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Research with Navy Marine Mammals Benefits Animal Care, Conservation and Biology

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The benefit and ethics of keeping marine mammals in captivity has been a source of debate for several decades. One of the center pieces of the debate is whether there is real benefit to marine mammals as a whole that results from research on captive marine mammals. The Navy Marine Mammal Program (MMP) keeps marine mammals for national defense purposes. However, in nearly 50 years of existence, the MMP has also been a leader in marine mammal research. The results of the research conducted by the MMP has not only benefited the care of marine mammals in captivity, but has directly and indirectly improved our understanding of the behavior, physiology, and ecology of animals in the wild. Research conducted with the MMP marine mammal population has produced demonstrable improvements in veterinary care and has lead to some of the earliest advances in providing guidelines for mitigating the impact of sound on wild marine mammals. Additionally, our understanding of echolocation, diving physiology, and husbandry behaviors has greatly benefited from MMP research. Future and current work conducted by the MMP will continue to add to the knowledge base of marine mammal biology while contributing to their care and conservation.

The primary purpose of the United States Navy Marine Mammal Program (MMP) is to support the operational Navy. The Navy has three “systems” of bottlenose dolphins (*Tursiops truncatus*) that perform underwater mine detection, a combined dolphin and California sea lion (*Zalophus californianus*) system that interdicts aquatic intruders, and a sea lion system that recovers objects from the sea. The MMP has supported the operational Navy for decades. For example, in 1970, during the Vietnam War, MMP dolphins were deployed to Cam Ranh Bay to protect an ammunition pier from water-borne attacks.

The Navy’s involvement with marine mammals started on a very different note. Navy interest in dolphins began in 1959 when Navy scientists began experiments with a Pacific white-sided dolphin (*Lagenorhyncus obliquidens*) housed at Marineland of the Pacific near Los Angeles. The initial work was based on a desire to determine characteristics of dolphin swimming that could be capitalized on to reduce drag and improve torpedo design. A Marine BioScience Facility was established north of Los Angeles at Point Mugu in 1962 and Navy scientists began to collect animals for experiments in the open ocean where the

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animal's full capabilities could be assessed. The apparent utility of marine mammals in several capacities was realized by 1965. Of particular interest was how marine mammal sensory systems might benefit the Navy and how marine mammals might be employed to assist the Navy in tasks performed in the ocean. It was at Point Mugu that a young dolphin named "Tuffy" participated in a study called Sea Lab II. Tuffy, a juvenile dolphin at the time of the program in 1965, delivered tools and messages to aquanauts housed some 200 feet below on the sea floor. Tuffy's affinity for and willingness to interact with human trainers and aquanauts (Ridgway, 1987) demonstrated a great potential for interspecies accomplishment that soon grew into a larger, more formalized program. In the latter half of the 1960s, Tuffy and several other dolphins helped to recover Regulus missile cradles, practice mines, and ASROC practice rockets from the sea floor. The program expanded considerably during that time.

Efforts at the Point Mugu facility began relocating in 1967 in order to forward the research and operational efforts of the MMP. A sister laboratory was established in Kanehoe Bay, Hawaii and another in San Diego; the Point Mugu facility was closed in 1970. The research projects increased over time and the Navy involved more and different species of marine mammals to explore their different capabilities. Killer whales (*Orcinus orca*), pilot whales (*Globocephala* spp.), belugas (*Delphinapterus leucas*), and Stellar sea lions (*Eumatopias jubatus*) all participated in the program at one time or another. However, the MMP eventually settled on the use of bottlenose dolphins and California sea lions to meet most of their operational needs as both species were found to be robust and adaptable to numerous tasks.

Over the 48+ years the MMP has been in existence, a plethora of research projects investigating marine mammal health, physiology, behavior, biosonar, and diving have been completed. The program has generated over 1000 research articles in its history (Department of the Navy, 1998), making it one of the largest contributors to the knowledge of marine mammals in the world. In the following article, some of the contributions of the MMP to our current body of marine mammal knowledge are summarized. In particular, those studies related to the health and conservation of marine mammal species are presented.

Environmental Stewardship–Sound and Marine Mammal TTS

The entrance of the MMP into environmental issues began in earnest with studies of temporary threshold shift (TTS)—a temporary noise-induced hearing loss—in marine mammals. During the mid 1990s, with an increasing awareness that anthropogenic sound could potentially negatively impact marine mammals, TTS was under consideration by the National Marine Fisheries Service (NMFS) as criteria for harassment of marine mammals under the Marine Mammal Protection Act (MMPA). At that time, no data existed on the levels of sound required to induce TTS in any marine mammal. The first study of TTS involving bottlenose dolphins was conducted by the MMP and involved the measurement of levels of sound required to cause a TTS from 1s tonal signals at frequencies of 3, 20, and 75 kHz (Ridgway, Carder, Smith, Kamolnick, Schlundt, & Elsberry, 1997). Work with tonal signals continued in the years to come, with the addition of belugas as subjects and with improvements in techniques that permitted more control over the acoustic environment and the ability to assess the impact of sound exposure across multiple frequencies of hearing simultaneously (Finneran, Carder, Schlundt, & Dear, 2009; Finneran, Carder, Schlundt, & Ridgway, 2005; Finneran, Schlundt, Branstetter, & Dear, 2007; Schlundt, Finneran, Carder, & Ridgway, 2000). Importantly, the results of the tonal exposure studies became the foundation for decisions by the NMFS on the exposure thresholds required to trigger harassment in cetacean species. Although the current manner in which regulatory harassment is determined in marine mammals has been expanded to include behavioral disturbance without the occurrence of TTS, the use of exposure thresholds inducing TTS determined at the MMP continue to be used for assessing the potential impact to marine mammals from acoustic sources and for establishing mitigation procedures for operating sound sources in the ocean. To date, the information from these studies has been implemented in numerous environmental assessments and environmental impact statements (U.S. Navy, 2008a, 2008c, 2008d).

With the realization that impulsive signals from military and industrial sources were an important component of ocean noise, studies of TTS at the MMP were expanded in the late 1990s to address the exposures required from impulsive signals to cause TTS. These studies, concerned primarily with addressing the potential impact of explosives on marine mammals, used an underwater explosive simulator, seismic water gun, and arc-gap transducer to determine the characteristics of the impulsive signals that produced TTS in sea lions, dolphins and belugas (Finneran, Dear, Carder, & Ridgway, 2003; Finneran et al., 2000; Finneran, Schlundt, Dear, Carder, & Ridgway, 2002). As with data collected on tonal signals, the information on the tolerances of sea lions, dolphins and belugas to impulsive sounds proved valuable to estimating the environmental impact resulting from explosive sources (U.S. Navy, 2008b). Today, there is still keen interest in the impact of impulsive signals to marine life. Studies within the MMP continue to address the recovery of the auditory system to noise induced threshold shifts, particularly following multiple but temporally separated exposures.

Audiometry

Fundamental to understanding the impacts of anthropogenic sound on marine mammals is a clear understanding of the hearing capabilities of the animals exposed to the sound. Sounds outside an animal’s range of hearing, or within frequencies to which they are insensitive, are likely to have no to minimal impact unless they are of such magnitude as to cause tissue trauma. Conversely, both physiological impacts and behavioral responses may be more easily incurred at frequencies to which animals are particularly sensitive. The MMP was the early pioneer in the study of animal hearing, first through the use of behavioral methods to determine the range of hearing and sensitivity of dolphins (Johnson, 1966), and later through the use of auditory evoked potentials (AEP) (Ridgway, Bullock, Carder, Seeley, Woods, & Galambos, 1981; Seeley, Flanigan, & Ridgway, 1976), a neurophysiological method which can be used to measure hearing sensitivity. Through access and testing of AEP methods on MMP dolphins, the approach has been benchmarked against behavioral audiometry for dolphins resting in water and resting in air (Finneran & Houser, 2006; Houser & Finneran, 2006a). This latter methodology had important implications for application of the technique in stranding situations.

A system for performing AEP tests, called the Evoked Response Study Tool (EVREST), was developed within the MMP and proofed through studies with MMP dolphins. The system is both portable and battery operated and permits real-time, objective estimations of hearing thresholds in marine mammals (Finneran, 2008, 2009). The system also permits multiple frequencies to be tested simultaneously; whereas the use of AEP methods to test single frequencies reduced the time of obtaining dolphin audiograms from months to approximately an hour, the ability to test multiple frequencies reduced testing across the range of hearing to minutes (Finneran & Houser, 2007; Finneran, Houser, Blasko, Hicks, Hudson, & Osborn, 2008). The portability of the system and the reduction in testing time necessary for obtaining audiograms has opened the door for researchers to deploy to stranding sites or other marine mammal facilities to collect audiometric data. This has permitted the collection of data on species for which audiometric data did not exist (Finneran, Houser, Mase-Guthrie, Ewing, & Lingenfelser, 2009b) and allowed the first ever measures of population level hearing data in a marine mammal (Houser & Finneran, 2006b; Houser, Gomez-Rubio, & Finneran, 2008). The collections of these types of data directly address the need for a basic understanding of species hearing and the variations in hearing that result from age, gender and environmental factors. In addition, it provides the ability to study issues of clinical care, such as the impact to hearing resulting from the treatment of certain antibiotics (Finneran, Dear, et al., 2005). In 2008 and 2009, two EVREST systems were created for use by stranding networks in Cape Cod and the coast of California. This capability, which is available due to studies conducted on animals of the MMP, has the potential to expeditiously increase our knowledge of hearing in novel species, increase population-level understanding for species in which data exist, and provide better clinical assessments and care of stranded odontocetes.

Although development of AEP methods has focused predominantly on odontocetes, there are efforts underway to expand the methods to other species and optimism about the potential for one day using the techniques for testing hearing in mysticete whales. A broad-scale effort is underway at the MMP to benchmark AEP audiometric methods against behavioral audiometry in California sea lions (*Zalophus californianus*) and then apply the methods to the MMP sea lion population. As with the bottlenose dolphins, this will provide population-level assessment of hearing in a pinniped species, albeit limited to only males. Partnerships between the MMP and other institutions also continue to expand the AEP methods to other pinniped species (Houser, Crocker, Kastak, Mulsow, & Finneran, 2007; Reichmuth, Mulsow, Finneran, Houser, & Supin, 2007), including those that approach the size of neonate mysticetes (Houser, Crocker, & Finneran, 2008).

Non-Auditory Responses to Sound Exposure

Federal agencies are currently required to consider more than TTS in an analysis of the potential impact of acoustic operations on marine mammals. Other considerations are significant behavioral responses (i.e. disruption of behaviors important to survival and reproduction), and the accumulation of stress associated with sound exposure that results in negative biological consequences for an individual or population (National Research Council (NRC), 2005). Ideally, such impacts would be ascertained and understood in the context of wild populations of marine mammals. However, field research endeavors are costly and time consuming and it will be many years before sufficient data is accumulated from field studies to adequately address these outstanding issues. Conversely, the use of animals maintained at facilities provides opportunities to address some of these questions.

Relatively little is known about the acute or chronic stress response resulting from either acute exposure to anthropogenic sound or the long-term exposure resulting from increased ocean noise. Some of the few studies on acute responses to high level sound exposure were conducted at the MMP with dolphins and belugas (Romano et al., 2004). These studies demonstrated a neural-immune response in a beluga and dolphin that was related to sound exposures created by both a seismic water gun and a tonal source. The results were varied between individuals in both type and magnitude and highlighted the difficult nature of working with small numbers of animals. Nevertheless, at the time of the study, only two other studies had looked at stress resulting from sound exposure, either through analysis of stress hormones or via monitoring of heart rate (Miksis, Connor, Grund, Nowacek, Solow, & Tyack, 2001; Thomas, Kastelein, & Awbrey, 1990).

Determining behavioral reactions to sound exposure that have consequences to marine mammal survival and reproduction are difficult to obtain in the wild. It is no surprise that initial methods of estimating impacts relied once again on behavioral responses of marine mammals maintained at facilities and participating in acoustic studies. Much of the data used by the U.S. Navy for predicting behavioral reactions that equate to “significant” are derived from the post-hoc analysis of behavioral reactions of MMP dolphins and belugas observed in studies of sound-induced TTS (Finneran & Schlundt, 2004). These are the majority of the data that form the basis of the “risk functions” currently used by the U.S. Navy in a number of environmental impact statements (U.S. Navy, 2008a, 2008c, 2008d). Being derived in a post-hoc manner and from a study that was not designed to investigate behavioral reactions, it is acknowledged that the responses observed in the TTS studies have limited applicability to estimating behavioral reactions in wild marine mammals. As a balance between current need and the future gathering of more directly applicable behavioral reaction data in wild marine mammals, a study is currently underway at the MMP to qualify and quantify the magnitude and duration of both behavioral and physiological reactions to sonar-like signals. This controlled exposure study is utilizing large numbers of dolphins and sea lions to increase the robustness of the data collection. Animals are naïve to the sound exposure prior to participating in the study and each animal is only tested once. Levels of sound received by the animals range from near ambient to 185 dB re 1 µPa and multiple animals are tested at each exposure level. Behavioral reactions are noted and scored according to a severity scale with the resulting data purposed for supporting the development of more robust risk functions. In addition, heart rate is recorded on several of the animals and blood corticosteroids and catecholamines are observed to determine if there are acute or chronic stress responses related to the sound exposures. Collectively, the study should provide the most comprehensive assessment of behavioral reactions to sonar-like signals conducted to date with the added benefit of monitoring physiological responses associated with stress (Houser, Yeates, Crocker, & Finneran, 2009).

Clinical Care and Research

The U.S. Navy is committed to providing the highest level of care to its marine mammals and the MMP provides a comprehensive medical program for the detection, treatment and prevention of disease. As a result of this effort, many milestones in marine mammal medicine have been made through the decades of the MMP's existence (Ridgway, 1965, 1972, 2008). Work at Point Mugu in the 1960s led to the first textbook aimed at providing basic scientific information, anatomy, general biology, physiology, husbandry, and behavior, useful for caring for marine mammals and diagnosing their diseases (Ridgway, 1972). Several areas in which work with MMP dolphins and sea lions have advanced, or are anticipated to advance, the overall care of marine mammals at parks and aquaria and stranding facilities are reviewed below. In addition, health related research and its application to understanding the health of wild marine mammals is discussed. The list is by no means exhaustive, but serves to highlight the accomplishments that have impacted our current understanding of marine mammal health and disease.

Anesthesia

The handling of marine mammals for purposes of providing veterinary care can be dangerous to both the animal and the clinician. In the early days of the MMP, with the realization that sea lions would require a humane method of immobilization for examination and treatment, the sea lion "squeeze cage" was developed (Ridgway & Simpson, 1969). This device, which is still widely used today in wild and captive otariids, provides a means to safely immobilize otariids and protect animal handlers from injury. Although the squeeze cage provides an adequate means of temporarily restraining sea lions for evaluation and treatment, the development of gas anesthesia methods at the MMP paved the way for techniques used today (Ridgway & Simpson, 1969). Halothane anesthesia techniques developed at the MMP were demonstrated to be far superior to available injectable agents, which usually produced a mixture of complications including prolonged recovery, loss of thermoregulatory control, and respiratory distress. Over the decades since its development in sea lions, the gas anesthesia technique for otariids has improved and the efficacy and safety margins of the gas anesthetics used (e.g., isoflurane and sevoflurane) has increased. Gas anesthesia is now widely used as a safe and humane method of otariid immobilization in both captive and wild populations (Dold & Ridgway, 2007; Heath, DeLong, Jameson, Bradley, & Spraker, 1997; Horning, Haulena, Tuomi, & Mellish, 2008; Petrauskas, Atkinson, Gulland, Mellish, & Horning, 2008; Sousa, Hurley, & Costa, 1998).

Anesthesia in dolphins is a tenuous undertaking but is sometimes necessary for critical care cases (e.g., surgical procedures have occasionally been required in animals that have swallowed foreign objects). Until the 1960's, efforts to anesthetize dolphins largely met with failure and loss of the dolphin (reviewed in Ridgway, 2008). Initial successes with dolphin anesthesia were made with the use of nitrous oxide and the application of the Bird respirator, a device which mimicked the peculiar breathing pattern of the dolphin (Nagel, Morgane, & McFarland, 1964,1966; Ridgway, 2008). This approach proved to be effective at anesthetizing dolphins, but the plane of anesthesia was not deemed sufficient for major surgical procedures. Anesthetic procedures for dolphin surgery were reported by Ridgway (1965) and later, work conducted at the MMP as a joint effort between Drs. Sam Ridgway and James McCormick would lead to a more effective method of anesthesia suitable for surgical procedures (Ridgway & McCormick, 1967, 1971). The approach, which utilized halothane and implemented more rigorous monitoring procedures, has been used a number of times in efforts to save the lives of dolphins in critical care situations. Although the gas anesthetic may have changed, the procedure endures as the method available for major surgical procedures.

Disease states, epidemiology and clinical care procedures

The veterinary staff of the MMP has spent decades working on the detection, isolation and identification of viral and bacterial pathogens and environmental contaminants that can affect the marine mammals within its population and elsewhere. Studies conducted at the MMP on the bioaccumulation of trace metals, polychlorinated biphenyls (PCBs) and organochlorines (OCs) in dolphin tissues has provided not only basic information on the levels of these compounds in tissues and milk, but also information on contaminant dynamics between tissues (e.g., blood vs. blubber), its maternal passage to offspring via milk production, its potential impact to reproduction, and its relationship to age and gender (Reddy, Echols, Finklea, Busbee, Reif, & Ridgway, 1998; Reddy, Reif, Bachand, & Ridgway, 2001; Ridgway & Reddy, 1995; Sorensen, Venn-Watson, & Ridgway, 2008). Veterinary work with MMP dolphins has resulted in observations of unusual species interactions (e.g., skin infestations of delphinids), allowed identification of bacterial and viral disease states, permitted the characterization of novel dolphin viruses, and resulted in the development of methods for detection of the viruses (Jensen, Lipscomb, Van Bonn, Miller, Fradkin, & Ridgway, 1998; Miller, Padhye, Van Bonn, Jensen, Brandt, & Ridgway 2002; Nollens et al., 2008; Ridgway, Lindner, Mahoney, & Newman, 1997; Van Bonn, Jensen, House, House, Burrage, & Gregg, 2000; Venn-Watson et al., 2008). In a collaborative effort between the MMP and academic researchers, virus detection methods were used to characterize the distribution of parainfluenza virus across wild dolphin populations and those under human care (Venn-Watson et al., 2008). Similar comparisons have been made between the MMP and wild populations with respect to immunological factors (Ruiz et al., 2009). As has been demonstrated by these efforts, long term monitoring of physiology and health in a managed population of animals provides comparative and baseline information for the understanding of bioaccumulation, disease, and epidemiological processes in wild populations.

The long-term monitoring of, and investment in, the animals of the MMP has permitted the development of diagnostic techniques and clinical treatments that has increased the longevity and quality of life of the MMP animals. These advances, which are shared with other veterinarians during regular meetings of the International Association for Aquatic Animal Medicine (IAAAM), have broad impacts to the treatment and care of both captive and wild (e.g., stranded) marine mammal populations. Advances in ultrasonography, endoscopy (Van Bonn, Cranford, Chaplin, Carder, & Ridgway, 1997), and biomedical imaging (*see below*) at the MMP have promoted the earlier detection of pathological conditions, enabling earlier treatment and better prognoses for afflicted animals. The identification of iron overload disease in dolphins subsequently resulted in a treatment procedure involving phlebotomy to reduce the iron load carried by an animal (Johnson, Venn-Watson, Cassle, Smith, Jensen, & Ridgway, 2009). The identification of the consumption of indigestible objects (e.g., sea grass) in a small percentage of the population led to the development of treatment plans for mitigating this behavior (Meck, Jensen, Van Bonn, & Fradkin, 1998). From advanced technological approaches to the implementation of effective management plans resulting from basic behavioral observations, the long term but daily access to the animals of the MMP has produced valuable knowledge for veterinarians addressing marine mammal pathologies.

Medical imaging

Early on, the MMP implemented the use of X-Ray as a diagnostic tool for dolphins and sea lions (Miller & Ridgway, 1963; Sweeney, 1974), a tool which was commonplace by the 1980s. The MMP is now a leader in applying computed tomography (CT) and magnetic resonance imaging (MRI) to improve animal health care. Both CT and MRI have been used to study the post-mortem tissues of marine mammals for more than 20 years (Cranford, 1988; Cranford, Amundin, & Norris, 1996; Cranford et al., 2008; Ketten, 1997; Ketten & Wartzok, 1990; Marino, Murphy, DeWeerd, et al., 2001; Marino, Murphy, Gozal, & Johnson, 2001; Marino, Sherwood, Delman, Tang, Naidich, & Hof, 2004; Marino, Sudheimer, McLellan, & Johnson, 2004; Marino, Sudheimer, Pabst, et al., 2004; Marino, Sudheimer, Pabst, McLellan, & Johnson, 2003; Montie, Schneider, Ketten, Marino, Touhey, & Hahn, 2007, 2008; Ridgway, Marino, & Lipscomb, 2002). Within the last decade, the MMP has spearheaded the use of CT and MRI, as well as functional imaging modalities (positron emission tomography (PET) and single photon emission computed tomography (SPECT)), to study the physiology and anatomy of living marine mammals. The first of these studies demonstrated the relationship between air spaces and bony structures in a living dolphin, the distribution of blood flow within the dolphin's cranial tissues, and the relative metabolism of the dolphin's brain tissues (Houser et al., 2004). Follow-on work demonstrated intriguing relationships between reductions in blood flow to one hemisphere of the brain, variations in regional brain metabolism, and the condition of unihemispheric sleep in the dolphin (Ridgway et al., 2006). Although these studies did not directly address animal health issues, they provided insight on the physiology and functional anatomy of the bottlenose dolphin that would not otherwise have been obtained and increased our overall understanding of how this species works. In addition, the methodologies for training and handling animals for the scanning procedure have been migrated to the clinical setting so that CT has become more available for diagnosis and tracking the progress of treatment.

The veterinary staff at the MMP now capitalizes on the ability to perform biomedical scans to enhance the care of MMP dolphins. Computed tomography is used to investigate osteological problems, MRI is used to study soft-tissue pathologies in sea lions and dolphins (Blankenship, Dold, Jensen, Smith, Bonn, & Ridgway, 2008), and PET scans are used in the performance of renal scintigraphy. The use of biomedical imaging techniques is not routinely performed on MMP marine mammals, but neither is it uncommon. The continued use of biomedical imaging methods will enhance our understanding of marine mammal pathologies and pathogenesis. As the availability of biomedical scanners increases, more marine parks and aquaria will likely begin to utilize them for diagnostics. The use of biomedical scanners by stranding networks to study marine mammal biology and health is already growing (Montie et al., 2009). In the end, the use of biomedical imaging scanners will only improve our care and treatment of injured and diseased marine mammals. The MMP will continue to lead in that regard, by promoting the use of diagnostic imaging techniques traditionally unavailable to the marine mammal community.

Husbandry and research behaviors

The performance of husbandry behaviors is essential to the effective management of animal health. Behaviors such as dolphin fluke presentations for the collection of blood samples, stationing and body presentation for ultrasound inspections, voluntary opening of the mouth for inspection of teeth and gums, and body positioning for milk or semen collection are all fairly common these days. However, there was a time when these husbandry behaviors were not in use and the need to perform veterinary exams required forced restraint. Many of the husbandry behaviors common today were started or improved through training efforts with MMP dolphins and sea lions utilizing positive reinforcement methods. Most notable of these may be the voluntary presentation of the fluke for blood draws. This behavior was pioneered by C. S. Johnson during the early years of the MMP in 1964, presumably because Johnson was "annoyed" by blood draws interfering with his research (Ridgway, 2008; Ridgway, personal communication). Johnson also trained his dolphin to present itself for all sorts of veterinary inspections of the mouth, chest, etc. Additional conditioning for milk collection (along with the development of a milk collection device), nasal passage endoscopy, and improvements in voluntary transport procedures were pioneered at the MMP (Chaplin, Kamolnick, Cranford, Van Bonn, Carder, & Ridgway, 2000; Kamolnick, Reddy, Miller, & Curry, 1997; Ridgway, 2008). Without the development of these and other husbandry behaviors, marine mammal veterinary medicine would likely be a much more stressful practice for both animal and practitioner. The efforts placed into the development of voluntary husbandry behaviors have contributed to improvements in the quality of life of captive animals; through the use of positive reinforcement, voluntary behaviors have reduced the stress to animals and enabled better veterinary care to be provided.

Similarly, the training of husbandry behaviors contributed to the development of research behaviors that facilitated the performance of research projects throughout the history of the MMP. For example, in the 1980s, MMP trainers developed methods for training dolphins and belugas to respond by whistling or burst pulsing to different computer generated sounds so that acoustic response times could be measured and behavioral audiograms could be collected more rapidly (Ridgway & Carder, 1988, 1997; Ridgway, Carder, Kamolnick, Skaar, & Root, 1991). This methodology allowed for the first audiograms collected in the open ocean at depths up to 300 m (Ridgway, Carder, Kamolnick, Smith, Schlundt, & Elsberry, 2001). This ability to have dolphins rapidly interacting with computer programs to carry out response paradigms has greatly facilitated behavioral audiometry and TTS measurements (Finneran et al., 2000, 2002; Finneran, Carder et al., 2005; Schlundt, et al., 2000). Additionally, the dolphin's response time gives a good idea of the animal's perception of stimulus strength allowing a better comparison of different acoustic or visual stimuli (Ridgway et al., 2009; Ridgway & Carder, 1997).

General Biology

Echolocation

Although dolphin echolocation was discovered with the first animals to be captured and maintained at Marine Studios in Florida in the 1950s (McBride, 1956), considerable advancement in understanding dolphin echolocation has been made in the MMP. This is especially notable in the work of Evans and Powell (Evans & Powell, 1966) on echolocation discrimination and the collaborations of Evans and Norris (Norris & Evans, 1967; Norris, Evans, & Turner, 1966). In the 1970s and 1980s a great body of work on echolocation was compiled by MMP researchers, especially W. L. Au, P. Nachtigall, R. Penner, J. Kadane, E. Murchison, and P. W. Moore (see Au, 1993 for review). We know that animals in the wild echolocate because of the numerous experiments done with trained animals since the first discovery in Florida. If it were not for the numerous experiments on trained animals, one wonders if we would still be debating the function of those clicks we record from odontocetes at sea.

Obtaining information from tagged animals at sea

MMP researchers W. E. Evans and J. S. Leatherwood pioneered the use of tagged dolphins for obtaining information on wild dolphin behavior and distribution (Evans, Hall, Irvine, & Leatherwood, 1972; Evans & Leatherwood, 1972). They tracked dolphins and followed herd movements, recording dive depths, dive profiles and other relevant biological data. Hui later looked at dolphin movements using telemetry data from tagged dolphins, showing that they did not follow magnetic fields in the ocean (Hui, 1994). Today, sophisticated tags are extensively employed to obtain information on cetaceans in various wild populations.

Marine mammal diving

Early in the MMP there was interest in what might be learned from diving animals like dolphins, whales, and seals that might give clues to human diving diseases such as decompression sickness, aeroembolism, nitrogen narcosis and high pressure nervous syndrome (*c.f.* Ponganis, Kooyman, & Ridgway, 2003). In the late 1960s, open ocean work with the dolphin, Tuffy, demonstrated that dolphins could make dives to 300 m with no ill effects. This was the first demonstration that dolphins could dive to these depths. The experiments showed that the breath-hold diving dolphin could rapidly return to the surface from these depths without any problem of developing symptoms of decompression sickness (Ridgway, Scronce, & Kanwisher, 1969). The secret was in the dolphin's flexible thorax that allowed the lungs to collapse with increasing dive depth. This collapse limited nitrogen absorption in the blood and thus mitigated problems (symptoms) associated with decompression sickness. In the 1970s, MMP investigators addressed the issue of repetitive, rapid dives to a shallower depth of 100 m. Trained dolphins dived to 100 m and returned to the surface 20 to 25 times within a period of one hour. With this rapid, repetitive dive schedule, dolphins did build up nitrogen in their muscle. The level of nitrogen in the dolphins at the end of the dive schedule was at a level where nitrogen bubbles were thought to potentially develop (Ridgway & Howard, 1979). However, the dolphins were ready and willing to repeat this rapid dive schedule and showed no ill effects from the effort.

The question of diving diseases and bubbles in blood and other tissues of cetaceans has recently been revisited by several authors (Fernández et al., 2005; Houser, Howard, & Ridgway, 2001; Jepson et al., 2003; Moore et al., 2009; Moore & Early, 2004; Zimmer & Tyack, 2007). Of particular note, scientists who investigated a mass stranding of beaked whales off the Canaries in 2002 noted that the animals showed signs of acute gas and fat emboli formation in their soft tissues and vasculature. They suggested sonar exercises that occurred proximate to the strandings might have contributed to the development of symptoms similar to decompression sickness in the stranded whales, potentially as a result of altered dive behavior (Fernández et al., 2005). In another study, Moore and Early (2004) found lesions in sperm whale bones suggestive of osteonecrosis. Among other causes, osteonecrosis can result from a history of repetitive decompression insults in human divers.

In an effort to determine if vascular bubbles could be observed in a repetitively diving cetacean, researchers at the MMP trained a dolphin to dive repetitively to depths between 30 and 100 m and to remain at depth for a period of time on each dive in order to increase nitrogen gas absorption (Houser et al., 2009). At the end of 10-12 dives a portable ultrasound was used to investigate for the presence of vascular bubbles. No bubbles were observed after any of the dive series. However, bubbles in the tissue of stranded cetaceans may have many causes, and the authors suggested that the stranding itself may contribute to bubble formation if the vascular dynamics of the cetacean is compromised so that nitrogen gas from slowly off-gassing tissues is not effectively removed. Currently, the relationship between stranding, sonar, and the presence of gas and fat emboli is still a puzzle that requires further investigation.

Conclusion

The existence of the MMP provides access to a unique marine mammal population that has greatly added to our knowledge of marine mammal biology and veterinary medicine. The ability to continuously monitor the behavior and health of the MMP animals has established this population as a system that can be used as a benchmark for other populations with respect to contaminants and disease transmission, as well as a system for evaluating and improving population health surveillance methods (Reddy et al., 2001; Wong, Van Bonn, Smith, Jensen, Lomax, & Ridgway, 2003). The ability to train MMP animals for involvement in research has greatly increased the value of this population as it has permitted the expansion of our knowledge of many aspects of marine mammal biology, and that of the dolphin and sea lion in particular. Of current interest, experimental work conducted at the MMP has dramatically improved our understanding of how sound impacts marine mammals. As anthropogenic sound is increasingly acknowledged as an ocean pollutant, information on the impact of sound to marine mammals (and other marine life) becomes more essential for effectively managing the interaction between marine mammal populations and anthropogenic sound production. The same can be said of other anthropogenic and natural factors that directly and indirectly affect dolphins and sea lions; being top level predators in the ocean, these species can be good indicators of ocean health and habitat flux.

Criticisms that captive marine mammals offer little in the legitimate contribution of understanding marine mammal biology or aiding conservation exist (e.g., Rose, Parsons, & Farinato, 2009). These criticisms are more often targeted toward display facilities, but the MMP has received its share of similar criticisms. The MMP is distinctive in that it is “not” a display facility, but one that maintains marine mammals for national defense purposes. Certain defense requirements are met because of the dive capabilities and acute underwater hearing of the dolphin and sea lion and the biosonar capability of the dolphin. Nevertheless, the existence of the program has produced decades of research that has advanced our understanding of marine mammal biology. The program boasts hundreds of research articles dealing with marine mammal hearing, sound production, physiology, diving, hydrodynamics, breeding, ageing, and veterinary medicine (Department of the Navy, 1998). In addition, the MMP has facilitated the efforts of many marine mammal scientists and sponsored and trained students and post-doctoral associates interested in marine mammalogy. The program has provided access to research subjects, cutting-edge technology, and decades of scientific expertise that exists within the program. Many of the individuals that have come through the program are now leaders in the field of marine mammalogy and they are addressing today's pressing scientific questions regarding marine mammals.

The existence of the MMP has been a benefit to marine mammals, both captive and wild. Either through improvement in conservation practices, advances in veterinary care and management, or through improvement in our understanding of the overall biology of marine mammals, the MMP has served as a unique population from which we have and will continue to learn.

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