenose dolphins along with previously collected data on harbor porpoises, showed that the biosonar clicks were produced by the right phonic lips and whistles by the left, putting the controversy to rest.

The use of finite-element modeling (FEM) of acoustic propagation in the head of dolphins is the latest area of research in dolphin biosonar. Cranford et al. (2008) used FEM to study sound propagation in a beaked whale head and found a "previously undescribed 'gular pathway' for sound reception." I am collaborating with Chong Wei and his adviser Yu Zhang from Xiamen University, China, in applying FEM techniques to study the propagation of clicks in the head of the Chinese river dolphin (*Lipotes vexillifer*), harbor porpoise, and bottlenose dolphin. Our results suggest that reflections off the skull and air sacs are the major contributor to the formation of the biosonar beam, with the melon having mainly a channeling and only a minor focusing role.

There are many areas of research that need to continue to fully understand the biosonar of dolphins. One of the greatest challenges is to determine how they perform complex target discrimination and recognition and to mathematically describe the process. Their capability in discriminating and recognizing targets lying or buried in the ocean bottom far surpasses any technological sonar, and understanding the biosonar process has many civilian and military applications.

Acknowledgments

Biosketch

Whitlow Au is a bioacoustician who has studied the dolphin sonar system for over four decades. He is a former president of the Acoustical Society of America and the first chairperson of the Animal Bioacoustics Technical Committee. He also is the first silver medal recipient in Animal Bioacoustics. Whit obtained his Bachelor's degree in Electrical Engineering from the University of Hawai'i and Master's and PhD degrees in Electrical Engineering from Washington State University. He is currently semiretired as a research professor at the Hawai'i Institute of Marine Biology.

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