FINAL REPORT

The Behavior and Sensory Biology of Sharks

Contract N00014-76-C-0142
and predecessor, N00014-67-A-0201-0008

by

Arthur A. Myrberg, Jr.

UM-RSMAS - 81003 December, 1981
Rosenstiel School of Marine and Atmospheric Science
University of Miami

The Behavior of Sharks

Final Report
To
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and its predecessor, N00014-67-A-0201-0008

by
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Principal Investigator

Miami Florida 33149
December, 1981
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Dr. Warren W. Wisby
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Overview

This report covers the major reports and publications which arose from a program of research dedicated to the study of the behavior and sensory biology of sharks as contracted by the Oceanic Biology Program, Office of Naval Research, Department of the Navy, to the principal investigator during the period 1971 to 1980. Twenty-three reports are summarized briefly below. Progress reports and abstracts of proceedings before peers at numerous national and international scientific meetings are not provided since their content would be redundant to that summarized in the major reports. Papers were presented either by Arnold Banner, A. Peter Klimley or Arthur A. Myrberg at meetings of the Acoustical Society of America, the International Congress of Acoustics, the American Society of Ichthyologists and Herpetologists, the Animal Behavior Society, the International Ethological Conference, the American Psychological Association, the American Society of Zoologists, the American Association for the Advancement of Science, and the American Institute of Biological Sciences.

We believe that the efforts expended during the tenure of the above contracts have provided a significant increase in man's knowledge and insight about shark behavior and the acoustical biology of sharks. The contracts emphasized field studies; most facets of the program were conducted either over the coral reefs of south Florida, over the deep waters of the Florida Straits, in the shallow waters of the Bahamas or within the Tongue of the Ocean, Bahamas. Extensive information was gained on the qualities of underwater sounds which result in rapid attraction of many species of sharks, both shallow water and epipelagic forms. In depth studies also examined qualities of acoustical signals which could aid in causing rapid withdrawal from the vicinity of an operating sound-source. Such withdrawal was proven under natural, as well as semi-natural conditions.

The ethology of sharks was also studied subsequent to attraction, as well as under more controlled conditions in a semi-natural environment. Behavior activities were described for the silky shark, Carcharhinus falciformis, and the oceanic whitetip shark, C. maori. Clear species-typical action-patterns (MAP's) were also described for Sphyrna tiburo and its social organization was examined in detail. That organization apparently consisted of a dominance-hierarchical system in which females shied away from males and dominance was based on size.

Various of the studies reported below were conducted wholly, or in part, in areas under the jurisdiction of various offices. We wish to thank, at this time, the Government of the Bahamas for allowing us to use its territorial waters for numerous tests, Wometco Enterprises for allowing the use of various systems at the Miami Seaquarium (we are particularly indebted to Mr. Warren Zeiller, Director of the Miami Seaquarium for his total cooperation whenever requested), the Biscayne National Monument, United States National Park Service (especially James W. Todd and James T. Tilmant), and finally the officers and staff of the Atlantic Undersea Test and Evaluation Center (AUTEC), West Palm Beach, Florida and Fresh Creek, Andros Islands, Bahamas for their collaboration and cooperation during field tests within the center's ranges, located in the Tongue of the Ocean.
Summaries of Efforts


Acoustic pressures and particle velocities were measured at several distances from both pulsed multipole and continuous monopole broad-band sound sources, in a shallow bay. Pressure attenuation was less for pulsed than for continuous signals in the range of 80 to 640 Hz. Relationships of particle velocity to pressure amplitudes were determined, using a reference level common to both. The ratios of these parameters were found to remain constant for all distances beyond 1 m from the sources for frequencies from 20 to 640 Hz. These ratios were also valid for ambient noise measured at this location. Particle motion appeared to be primarily vertical and to attenuate at the same rate as pressure once this ratio had been attained. Shallow-water marine organisms may thus receive nearfield stimuli at relatively great distances from sources.


Relatively little information is available concerning the biological significance of sensory capabilities to fishes. This study was directed at determining the role of hearing in predation by young lemon sharks. It consisted of the following stages: (1) a test site was established in Biscayne Bay, Florida, where sharks were common during much of the year: (2) the relative importance of various local organisms as prey was determined from analyses of stomach contents: (3) sounds produced by prey, and other common species, were recorded and analyzed: (4) acoustic attenuation rates at the site were established: (5) mean ambient noise levels were determined: (6) biological and instrumental sounds were played back at the site, and associated responses of sharks were observed.

Responses to various sounds, and during control periods, were compared and their relative attractiveness was statistically analyzed. Differences were evident, but were not entirely related to the importance of the source as prey.

Maximum distances at which sharks responded to attractive signals were determined, these subsequently related to associated signal-to-noise levels. These were then compared to thresholds obtained in the laboratory. Excellent agreement was noted.

Sharks detected biological sounds only when within 5 meters of the source. This limit was determined both by the rapid attenuation rates prevailing, and by low signal levels associated with the small size of natural prey. However, auditory detection distances generally did exceed the estimated visual range. The experimental results and observations made during this study indicate that hearing is useful in alerting sharks to the presence and location of prey.

A design and calibration data are presented for velocity hydrophones which operate vertically or horizontally. The simplicity of construction, broad frequency range, and relatively high sensitivity of these units make them particularly practical for use in bioacoustic research.


Many kinds of sharks are dangerous and apparently unpredictable predators whose behavior is virtually unknown. This is because they are difficult both to maintain in captivity and to observe in the field. The purpose of this report is to review the behavioral information presently available on sharks and, more importantly, to suggest approaches which will accelerate progress in understanding the activities of these animals. Shark behavior has been investigated within the methodological frameworks of both comparative psychology and ethology. Thus, the underlying philosophies of these disciplines are briefly discussed. Six approaches for investigating the activities of sharks are presented. Approach I involves intuitive studies drawing upon natural history notes and fisheries statistics, and is typified by Springer (1967). This work set the stage for future quantitative research. Approach II is also intuitive. Here, as typified by Klausewitz (1962), inferences about behavior and ecology are drawn from morphologic and taxonomic considerations. Results appear to be useful in only the broadest of applications. Approach III, an ethological approach which we term "structure of behavior," rests upon direct observation of behavior. The basic rationale underlying this technique, including examples of field and laboratory studies with sharks, is given. While we are at a beginning stage in studying the ethology of sharks, the approach appears to hold great promise. Approach IV, the study of activity rhythms in sharks is reviewed. Little is known about such rhythms, which represent short-term temporal activity. Practically nothing is known about long-term activity, i.e., behavioral ontogeny. In Approach V, psychological studies of learning are reviewed with emphasis on habituation, operant and classical conditioning in sharks. It is concluded that learning plays an important role in the lives of sharks and that they are clearly not the stupid, blindly swimming creatures of folklore. In Approach VI, studies of sensory physiology using behavioral techniques are briefly discussed. Results lead to the conclusion that sharks are well adapted to detect and respond appropriately to a wide variety of environmental stimuli. Though the difficulties are real and many, the report ends on an optimistic note, and it is felt that continued effort will unquestionably lead to a significant increase in our understanding of these fascinating animals.

This paper briefly considers the following subjects: hunger-motivated attacks, stimuli for a predator, chemical substances detected by sharks, underwater sound and its trigger effect relative to attack, the role of vision in attacks, electrical fields, victims wounds, and new repellent possibilities.


This report considers the facts and 'misfacts' concerning the maximum length of the white shark, *Carcharodon carcharias*. Segments deal with: the problems which have been encountered in measuring the length and weight of large fishes in general, the 36 1/2-foot fallacy which supposedly was established in the late 1800's by the noted ichthyologist, Albert Gunther from the British Museum, and finally the more realistic size-figures, based on measurements made by John Randall, a present-day expert in the field who re-studied the older data and came up with extremely different figures. Also, new estimates of the fossil shark, *C. megalodon* are given, based on new measurements of teeth size.


The acoustical factors responsible for eliciting rapid withdrawal (180° turn and departure) from the vicinity of a sound source by adult lemon sharks were investigated. Four sounds were examined on separate days: (1) killer whale scream, (2) 500 to 4,000 Hz noise-band (same bandwidth as the scream), (3) 500 Hz pure tone, and (4) 150-300 Hz pulsed noise-band. While the scream elicited more withdrawals than the pulsed noise-band and pure tone at similar sound pressure levels, it elicited fewer responses than the continuous noise-band. The latter result was also obtained when the scream and the continuous noise-band were played back (in alternation) on the same day. The relative effectiveness of these various sounds in eliciting withdrawal, thus, does not stem from a species-specific recognition of a predator's call. Although sharks continued to approach the source of the 150 to 300 Hz, pulsed noise-band when small incremental changes were made in sound pressure levels, withdrawal was elicited when increases involved considerable change. This suggests that withdrawal was based on stimulus magnitude and/or rate of level rise. Sharks were then exposed to one rate of increase (96 dB/sec) at several magnitudes above broad-band ambient level (3, 6, 9, 12, 15, 18 dB) and several rates (6, 24, 96 dB/sec) at one magnitude (18 dB). Findings showed that withdrawal depended upon both the magnitude and rate of increase in level of stimulus. Trials during a given day did not affect the occurrence of withdrawal on successive days. A decrease in response was noted when water temperature dropped below 21°C.

This report considers the influence of underwater in directing the behavior of selected marine animals. It deals initially with marine mammals, both odontocete, and mysticete whales, as well as pinnipeds. This is followed by sections on teleost and cartilaginous fishes, with a final small summary of present knowledge about specific invertebrates, e.g., fiddler crabs (Uca) and the lobsters, Panulirus argus and P. interruptus.


Reprints include five published studies on the acoustic biology of selected species of sharks found in the waters off Florida and the Bahamas. Interest was directed primarily at determining: 1) which types of underwater sounds (instrumental, as well as biological) were effective attractants for sharks, 2) those parameters of a sound which were apparently used by these animals for purposes of rapid, oriented movement to a sound-source, and 3) what might be the biological significance attached to excellent hearing ability and rapid movement to a given sound-producer.


The difficulties, encountered in carrying out any type of biological research directly in the ocean, are many and varied, indeed. To reduce this impact for one rather small but rapidly developing field animal behavior various tools now provide scientists the opportunity not only to observe directly phenomena of interest, but also to collect data over sufficient periods of time so that meaningful analyses are assured. One such tool, underwater television, has been a most important tool for various phases of behavioral research carried out at the Rosenstiel School of Marine and Atmospheric Science, University of Miami. The rationale for its use is discussed, and a brief history of the evolution of the tool is provided.
The aggressive behavior of sharks towards humans and their possessions has been of great concern for many years. Although our knowledge about various morphological and physiological functions of selected species has, without question, increased significantly in recent years, our greatest ignorance about sharks still centers on that aspect of their biology that relates most directly to their hazardous nature—behavior.

Reasons for this ignorance include: (1) the extreme difficulties in maintaining most species under laboratory or semi-natural conditions, (2) the lack of suitable facilities for observing animals of their size and mobility, (3) the high cost of field studies on free-ranging requiem sharks when direct observations are required, (4) the present inability to apply sophisticated behavioral methodology and analyses to the moments of wide-ranging animals and, finally, (5) the inevitable danger that is associated with long-term, close-in observations of large sharks in their natural state. These and other limitations and restrictions hinder adequately controlled and repeatable behavioral observations. In turn, very few scientists direct their interests and efforts toward these enigmatic animals.

Despite these difficulties and the "limited work force," various important and, in fact, rather startling finds have recently come forth, centering on the behavior and sensory biology of these animals. To date, the findings have been documented in only a few species. A summary of the work of various investigators in studying primarily young or juvenile animals indicates the sophistication of this group of fishes. Direct knowledge of the gray or requiem sharks, i.e., those of greatest interest to man, is scarce for the reasons noted previously.

For example, young lemon and nurse sharks do well in conditioning trials, i.e., events typically associated with birds and mammals. That sharks possess numerous species-typical postures and patterns of behavioral activities may serve as a basis for the prediction of behavior. For example, the "hunch" posture has been noted in members of three species under similar circumstances—the presence of a nearby intruder. "Give-way" behavior in bonnethead sharks and smooth dogfish indicates a clear social hierarchical organization operating in groups of these animals.

Facts about the sensory biology of sharks continue to be uncovered, and in the species studied, sensitivity to pulsed low sounds, excellent nocturnal and diurnal vision, biorhythms, and electrical sensitivity have been described.

This brief review points out that although much of our knowledge about the behavior of sharks in the past has been obtained from casual observations, we now have some accurate knowledge based on careful observation and measurements, although the amount is still extremely small. The point made is that such accurate knowledge is extremely difficult to obtain and hence is costly in many ways. However, if we are ever to understand the behavior of sharks and thus remove often the word "unpredictable" from general discussions about their behavior we must continue to study them carefully and accurately in the field as well as in the laboratory.


Reprints of five published studies are provided. They deal for the most part, with the effects of ocean noise on the behavior of selected marine animals, emphasizing, in the main, sharks. Other subjects include ocean noise spectra (physical as well as biological), hearing sensitivity vs. spectrum level noise, the biological significance of low frequency sound to free-ranging sharks, approaches to the study of the behavior of such animals, and finally, the enigmatic nature of shark behavior.


This is an extensive review of the relationships existing between the behavior of sharks and specific types of underwater sounds. It lists the species which have been attracted by sound - worldwide, and then summarizes the qualities of an attractive sound (spectral content, repetitive pulsing, and sound level). It then considers those acoustical qualities which appear unimportant for attraction. The behavior of sharks, subsequent to attraction, is then reviewed; and the final subjects deal with the antithesis of approach - withdrawal, and also directional hearing.


The present state of our knowledge regarding underwater ambient noise and its effects on selected marine biological systems is reviewed. The report is limited to relevant findings from marine fishes and selected
marine mammals since little or nothing is presently known about the subject in other groups. Only shallow, coastal regions off the Continental Shelf are considered since they represent the major habitats of those animals considered here. A general synthesis of ambient noise conditions for such regions is provided, including spectral curves for traffic (industrial), wind, rain, and selected sources of high level, biological noise. Sound detection and localization by fishes and marine mammals are considered in relation to various types of noise with frequencies ranging from less than 100 Hz to beyond 100 KHz. A preponderance of evidence exists from both laboratory and field studies that ambient noise can indeed affect audibility in such animals, especially in the regions of greatest sensitivity. Various simulations are provided in which auditory sensitivities of various fishes and mammals are placed into the context of specific levels of noise for the frequency ranges involved. The results, though speculative, strongly suggest that environmental noise does affect audibility. The implications which arise from such findings are covered in the final discussion.


Reprints are provided of three published studies on underwater sound and its effects on the behavior of sharks. Subjects include those species of sharks which have been attracted to sound sources, the physical factors which appear to be important or unimportant for an acoustical attractant, and the behavior of sharks in the vicinity of a sound source. Emphasis is directed also at those qualities of sound that promote withdrawal from a sound source by three species of sharks, Carcharhinus falciformis, C. longimanus (C. maori) and Negaprion brevirostris.


Behavioral activities of a colony of 10 bonnethead sharks, *Sphyrna t. tiburo*, held under semi-natural conditions, were examined over a period of six months. All sharks had attained, or were approaching, sexual maturity. Objectives of the study were to describe species-typical motor patterns and postures, to analyze the diurnality of patrolling activity and to characterize pattern(s) of organization underlying social interactions noted within the colony. Eighteen postures and patterns of movement were described, almost half of them having apparent social relevance. In specific instances, functional significance of a pattern was cautiously provided. Patrolling activity appeared to have a diurnal rhythm, with a peak occurring in the late afternoon; smaller individuals were more erratic in their patrolling. Finally, a clear but subtle social organization, based on a straight-line, size-dependent, dominance hierarchy was found. Though position within the hierarchy was not determined by sex, data indicated that all individuals, especially females, tended to shy away from larger males. Sexual differences in the performance of certain patterns of movement were also established.


Series of extensive field experiments were conducted over the deep waters of the Florida Straits and the Tongue of the Ocean, Bahamas to provide information on the differential attractiveness of various acoustic signals in the near sub-sonic range (10 to 20 Hz, 20 to 40 Hz, and 40 to 80 Hz) to free-ranging silky sharks (*Carcharhinus falciformis*) and oceanic whitetip sharks (*C. maori*). Ambient noise measurements were accurately determined in the study areas. Findings included ambient noise determination from 10 to 1000 Hz, demonstrated preferential attraction by sharks to sounds having frequency spectra between 10 and 80 Hz, and behavioral information on both species of sharks. A summary of all studies on the acoustic attraction of sharks is included in the discussion.


Field and laboratory studies were conducted on the use of underwater sound as a means to cause rapid withdrawal from an operating sound-source by various species of sharks found in the Florida Straits, Tongue of the Ocean, Bahamas and associated reef tracts. The study included species of
the genera, *Carcharhinus* and *Negaprion*. The findings, to date, leave little doubt that, given specific conditions, at least certain species of sharks can be made to withdraw for a reasonable period of time (measurable in mins.) from such a source playing back appropriate-level acoustic signals.


A series of field experiments was conducted over the deep water off the Florida Straits and the Tongue of the Ocean (TOTO) to investigate the attraction of silky (*Carcharhinus falciformis*) and oceanic whitetip (*C. maori*) sharks by low frequency acoustic signals. By carefully considering ambient noise levels in the areas of testing, additional insight was gained as to the adaptive value that underwater sound affords such animals in their environment. Difficulties in accurately measuring ambient noise levels at sea were surmounted by using an appropriate spar-buoy (described) and radio telemetry.

Three hundred forty two tests, carried out in the Florida Straits, showed that the two lower frequency signals (modulated noise bands of 10 to 20 Hz and 20 to 40 Hz) were more effective in attracting silky sharks than the third signal used (a modulated noise band of 40 to 80 Hz). One hundred ninety-eight additional tests, conducted at TOTO on a small resident population of silkies showed effective attraction but no significant difference in the responsiveness to the three test signals. Reasons for this difference are discussed. Oceanic whitetip sharks were attracted to all three test signals at the TOTO site and this species can now be added to the ever-growing list of sharks that are attracted by underwater sound. The relatively small number of sightings of the latter species did not allow us to examine differences in the attractiveness of the three test signals by statistical inference.

Additional data were obtained at the various sites. These included: (1) latency between onset of signal and arrival of sharks at the sound transducer, (2) time spent by sharks in visual range during sound transmission, and (3) time spent by sharks in visual range after sound transmission stopped. These, and other findings, are discussed. Discussion also includes those acoustical factors that are apparently responsible for the rapid attraction of free-swimming sharks to a sound source. These include spectral content, repetitive pulsing and sound level. Finally, mechanisms of sound-source localization by fishes are considered.


Studies undertaken in the Straits of Florida and the Tongue of the Ocean (TOTO), Bahamas, have established that silky sharks, *Carcharhinus falciformis*, while approaching a source of underwater sound, will withdraw
rapidly from its vicinity if specified changes occur in the nature of the transmitted sound. These changes include: 1) an increase in level of the sound being transmitted (approximately 20 dB) and 2) the abruptness by which that level is achieved. Augmenting factors may well also include sudden changes in the spectral or temporal qualities of the transmitted sound. Although a biological sound (killer whale scream) could elicit clear withdrawal, it possessed no unique quality; rather, more simply constructed sounds, possessing only a restricted band of frequencies and lacking frequency-modulation, were equally effective. Habituation of the response was apparent during successive tests. All results closely followed those obtained on lemon sharks, Negaprion brevirostris, during a concurrent study (reported elsewhere). In the presence of added stimulants (chopped, fresh fish) withdrawal could be elicited in small silky sharks for only a short time. Limited testing of oceanic whitetip sharks, Carcharhinus longimanus, showed that extremely limited withdrawal could also be elicited in that species.


Three experimental studies were carried out in the field to determine the effectiveness of various acoustic signals in attracting free-ranging silky sharks, Carcharhinus falciformis, to the immediate vicinity of an underwater sound source. These studies were carried out over the deep waters of the Straits of Florida, miles from the mainland, as well as at a moored buoy in the Tongue of the Ocean, Bahamas.

All of the octave bands of noise used in the tests resulted in attraction, with the level of attraction increasing as the frequency spectrum decreased, respectively, from 500-1000 Hz, to 250-500 Hz, to 75-150 Hz, and finally, to 25-50 Hz. Irregularly pulsed signals were also more attractive than regularly pulsed signals, with the latter increasing in attractiveness as the pulse rate increased from 1, to 5, to 10, and finally to 20 pulses/sec. Additionally, it was established that, at least under certain conditions, sharks can be drawn away from one vessel by transmitting irregularly pulsed, low-frequency signals from another vessel, stationed a few hundred meters distant.

Various behavioral actions of individual sharks, after approaching a sound source, are described. Also various practical considerations, arising from the findings, are discussed.
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**Abstract:**
A summary is provided of the research conducted under the above mentioned contracts from the years 1971 to 1980. A brief overview initiates the report; that is followed by brief summary of each 23 publications and technical reports generated during the tenure of the research contracts. These papers deal with underwater sound and its effects on the behavior of sharks, ocean noise and its possible effects on marine-animals, and the behavior of certain species of sharks from south Florida and Bahamian waters.