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Prelude to the anthology in memory of Donald Richard Nelson

There are few people on this planet who could not tell you something about the behavior of the sea creature known as the shark. Ask most people and they will likely cite voracious feeding and aggressive behaviors, but ask a shark scientist and you will get a very different answer. In truth, information on the natural behavior of sharks is known for only a few of the more than 350 species. Even less is known about their cousins, the more than 450 species of derived rays and skates. The main reason for this great void is that elasmobranch fishes are relatively large, wide-ranging, and live in an inhospitable and secretive environment. Thus they are relatively difficult to observe in the field or study under laboratory conditions. The same reasons explain why so little is known of how the sensory systems of these animals function in natural settings. As a result, much of what we know about the natural behavior of sharks and rays comes from brief field studies conducted without a premeditated paradigm or experimental design.

One extraordinary exception is the research from 1962–1997 conducted by Donald Richard Nelson, whom this anthology honors. Don was a diver, teacher, scientist and adventurer who arguably spent more time underwater observing these animals than any other human. His bold and numerous expeditions to study shark behavior and sensory biology in the field are unmatched. Perhaps most significant is that his enthusiasm and teachings have continued to stimulate many of his students and colleagues. Don's work, and that of his successors, will become even more significant as time progresses given the great academic pressures for successful grantsmanship and the current lack of funding resources for the study of shark behavior. In retrospect, Don has left a healthy legacy that will hopefully propel this field well into the future.

The symposium to honor the contributions of Don Nelson to the study of shark behavior was convened on 18 July 1998 at the annual meetings of the American Elasmobranch Society held at the University of Guelph (Figures 1–3). At the formal meeting there were 17 presentations that covered a wide range of topics on the sensory biology and behavior of sharks and rays. From the original symposium presentations, 14 scientific papers were contributed for this volume. The purpose of this publication is twofold. First, there has not been a scientific treatise published on the behavior of elasmobranch fishes for more than 20 years. In that time period, many new technologies were developed (some of which were pioneered in Don Nelson's laboratory) and applied to the study of shark behavior and sensory biology. Second, there is a new generation of young students who often find it difficult to consolidate information on elasmobranch behavior, or identify critical study questions. Thus, we asked authors of this volume to include a significant review of their study area, and also to identify at least 3 hypotheses that can be tested. It is our hope that this treatise will provide an impetus for scientists (young and old) to continue the study of shark behavior and sensory biology.

The articles that follow the introductions to Don Nelson can be separated into three categories: sensory biology, behavior and telemetry. The first paper is by symposium keynote speaker Art Myrberg, who in his own right is a founder of the study of shark behavior and sensory biology. His paper addresses the history and current status of research on how sharks hear and orient to sound sources in their natural world, which remains one of the most controversial questions in auditory biology. Karen Maruska then presents a detailed review of the lateral line system of sharks and rays, new comparative data on the poorly studied batoids, and an interpretation of this complex but poorly studied system in relation to elasmobranch natural behavior. In his paper on the electrosense, Tim Tricas argues for the 'neuroecology' approach to the study of elasmobranch sensory systems, and presents new information on how the skate and great white shark may use their respective electrosensory systems in the real world. John New's paper on the enigmatic cerebellum, a brain structure that is greatly enlarged in some sharks and batoids, identifies the intricacies of this sensorimotor interface and how it may function in the expression of behavior. John Montgomery & Mike Walker review the subject of shark posture, orientation and navigation where they emphasize the importance of integrating sensory system functions with natural behaviors. The work by Joe Sisneros & Don Nelson posthumously provides the history of the U.S. Navy's effort to develop an effective shark repellent and the subsequent discovery of pardaxin in the Moses sole. They then present new data on the irritant response of sharks to more economical



Figure 1. Participants in the Donald R. Nelson symposium sponsored by the American Elasmobranch Society at the University of Guelph on 18 July 1998. Standing in the upper picture are (from left to right) Scott Eckert, John New, John Montgomery, Sonny Gruber, Karen Maruska, Arthur Myrberg, Jr., Peter Klimley, Nancy Kohler, David Bodznick, Timothy Tricas, Fred Voegeli, Chris Lowe, Bob Heuter and in front, Joe Sisneros, Wesley Strong, Wes Pratt and Jeff Carrier. Photograph below shows Arthur Myrberg delivering his lively keynote presentation on shark hearing and acoustic orientation.



Figure 2. Ginger Nelson (upper photograph) thanks the American Elasmobranch Society for the symposium to honor the many accomplishments of her husband. Ginger was instrumental in establishing the Donald R. Nelson fund with AES, which promotes an annual student research award to encourage the study of the sensory biology and behavior of elasmobranch fishes. The Don Nelson symposium in Guelph was attended by many of his former students/advisees (lower photograph). From left to right are Joe Sisneros, John Morrissey, Ginger Nelson, Chris Lowe, William Fouts, Ron Abir and Tim Tricas.



Figure 3. Festivities at the American Elasmobranch Society banquet following the Nelson symposium. Social hour in which José Castro (left) describes the reproductive biology of sharks to unidentified graduate student (right) under the watchful eye of Art Myrberg (center). Co-organizers Tim Tricas (left) and Sonny Gruber (right) discuss the symposium and plan the publication of this volume. Mariko Gruber (seated at center) moderates.

substitute surfactants. Phil Motta & Cheryl Wilga give a much-needed update on the feeding mechanism of sharks and how modern techniques have advanced the study of the function and evolution of shark feeding behavior. Wes Pratt & Jeff Carrier's review of the reproductive behavior of sharks and rays also includes recent work on their gold mine of mating nurse sharks in the Florida Keys. The final part of the volume deals with applications of old and new technologies to monitor the movements and behavior of sharks and rays in the field. Nancy Kohler & Pat Turner provide a detailed history of how standard tagging techniques are used to study migration patterns of sharks. They then synthesize the major National Marine Fisheries effort in the United States and others conducted around the world. This is followed by a series of telemetry papers, the first of which is authored by Fred Sundström, Sonny Gruber and colleagues. They summarize past research conducted on the behavior and movements of sharks that use standard telemetry tracking techniques, and then provide new information on the movement patterns, activity, and homing behavior of juvenile lemon sharks around Bimini. The applications of ultrasonic telemetry used to study swimming physiology and endothermy in sharks is reviewed by Chris Lowe & Ken Goldman, and several timely studies in this area are proposed. This is followed by a review of the current state-of-the-art in remote monitoring equipment compiled by engineer Fred Voegeli and associates. The issue closes with two excellent field studies that demonstrate applications of new and exciting tracking techniques. The paper on archival tagging written by Grant West & John Stevens of CSIRO, Australia provides a remarkable example of how this new technology can provide unprecedented information on the vertical movements of large sharks. This impressive work is matched by that of Scott Eckert & Brent Stewart, who report their transoceanic satellite trackings of whale sharks. Clearly, new techniques applied to the field such as these will continue to reveal information that was only a dream for us a few years ago.

The guest editors would like to thank all the participants of the symposium in Guelph, and those who contributed papers in this printed volume. The symposium was made possible with the full support of the American Elasmobranch Society and its members. Special thanks are given to then AES president Phil Motta for his administrative support, Jeff Carrier for his never-ending technical and photographic assistance during the presentations, and Chris Lowe for his helpful assistance with details on this publication and the Nelson Fund. We also thank the more than 100 AES and ASIH members that formed the interactive audience at the Nelson symposium meeting. We extend our deepest appreciation to Eugene Balon for offering us pages in this journal, and his ability to bend with the wind as we tried to bring this event to press. Finally, we thank Ginger Nelson for her endless support of Don, and our efforts to crystallize his impact on the study of shark behavior.

Melbourne and Miami, Florida, 1 May 2000

Timothy C. Tricas Samuel H. Gruber

A note on shark drawings on the blank pages of this volume

Paul Vecsei & Sarah Heaton

We searched through shark publications and found, with the rare exception, that most lateral views of these creatures are rather poorly executed. While there exist many wonderful underwater photographs of sharks in their natural environment, scientific photographs stressing the morphological characters of these animals are much more difficult to find. At the beginning of this project, José Castro sent several slides of his lateral views of sharks. His images were taken at a great enough distance from the subject as to minimize the parallax distortions that plague this sort of picture.

Our technique was as follows. The slide was projected onto a Lintech 3000 illustration board so that the image was between 40 and 70 cm in length. With a pencil, we traced the contour and all details. Letter codes were used on the emerging sketch to indicate the tone or degree of density of the stippling that is to follow (see Figure 1a).

Stippling was used to indicate shape, tone and pattern. A base coat was applied using a 0.5 mm tip of the Kohi-Noor rapidograph. To give form and to smoothen out the rough appearance of the initial coat, a second and third coats were applied with a 0.25 mm tip. All aspects of detail were taken into account and the end result (up to 30 hours later) was a reasonable replica of a particular specimen (Figure 1b). José Castro evaluated the results during our visit to Mote Marine Laboratory. He reveiwed the illustrations, giving useful commentaries that sometimes lead to changes being made on a particular specimen.



Figure 1. Female of the oceanic whitetip, Carcharhinus longimanus, 185 cm long. Original by Sarah Heaton.