

CURRENT RESEARCH TRENDS IN CETACEAN BIOACOUSTICS

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1 INTRODUCTION

Advances in the study of cetacean bioacoustics over the last several years have been driven in part by the collective influence of technological improvements and the need to understand how anthropogenic sound impacts marine mammals. Improvements in memory storage, the miniaturization of acoustic sampling devices, and the availability of high sample rate data acquisition systems now permit scientists to obtain basic information on the hearing capabilities of many odontocete species, as well as cultivate a basic understanding of how acoustics play a role in the natural behavior and ecology of marine mammals. Both of these lines of research strive to fill a need to understand the sensitivities of marine mammals to sound and how anthropogenic sound might impact marine mammals at the individual and population levels.

Bioacoustic research has been further enabled by the increasingly common use of technologies traditionally applied to human medicine. Biomedical imaging systems, with nearly two decades of use in the study of post-mortem marine mammal samples, have now become useful for *in vivo* investigations. The miniaturization and portability of electrophysiological systems has also led to a major increase in the use of auditory evoked potentials (AEPs) to characterize marine mammal hearing capabilities and study odontocete biosonar.

In the following sections, discoveries in cetacean bioacoustics since the turn of the century are discussed. Many of these findings were made possible because of the technological advancements and technologies described above. As such, the review below categorizes the discoveries according to the technology that permitted them. In many instances we find that the discoveries made with disparate technologies have culminated in a better overall understanding of cetacean bioacoustics or produced further hypotheses regarding the production, reception and utilization of sound by these ocean dwellers.

2 THE GROWTH OF DATA ACQUISITION CAPABILITY

2.1 Technological Advances

Data acquisition systems (DAQS) have become increasingly capable of high through-put, multi-channel data collection while concomitantly remaining relatively affordable. Programmable digital signal processors (DSP) have decreased in power consumption, increased in dynamic range (12-bit to 16 and 24-bit), and diminished in size. Coupled with an increasing capacity in solid state memory and continuing reductions in the memory footprint, new opportunities for bioacoustic data collection have evolved. In the following sections several recent studies that capitalize on technological improvements in data acquisition are described. The first studies are those which have coupled the sampling of acoustic information with spatial representations of animal subjects. The latter studies utilized increased sampling rates and multi-channel data acquisition to better characterize the spatial variability within the biosonar beam.

2.1.1 Archival Data Loggers

The study of echolocation and vocal behaviour of wild odontocetes has traditionally been constrained by a need to use hydrophones fixed to a particular location and/or platform and spatially and variably separated from the animals under study. The coupling of acoustic data loggers to marine mammals so as to utilize them as autonomous platforms permitted the fixed co-location of sampling devices to a marine mammal. Efforts to deploy these types of archival data loggers began in earnest in the 1990's with its first successes in deployments on pinnipeds [1; 2]. Tagging efforts on cetaceans was largely hampered by the size of the first generation acoustic data loggers and ineffective means of long term attachments. Whereas the attachment of acoustic data loggers to pinnipeds was accomplished by epoxying instruments to the fur, the smoother skin of odontocetes heavily restricted non-invasive attachment methods and limited the time that data loggers could be attached.

Attachment methods for odontocete tagging have improved with the modification of various suction designs. However, a more important advancement has been the integration of the acoustic data logger with other sensor types permitting the recording of pressure, temperature and orientation of the animal concomitant with the collection of acoustic data. Information collected by these sensors allows sound production and reception to be analyzed in the context of the animal's diving behaviour. The most notable of these integration efforts to date has been the development of the DTAG by Mark Johnson and colleagues [3]. The DTAG has evolved since its inception, and as of the writing of this article boasts a 16-bit dynamic range, 96 kHz sampling rate, and 3-axis magnetometers and accelerometers for capturing the 3-dimensional movement of the tagged whale [4]. Future enhancements are certainly forthcoming.

The DTAG has been deployed on a number of different species of cetacean, including the sperm whale (*Physeter macrocephalus*) [4; 5; 6], northern right whale (*Eubalaena glacialis*) [7], and several species of beaked whale (*Ziphius cavirostris* and *Mesoplodon densirostris*) [8; 9; 10]. Data collected from these tag deployments has provided novel insight into sound production mechanisms and the manner in which free-ranging animals utilize biosonar for foraging purposes. For example, it is now known that *Mesoplodon* generally do not produce echolocation clicks within the upper 200 m of the water column and, on foraging dives, produce clicks with interclick intervals (ICI) ranging from 200-500 ms up until the terminal buzz on the approach to prey capture [10]. This behavior in sound production and its relation to prey capture was unknown until the deployment of the DTAG, and the application of the DTAG to the study of beaked whales has opened the door on the underwater behaviour of a marine mammal that is difficult to observe. The DTAG has also been extremely useful in advancing proximate studies of how anthropogenic sound might affect diving behaviour. The work of Nowacek and colleagues [7] was the first to document an acute change in the diving behaviour of the northern right whale resulting from exposure to an alarm signal designed as an alert to an approaching vessel. The results provided first-hand evidence of pronounced variation in underwater dive behavior resulting from an anthropogenic signal. Similar studies of the potential impact to sperm whales exposed to sound generated during seismic exploration have also been made with the DTAG. Results of those studies have demonstrated that seismic air guns are capable of generating sounds at frequencies outside those of interest for seismic exploration, but at levels and frequencies that may be of potential concern for the sperm whale [4].

The biosonar monitoring tool (BMT) was created by Steve Martin and colleagues [11] to specifically study dolphin echolocation. Unlike the DTAG, the BMT was created for use by a dolphin trained to carry the instrument during a target detection task in a cluttered bay environment. The BMT consisted of three acoustic recording channels - a click detection channel and two echo recording channels. Echolocation clicks were recorded from a hydrophone placed 1 m in front of the presumed location of the phonic lips and in line with the presumed maximum response axis (MRA) of the echolocation beam. Echo receivers consisted of biomimetic directional hydrophones, i.e. the receive beams matched those previously measured in the bottlenose dolphin. Like the DTAG, the BMT also contained accelerometers so that the 3-dimensional movement of the dolphin could be recorded during target searches and recreated for analysis at a later time. Results of the deployment of the BMT on two bottlenose dolphins demonstrated that considerable variation in

search strategies existed for animals performing the same task [12]. One dolphin searched slowly (tens of seconds), produced clicks with stereotypical frequency-dependent energy distributions, and always approached the target closely prior to verifying target presence by whistling. The other dolphin searched quickly (< 10 s) and produced clicks with variable frequency-dependent energy distributions. Both animals increased the received level of target echoes either by maintaining the source level (SL) of clicks and approaching the target or by maintaining a given distance from the target and increasing the SL during final echo-inspection. Temporospatial relationships between the animals and the targets during the echolocation task suggested that dolphins often initially detected the target well off of the MRA of the echolocation beam and then oriented toward the target for identification. The individual and collective behavior of the dolphins had implications for individual variability in search strategies as well as the adaptive control of echolocation. These results were essential to guiding follow-on research on dolphin echolocation beamwidths (see below) and interpreting the results of evoked potential audiometry studies (see below). Furthermore, the increase in echo received level following initial detection had implications for gain control in the dolphin, a topic that is of recent interest given the results of research on wild dolphins using a star array of hydrophones and those obtained with the study of echolocation using auditory evoked potential (AEP) methods (see below).

2.1.2 Hydrophone Array Studies

The hydrophone has long been the standard tool in the study of dolphin biosonar and it remains a staple tool today. Improvements in data acquisition have enabled higher resolution sampling of echolocation signals and the use of multiple hydrophones for recording. The use of these hydrophone arrays, both in the wild and in captive settings, have recently yielded exciting information on the adaptive control of echolocation in delphinids.

Whitlow Au and colleagues have been utilizing a symmetrical star array of hydrophones in the study of echolocation by wild odontocetes. The star array, which consists of a central hydrophone surrounded by 3 additional hydrophones, is useful in determining the distance of echolocating animals from the array and, by selecting only echolocation clicks recorded with maximum amplitudes on the center hydrophone, isolating clicks which are near the MRA of the sonar beam. Prior to the usage of the star array, accurate measurement of echolocation signals in the wild were difficult to obtain. The star array has been used to record the echolocation clicks of numerous odontocetes, including the Hawaiian spinner dolphin (*Stenella longirostris*), white-beaked dolphin (*Lagenorhynchus obliquegens*), killer whales (*Orcinus orca*), Atlantic spotted dolphins (*Stenella frontalis*), and pan-tropical spotted dolphins (*Stenella attenuata*) [13]. An exciting finding of recordings from these wild odontocetes has been the variation in source level of the echolocation clicks as a function of the range between the star array and the animals (Figure 1); that is, the source level of the echolocation clicks varies nearly as a function of $20 \log(R)$. The implications of these findings, as suggested by Au and Benoit-Bird [13], is that delphinids utilize a form of time-varying gain (TVG). In contrast to human-made systems in which the TVG is applied to the receiver, the delphinids are hypothesized to vary the level of the transmitted echolocation click according to the distance of the target. The control of the biosonar system in this manner would maintain a constant echo level throughout target approach. Given that many of the delphinids studied feed on schools of fish, the reduction in the amplitude of the echoes from the school is expected to vary as volume reverberation, or as $20 \log(R)$.

Work conducted by Patrick Moore and colleagues has recently demonstrated adaptive control over the width of the echolocation beam [14]. Using an array of 24 hydrophones spaced approximately 12° apart in the horizontal and 8.2° apart in the vertical planes, echolocation clicks were recorded from a dolphin performing a target detection task. The dolphin was required to station on a biteplate, thus fixing its head during the task, and either a metal sphere or cylinder was presented to the dolphin at progressively greater distances to the left or right of the presumed MRA of the echolocation beam. The results of the study demonstrated not only that dolphins were capable of detecting metal sphere and cylinder targets well off of the MRA of the echolocation beam, $21\text{--}26^\circ$ and $13\text{--}19^\circ$ respectively, but that the dolphin had a remarkable ability to vary the echolocation beamwidth in both the horizontal and vertical planes. Horizontal beamwidths in excess of 30° and

vertical beamwidths in excess of 25° were observed (Figure 2). The dolphin was able to nominally steer the echolocation beam 6° in the horizontal plane. The results of the study demonstrated that dolphins have remarkable control over the echolocation beamwidth and can manipulate it according to the echoic task being performed. The subject developed a noticeable search strategy which involved a consistent broadening of the beam when targets were progressively presented further off of the presumed MRA of the echolocation beam and directional steering of the beam toward the location of the target. The study demonstrated a remarkable flexibility in the dolphin's control over the echolocation beam that had not been previously described.

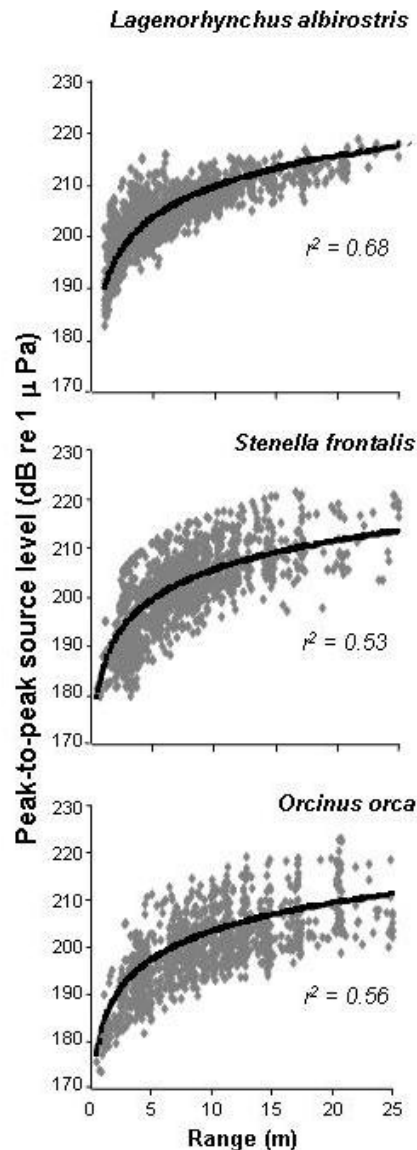


Figure 1. Source levels of three odontocete species measured in the wild as a function of distance between the array and animal. Reproduced from [13] with permission from W.W.L. Au.

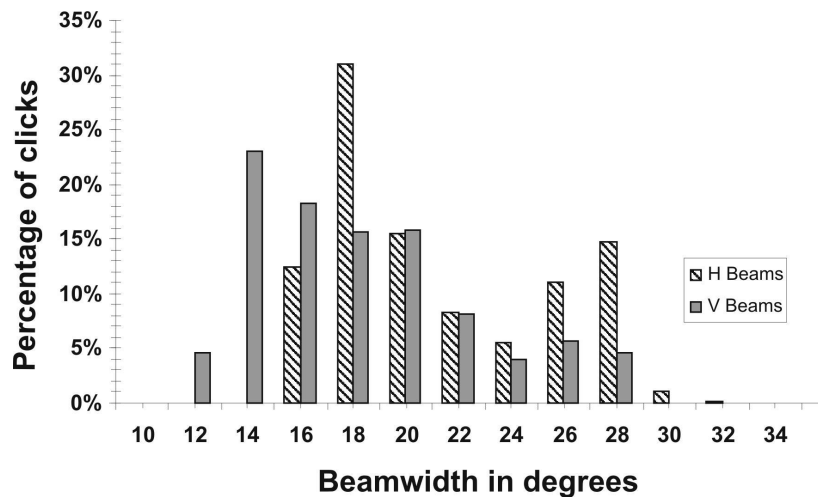


Figure 2. Distribution of horizontal and vertical beamwidths produced by a dolphin performing target detection tasks with the target off of the MRA of the echolocation beam.

3 APPLICATION OF BIOMEDICAL RESEARCH TOOLS

3.1 Auditory Evoked Potentials

Auditory evoked potentials (AEPs) are small electrical voltages produced by the brain in response to an acoustic stimulus. The measurement of AEPs in human clinical practice is long-standing and AEPs are commonly used to test the hearing sensitivity of humans that are incapable or unwilling to participate in behavioural audiometric tests. The use of AEPs to study dolphin hearing dates back more than four decades [15] but non-invasive means of studying brain neurophysiology in dolphins did not become commonplace until the 1980s. Since that time, a considerable amount of study of odontocete hearing capabilities has been conducted utilizing AEP methods, most predominantly by Alexander Supin and Vladimir Popov, e.g. [16; 17; 18; 19; 20; 21; 22].

Recent studies of echolocation in the false killer whale (*Pseudorca crassidens*) using AEP methods have demonstrated a constancy in echo-dependent AEP amplitudes that are independent of target strength and distance [23; 24]. The independence of the echo-dependent evoked response has been interpreted as a form of automatic gain control achieved through variation in hearing sensitivity and/or an increasing release of the echo-dependent AEP from masking by the click-dependent AEP resulting from distance-dependent delays in echo reception. In contrast, Beedholm and colleagues [25] argue that automatic gain control does not exist in the harbour porpoise (*Phocoena phocoena*). Echo-dependent AEPs recorded in a harbour porpoise utilizing the phantom echo paradigm demonstrated a reduction in amplitude that was dependent on echo amplitude but not echo delay. The results of these two AEP experiments, particularly when taken in consideration of the results of Au and Benoit-Bird [13] and that of Houser and colleagues [12], leaves the presence of use of gain control as a topic for much debate and research.

The use of AEPs for determining the hearing abilities of cetaceans has also become increasingly popular because of concern over the potential for anthropogenic sound to affect marine mammals and the speed at which audiograms can be obtained relative to behavioural methods (i.e. audiograms can be obtained in minutes to hours as opposed to many months). Fundamental to the issue of the impact of human generated noise on marine mammals is hearing sensitivity, which is known for less than 30 species of the over 100 species of marine mammal. Of these, the representation of hearing sensitivity is often restricted to tests performed on a single or a few subjects. Thus, hearing sensitivity is unknown for most species and is under-represented for all marine mammal species. AEP assessments of hearing sensitivity are made by monitoring the magnitude of the evoked response as a function of the stimulus level and use subjective or

objective signal detection methods to detect the evoked response. The stimulus of choice for use in odontocete AEP hearing tests is the envelope following response (EFR), an AEP that is phase-locked to the envelope of a sinusoidal amplitude modulated signal. This stimulus has a narrow frequency spectrum at the rate of amplitude modulation and is preferable to broader band stimuli such as tone pips or clicks. The EFR has recently been validated against behavioural audiometry in dolphins [26; 27] and a false killer whale [28]. It is providing opportunities to obtain information on species for which little to no audiometric information exists, including the Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*) [19], Risso's dolphins (*Grampus griseus*) [29], and a beaked whale (*Mesoplodon europaeus*). The technique has permitted the first determination of population level variability in hearing sensitivity for any species of marine mammal [30]. In that study, 42 bottlenose captive dolphins ranging in age from 4-47 years of age had their hearing tested using the EFR. As has been observed in humans and other mammals, the population of dolphins exhibited age and sex-related losses in hearing sensitivity. In general, the frequency range of hearing and sensitivity decreased with age (Figure 3) and males tended to have an earlier onset of hearing loss than females. Similar population-level quantitative characterizations of hearing sensitivity should be sought in other species, both wild and captive. By broadening the scope of the species for which information on hearing sensitivity exists and obtaining information on population level variability, a better understanding of animal tolerance to sound and contributing causes to hearing loss can be determined. Both are issues important to environmental stewardship and the promotion of animal welfare.

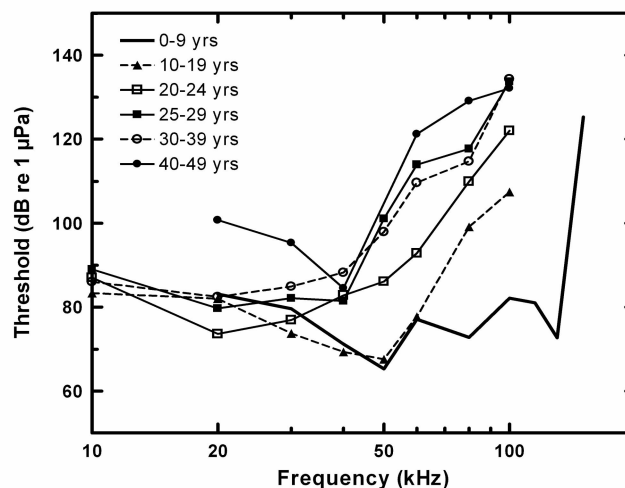


Figure 3. Mean audiograms for bottlenose dolphins grouped by age. Except for the 0-9 yr age group, plots are terminated at 100 kHz; there were a number of individuals for which data above 100 kHz was not obtained because the upper frequency limit of hearing was < 100 kHz. The plot for the 0-9 yr age group is extended so that the reduction in high frequency hearing for animals with a full range of hearing can be viewed for comparison. Reproduced from [30].

One additional finding that had exciting implications for the adaptive control of echolocation was the determination that one of the animals used by Steve Martin and colleagues in the BMT study (section 2.1.1) was profoundly deaf at all but a band of frequencies between 20 and 40 kHz (Figure 4). Interestingly, this is the same frequency band in which the animal placed most of the power within its echolocation clicks (Figure 5). The implication of this finding is that the dolphin was able to compensate for its hearing loss by controlling the frequency content of the click such that the usable frequency range of hearing was exploited. This finding suggests an acute ability to control the phonic lips in click production.

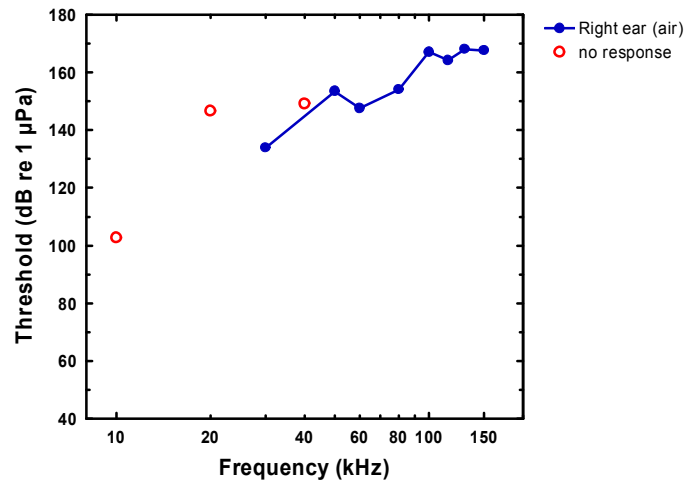


Figure 4. Evoked potential audiogram for a 26-year old male dolphin with profound hearing loss. Red circles indicate that no evoked response could be obtained. Reproduced from [30].

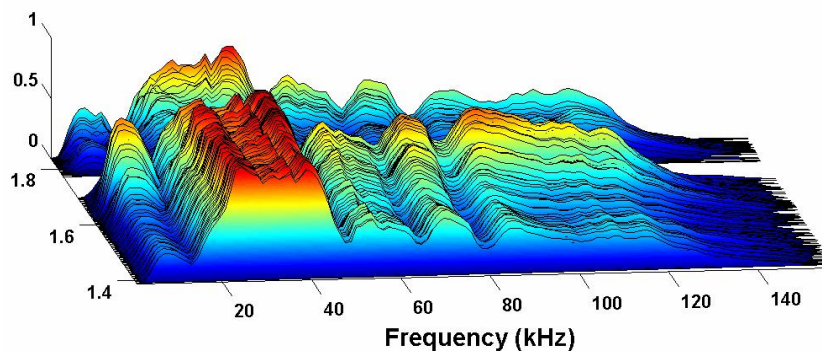


Figure 5. Power spectra of echolocation clicks emitted by the dolphin referenced in Figure 4 during an open water target detection task. Data from [12].

3.2 Biomedical Imaging

The use of biomedical imaging techniques, particularly magnetic resonance imaging (MRI) and computed tomography (CT), have been used to study *in situ* anatomy of cetaceans for about 20 years. The advantage of these approaches is that spatial and anatomical relationships between tissues are preserved, whereas dissection inherently destroys some of these relationships and introduces anatomical distortions. The use of these modalities continues today. However, the increased availability of biomedical imaging devices has opened up greater opportunities for facilities that have the capability to transport living marine mammals for scanning. Sam Ridgway and colleagues have, over the last several years, employed both single photon emission computed tomography (SPECT) and positron emission tomography (PET) to couple physiological function to anatomical structures imaged via CT and MRI [31; 32].

These first-of-their-kind *in vivo* studies demonstrated several anatomical and physiological characteristics that have relevance to dolphin biosonar. First, unlike scans from dead animals in which air spaces suffer from variable degrees of collapse, *in vivo* CT scans demonstrated detailed relationships of air spaces to the skull (Figure 6) and auditory bullae permitting a better understanding how the geometry of sound reception is impacted by reflective air spaces within the animal's head. Second, use of the radiolabeled injected Tc-99 to map cranial blood flow via SPECT demonstrated an extensive region of blood flow over the melon and within the mandibular fats. Although the vascularisation of the mandibular fats has long been known, the amount of blood flow

over the melon was surprising based upon the anatomy of the melon. Given that the melon is relatively metabolically inert, the function of the blood flow over the melon has been speculated to have a thermoregulatory capacity, possibly maintaining the temperature-dependent density of the melon (and mandibular) fats and preserving sound speed gradients within these fat bodies. Finally, recent work by Ridgway and colleagues mapping the uptake of fluoro-deoxyglucose (FDG) within the dolphin head via PET following acoustic stimulation has suggested some possible active participation on the part of the animal in hearing. The compound FDG is a proxy for glucose uptake and can be used to estimate the relative metabolism of tissues. Injection of FDG during unilateral auditory stimulation results in uptake of the radiolabeled compound by metabolically active tissues. Scanning of the dolphin head via PET following this procedure has, in some cases, demonstrated a disproportionate uptake of the compound in tissues surrounding the ear that is being preferentially stimulated. If the disproportionate uptake corresponds to an active process in tissues surrounding the ear during sound reception, it could have implications for processes such as automatic gain control and directional hearing in this species. However, much further work needs to be done analyzing FDG uptake under both acoustic stimulus present and absent conditions before a final assessment of the current findings can be made.

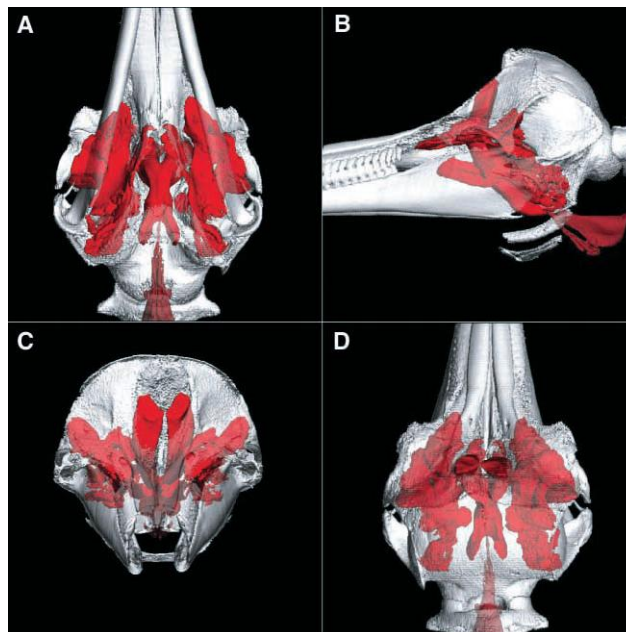


Figure 6. Spatial and morphologic relationship of the contiguous cranial air space (red) to the skull (white) of WEN. Panels correspond to the (A) ventral, (B) lateral, (C) anterior and (D) dorsal views. Discontinuous cranial air spaces, excluding the laryngeal air space (also in red), are not shown. Reproduced from [31].

4 WHAT IT ALL MEANS

Since the turn of the century, cetacean bioacoustic research has yielded exciting results that have advanced the basic understanding of cetacean biology and provided practical knowledge that can be applied to conservation and management efforts. In some instances, the findings have contradicted previous thought. In others, they have produced more questions related to proximate function and ultimate functionality. Following are some points for thought that arise from recent findings.

Data collected from wild dolphins using the star array suggest that odontocetes apply time-varying gain to biosonar pulses as a function of distance between animal and target. In contrast, trained animals searching for targets in the natural environment are observed to either increase the amplitude of echolocation clicks at a constant distance from a target, once it is detected, or

approach the target while maintaining constant click amplitude. Whereas the former scenario serves to maintain echo amplitude across a range of distances, the latter serves to increase the amplitude of the received target echo. If odontocetes practice gain control during target searches, under what circumstances and in what manner is it applied? If, as suggested by Au and Benoit-Bird, time-varying gain is applied to volume reverberant targets to preserve echo amplitude, then maybe gain is also applied to increase the amplitude of the echoic response when the target is a point source. In the former case, tracking of the volume would be more important than identifying individual targets (i.e. a school of fish is more important than an individual fish). In the latter, capitalizing on echo highlights would be key to positively identifying the target amidst clutter. The issue of gain control, its presence and use, are open to further debate because of the neurophysiological findings: in one species, the false killer whale, gain control has been posited as a variable hearing sensitivity response; in another, the harbour porpoise, there appears to be no evidence of gain control during echolocation. In each of these behavioural and neurophysiological studies different species of odontocete were used, different experimental approaches were applied, and the subjects were studied under different motivational forces. Differentiating if, how, and when gain control is used by odontocetes will require future studies to invoke controls that permit task and species-specificity to be teased out as variables. One issue in need of immediate resolution is determining whether metabolic processes in tissues surrounding the ears increase when the ear is stimulated by sound. If so, then the possibility that animals may be actively controlling the sensitivity of individual ears needs to be considered. For instance, could the volume of sinus air surrounding the auditory bullae be preferentially varied to attenuate or accentuate the reception of echoes at the contralateral and ipsilateral ears?

The adaptive control of echolocation has been typically related to source level variation and shifts in the peak frequency of clicks as a result of variations in ambient noise levels. Echolocation beamwidths for odontocetes have traditionally been quantified as an average width while beamwidth variability is often not considered. Data collected during off-axis detection tasks demonstrate that dolphins can generate 3-dB beamwidths in excess of 30° in the horizontal plane and 25° in the vertical plane, and have a much greater control over the beamwidth than has traditionally been attributed to them. Where it has previously been postulated that time-varying gain is not under conscious control of the dolphin, the results of the off-axis detection task demonstrates conscious control over beamwidth with beamwidth variability corresponding to task. These results have broad implications for understanding how odontocetes might use echolocation in the wild and suggest that considerable caution should be used when estimating beamwidths using sparse hydrophone arrays or limited sets of echolocation data. If the ability to modulate beamwidths exist, it is probable that it has a functional capacity in foraging in navigation

Recent behavioural, anatomical and physiological findings continue to generate speculation on how the anatomy of the dolphin contributes to biosonar production and echo reception. The identification of blood flow in the melon, coupled with prior knowledge of vascularisation of the mandibular fats, argues for a temperature regulatory function. Given that the acoustic fats are relatively metabolically inert, the need for blood to deliver oxygen to the tissues becomes less important. However, the lipid densities are affected by temperature and it seems reasonable that the preservation of blood flow to these tissues stabilizes density gradients when animals experience water temperature changes, either by season, region, or depth of the water column. The observation of nominal beam steering begs the question as to how steering is accomplished. Subtle manipulation of the melon by the dolphin has been observed during off-axis detection tasks suggesting that muscular control of the melon's geometry could be a contributing factor. Another possible mechanism of beam steering is through the phase shifting of two sound generators. The presence of two sets of phonic lips provides the mechanistic basis for this process, and prior echolocation work has suggested independent use of the phonic lips in click generation. Indeed, the adaptability of the dolphin in modulating the frequency content of echolocation clicks to accommodate for hearing loss suggests that the dolphin has considerable control over operation of the phonic lips.

The potential for anthropogenic sound to impact marine mammals remains of considerable concern. Recent findings suggest that dolphins, like humans and terrestrial mammals, lose their range of hearing and hearing sensitivity as they age. It seems reasonable to assume that this pattern will

extend to other marine mammals. Thus, when considering population level effects resulting from a broad range of sound sources, how does one take into consideration the variability in hearing sensitivity within the exposed population? Recent findings from acoustic data loggers and dive recorders deployed on cetaceans have provided insight not only on how sound is used in foraging, but on the types of sounds that can produce behavioural reactions in marine mammals. The issue of behavioural disturbance is a hotly debated topic with relatively little controlled experimentation to defend any particular stance on the onset or severity of behavioural responses to sound exposure. The continued use of tags that utilize both dive recorders and acoustic sensors will likely be the most effective means of addressing questions regarding the behavioural reaction of wild marine mammals to anthropogenic sound exposures.

The field of cetacean bioacoustics is at the onset of a new age, driven by novel capabilities and a requirement to better understand how marine mammals use sound in niche exploitation. The answers to emerging questions will hopefully be elucidated as better technologies are developed and as innovative research designs are created. However, as we learn more about cetacean bioacoustics, we are certain to uncover some surprises along the way that lead to the generation of new ideas regarding the generation, reception and processing of sound by cetaceans.

REFERENCES

- [1] W.C. Burgess, P.L. Tyack, B.J. Le Boeuf, and D.P. Costa, A programmable acoustic recording tag and first results from northern elephant seals. *Deep-Sea Research part II* 45 1327-1351. (1998).
- [2] D.P. Costa, D.E. Crocker, J. Gedamke, P.M. Webb, D.S. Houser, S.B. Blackwell, D. Waples, S.A. Hayes, and B.J. Le Boeuf, The effect of a low-frequency sound source (acoustic thermometry of the ocean climate) on the diving behavior of juvenile northern elephant seals, *Mirounga angustirostris*. 113 1155-1165. (2003).
- [3] M.P. Johnson, and P.L. Tyack, A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* 28 3-12. (2003).
- [4] P.T. Madsen, M. Johnson, P.J. Miller, N. Aguilar Soto, J. Lynch, and P. Tyack, Quantitative measures of air-gun pulses recorded on sperm whales (*Physeter macrocephalus*) using acoustic tags during controlled exposure experiments. *J Acoust Soc Am* 120 2366-2379. (2006).
- [5] W.M.X. Zimmer, M.P. Johnson, A. D'Amico, and P.L. Tyack, Combining data from a multisensor tag and passive sonar to determine the diving behavior of a sperm whale (*Physeter macrocephalus*). *IEEE Journal of Oceanic Engineering* 28 13-28. (2003).
- [6] W.M.X. Zimmer, P.T. Madsen, V. Teloni, M.P. Johnson, and P.L. Tyack, Off-axis effects on the multipulse structure of sperm whale usual clicks with implications for sound production. *Journal of the Acoustical Society of America* 118 3337-3345. (2005).
- [7] D.P. Nowacek, M.P. Johnson, and P.L. Tyack, North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. 271 227-231. (2004).
- [8] W.M.X. Zimmer, M.P. Johnson, P.T. Madsen, and P.L. Tyack, Echolocation clicks of free-ranging Cuvier's beaked whales (*Ziphius cavirostris*). *Journal of the Acoustical Society of America* 117 3919-3927. (2005).
- [9] M. Johnson, P.T. Madsen, W.M.X. Zimmer, N. Aguilar de Soto, and P.L. Tyack, Beaked whales echolocate on prey. *Proceedings of the Royal Society of London B* 271 S383-S386. (2004).
- [10] P.T. Madsen, M. Johnson, N. Aguilar de Soto, W.M.X. Zimmer, and P. Tyack, Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *The Journal of Experimental Biology* 208 181-194. (2005).
- [11] S.W. Martin, M. Phillips, E.J. Bauer, P.W. Moore, and D.S. Houser, Instrumenting free-swimming dolphins conducting an open water echolocation search task. *Journal of the Acoustical Society of America* 117 2301-2307. (2005).
- [12] D.S. Houser, S.W. Martin, E.J. Bauer, M. Phillips, T. Herrin, M. Cross, A. Vidal, and P.W. Moore, Echolocation characteristics of free-swimming bottlenose dolphins during object

- detection and identification. Journal of the Acoustical Society of America 117 2308-2317. (2005).
- [13] W.W.L. Au, and K.J. Benoit-Bird, Automatic gain control in the echolocation system of dolphins. Nature 423 861-863. (2003).
- [14] P.W. Moore, L.A. Dankiewicz, and D. Houser, Off-axis target detection by an echolocating bottlenose dolphin, Symposium on Bio-sonar Systems and Bio-acoustics, Loughborough, England. (2004).
- [15] T.H. Bullock, A.D. Grinnell, E. Ikezono, K. Kameda, K. Katsuki, M. Nomoto, O. Sato, N. Suga, and K. Yanagisawa, Electrophysiological studies of central auditory mechanisms in cetaceans. Zeitschr vergleich Physiol 59 117-156. (1968).
- [16] V.V. Popov, and A.Y. Supin, Characteristics of hearing in the beluga *Delphinapterus leucas*. Doklady Akademii Nauk SSSR 294 1255-1258. (1987).
- [17] V.V. Popov, and A.Y. Supin, Contribution of various frequency bands to ABR in dolphins. Hearing Research 151 250-260. (2001).
- [18] V.V. Popov, A.Y. Supin, and V.O. Klishin, Auditory brainstem response recovery in the dolphin as revealed by double sound pulses of different frequencies. Journal of the Acoustical Society of America 110 2227-2233. (2001).
- [19] V.V. Popov, A.Y. Supin, D. Wang, K. Wank, J. Xiao, and S. Li, Evoked-potential audiogram of the Yangtze finless porpoise *Neophocaena phocaenoides asiaeorientalis* (L). Journal of the Acoustical Society of America 117 2728-2731. (2005).
- [20] A.Y. Supin, M.G. Pletenko, and M.B. Tarakanov, Frequency resolving power of the auditory system in a Bottlenose Dolphin (*Tursiops truncatus*). in: J.A. Thomas, R.A. Kastelein, and A.Y. Supin, (Eds.), Marine Mammal Sensory Systems, Plenum Press. 287-293. (1992).
- [21] A.Y. Supin, and V.V. Popov, Envelope-following response and modulation transfer function in the dolphin's auditory system. Hearing Research 92 38-46. (1995).
- [22] A.Y. Supin, and V.V. Popov, Frequency-modulation sensitivity in bottlenose dolphins, *Tursiops truncatus*: evoked-potential study. Aquatic Mammals 26 83-94. (2000).
- [23] A.Y. Supin, P.E. Nachtigall, W.W.L. Au, and M. Breese, Invariance of evoked-potential echo-responses to target strength and distance in an echolocating false killer whale. Journal of the Acoustical Society of America 117 3928-3935. (2005).
- [24] A.Y. Supin, P.E. Nachtigall, W.W.L. Au, and M. Breese, The interaction of outgoing echolocation pulses and echoes in the false killer whale's auditory system: Evoked-potential study. Journal of the Acoustical Society of America 115 3218-3225. (2004).
- [25] K. Beedholm, L.A. Miller, and M.-A. Blanchet, Auditory brainstem response in a harbor porpoise show lack of automatic gain control for simulated echoes. Journal of the Acoustical Society of America 119 EL41-EL46. (2006).
- [26] D.S. Houser, and J.J. Finneran, A comparison of underwater hearing sensitivity in bottlenose dolphins (*Tursiops truncatus*) determined by electrophysiological and behavioral methods. Journal of the Acoustical Society of America 120 1713-1722. (2006).
- [27] J.J. Finneran, and D.S. Houser, Comparison of in-air evoked potential and underwater behavioral hearing thresholds in four bottlenose dolphins (*Tursiops truncatus*). Journal of the Acoustical Society of America 119 3181-3192. (2006).
- [28] M.M.L. Yuen, P.E. Nachtigall, M. Breese, and A.Y. Supin, Behavioral and auditory evoked potential audiograms of a false killer whale (*Pseudorca crassidens*). Journal of the Acoustical Society of America 118 2688-2695. (2005).
- [29] P.E. Nachtigall, M.M.L. Yuen, T.A. Mooney, and K.A. Taylor, Hearing measurements from a stranded infant Risso's dolphin, *Grampus griseus*. The Journal of Experimental Biology 208 4181-4188. (2005).
- [30] D.S. Houser, and J.J. Finneran, Variation in the hearing sensitivity of a dolphin population obtained through the use of evoked potential audiometry. Journal of the Acoustical Society of America 120 4090-4099. (2006).
- [31] D.S. Houser, J.J. Finneran, D.A. Carder, W. Van Bonn, C. Smith, C. Hoh, R. Mattrey, and S.H. Ridgway, Structural and functional imaging of bottlenose dolphin (*Tursiops truncatus*) cranial anatomy. The Journal of Experimental Biology 207 3657-3665. (2004).
- [32] S. Ridgway, D. Houser, J. Finneran, D. Carder, M. Keogh, W. Van Bonn, C. Smith, M. Scadeng, R. Mattrey, and C. Hoh, Functional imaging of dolphin brain metabolism and blood flow. Journal of Experimental Biology 209 2902-2910. (2006).