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Shark Research Present Status and Future Direction

Conference on shark research (1974 : Naval Postgraduate School , Monterey, California)

Arlington, Va. : Office of Naval Research. Dept. of the Navy

SHARK RESEARCH

Present Status and Future Direction

Oceanic Biology Program

April 1975

OFFICE OF NAVAL RESEARCH
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In the summer of 1974 a three day workshop was convened by the Office of
Naval Research. Purpose of the workshop was to access the present status of
shark research and to discuss areas of potential future research. The
results of these discussions constitute the main portion of this report and
include the following recommendations:

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20.   Abstract (Continued)

    1.   A proposed "Guide to the Sharks of the World" to be produced by a multiplicity of authors in a loose leaf format in order to insure wide dissemination of accurate and up-to-date information about the identification and biology of sharks.
    2.   A proposed "Systematic Catalogue of Sharks and Rays of the World" intended as a companion to the guide listed above but containing more technical information for specialists.
    3.   A proposed Shark Data Bank where potentially useful ecological data on sharks may be gathered and collated as contributed, perhaps much of it collected incidental to other marine research.
    4.   Concentrated ecological and behavioral studies on a variety of representative and preferably ubiquitous species of sharks such as the great white shark, tiger shark, bull shark, or oceanic whitetip.
    5.   Expansion of research using the most advanced ethological techniques for investigating social, rhythmic and feeding behavior, especially toward a quantification of the results.
    6.   Continuation of research: behavioral, physiological and anatomical; on shark sensory systems: acoustic, chemical, visual and electric; as well as on a number of other systems: central nervous system, orientation mechanisms and the osmoregulatory system.
    7.   The establishment and maintenance of an effective reporting system for shark incidents, perhaps within the framework of a re-established Shark Attack File with its attendant function of analysis and reporting.
    8.   Improved dissemination of information about sharks in relation to man including medical treatment for shark attack injuries and the reassessment of accurate and current information in training programs.
    9.   Discontinuance of the purchase of Shark Chaser by the Department of Defense along with the objective assessment of all proposed deterrents especially in light of technical and operational requirements.
    10.   An accurate assessment and further investigation of the problem of sharks attacking and biting mooring lines and equipment, especially through the establishment of a central clearing house for the collection and study of fishbite incident reports.

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PREFACE

In the summer of 1974, during the three day period 30 July through 1 August, a conference on shark research was held at the Naval Postgraduate School in Monterey, California. Convened by the Oceanic Biology Program (Code 484) of the Office of Naval Research, the conference brought together a number of people concerned with sharks and shark research including scientists and representatives of the Air Force, Army, Coast Guard and a variety of Navy commands. The purpose of the conference was to assess the present status of shark research and to discuss areas of potential future research. The results of these discussions constitute the main portion of this report and appear as Section III.

The report itself was produced in rough form by the attendees during the conference. The attendees were divided into three working groups each with its own chairman: Whole Organism Studies, Dr. Richard H. Rosenblatt, Scripps Institution of Oceanography; Studies of Systems and Organs, Dr. Thomas B. Thorson, University of Nebraska; Studies of Sharks in Relation to Man, Mr. F. G. Wood, Jr., Naval Undersea Center, San Diego. Dr. Rosenblatt also acted as overall chairman of the conference. Each working group produced its own section of the final report. These sections were combined and comments were solicited from all attendees which were then incorporated into the final report.

It is obvious that without the intensive and conscientious efforts of all participants, this report could not have been completed in as short a time. Sincere thanks are due to all of them and especially to the chairmen who gave so willingly of their time. Thanks are also due to the faculty and staff of the Naval Postgraduate School in Monterey, particularly LCDR Calvin Dunlap who handled the local arrangements. The facilities and setting of the school were most conducive to the deliberations and successful attainment of the goals of the conference. The help with logistics provided by Ms. Mary Frances Thompson of the American Institute of Biological Sciences is also appreciated.

Finally, during the time that this report was in preparation, the participants were saddened to hear of the unexpected passing away of one of their members. Dr. Albert Tester of the University of Hawaii, who contributed unstintingly of his time, knowledge of, and experience with sharks, will be missed by his colleagues. His memory and the many contributions he made to our knowledge of sharks will live on.

> Bernard J. Zahuranec
> Editor and Workshop Convener
> Washington, D.C.
> April 1975

INTRODUCTION

Since the Second World War, the United States Navy has supported basic and applied research on elasmobranchs. This has resulted in a great advance in our knowledge of sharks, their capabilities and recently, their behavior, including the publication of numerous scientific papers and two major volumes about sharks: Sharks and Survival, edited by P.W. Gilbert (1963) and Sharks, Skates and Rays, edited by P.W. Gilbert, R.F. Mathewson and D.P. Rall (1967). Research on sharks has given us some appreciation of the remarkable abilities of these animals which are so primitive, yet are so well adapted for the role they play in the environment. Undoubtedly, future research efforts will enable us to know them still better.

The sharks are part of the major group of non-bony fishes known as elasmobranchs which include the skates and rays. The sharks are primarily carnivores and many of the larger species apparently are the top predators in their environment. This role is not widely appreciated and not well understood. In fact, the exact position and role of most of the species of sharks in the marine ecosystem is poorly known despite the large size and spectacularity of most kinds of sharks.

The main areas of shark research discussed at the Monterey Conference included those which, in the past, had been judged to be of most interest to the U.S. Navy. These research areas have a more direct bearing on the capabilities of sharks to act as predators on humans. Intentionally, no attempt was made to cover all aspects of elasmobranch research since these can be as diverse as the entire discipline of biology. In fact, it was suggested that a second workshop be held in the future, concentrating on those aspects of elasmobranch biology such as immunobiology, cellular metabolism, pathology, etc., wherein the elasmobranch is essentially utilized simply as another kind of experimental animal of convenience or choice. In addition, because the conference was in the nature of a workshop discussing areas of potential future research, this resulting report cannot be considered a review of the entire field of elasmobranch research, even in those topics specifically covered and represented by the participants.

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RECOMMENDATIONS

PART A.   WHOLE ORGANISM STUDIES

1.   Systematics and Distribution of Sharks

a.   Present Status and General Recommendations

Since the publications of Bigelow and Schroeder's monumental works in 1948, much knowledge has been accumulated about the biology and identification of the over 300 species of sharks.

Many problems relating to the classification of sharks have been resolved in the past decade, in many cases as a result of ONR support. Whereas, in the 1950's for example, identification of many species of dangerous sharks was hampered by the chaotic state of taxonomy, it is now possible, at least for specialists, to identify these species with a high degree of certainty.

However, dissemination of this improved knowledge to the greatly increased number of people interested in sharks has been slow and inefficient.   Implementation of the recommendations in this report would facilitate the widest distribution of this information to the greatest possible audience.

We recognize that users of this information fall into two large groups, the interests of which may overlap. Accurate identification is essential, for example, by those persons in shark-infested areas in order to assess the degree of danger to which they may be exposed. A diver working in an area where there may be many individuals of a harmless species may be greatly aided by this knowledge. Conversely, the accurate identification of dangerous species and some general knowledge of their habits will suggest appropriate caution for protection of personnel and in the planning of operations. In the event of attack, accurate identification of the shark involved is essential in any report of the incident; incorrect identification will lead to future misunderstandings.

Accurate identification is also essential to those studying the physiology, behavior, medical, and bionic aspects of sharks. For example, a behavioral scientist who documents a lack of territorial aggression in a misidentified species may dangerously mislead personnel who encounter a similar species that is territorially aggressive.

Trustworthy identification of dangerous sharks in both the laboratory and in the field will insure efficient use of research and mission funds. Research experiments or field encounters involving misidentification may lead to the waste of resources and the endangering of personnel.

We recommend assembly of two manuals which would disseminate present and future knowledge to all groups associated with shark biology. The first, "A Guide to Sharks of the World," would allow ease of identification, and provide general information on distribution and pertinent habits. The second, "A Systematic Catalogue of Sharks and Rays of the World," would provide a universal reference list allowing increased stability of

species names and better communications among observers of sharks throughout the world.

b. Proposed "Guide to Sharks of the World"

This book should be produced in a loose-leaf three-hole notebook format similar to some Naval Oceanographic Office publications. This would allow future revision, the participation of a number of appropriate specialists as authors, addition of new observations, and immediate production of sections on well-known sharks, with the eventual addition of information on species which are presently under study. This concept is being successfully used by the United Nations Food and Agriculture Organization in its production of species identification sheets for fishery workers and fishermen in the Mediterranean and Black Seas (Fischer, 1973).

A short introductory chapter including diagrams and a glossary would instruct the reader in the use of the book. A second chapter similar to that of Gilbert (1963a) and Baldridge (1974), should be devoted to advice for persons in the water who may encounter sharks. A simple, brief index would direct the user to the appropriate subsection of species accounts. Each species account would follow a uniform format consisting of 1-2 pages, and include the author and date of issue.

A typical account would include the following information:

1) English common names (if one exists).

2) Proper scientific name (further information can be sought in the companion catalogue; see below).

3) Accurate line drawings of a side view of the whole shark, vertical view of head, representative teeth or tooth sets, and any other significant characteristics.

4) Diagnostic external characters.

5) Statement of dental formula and significant vertebral counts.

6) General distribution map.

7) Natural history notes including size range, size at maturity, food habits, depth range, and whether oceanic, inshore, or deep-water.

8) Significant behavioral information including possible agonistic display, territoriality, and implication in human attack. (If a species is known to be relatively harmless, this can be stated in such a manner that caution is still preserved).

9) Any important economic significance.

10) Short list of references for wider information.

An appendix would advise the reader on a uniform procedure by which to record written and photographic information in the event that the guide does not allow positive identification of a possible rare species, or in the event that a significant behavioral or ecological observation is made. Sample forms to be sent to the Shark Data Bank (described in Ecology section below) should be included.

A second appendix would include a list of dangerous shark species likely to be found in a specific area, e.g., the open ocean tropical Pacific, the coast of Asia, etc.

c. Proposed "Systematic Catalogue of Sharks and Rays of the World"

This manual is intended as a more specialized companion to the "Guide" and would be of greatest use to researchers in interpreting the work and observations of others. In the past, a number of scientific names have been used for a single species, usually resulting in confusion. This catalog would indicate the correct name and list other names that have been incorrectly used in the past. It would also include a significant bibliographic references and technical information such as type localities and an index of names.

d. Production and Coordination

Much of the necessary information has already been accumulated and merely needs to be collated and edited. In several cases, however, studies must be undertaken to fill gaps in our knowledge. Primary examples are the taxonomy of the lemon shark genus Negaprion and the stingray family Dasyatidae.

It is anticipated that the existing editorial staff of an organization such as the American Institute of Biological Sciences could effectively conduct the necessary editing and coordination under contract arrangement. Under AIBS aegis it might also be possible to partially underwrite production costs by subscription sales of the manuals.

2. Ecology of Sharks

a. Present Status and General Recommendations

Ecological studies of sharks are of interest in a purely scientific sense because sharks are among the top carnivores in most marine ecosystems. More pertinent to the present purposes, basic ecological data (particularly on population dynamics) are needed to predict abundance and size composition of shark populations at a given place or season, to evaluate the effectiveness of shark control programs, and to reliably extrapolate results of laboratory studies to the field situation.

Intensive ecological studies have been made on very few species of sharks, notably the spiny dogfish (Ford, 1921; Hickling, 1930; Templeman, 1944; Holland, 1957), soupfin shark (Ripley, 1946), school shark (Olsen, 1954), scalloped hammerhead (Clarke, 1971), and sand bar shark (Springer, 1960). In most of these cases, knowledge of the species' ecology is still incomplete, and no intensive studies have been conducted on really significantly dangerous species. It is clear that more ecological data, (e.g., seasonal and spatial changes in abundance, age and growth, reproductive potential, food habits) are needed, particularly for dangerous species.

The paucity of reliable ecological data on sharks is, in a large part, due to the difficulty and expense involved in collecting and handling sufficient numbers of specimens. It is no accident that most studies

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have involved data collected by either shark fisheries or control programs. While such sources are useful, they are limited in number and most have already been tapped. Furthermore, for obtaining ecological information, sampling programs operated for such purposes as fisheries or control efforts are less effective than sampling programs designed by an ecologist.

Thus, it is unrealistic to expect thorough studies of all species of sharks or even all dangerous ones. Consequently, we recommend two main thrusts in ecological studies of single species: 1) Establishment of a uniform reporting and storage system for ecological data on all species, and 2) Concentrated studies on a few representative and preferably ubiquitous species.

b. Proposed Shark Data Bank

Obviously, there are in existence, potentially useful ecological data on sharks, much of them collected incidental to other marine research. Such data are unlikely to ever be published. Furthermore, it is likely that, with encouragement, even more useful ecological data could be collected by marine scientists in the future.

To make such data more widely available, we recommend production and distribution of a standard, computer-compatible data reporting format, centralized storage of these data, and their availability to interested scientists. The format should include species, size, sex, reproductive condition, stomach contents, wounds, parasites, etc. of the specimen, and collection data such as location, time, depth, temperature, bottom type, and gear. We suggest that instructions and data sheets be included in the synoptic "Guide to the Sharks of the World" mentioned above and that the National Oceanographic Data Center (NODC) is the likely service agency for deposition and dissemination of the data.

Such a data bank would be useful in several respects. First, by central collection of data from widely scattered sources it seems likely that a more coherent picture of the ecology of even rarely studied species (e.g., the great white shark) will emerge. In addition, given that the data may not be sufficient or reliable enough for publication, it could at least serve as a preliminary base for intensive studies and could help to indicate to what extent data from an extensive study of one species can be extrapolated to others. Finally, the existence and distribution of a standardized data format would stimulate taking and recording of ecologically pertinent data by non-specialists who might ordinarily make no or limited notes on sharks taken incidentally.

c. Proposed Single Species Investigations

It is further recommended that intensive ecological studies be carried out for the few species which constitute the principal hazard to man in the sea. Though positive identification of the sharks which have attacked humans is rarely obtained, enough such information is available to implicate the great white shark, Carcharodon carcharias, and the tiger shark, Galeocerdo cuvier, as clearly the most dangerous to man.

The white shark is a large circumglobal pelagic species, more often

encountered in temperate waters than tropical, but nowhere abundant (Bigelow and Schroeder, 1948; Limbaugh, 1963; Lineaweaver and Backus, 1970). Remarkably little is known about this shark; for example, there are still no reliable data on the number of young that may be found in a single female. Much effort would have to be expended to gather information on this species, but we feel that some attempt should be made to advance our knowledge of this most-feared species. Tracking of single individuals to which sonic tags have been affixed, for example, would be of great interest.

No excuse exists for the paucity of data on the tiger shark which is one of the most abundant and widespread species of tropic seas. A broad-based detailed study of this species could profitably be undertaken, utilizing methods which would allow comparisons with life history data gathered for other pelagic species.

Because of their great abundance and the threat they pose to survivors of air and sea disasters well off-shore (Suda, 1953; Strasburg, 1958; Limbaugh, 1963; Nelson, 1969; Lineaweaver and Backus, 1970; Myrberg, et al, 1972), the oceanic white tip shark, Carcharhinus longimanus (= C. maou), the silky shark, C. falciformis, and the blue shark, Prionace glauca, should be investigated. For these three species, unpublished data are available from tuna longline fishing, particularly from Japanese fishery research vessels.

Studies should also be carried out on at least one of the ubiquitous near-shore species of Carcharhinus or Negaprion. Emphasis may well be given to the proven dangerous species of Carcharhinus (Davies, 1964; Johnson and Nelson, 1973) such as the bull shark, C. leucas, grey reef shark, C. amblyrhynchos (= C. menisorrah), or to the lemon shark, Negaprion sp. (Springer, 1950; Banner, 1968). However, it should be noted that studies of a smaller, less dangerous, but more feasibly investigated species, such as the blacknose shark, C. acronotus, or the reef blacktip shark, C. melanopterus are not necessarily worthless from the practical standpoint. Some of the basic biological information obtained for one species of a genus may be extrapolated to other members of the genus. Such comparative data are also needed to determine the roles that these common species play in the ecosystem.

d.   Inter-Specific Relationships

The most pertinent aspect of inter-specific relationships of sharks involves their feeding habits. Although scattered data exist on food items of sharks, much more work is needed on stomach content analyses, particularly with regard to species of prey. The available data suggest that most sharks are opportunistic feeders without clear preferences; this view may have resulted simply from lack of information or poor identification of prey. Limited studies have been carried out on natural predator-prey relationships, i.e., preference, availability and abundance of prey, habits of prey species, and their relationship to the shark's ability to detect or capture them (see Banner, 1972).

Interspecific shark predation is of particular importance. It is known, for example, that the young of sandbar sharks, Carcharhinus milberti, and "puppy" sharks, C. porosus, are important food items for the

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dangerous bull shark C. leucas. Thus, predation by the bull shark may be a natural control on the populations of other shark species. Conversely, the availability and abundance of the prey shark species may affect the distribution and abundance of the predator.

Information is also lacking on competition. In many localities quite similar species with apparently identical food habits seem to occupy the same habitat. A good example is the relationship between the silver-tip and Galapagos sharks, which are often found together at offshore islands (Limbaugh, 1963).

3. Behavior of Sharks

a. Introduction

Early investigations of shark behavior centered on the study of captive animals with experiments demonstrating responsiveness under various stimulus situations. While profitable research still continues along these lines (e.g., Banner, 1967; Davies et al., 1963; Gruber, 1967; Hodgson and Mathewson, 1971; Graeber et al., 1973; Kleerekoper, 1967; Kuchnow and Gilbert, 1967; Tester and Kato, 1966), technical developments have recently permitted significant strides in studying these animals under natural conditions (Banner, 1972; Hodgson, 1971; Myrberg et al.,1969a, 1969b, 1972b). Continued developments along these and other avenues will aid dramatically in answering questions unresolved by previous research.

b. Social Behavior

Existing knowledge of social behavior in sharks is based largely on fishery catch statistics and anectodal accounts. As discussed above, recent technical developments and refinement of analysis, as used by workers in various behavioral disciplines, will surely provide the opportunity for obtaining a greater understanding of the social activities carried out by these animals. Examples of such technical developments include the use of underwater habitats, closed-circuit television, tele-metry and photography (see Herrnkind, 1974). Examples of the refinement of analyses alluded to above include the use of information and communica-tion theory; sequential, pattern interval, and time series analysis; the ethogram; and various types of level-adequate motivation and situation analyses (see Hinde, 1970; Marler and Hamilton, 1966; Myrberg, 1972a). It is essential that innovative programs continue to incorporate quanti-tative, as well as qualitative, information in their methodology.

Various statements have appeared in the literature, regarding the social organization and group structure of sharks (e.g., Springer, 1967); yet, quantitative information exists presently for only two species: the smooth dogfish, Mustelus canis, (Allee and Dickinson, 1954) and the bonnet-head shark, Sphyrna tiburo, (Myrberg and Gruber, 1974). Virtually nothing is known about shark behavior in the following broad areas: territoriality, species recognition and interactions, reproductive behavior, agonistic behavior and other sequentially related activities. Such knowledge is critical in understanding, predicting and controlling any interaction between sharks and man, including that of shark attack. For example, a

recent study has indicated that some attacks are motivated by social factors rather than feeding (Baldridge and Williams, 1969). Understanding the causal factors which underlie behavior will require experimental manipulation and comparative behavioral analysis among a variety of representative species. An important aid in this regard will be to obtain and standardize dossiers of behavior patterns (i.e., ethograms) such as those initiated by Myrberg and Gruber (1974) for the bonnethead shark and by Johnson and Nelson (1973) for the gray reef shark. These will not only provide the opportunity for comparative analysis, but they will also be vital in planning, analyzing and interpreting future observations from both the field and laboratory.

c. Rhythmic Behavior

The universality of rhythms in biological systems is now established, and recent studies indicate that sharks are not exceptions (Hobson, 1968; Myrberg and Gruber, 1974; Nelson and Johnson, 1970; Randall, 1967; Springer, 1963; Graeber, 1974). For example, diel rhythms, regulated by the daily light cycle, are known to determine the activities of tropical reef fishes (Hobson, 1965, 1968, 1972; Collette and Talbot, 1972). Their influence on the behavior of sharks, however, is less well known. Quantitative information exists on only a few species (horn, swell, angel and blue sharks), all of which are basically nocturnal (Nelson and Johnson, 1970; Standora et al., 1972). We are not aware of any information on rhythms related to moon phase and only little that is related to tidal cycles. Seasonal or other long term rhythms are only slightly better known. For example, migrations have been studied by various tagging programs (Davies and Joubert, 1967; Kato and Carvallo, 1967; Olsen, 1953, 1954; Springer, 1960; Tester, 1969), but they still remain poorly understood. Since long-term tagging programs generally yield low return for the effort expended, we recommend their support only where a well established fishery permits adequate recovery.

Controlled studies, demonstrating endogeneity, have been conducted for only two species - certain circadian rhythms of the horn and swell sharks (Nelson and Johnson, 1970). The effects of exogenous factors on rhythms, other than those involving the daily light cycle, are virtually unknown.

The most profitable line for future research would seem to center around the daily routines of sharks under natural or semi-natural conditions. Recent advances in ultrasonic telemetry and direct observations offer much promise in this area (Herrnkind, 1974; Myrberg, 1973; Standora et al., 1972). Knowledge of daily movements, levels of responsiveness and habitat preference will aid in predicting and perhaps controlling those activities of sharks that conflict with the interests of man.

d. Feeding Behavior

We know of only one significant experimental study of feeding behavior in free-ranging sharks (Gray reef, blacktip reef and reef whitetip sharks - Hobson, 1963); yet, since the experimental design demanded that food be presented to the sharks, natural feeding was not involved. There are scattered, anecdotal accounts of natural feeding (e.g., Bullis, 1961; Eibl - Eibesfeldt and Haas, 1959), but quantitative observations have not

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been attempted. Some information on food preference is available from fishery catch statistics and the food habits of a few species are known from studies of gut contents (e.g., the lemon shark - Banner, 1972; Clark and von Schmidt, 1965; Randall, 1967).

Obviously, feeding is essential behavior for sharks and in the case of interactions with man - perhaps their major activity. Thus, although studies of natural feeding are difficult to accomplish, programs of research incorporating innovative techniques for the field deserve high priority. Some attacks on man may well be motivated by social factors, as noted above but undoubtedly feeding motivates others. Certainly, the danger from shark attack is acute during certain types of group feeding, such as those culminating in the "feeding frenzy."

e. Responses of Sharks to Specific Stimuli

Numerous studies have been conducted on the responsiveness of sharks, both captive and free-ranging, to specific stimulus situations, often somewhat artificial in nature due to a desire to control certain con-founding variables. The aim of such studies has often been to determine not only the gross stimuli "perceived" by the subjects, but to provide insight into more specific factors which are associated with a given sensory modality, such as sensitivity, masking, adaptation, activation of response by selective factors, etc. It is hoped that future efforts along such lines will continue to contribute to a better understanding of how free-ranging sharks detect and locate objects of interest within their sphere of influence.

When interest is directed at determining the range and sensitivity of sensory modalities, programs often incorporate conditioning paradigms (behavioral or physiological) or electrophysiological techniques. These subjects will be covered in a later portion of this report.

1) Acoustic Stimuli

It had long been suspected by fishermen and divers that many sharks were highly responsive to water-borne sounds (Eibl-Eibesfeldt and Haas, 1959; Hobson, 1963; Wright, 1948). That suspicion has now been elevated to conclusive fact, our knowledge being greatly augmented since the initial demonstration of shark attraction by low frequency sounds (Nelson and Gruber, 1963). The phenomenon of acoustic attraction appears widespread among the active, predatory species; to date, such attraction has been experimentally shown by members of at least 20 species, covering five families (Banner, 1968, 1972; Limbaugh, 1963; Myrberg, 1969, 1972b; Myrberg et al., 1969a & b, 1972; Nelson and Johnson, 1970, 1972; Nelson et al., 1969; Richard, 1968). In general, the most effective sounds for attracting sharks are low frequency (800 Hz or below - with attractiveness apparently increasing with decreasing frequency to, at least, 10 Hz) and of a pulsed nature, i.e., apparently simulating hydrodynamic or other sounds produced by wounded (struggling) or actively feeding, or otherwise milling, fishes. These conditions are believed to represent feeding opportunities for large predacious fishes - sharks included. Erratic or intermittant pulsed presentations appear more effective than those having pulses of a constant repetition rate. Yet, within the latter group, the more rapid the rate, the more attractive the sound, at least up to 20 pulses/sec.

Differential attraction does not seem related to either a temporal summation of acoustic energy within a given band or, with reason, to the pulse duration. Continuous signals, sounds having a single pulse, or those having relatively long interval are rarely attractive.

One study addressed the difficult problem of determining the biological significance of acoustic stimuli in the predatory behavior of the lemon shark (Banner, 1972). Similar field studies are encouraged for other species, where possible. Efforts have also centered on determining those variables within the acoustic stimulus itself, that sharks attend to, i.e., particle displacement or associated functions (Banner, 1967), the frequency spectrum (Myrberg et al., 1969b and 1972) and pulse character and intermittancy (Myrberg et al., 1972; Nelson and Johnson, 1972). Such research provides not only information on the acoustical modalities of sharks, but also a method whereby free-ranging sharks can be brought to a specific location for experimental purposes (e.g. Evans and Gilbert, 1971), as well as for monitoring shark-shark and shark-diver interactions (e.g., Myrberg et al., 1972). Recent findings have also suggested the possibility of repulsion of certain species of sharks by acoustic means under specific circumstances (Banner, 1972; Myrberg, 1974); this line of research should be explored further.

2) Chemical Stimuli

Detection of and orientation to various chemical stimuli by sharks have also been important subjects of study during the past decade (Baldridge, 1966, 1969 a & b, 1971; Hobson, 1963; Hodgson, Mathewson and Gilbert, 1967; Katsuki et al., 1969; Kleerekoper, 1967; Tester, 1963). The effectiveness of these stimuli in attracting sharks from a considerable distance is directly related to water currents. As above, attractive stimuli have been those which apparently represent wounded or distressed prey. There has been little success in using chemical stimuli as repellents as discussed in a later section of this report. Such repellents appear generally ineffective in driving sharks from their prey, with one possible, recently discovered, exception (Clark, 1974). Another recent study has also shown two distinct ways in which sharks use olfaction to locate odor sources (Hodgson and Mathewson, 1971). Yet, much remains to be learned. Innovative studies of the chemical modalities of sharks deserve continued support.

3) Visual Stimuli

Laboratory studies of vision in sharks have brought forth much information about the capabilities of the modality (see next section), but field work, to determine the role of vision in behavior of these animals is virtually unknown (a few exceptions include studies by Johnson and McFadden, 1971 and Tester et al., 1968). Yet, observed interactions among sharks, such as threat and mutual interaction displays (Church, 1961; Johnson and Nelson, 1973; Myrberg and Gruber, 1974) clearly indicate that vision is an important modality in the lives of these animals. In feeding, for example, vision is thought to direct the final approach of many sharks to prey (Gilbert, 1966). Research directed at the functional significance of the modality is badly needed, perhaps with focus on the use of models, reflected images and other controlled stimuli.

4) Electric Stimuli

The ampullae of Lorenzini have been identified in the shark,

Scyliorhinus canicula, and the ray, Raja clavata, as sensitive electrical
receptors, used to detect minute electric fields as discussed in greater
detail in the next section. Orientation to such fields produced by prey
has been demonstrated in the laboratory (Dijkgraaf and Kalmijn, 1962,
1963; Kalmijn, 1966, 1971, 1972) and though the distance over which this
modality operates is apparently quite limited, its extreme sensitivity
(0.01 μv/cm) strongly indicates a critical role in prey detection.
Speculation has also brought forth the possibility that such sensitivity
could aid in navigation or obstacle avoidance in turbid water based on
the awareness of changes in the earth's magnetic field (Kalmijn, 1972,
1973, 1974). Although these findings certainly do not rule out the
possibility of a multi-functional role for the ampullae of Lorenzini in
elasmobranch fishes, it is obvious that this modality should be examined
in additional species and the phenomenon of electroreception be examined
by extensive field investigations, when methodology permits.

PART B.   STUDIES OF SYSTEMS AND ORGANS

     A quick tally of physiological papers in the last several symposia on
shark research reveals especially heavy representation of studies in the
areas of neurobiology and of osmoregulation. Thus, our emphasis here
upon those same areas may reflect the continuing major thrusts of physio-
logical research on sharks. The perspectives which follow are organized
around the various functions involved, with suggestions of promising areas
of future research in each section.

     1. Visual System

     This report covers that modality whose adequate stimulus is photic
energy and whose function is to detect and transform spatial-temporal
photic information to a frequency modulated neural signal which eventually
informs the organism about its external environment. The elasmobranchs
possess such a system which fits the general vertebrate plan. This system,
however, has become uniquely adapted to the individual behavioral, physio-
logical and environmental requirements of the animal it serves. These
visual adaptations are so sophisticated that one gets the impression that
vision must play an important role in the lives of some, if not all,
sharks.

     Tinbergen (1952)has correctly pointed out that the first task in
investigating the behavior of an animal is a careful study of its sensory
capacities. Such studies, typically involving psychophysics and neuro-
physiology not only provide data on the physiological mechanisms subserving
a particular modality, but give some understanding of properties of the
organism's physical world. Clearly, each animal has its own "Merkwelt"
or perceptual world which frequently is very different from our own. Thus,
in observing an animal it must be clearly understood that certain stimuli
can influence, indeed, release behavior and, equally important, other
stimuli can never affect the animal's activities. It is for these reasons
that the sensory systems of sharks are being studied in both laboratory
and field.

In the most recent review of vision in sharks, Gilbert (1963b) made no mention of photochemistry, neurophysiology or psychophysics, reflecting the limited information available at that time. Lately, knowledge of the visual system has rapidly increased as a result of research in diverse biological disciplines. Typically, experimental studies center on questions such as: what is the structure of the visual system; how do the component parts work; and what is the biological function or importance of the system. The significance of these questions relates to elucidation of physiological mechanisms of vision and their behavioral correlates.

a. Anatomy

Recent advances have been made in the areas of: 1) retinal history, both at the light and electron microscope level (Hamasaki and Gruber, 1965; Gruber, Gulley and Brandon, in press; Stell, 1973); 2) retino-tectal projections and the central visual pathway (Ebbesson, 1972; Graeber, Ebbesson and Jane, 1973 - see page 21); 3) pineal apparatus (Rudeberg, 1969; Hamasaki and Streck, 1971; Gruber et al., 1975); and 4) tapetum and iris (Denton and Nichol, 1964; Kuchnow and Gilbert, 1967; Wang, 1969). Thus, the structure of the visual system, already reasonably well known, continues to be profitably investigated. Two areas of future study on the structure of the visual system could produce useful data:

1) An ultrastructural investigation of receptor cytoarchitecture and the synaptic relations within the retina with emphasis on the outer plexiform layer. Such a study would aid in interpretation of neurophysiological results and visual data in general.

2) The function of the eye as an optical system including refraction, cardinal planes, nodal points, accommodation, preretinal absorption and spectral reflection from the tapetum. These data could be utilized in producing a schematic or model eye. Thus, levels of photic stimuli impinging on the cornea could be specified at the receptor level. In addition, the physical limitations of the dioptric parts of the eye would be known.

b. Physiology

Areas encompassed within visual physiology include: 1) vegetative physiology of the eye such as nutrition of the lens, cornea, iris and retina; 2) photobiology, including identification of visual pigments, kinetics of bleaching and photoproducts; 3) neurophysiology, including electroretinograms (ERG's), intercellular records such as S-potential, intracellular or single unit records and resultant data on frequency codes, receptive fields, and visual mechanisms; 4) psychophysics, including conditioned responses and natural orientations providing information about visual capabilities, stimulus limits and visual mechansisms involved with behavioral functions.

While more is known about the neurophysiology of vision in elasmobranchs than many other organisms, these studies are still in their initial stages. Several electroretinographic studies have been accomplished (Dowling and Ripps, 1970; Green and Sigal, 1973; Gruber, 1973;

Hamasaki and Bridges, 1965; and Kobayashi, 1962), and S-potentials have been reported on (Dowling and Ripps, 1971; Tamura and Niwa, 1967). Receptive field mapping by single unit technique (Naka and Witkovsky, 1972) and tectal studies have also been accomplished. Although much data on visual mechanisms has been derived from ERG studies, single unit analyses are lacking, especially in the higher visual centers (see page 21).

Little is known of the vegetative physiology of the eye. Visual pigments from several elasmobranchs have been extracted and characterized (Denton and Shaw; 1963; Bridges, unpublished). The more revealing techniques of microspectrodensitometry have not been attempted on shark retinas.

c. Behavioral Aspects

Few psychophysical studies on vision have been reported though training experiments have yielded reliable data on dark-adaptation, brightness discrimination, critical frequency of flicker-fusion, visual sensitivity, color discrimination and pattern discrimination (Aronson et al., 1967; Clark, 1959; Graeber et al., 1973; Gruber, 1975). These data have tended to confirm the results of physiological studies and have strengthened the view that sharks have an extremely functional visual system. Any discussion of visual capability must account for both visual acuity and light sensitivity. Thus, when one asks if an animal has "good vision" the inquiry may concern either spatial resolution (acuity) or how well an animal can see in dim light (sensitivity). We can state that sharks have extremely good vision regarding sensitivity factors. Their sensitivity to light spans the visible spectrum, from blue to deep red and they are ten times more sensitive than man under similar test conditions. Nothing at all is known of spatial resolution in these creatures. Some estimates have been made, based on packing density of photoreceptors (Franz, 1931) but these are largely speculative. The temporal resolution of sharks is similar to man's and is the type associated with a duplex retina. Thus, under high illumination a shark can detect, as flashing, light which is intermittently blocked 40 times per second. This has theoretical implications with regard to function of cone photoreceptors and practical implications on how fast a shark can swim without its visual world blurring.

The large gap here is in visual acuity. This factor is amenable to analysis by physiological and behavioral techniques and should be undertaken. By determining parameters such as the spatial modulation transfer function, practical knowledge can be gained on the ability of sharks to distinguish two contours as separate. Additionally, theoretical data on size tuned channels in the sharks visual system could be derived.

Another area of importance concerns qualitative aspects of vision: for example, do sharks possess trichromatic color vision? Again, for both theoretical and practical reasons the nature and importance of color vision must be revealed.

Finally, as mentioned in the previous section, the role of vision in the field behavior of sharks is virtually unknown. Not only does little useful information exist on the behavior of sharks in general, but it is also conceptually difficult to establish criteria for determining the

relative importance of visual stimuli in the field or the effects of visual stimuli on motivation. This is an area which can bridge the gap between field and laboratory studies and strong consideration should be given to any promising studies of this kind. The main difficulty with this type of investigation involves adequate and reliable methodology. Until this is properly developed, we will still be guessing!

In summary, knowledge of visual structure and function has rapidly advanced during the past decade: several investigators are applying methods from various disciplines to the study of vision in elasmobranchs. It is now possible to make definitive statements on visual capability in these animals and the picture which emerges is quite different from classical descriptions. Still, as in other phases of elasmobranch biology tangible progress in understanding the visual system in sharks is just beginning.

2. The Chemical Senses

The senses of smell and taste are closely involved with the feeding and attack behavior patterns of sharks. As a consequence, research on these senses of sharks has had a long history. When G.H. Parker published his classic summary of "Smell, Taste, and Allied Senses in the Vertebrates" (1922) there were already many descriptions of the gross morphology of chemical sense organs of sharks. Some of Parker's colleagues had also studied the effects of plugging one nostril in a shark (resulting in circular movements), and attempts were being made to determine the groupings of chemicals which stimulated olfactory, gustatory, and skin chemoreceptors of sharks. However, the latter studies, on modalities of effective stimuli, were completely inconclusive.

During most of the intervening half century, research on the chemical senses of sharks has been essentially a refinement of behavioral studies and anatomical investigations which could have been appreciated by Parker and others early in this century. Screening programs for repellents, tests of the attractiveness of various potential food substances, and comparative anatomical studies have dominated the field. A few field studies on feeding behavior of pelagic sharks under natural conditions were made, but mainly on a catch-as-catch-can basis, often in conjunction with natural history expeditions primarily concerned with other objectives. Tester (1963) has given a valuable summary of that phase of the studies on chemical senses of sharks. He noted that there was a need for:

1) Electrophysical studies of receptor function, already in widespread use on other sensory systems of other animals.

2) Electro-dissection or other precise techniques of neurosurgery to localize functions within the CNS concerned with the chemical senses.

3) Tests with pure single chemicals which trigger important patterns of behavior in sharks.

4) Determination of chemically-mediated patterns of behavior in sharks of other kinds and in other circumstances, beyond the few species and laboratory situations most studied.

The call for some shift of focus was in no way a repudiation of the value of anatomical and behavioral studies. Certainly the ultimate test of insights is in their applicability to understanding the behavior of intact animals in their normal environments. However, the major shift indicated at this time was toward more molecular and cellular levels of investigation.

During the 1960's and 1970's, modern electrophysiological methods have been applied to analyzing the chemical senses of various elasmobranchs. The first breakthrough came with the recordings of electrical activities of masses of cells in various parts of the shark's brain -- the electro-encephalograph (EEG) -- which provided a picture of the functions of various surface areas of the brain (Gilbert, Hodgson, and Mathewson, 1964). It was found that variations in EEG patterns could be correlated with chemical stimulation and with behavior patterns of lemon sharks (Negaprion), nurse sharks (Ginglymostoma) and bonnet sharks (Sphyrna tiburo). In some of these studies chronically implanted brian electrodes were used, and responses of sharks to pure chemicals were tested in a hydrodynamic tunnel (Hodgson, Mathewson and Gilbert, 1967).

Very recently, electrophysiological recordings have been made from the olfactory tracts of hammerhead sharks exposed to chemical stimuli. This was done by a student at the University of Hawaii (A. L. Tester, personal communication).

Amino acids, short-chain tertiary amines, and purified hemoglobin (human and bovine) have been found especially effective in altering EEG patterns, and in eliciting typical orientation behavior -- either klino-taxis or rheotaxis -- in lemon and nurse sharks (Hodgson and Mathewson, 1971). Results similar to those obtained under controlled laboratory conditions have been observed with open-sea tests using these purified chemicals, making observations by a remotely-controlled underwater tele-vision camera, (R.F. Mathewson and E.S. Hodgson, personal communication).

The linking of electrophysiological analysis with field studies of behavior, and the limitation of stimulation to single pure chemical stimuli, bring the study of shark chemical senses to a new level of sophistication and usefulness. Laboratory EEG analysis has good predictive value for behavior of sharks in open sea. Furthermore, the use of single pure chem-icals gives access to future studies on exact chemical mechanisms of stimulation. We can now ask a whole series of new questions about olfaction and taste in sharks:

1) What is the mechanism of interaction between a chemical stimulant and the receptor cell membrane?

2) Once more is known about that, it would be possible to investigate specific blocking agents of anti-metabolites which might interfere with these specific processes. In other words, how might the specific mechanism of stimulation be modified, and possibly controlled?

3) How can we get single cell, or few-fiber experimental prepar-ations, to reveal the action potentials which must certainly be involved in stimulation by chemicals? Additional studies of the ultrastructure of olfactory nerves, and taste

receptors, may indicate the best ways of solving this
problem.

4) How are the immediate effects of chemoreceptor stimulation
coded into patterns of afferent impulses which enable sharks
to discriminate various chemical stimuli? And how many
types of chemical structure or modalities of stimuli, are in
fact detected?

Probably the most powerful tools to study mechanisms of chemical
stimulation include both electrophysiological methods, to detect receptor
responses, and radio-isotope techniques, to label and follow the distri-
bution of chemical stimuli. The first tests with labeled stimuli have
recently been completed and suggest that neural mechanisms of behavior
are somehow automatic, once initiated, and play out a sequence of re-
sponses that is independent of the initial stimulus (E.S. Hodgson,
R.F. Mathewson and A. Karsten, personal communication). This opens up
additional new perspectives in the study of innate, more or less auto-
matic responses "wired into" the CNS of the shark; it is possible that
many feeding and attack behavioral patterns fall into this category, and
consequently they deserve further study.

Many physiological studies of the chemical senses are handicapped by
lack of knowledge of the fine structure of the tissues involved. To
our knowledge, no electron microscope studies have been made on the ultra-
structure of either olfactory or gustatory sensory cells in elasmobranchs.
It would be worthwhile to determine more precisely how an olfactory cell
differs from a gustatory cell, whether cilia or villi are present on the
exposed surface, the nature of organelles, the nature of innervation,
etc. The barbels of bottom feeders, such as Ginglymostoma, should be
studied for the presence of external taste buds and how they compare in
structure with those of teleosts.

A further limitation has been that most physiological studies on the
chemical senses have been done with four or five species in the genera
most readily maintained in captivity: Mustelus, Squalus, Negaprion,
Ginglymostoma, and (very recently) Sphyrna. It is obvious that with some
250-300 species of sharks, each specially adapted to its own environment,
it sometimes involves unwise extrapolations to attempt predictions about
the physiology and behavior of other species, or even of these better-
studied species in other areas of the world. Careful physiological
studies require adequate laboratory facilities and with the development
of new marine laboratories there may be opportunities for highly desirable
comparative studies on additional species of sharks.

3. Acousticolateralis System

This is a complex sensory system which is deeply involved in shark
predation and defense. It is comprised of the sensory canals of body and
head, the pit organs, the ampullae of Lorenzini and the ear. Basically,
the sensory organ is the neuromast and the actual receptor of the organ
is the hair cell (Dijkgraaf, 1963).

a. Sensory Canals

The gross morphology and histology of the sensory canals, their

tubules and their neuromasts are reasonably well known for sharks and rays from the works of older authors, augmented by more recent studies, e.g., Tester and Kendall (1969) for Carcharhinus. The orientation of the tubules and tapering caudad bore of the canal provide for a slow tailward flow of seawater through the canal. The rate of flow should be determined for several species. The function of peculiar vesiculated cells adjacent to the neuromast in the canal epithelium, greatly elaborated in the anterior head canals, should be investigated. The recent study of Liddicoat and Roberts (1972), showing the canal fluid of dogfish to have the same ionic content as seawater, should be repeated for other species. These latter studies would contribute to our knowledge of ionic regulation of body fluid, and the part played in establishing a sodium-potassium ratio optimal for electrogenesis in the hair cells.

The fine structure and orientation of hair cells of the canal organ has been studied extensively in teleosts but not in sharks. Roberts and Ryan (1971) have made Electron Microscope (EM) studies in Scyliorhinus. Similar studies should also be undertaken in other common sharks, including both bottom-dwelling and pelagic species in order to contribute to our knowledge of how a hair cell functions as a receptor of displacement waves. Items of interest are (1) the orientation of hair cells along the canal with respect to the position of the kinocilium (movement in one direction produces excitation and in the oposite direction, inhibition); (2) the presence of different types of hair cells; (3) the nature of organelles; and (4) the presence of both afferent and efferent synapses.

Roberts and Russell (1970) and Roberts (1972), again working with Scyliorhinus, have made the only study in sharks of the source of efferent activity that modulates the afferent firing of the hair cells in the canal organ. Since the results are not clear cut, the work should be repeated and expanded, preferably with other species. This work is essential to a complete understanding of how the canal organ functions as a receptor of displacement waves.

Given that the ordinary lateral-line organs are displacement receptors, the following questions arise (cf. Dijkgraaf's lateral-line review, 1963): (1) What are the displacements that sharks detect in their daily life? Here we should distinguish between (a) displacements imposed upon the animals from external sources, in which case the receptor system operates in a passive mode, and (b) displacements resulting from the animal's own activity relative to the environment with the receptor system operating in active mode. (2) What may be the biological significance of the various displacements (e.g. detection of other animals by the displacements re- sulting from their swimming or ventilation movements, detection of objects by the distortions they cause in the sharks' own "underwater bow waves")? (3) How do sharks mechanically relate to their environment? How do they integrate the information from their spread-out lateral-line organs, and how do they analyze the spatial and temporal aspects of natural displace- ment fields? To answer these questions, the physics of the pertinent displacement fields should be studied more rigorously, the biological relevance should be determined in well-planned behavioral tests, and the central processing of the total receptor input should be investigated by recording the electrophysiological responses of peripheral nerves and central nuclei.

b. Pit Organs

The gross morphology, histology and innervation of these organs have been described in several species of sharks by Budker (1938), Tester and Nelson (1967) and Tester and Kendall (1967). They resemble the canal organs and, in fact, have been called free neuromasts by some authors. However, there is doubt as to whether they actually have a cupula or whether the sensory surface is merely coated with an undefined mucus layer. There is still some question as to whether they have cilia: only a brush-like fringe can be seen under the light microscope. The only EM work to date is referred to by Katsuki, Hashimoto and Kendall (1971) who state "Hama and Yamada (in preparation) confirmed electron-microscopically the ciliary structure of the hairlike process in these sensory cells." There is need for further EM studies of the pit organs of sharks to further elucidate the fine structure of the sensory cell and to compare it with that of the lateral line hair cell. Suitable preparations are difficult to make because of protective modified scales.

The function of the pit organ is still uncertain. Onada and Katsuki (1972) imply that it has the dual function of mechanoreception and chemo-reception. In earlier papers, Katsuki and his co-workers have implied, from electrophysiological experiments, that it is primarily a salinity detector. How its true function or functions (from the shark's point of view) can be determined is problematical. Since it apparently does have mechanoreceptive functions it may contribute to the sharks ability to orient and home in on a near field sound source, or it may serve to detect changes in flow pattern. Further electrophysiological experiments, augmented by behavioral experiments, should be undertaken to clarify its alleged mechanoreceptive and/or chemoreceptive function. For behavioral experiments, some method will have to be devised to occlude or otherwise nullify either the sensory canals or the pit organs, both of which are serviced by the same nerve, in order to investigate their functions separately. It may also be necessary to occlude the ampullae of Lorenzini and the ear when studying the response to displacement waves.

c. Ampullae of Lorenzini

These unique organs, located on the dorsal, ventral, and lateral surfaces of the shark's head, have been subject to many morphological, electrophysiological, and behavioral studies over the years. The organ is a flask-like tube with an opening on the head and is filled with a mucoid jelly. Its blind end has a central plate and several out-pouchings lined with sensory epithelia. EM studies by Waltman (1966) show that the pear-shaped sensory cells have a cilium or hair with a supporting structure that differs from that of the "ordinary" lateral-line haircell. Despite this and other differences, the ampullae are still considered to be "specialized" lateral-line organs.

Excised ampullae of Lorenzini have been shown by many authors (see Murray, 1974) to respond to a variety of stimuli: thermal, mechanical, chemical, and electrical. Nerve recordings from free-swimming sharks (Scyliorhinus) revealed, however, that in situ ampullae, though still very sensitive to weak electric fields, do not appreciably respond to mechanical perturbations nor to thermal gradients in the water (Kalmijn, 1972, 1974). These results accord with the location of the sensory epithelia deeply

buried under the skin. Obara and Bennett (1972) recently presented a novel theory and preliminary experimental evidence regarding the receptor mechanism of the ampullae of Lorenzini in an effort to explain their high electrical sensitivity and the anomalous polarity of response.

It seems now generally agreed that the ampullae of Lorenzini function as electroreceptors. It has been shown by Dijkgraaf and Kalmijn (1962, 1963) that sharks and rays respond to very weak electric fields of the order of 0.1 μV/cm, and that their high electrical sensitivity is due to the ampullae of Lorenzini. Subsequent studies (Kalmijn, 1966) lowered this threshold to 0.01 μV/cm, representing the greatest electrical sensitivity known in the animal kingdom. Further behavioral experiments by Kalmijn (1971) showed that both Scyliorhinus and Raja are able to detect flatfish buried in the sand by virtue of the bioelectric potentials that the prey produce. The predators cued in on the flatfish's bioelectric fields from distances up to 10-15 cm. Because of the biological significance of this response, Kalmijn concluded that sharks and rays are endowed with an acute electric sense and that the ampullae of Lorenzini are true electro-receptors.

The high electrical sensitivity of sharks and rays allows for some interesting speculations. If the animals are capable of interpreting the large-scale electric fields induced by open-ocean streams flowing through the earth's magnetic field, they may sense upstream and downstream directions, e.g. for compensating unwanted drift or for gaining passive transport. If the animals are capable of appreciating the electric fields that they produce when swimming through the earth's magnetic field, they may even sense the actual compass directions. The feasibility of orienting with respect to uniform electric fields has recently been demonstrated in successful training experiments on catfish and weakly electric fish. More-over the shark Triakis was found to respond in a frightened manner to local, experimentally induced non-uniformities in the earth's magnetic field (Kalmijn, 1973, 1974). Since understanding the principles of shark navi-gation and open-ocean orientation in general is of utmost importance, these advanced studies should be pursued tenaciously despite their inherent bio-logical, physical, and technological difficulties.

Although there is good evidence that the ampullae of Lorenzini serve an electroreceptive function, this does not necessarily rule out multi-functional performance, e.g. the ampullae may serve as mechanoreceptors to enable sharks to distinguish between the texture of objects in "head bumping", though the ordinary lateral-line organs and the free nerve endings could be involved as well. The responses of the ampullae of Lorenzini to stimuli of various modalities should be critically examined in other sharks and rays, particularly the pelagic species, using both electro-physiological and behavioral techniques. A fruitful approach in the invest-igation of the ampullae of Lorenzini may be through the use of recently developed locomotory monitoring techniques under controlled conditions (Kleerekoper, 1969).

d. The Ear

The gross morphology and histology of the elasmobranch ear has been known since the classical work of Retzius in 1881, and has been updated for Squalus acanthias by Quiring (1930), for Raja clavata by Lowenstein,

Osborne and Wersall (1964) and for Carcharhinus by Tester, Kendall and Milisen (1972). The fine structure of the sensory epithelia of the ear of Raja, including the orientation of the hair cells, has been determined by Lowenstein, Osborne and Wersall (1964). Rauchbach and Arenberg (1972, 1973) have demonstrated the use of the scanning EM (SEM) to show the structure of hair cells of the ear of Negraprion and have diagrammed their orientation. J. Corwin (U. of Hawaii graduate student) is presently using both transmission EM (TEM) and SEM to study hair cell orientation in Carcharhinus, particularly with respect to the little known organ, the macula neglecta. EM work should be continued and extended to other genera to provide a firm basis for the interpretation of electrophysiological experiments designed to illucidate how the ear functions in hearing. Other functions of the ear -- equilibrium and muscle tonus maintenance -- have been worked out for the ray by Lowenstein and Sand (1940a and b) and by Lowenstein and Roberts (1950). This work should be extended to other sharks.

There have been many papers in recent years on hearing in sharks, including both tank experiments and studies with free-swimming animals in their natural environment. Although it has been shown that the response varies with the nature of the sound (continuous, pulsed, train, etc.) and that the response is directional, it has not yet been established whether the stimulus is received through the lateral line, the ear, or both.

There is need for determining if ahd how the ear participates in hearing. Much can be learned from electrophysiological studies of microphonics in various parts of the ear of an immobilized submerged shark, utilizing an underwater sound source as stimulus. There are indications that the macula neglecta may be a main organ of hearing in rays (Lowenstein and Roberts, 1951) and in sharks (Faye, Kendall, Popper and Tester, 1974). Further electrophysiological experiments, with particular attention to this organ, should be undertaken.

It might be possible to perform diagnostic behavioral experiments to clarify the role of the ear in hearing, subjecting sharks in tanks or in cages in the open environment to underwater sound sources. However it would be difficult to ablate the ear without causing problems in equilibrium and it would be difficult to ablate the lateralis system because of its complexity. The possibility exists of correlating behavioral and electrophysiological observations by inserting electrodes into the macula neglecta of both ears and telemetering the responses. However, it is difficult to implant electrodes without damaging other parts of the ear and it is difficult to firmly anchor the electrode assembly to the skin. It should be possible to overcome those technological problems in the future.

4. Other Systems

a. Central Nervous System

In sharks, as in any organism, the understanding of an integrated behavior pattern should involve the study of various relevant components of the central nervous system. During the past few decades, such attempts to understand the nature of shark attacks have centered primarily on

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investigating sensory systems at the peripheral level. Typical has been the emphasis on olfaction and vision and their roles in guiding behavior.

Although these latter studies have led to some interesting and worthwhile findings, it is our belief that in order to understand and predict shark behavior, it will first be necessary to correct the lack of emphasis which has been placed on studying the shark central nervous system. It is here where the necessary integration of various sensory inputs occurs and where the animal's motivational state and past experiences exert their influence on behavior. By having dwelled on studies of isolated physiological systems, shark research is at a point where we now know a fair amount about both the effective stimulus modalities and mechanisms of shark sensory physiology but almost nothing about how such sensory information gets translated into actual response patterns. As a result, the stage is set for a new, more molar type of research into the psychobiology of shark behavior. The scope of this research program should eventually encompass such topics as central cross-modal sensory interaction, sensori-motor integration, and neural arousal mechanisms with an emphasis on the behavioral implications of these central neural processes. Hopefully, the following brief description of some such work already begun in sharks and other fishes will help clarify the type of research program we believe could be profitably pursued.

1) Central Sensorimotor Integration

As Ebbesson (1970, 1972) has pointed out, several of the revolutionary developments in neuroantomical technology have recently been applied to study elasmobranchs. Use of these methods, e.g., Nauta and Fink-Heimer degeneration techniques, electron microscopical analysis, etc., has led to a marked change in our understanding of the structure of the shark brain and, in many instances, a complete reversal of traditional beliefs (Ebbesson & Heimer, 1970; Ebbesson & Ramsey, 1968; Ebbesson & Schroeder, 1971; Graeber & Ebbesson, 1972). For instance, work on the olfactory inputs to the brain has shown that only a relatively small portion of the shark forebrain (formerly called the "smell brain") received any information regarding olfactory stimuli (Ebbesson, 1972; Ebbesson & Heimer, 1970). However, due to the rather limited attention given to central nervous system investigations in elasmobranchs, there is still a large void to be filled concerning how the brain processes olfactory as well as other sensory information.

In this regard, there has been practically no work done since the turn of the century on relating brain anatomy and physiology to actual behavior. Nevertheless, a recent series of studies has demonstrated the fruitfulness of this approach (Graeber & Ebbesson, 1972; Graeber, Ebbesson & Jane, 1973; Graeber, et al, 1972). Here relatively standard methods of behavioral analysis were used to study the contributions of various central nervous system structures to visually guided behavior in the nurse shark, Ginglymostoma cirratum. Contrary to traditional belief it was found that the processing of visual information into action involved much more than the midbrain optic tectum. Instead, by depending heavily on both thalamic and telencephalic nuclei, the central processing of visual cues in sharks may more closely resemble that in mammals and reptiles.

These findings obviously suggest that the neural basis of visually guided shark attack is more complicated that previously imagined. They

also indicate an increased capability for multi-modal sensori-motor integration. Hence, it is not surprising to the neurobiologist that shark behavior is apparently less stereotyped than often conceived on the basis of the shark's traditionally primitive simple brain. The naivete of this old notion is further pointed out by recent field studies (Johnson & Nelson, 1973) and Baldridge's (1974) analyses which have demonstrated the variability and unpredictability of shark attacks on humans.

Similar studies on the central neural mechanisms integrating vibratory tactile, electrical, and olfactory cues into response patterns are sorely needed and now appear feasible. Some such work has been initiated by Roberts, who has investigated the motor end of the stimulus response chain in dogfish. (Roberts, 1969a, 1969b; Roberts & Russell, 1972).

Another intriguing and promising approach to brain-behavior studies in sharks has been suggested by Okado and his colleagues (1969). Their delineation of the substantial morphological differences among the brains of different species strongly argues for a comparative strategy to answer some of the questions about the relationships between brain structure and behavior. This has yet to be tried amidst a laboratory setting.

As might be expected from the newly discovered complexity of the shark forebrain, shark behavior has recently been shown to be more flexible than previously thought. A number of learning experiments have demonstrated that both lemon and nurse sharks can be trained as easily as many mammals and can retain learned tasks for a considerable period of time (Aronson, 1963; Aronson et al, 1967; Clark, 1959; Graeber, 1972; Graeber & Ebbesson, 1972). The importance of such learning studies should not go unrecognized. Much of the progress which has been made in relating brain structure and physiology to behavior in mammals has resulted from experiments employing learned tasks to assess the effects of experimentally varying central neural states. It is now possible to apply similar behavioral technology to learning more about shark brain function. Moreover, the learning data underscore the important contribution of past experience in determining the momentary response tendencies of these animals. Consequently, it can be expected that experiential factors will influence the effectiveness of any technologies intended to thwart or predict shark behavior, especially in a given locale.

The hypothalamus and related areas of the brain have been shown to be the focal point for arousal or motivational systems related to feeding and attack in fishes as well as other vertebrates. For this reason a separate section dealing with this important topic in sharks and bony fishes is included below.

2) Neural Mechanisms of Feeding and Aggression

Feeding patterns have been described for many sharks maintained in captivity and in the wild (Clark, 1963; Gilbert, 1970; Graeber, 1974; Hodson et al., 1967; Kalmijn, 1971; Randall, 1963; Springer, 1967; Tester, 1963). The presence of chemical stimuli such as are released from freshly killed animals can cause considerable attraction of sharks and may result in a so-called "feeding frenzy" in which sharks are known to bite at anything that moves. Some of the sharks themselves may be eaten during this

activity. The description of this "feeding frenzy" is suggestive of some of the responses that have been evoked by electrical stimulation of the hypothalamus (inferior lobe) and midbrain in teleosts (Demski and Knigge, 1971; Demski, unpublished observation), in which the stimulated animals swarm around rapidly attacking many different objects which included food, gravel, debris, other fish and other inanimate objects. It should be noted that in some stimulations arousal seemed to be less intense and the fish either attacked only another fish or snapped at food objects or gravel. Similar arousal and feeding activity in fishes has been evoked by stimulation of the olfactory tracts (Grimm, 1960), anterior commissure (Fiedler, 1964), and the area near the medial forebrain bundle (Demski, 1973). These observations, along with the results of studies that indicate that olfactory cues alone can trigger similar activity in several teleosts (Grimm, 1960; Demski, 1973), suggest that the arousal and snapping activity evoked from the fish hypothalamus may be related to activation of normal forebrain olfactory input to the hypothalamus that runs in the medial forebrain bundle (Demski, 1973). It also seems reasonable to suggest that an analogous situation may exist in sharks which have a similar forebrain bundle input into the periventricular portion of the hypothalamic inferior lobes (Demski, 1974; Ebbesson, 1972), and which are also greatly aroused by olfactory cues. Consistent with this idea are reports of increased electrical activity in the forebrain of nurse, lemon and bonnet head sharks in response to perfusion of the nasal openings with extracts of normal food substances (Gilbert et al., 1964). Thus it would be interesting to know if stimulation of the hypothalamus and forebrain olfactory pathways in this group would evoke similar responses to those observed in teleosts.

In addition to olfactory information, the hypothalamus in various teleosts is reported to receive visual, gustatory and possibly acoustic inputs (see Ariens Kappers et al., 1936; Aronson, 1963; Schnitzlein, 1964; Tuge et al., 1968). Thus the hypothalamus may be one of the major sensory integrative centers in the fish brain. Its main output pathways run to the cerebellum, brain stem motor nuclei and possibly spinal cord as well (see above references); this suggests that it is likely to strongly influence motor systems. The above anatomical considerations led Herrick (1905) to postulate that the teleost hypothalamus is a sensorimotor correlation center which is involved in feeding activity. As mentioned above, the results of electrical stimulation experiments are consistent with this idea. Internal stimuli such as blood glucose levels may also be important in determining the hypothalamic activity in fishes in a similar manner as proposed for mammalian species (see De Groot, 1967). Thus the study of teleost and shark hypothalamus may give valuable insight into the role of many sensory factors in the determination of predatory behavior of sharks.

Many shark attacks may be agonistic in nature rather than related primarily to feeding (Baldridge and Williams, 1969; Johnson and Nelson, 1973). If this is the case, it is likely that hypothalamic mechanisms similar to those described for feeding are also involved since, in teleosts, electrical stimulation of the hypothalamus frequently evokes both prey catching as well as intraspecific aggression (Demski and Knigge, 1971; Demski, 1973).

Considerable information on the neural mechanisms of feeding and aggression in sharks may be derived by repetition of experiments carried out in teleosts and other vertebrate groups since there are at least

general similarities in the hypothalamic mechanisms for these responses
in many species. The following types of studies should lead to valuable
contributions in this field: electrical stimulation of the hypothalamus
in free-swimming sharks; study of the effect of lesions of the hypothalamus
and related areas on feeding and attack; and analysis of the detailed
anatomy, electrophysiology and pharmacology of the shark hypothalamus and
its related areas.

b. Orientation Mechanisms

In all animals, the capability to perform movements whose direction
is related to environmental cues is of paramount significance and will be
referred to as "orientation" in this statement (Schone, 1973). In fishes,
its survival value is obvious in many critical biological functions: the
localization of prey or predator, mate and spawning site, advantageous or
noxious physical and/or chemical conditions. In all these circumstances,
locomotion must be directed or oriented in relation to environmental stim-
uli, singly or in combinations, perceived through sensory mechanisms, and
evaluated by the central nervous system. In spite of the impressive
array of functions which directly depends on the capability of orientation,
the mechanisms by which physical and chemical cues are used in directing
locomotion are insufficiently known at best in the higher fishes and
almost entirely speculative in the elasmobranchs.

The available information regarding sharks refers almost exclusively
to the localization of food sources and the role of chemical and acoustic
cues in orientation (Parker, 1910; Sheldon, 1911; Parker and Sheldon, 1913;
Aronov, 1959; Teichmann and Teichmann, 1959; Pavlov, 1962; Tester, 1963;
Hobson, 1963; Kleerekoper, 1963; Myrberg et al., 1969 and 1972; Nelson and
Johnson, 1972). The effectiveness of orientation through chemoreception
in the absence of other directional cues has been a topic of much specu-
lation and some descriptive and quantitative experimentation (Kleerekoper,
1962, 1965, 1967 a and b, 1969; Mathewson and Hodgson, 1972). These
investigations have indicated that accurate localization of a chemical cue
by elasmobranchs is affected by and dependant on water flow. A recent
laboratory study, employing electronic techniques and time series analyses
of various locomotor variables, monitored during many hours, quantified
the relationship between chemical cue and water flow in the orientation of
Ginglymostoma cirratum (Kleerekoper et al., 1975). It was established
that accurate localization of a chemical cue was dependent on flow of the
medium. In the absence of such flow, localization became generalized.

Elegant experiments on electrical orientation have been performed in
both sharks (Scyliorhinus, Triakis) and rays (Raja, Platyrhinoidis). Well-
aimed feeding responses were evoked and directed by the bioelectric fields
that prey (e.g. the flatfish Pleuronectes) produce (Kalmijn, 1966, 1971,
1972). At short range (a few inches), electrical cues appeared to dominate
chemical cues. The acute electric sense of sharks and rays may well play
an important part in the animal's daily life (Kalmijn, 1974).

Orientation in sharks by acoustical cues has been studied in recent
years by various workers (Nelson and Gruber, 1963; Banner, 1968, 1972;
Myrberg, 1969; Myrberg et al., 1969, 1972; Nelson and Johnson, 1970, 1972)
who have provided evidence for the possible role of low frequency sounds
in the localization of prey by these animals. Attempts to demonstrate

orientation through sound in teleosts have been inconclusive and the physical basis for an orientation mechanism using acoustical cues seems difficult to formulate.

A physical theory of electrical orientation with respect to open-ocean streams and to the earth's magnetic field has recently been developed (Kalmijn, 1973, 1974). Now that we know the high electrical sensitivity of the animals and the strengths of the pertinent stimulus fields, it seems quite feasible that electro-orientation aids short- and long-range navigation in sharks and rays.

The possible significance of other sensory cues for orientation in sharks has hardly been considered experimentally. Although the lateralis system has been studied to a considerable extent in these animals, its role in orientation is unknown. Orientation through temperature perception and vision has not been investigated. Particularly, the possibility of perception of and oriented response to polarized light deserves early investigation in view of recently demonstrated capabilities of some teleosts in response to the e-vector of a polarized laboratory "sky" (Kleerekoper et al., 1973) and in field experiments (Waterman, 1973). In particular, the interaction of two or more cues in locomotor orientation in sharks merits urgent attention. Apart from the recent experiments on flow-chemical and electrical-chemical cue interaction, no work has been done in this area. Many of these fields of research will have to be attacked initially in the laboratory so that quantitative approaches can be used. Recent monitoring and statistical techniques would enhance the chances of success. New telemetric techniques now offer possibilities in the field for the coarser tracking of movements of sharks and for the design of meaningful experimentation. Whether in the laboratory or in the field, it should be emphasized that short term experiments on locomotor orientation do not inspire confidence in view of the great variability in this behavior over time. This variability can be statistically accounted for in stochastic models of locomotor behavior extending in time.

c. Osmoregulation

The biology of the shark's nervous system, both motor and sensory, is of obvious importance to its efficiency as a predator and its threat to man. Perhaps less apparent, yet a most important aspect of the shark's physiology, is the way it maintains water and solute balance under conditions which tend to disrupt it, i.e., its osmoregulatory mechanisms.

Earlier work on elasmobranch osmoregulation has been reviewed, and much of the recent work reported, in two symposium volumes: Gilbert, Mathewson, and Ralls (1967); and Goldstein (1972).

In broad outline the major features of the osmoregulation of marine elasmobranchs have been fairly well worked out. Instead of regulating the solute content of the body fluids well below that of the sea water, with the expenditures of much energy, as is done by marine teleosts, elasmobranchs accumulate large quantities of organic substances, especially urea, and to a lesser extent trimethylamine oxide. These are retained in quantities sufficient to make the body fluids hyperosmotic to sea water and thus provide water for a limited quantity of urine, relatively concentrated, but still hypotonic to the serum. Excess salt is excreted by

way of the rectal gland.

In freshwater teleosts, the osmotic imbalance between body fluids and environment is reversed, since the salt content is regulated at only a very slightly lower level than in the marine teleosts. But when euryhaline elasmobranchs such as the bull shark Carcharhinus leucas and the sawfish Pristis perotteti move from the sea to fresh water the imbalance is not reversed but simply increased. The osmotic influx of water therefore increases and the quantity of urine increases accordingly and its concentration is reduced, both by a factor of 15 to 20. The urea content of the body fluids decreases to about 30 to 50 percent of the marine level, and presumably the rectal gland stops excreting salt. When the elasmobranchs return once more to the sea, they revert to the marine osmoregulatory pattern.

The completely freshwater stingrays of South American rivers (family Potamotrygonidae) have abondoned the accumulation of urea as an osmoregulatory agent and are unable to retain urea even in response to transfer into saline water. Essentially they deal with their osmotic problems as freshwater teleosts. In contrast to these rays, freshwater stingrays of the Benue River of Nigeria (family Dasyatidae) deal with their osmotic problems essentially as the euryhaline shark and sawfish, retaining urea, but at a reduced level.

In recent years, more studies have been conducted in the general area of osmoregulation than in any other area of elasmobranch physiology except perhaps neurobiology. Many facets of the overall problem have been at least touched on, for instance, the biosynthesis of urea and trimethylamine oxide and the influence of various experimental regimens on that synthesis and the enzymes involved; the influence of various substances, procedures and environmental salinities on urea levels; membrane transport of urea and various inorganic ions; retention of urea by tubular reabsorption and gill membrane impermeability; various aspects of rectal gland function; and the influence of endocrine secretions on osmoregulation.

Nevertheless, much remains to be learned before we have a reasonably complete understanding of how elasmobranchs deal with their osmoregulatory problems, especially as they move between areas of differing environmental salinities.

No aspect of osmoregulation is fully understood and any of the areas mentioned above would profit by study in greater depth and particularly by comparison of a greater variety of species. Perhaps most enlightening would be the application of already used techniques and experimental procedures to the truly euryhaline species. In this way the rates and directions of the processes that make up the total osmoregulatory function can be watched under controlled manipulations in species that are able to make the requisite changes to accommodate to both sea water and fresh water.

In the past, many attempts have been made to observe changes when a shark is transferred from sea water to fresh water, but almost invariably the wrong species have been selected -- species that are not truly euryhaline and therefore are not fully able to make the necessary physiological adjustments. Therefore, when placed, for instance, in 50 percent sea water for several hours, they retain excessive water, are unable to

retain their normal salt concentration, their hematocrit falls, and they soon die unless returned to their accustomed habitat. On the contrary, Carcharhinus leucas and Pristis perotteti in fresh water are able to maintain their water and salt balance and normal hematocrit values indefinitely. The problem has been to obtain and maintain in captivity the small specimens most desirable for such studies. Given the necessary holding facilities and a dependable supply of experimental animals, these species are potentially a most valuable source of information, until now largely out of reach.

5. Closing Statement

By virtue of expertise represented or lacking on the committee, this portion of the report deals primarily with certain topics and neglects others. Lack of treatment of an area does not imply that the area is unimportant or is not an appropriate subject for research. Various aspects of reproductive physiology, immunobiology, pharmacology, and cell biology and metabolism have been studied in recent years by a number of investigators whose publications suggest fruitful lines of future research. The digestive process, muscle physiology, endocrinology, and parasitology have received less attention but they also offer ample opportunity for investigation in elasmobranchs. These and other areas may also be of primary interest and be expected to produce important results.

It is gratifying to note the progress that has been made in the neurobiology, sensory physiology, and osmoregulation of elasmobranchs during the last decade. Several promising areas of research have been indicated in this report. If implemented, these should provide additional fundamental information to explain the behavior of sharks and how they respond to environmental stimuli.

Various techniques and methods are common to diverse experimental studies on sharks and other elasmobranchs. At present, there are no readily available sources to which a researcher can refer in designing and carrying out studies on sharks. In addition, many important parameters related to the handling and maintenance of sharks are presently not known. For these reasons, it is important that workers in the fields of experimental physiology and behavior of elasmobranchs be brought together to exchange information and collate and publish the available data on experimental techniques. Included in such a symposium should be the following topics:

1. Electrode implantation techniques.

2. Stressful effects of captivity and handling.

3. Effects of pharmacological agents normally used as anesthetics, etc.

4. Pathobiology and nutrition.

5. Maintenance techniques including the use and composition of physiological solutions.

PART C.   STUDIES OF SHARKS IN RELATION TO MAN

1.   <u>Nature and Significance of Hazard to Man</u>

a.   Introduction

Although statistically infrequent, shark attack remains a significant physical and psychological problem for naval personnel. The circumstances under which sharks constitute a threat are primarily the following:

(a) Survival situations (air and sea disasters)

(b) Swimmer/diver operations

(c) Recreational swimming and diving

An indirect personnel hazard could result from shark-inflicted damage on deep-sea navigational buoy moorings or surveillance equipment (see Part C, Section 2).

Assessment of the problems requires collection and analysis -- on a continuing basis -- of accurate data. The effectiveness of. such as assessment is largely dependent on the availability of objective reports.

In the past the Navy supported, through ONR, the establishment and maintenance of such reporting procedures by means of the Shark Attack File. In 1967 support for this program was terminated, and no systematic collection of incidents has been possible since that time. The final report from this project (Baldridge 1973, 1974) resulted in the most complete analysis of shark attacks yet produced.

Emerging from the purposes of the Shark Attack File was Bureau of Medicine Instruction 6400.2A which required a world-wide reporting of shark attacks on naval personnel and civilians under naval jurisdiction. No reports of attacks on naval personnel have resulted, although independent documentation has indicated that personnel covered by that instruction have indeed been victims of shark attack. An effective reporting procedure is seen as mandatory (a) because of the need to identify possible causative and predictive factors of attack on man, (b) to provide an enlightened basis for development of anti-shark measures, (c) to identify changing trends in location and pattern of attacks, and (d) to provide information of such nature and accuracy as to allay unnecessary fears about shark attack.

b.   Hazards

1) Physical Hazard

Shark injuries are often massive and usually characterized by shock, trauma, and loss of blood, not unlike combat injuries. The treatment procedures are virtually identical in both situations. It is only in recent years that the importance of immediate on-site preliminary treatment for this type of injury has been recognized. The work by Davies and Campbell (1962) has dramatically demonstrated the value of having plasma available for immediate use on the beach before transporting the victim to a facility for more intensive care.

Pathogenic organisms such as haemolytic streptococci (ibid.) from the shark's mouth may constitute an additional serious complication.

Current medical practices, both military and civilian, do not reflect these findings.

2) Psychological Hazard

There is understandably a widespread apprehension of sharks and the possibility of shark attack, despite the relatively low incidence of attacks. Abundant evidence indicates that apprehension, even in the absence of a shark sighting, has an adverse effect on performance, whether in a survival situation or in the execution of an operational task. Apprehension lessens the individual's chances for survival or diminishes the operator's ability to accomplish his mission.

A message (272349Z Aug 74) from the Commander, Amphibious Forces Pacific, to the Naval Scientific Advisory Program requesting test and evaluation of a wet suit incorporating shark-bite resistant material (KEVLAR ; see Physical Deterrents) was prefaced with the following statement:

> The shark hazard to Navy Divers has been a
> continual threat over the years, both in the
> sense of producing actual casualties and in
> the psychological effect of degrading effect-
> iveness of divers who must work in waters in
> which sharks have recently made an attack.

Official concern with possible hazards is also reflected in the basic UDT/SEAL training lesson plan having to do with dangerous marine life. This states: "The appearance of a shark as large as the diver or two or more sharks in the diving area should be sufficient reason for the diver to terminate his diving activities and leave the water."

Examples of operator apprehension and official concern leading to mission interference can be cited:

> In a night-recovery training exercise prior to
> the splashdown of Apollo 15, the practice capsule
> was in the water and the UDT personnel were in the
> process of attaching the flotation collar. Three
> helicopters containing the primary recovery team
> and two reserve teams were overhead shining spot-
> lights on the capsule.* At this point, the officer-
> in-charge, also overhead in a backup helicopter,
> noticed that at least six sharks were circling the
> capsule. The training operation was immediately
> aborted. With realization of the disastrous
> implications the shark hazard presented, recovery
> personnel were subsequently equipped with CO_2 darts
> (see Physical Deterrents).

*In operational or survivor recovery operations utilizing helicopters, there exists the possibility, still unconfirmed, that the beat of the rotors on the water sends out low frequency vibrations similar to those that are known to attract sharks (see page 9).

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On 21 April 1963, a naval officer assigned to Underwater Demolition Team TWENTY TWO, LTJG J.W. Gibson, was attacked and fatally wounded by a shark at the head of Magens Bay, St. Thomas, Virgin Islands. The shark was caught on the following day and positively identified as the perpetrator of the attack by the undigested remains of the victim found in its stomach.

Personnel of UDT-22, which had been deployed to the Virgin Islands for advanced training, recall that apprehensions about the possibility of shark attack rose sharply after the death of LTJG Gibson. The rationale for the attack most frequently expressed by UDT personnel on scene was that the shark was "sick" and its attack was therefore extremely unusual.

A training exercise conducted a few days after LTJG Gibson's death, involving diver lock-out from a submarine, was cancelled after two pairs of divers locked-out and reported seeing sharks that appeared aggressive. Operations were not resumed that day, and the submarine returned to port. On the following day the operation was successfully completed, with no sharks sighted.

During the Fall of 1969, a classified underwater construction project was carried out by divers of · Underwater Demolition Team ELEVEN. In one stage of the project, use of underwater explosives was required on a daily basis. Diving operations were frequently hampered by aggressive behavior of the numerous sharks that unfailingly appeared in the work area after the detonation of the explosives. The sharks congregated in such large numbers after each detonation, and their behavior was so menacing, that resumption of work was delayed up to two hours on several occasions.

When work was resumed it was necessary to put two pairs of divers into the water; one pair to work and one pair to watch for and ward off sharks that approached too closely. Work dives were often terminated when persistently aggressive sharks forced divers to leave the water. The officer-in-charge requested permission to arm his divers with powerheads, but authorization was not granted because of the potential danger to personnel posed by the powerhead itself and concern that the thrashing and bleeding of a wounded shark would serve to attract more sharks.

c. Countermeasures

Advisable behavioral countermeasures which should be incorporated into training materials have been set forth in detailed fashion in an ONR report (Baldridge, 1973).

1) Personnel Training

Because shark attacks are rare, very little aircrew and UDT/SEAL
training is devoted to shark hazard. UDT/SEAL training for example,
includes only a two-hour lecture on dangerous marine life. Ordinarily,
this minimal information regarding sharks is not a matter of concern.
However, when an individual is in a survival situation, or sharks are
encountered in swimmer/diver operations, a knowledge of shark behavior and
proper response to shark activity may become crucial. The extent of
coverage of training information should range from simple and accurate
basics for aircrewmen to more detailed information for UDT and SEAL
personnel whose normal sphere of operations is underwater. Examples of the
kind of information that swimmer/diver personnel could use are: distin-
guishing features of dangerous species of sharks, recognition of distinctive
threat postures which may precede attack, and knowledge of characteristic
activity patterns, such as the movement of blue sharks from open sea to
shallow coastal waters at dusk, with return to deeper waters at dawn.

This behavioral information, only recently acquired by ONR contractors,
illustrates the desirability of frequently updating training manuals and
films. Training materials currently in use contain a great deal of out-
of-date and inaccurate information. The U.S. Navy Diving Manual, for
example, emphasizes the danger of killer whales, even though there has
never been a documented record of an attack on a human. The Air Force
film entitled Shark Defense (TF-5589-B) also contains inaccurate information
("it is difficult for sharks to make sharp turns"), and advocates a number
of courses of action which are either ineffective (for example, tearing up
bits of paper and scattering them on the water) or inadvisable (rubbing
bare fingers on the rubber life raft, to make a sound which, in actuality,
might attract sharks). While this film is 10 years old, it is still being
shown.

Proper training not only saves lives but also facilitates the success-
ful and expeditious accomplishment of tasks and missions.

2) Chemical Deterrents

Although a number of devices for deterring sharks have been proposed,
(Gilbert and Gilbert, 1973), the standard deterrent issued to military
personnel since World War II is a cake of water soluble wax containing 80%
nigrosine dye and 20% copper acetate, called "Shark Chaser." In early
tests it was reportedly effective in repelling several species of sharks.
However, a mounting body of evidence has now conclusively demonstrated
that Shark Chaser has no significant deterrent value against most dangerous
sharks. Even such psychological benefits as it may have provided have
diminished with the growing awareness that it does not afford effective
protection. But the inefficacy of Shark Chaser has not been clearly demon-
strated in operational use (a shark exposed to Shark Chaser may have had no
intention of attacking in the first place), and no practical, effective
substitute has become available. Moreover, it is only recently that the
growing body of evidence from observations and controlled experiments (Kato,
1962) has conclusively established the lack of value of this chemical
deterrent.

For the above reasons Shark Chaser is still issued to military per-
sonnel. In the period from November 1969 through February 1974, the

Department of Defense purchased 84,450 packets at a cost of approximately $345,000. In addition, each packet comes boxed in a cardboard container that bears a two-year expiration date, which probably accounts for the continuing purchase of 15,000 to 20,000 packets per year. (This information obtained from Naval Air Systems Command Code 531 as supplied by Defense General Supply Center, Richmond, Va.)

Although an effective substitute for Shark Chaser is clearly needed, it is questionable whether any chemical deterrent which diffuses to form a cloud around the user is practical. The quantity of material required to maintain an effective concentration for the desired period of time and the problem of insuring complete envelopment are among the reasons why such chemical deterrents appear to offer little promise (Baldridge, 1969a and b).

However, the recent discovery of a biological substance that has a unique deterring effect of sharks requires further investigation. A flat-fish, Pardachirus, which occurs in the Red Sea and Indian Ocean, secretes a milky substance that at certain levels of dilution, is highly toxic to a number of forms of life and extremely aversive to sharks. It has been demonstrated that a shark will not close its jaws on the living fish and that under experimental conditions the substance affords protection to other kinds of fish that the shark would otherwise eat. The substance acts with remarkable rapidity; even fish enveloped by a shark's open jaws have later shown no scratch or mark (Clark and Chao, 1972; Clark, 1974).

3) Physical Deterrents

Protective devices may be either active or passive. Of passive devices for individual protection in a sea survival situation, one promising device, the Shark Screen, appears to be an inexpensive, practical, and highly effective means of preventing shark bite (Johnson, 1968). Shark Screen is a bag of thin, tough plastic with a collar consisting of three inflatable rings. The user partially inflates one of the rings by mouth and gets into the bag. He then fills it with water by dipping the edge so that it becomes turgid, presenting to any shark a large, solid-looking black object. The rings can be fully inflated at leisure. The bag retains any fluids or wastes which might attract and arouse a shark. It also effectively attenuates the bioelectric and galvanic fields produced by the person and his gear, which otherwise might elicit attack through the shark's acute electric sense (Kalmijn, 1971). It is believed that minor packaging and material problems can be solved so that the final product will occupy no more space than that now required for a packet of Shark Chaser.

A new material called "KEVLAR" developed by Dupont is being used for bullet-proof vests and jackets. Preliminary tests indicate that it offers promise as a sharkbite resistant material which could be incorporated into wet suits.

A variety of devices for actively deterring sharks have been developed or proposed, most of them for use by a diver (as opposed to devices for area protection). In assessing these a number of factors must be taken into consideration, including practicality, cost, reliability, effectiveness, and safety for the user. A device practical for sport divers might be prohibitively burdensome for UDT/SEAL personnel. Cost, within reasonable limits, must be balanced against portability, effectiveness, and reliability.

Simplest and cheapest of devices in use is a short club, the "shark billy," which is rated moderately effective. At the other extreme are electrical or electronic shield devices which are expensive and complex. So far these have not proven to be effective and in some instances have constituted a hazard for the user (Gilbert, 1968).

Conventional power heads or "bang sticks" are relatively inexpensive and have some effectiveness, but are not readily reloaded. The recently developed "Sea-Way" power head is highly effective and easily reloaded, but, like bang sticks, would be of limited utility to military divers who are often burdened with other gear and sometimes required to operate clandestinely.

The electronic dart, which is designed to electronarcotize a shark, and the CO_2 dart, which injects carbon dioxide into the shark under high pressure (Langguth, 1972), are moderately effective but relatively expensive, and unless equipped with extension poles (which reduce their portability) require that the user be in very close contact with a shark.

One novel device, the drogue dart, is a barb with a small parachute attached. When the barb, mounted at the end of a pole, is implanted in a shark it breaks away and the parachute provides an off-balance impediment to the shark's swimming. This device, while cheap and effective with small sharks, has not been tested with large sharks.

Recent accounts of acoustic devices that repel sharks warrant investigation (see Banner, 1972; Myrberg, 1974), although they raise questions of cost and practicality. The great advantage of an acoustic device, assuming that there is a sonic stimulus which will repel sharks, is that it would operate at a distance. A disadvantage is that it could not be used in clandestine swimmer/diver operations.

In summary, no existing device satisfactorily meets the specifications for military swimmer/diver use, although some have utility in special circumstances.

4) Area Protection

Area protection may at times be desirable at an underwater construction site or a recreational bathing area. Again, no wholly satisfactory device or system is known, each being deficient in one respect or another. A net enclosure is effective but expensive and usually impractical. Gill-netting and fishing for sharks have proved effective in Australian beaches but are expensive, long-term measures. An electrical device called "Shark Shield" has seen some use by shrimp fishermen to keep sharks out of their nets, but it is expensive and of limited practicality for area protection (Gilbert and Gilbert, 1973). The possibility of attracting sharks away from the area of concern by means of acoustic techniques developed in the course of ONR-sponsored research might prove moderately effective but has obvious drawbacks.

The fact that porpoises have on occasion been known to attack and kill sharks has led to the suggestion that they be specially trained to provide protection for swimmers and divers. In an ONR-sponsored project conducted at the Mote Marine Laboratory a bottlenose dolphin was indeed trained to harass a large sandbar shark and drive it out of the pool, but when a bull

shark, one of the species known to be dangerous to man (and, probably, porpoises) was introduced, the porpoise exhibited flight behavior and refused to respond to any commands (Irvine, et al., 1973). While not conclusive and providing little optimism for development of a porpoise anti-shark system the experiment raised the intriguing question of what sensory cues were used by the porpoise in distinguishing two rather similar species of carcharhinid shark.

d. Principal Recommendations

1) The establishment and maintenance of an effective reporting system for shark incidents.

2) Re-establishment of the Shark Attack File with its attendant function of analysis and reporting.

3) Dissemination of information regarding need for treatment at the recovery site of shock and trauma of shark-attack injury.

4) Incorporation of current and accurate information in training programs and training aids.

5) Discontinuance of purchase of Shark Chaser by DoD.

6) Objective assessment of proposed deterrents with consideration to R&D and operational requirements.

2. Nature and Significance of Hazard to Moored Systems*

a. Introduction

Deployment of moored systems for the collection of oceanographic, meteorological, or surveillance data over extended periods of time has prompted an investigation of factors responsible for equipment loss within the rated life of moorings, which could not be attributed to hydrodynamic forces or encounter with surface craft or submersibles.

b. Discussion

Evidence accumulated from a comprehensive review of the limited literature reveals that sharks, including the oceanic whitetip Carcharhinus longimanus, mako shark Isurus oxyrinchus and blue shark Prionace glauca are incriminated in the biting and slashing of deep-sea moorings (Starkey, 1974; Stimson and Prindle, 1967). This has been verified by dental impressions and recovery of tooth fragments from various types of plastic cable armor to depths of approximately 1500 feet. Histograms of biting recorded on experimental moorings in Atlantic waters near Bermuda indicated that bites occurred with greatest frequency near the permanent thermocline (Turner and Prindle, 1967). Apparently, "fishbite" on mooring lines and cables is less of a problem in the Pacific, although detailed evidence is lacking.

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*This material was prepared by Roland J. Starkey, Jr., Environmental and Ocean Science Laboratory, General Electric Company, who was unable to attend the workshop.

For the most part, trials with baited samples of armored cable in tensile frames have been unsuccessful, although in one case Prionace glauca punctured samples of polyethylene and polycarbonate in trials conducted off the southeast coast of Massachusetts (Stimson and Prindle, 1967). Studies of this kind cannot be considered realistic since they fail to stimulate the stratification of the moorings' physio-chemical and biological environment.

It has been theorized that sharks usually do not exert maximum biting strength on cables because they are attracted to foreign objects on or in the immediate vicinity of the cables, rather than to the cables themselves. Walden and Panicker (1973) ascribe the "dental floss effect" to a slashing phenomenon. This may occur when the shark is casually searching for food, and the cable is rapidly drawn across the tip of one or more teeth as a result of whip-lash motion mediated by fluctuating currents or by movement of surface or sub-surface buoys. From an operational standpoint, slashing at any depth may expose one or more conductors, interrupting data collection, decreasing tensile strength, and contributing to the premature loss of an entire system. For these reasons various studies are being conducted to develop armor for multiple-conductor cables so that they will be resistant to attack by sharks and other fishes but still possess the tensile strength and characteristics (including diameter, weight, flexibility, etc.) necessary for deep-sea deployment of navigational buoys as well as instrument packages (Hartman, 1972; Preston, et al., 1973).

Concurrent interest has developed in investigating factors attracting sharks, and countermeasures suitable for use in shallow and deep-water applications. One factor under consideration is low-frequency sound generated by cable movement, generally referred to as "strumming", which may be similar to the low frequency vibrations that are known to attract sharks (Myrberg et al., 1969 a & b, 1972b; Nelson and Gruber, 1963; Nelson and Johnson, 1972; Nelson et al., 1969). Various types of anti-strumming devices are currently in use or undergoing evaluation to determine their effectiveness. The simplest involves the application of polyethylene ribbons at regular intervals along the length of the cable. Quantitative data are not available to confirm the efficacy of this method.

Based on examination of recovered deep-sea moorings it has also been hypothesized that sharks may be attracted to cables by visual clues elicited by an assortment of bioluminescent organisms accumulating on the cables' surface (Turner, 1965). Flashes of light would be triggered by mechanical stimuli as the cable strums, possibly evoking a positive phototropic response.

The high frequency of biting reported near the permanent thermocline suggests that a higher concentration of food organisms may exist there. This could increase the incidence of random encounters and expression of the "dental floss" effect.

Olfactory clues from chemical messengers cannot be discounted, since recovered moorings are often covered with a variety of unidentifiable decaying biological materials. This is generally referred to as "Sea Snot" and is frequently seen in the Bermuda area (Gifford, 1973). Garbage is also found on deep-sea mooring cables, and similarly could be expected to attract sharks and smaller fishes as aromatic degradation products are continuously

leached into the water.

Other possible attractants include current meter rotors (Walden and Panicker, 1963), hydrophones, or any equipment which could contribute to sound propagation, owing either to moving parts or to in-line sensor housings larger in diameter than the cable.

It has been speculated that shark attack on scuba divers could be provoked by galvanic currents generated by dissimilar metals of the regulator, tank, and backpack strap (Klimley, 1974). Similar currents may be produced in cables when care isn't taken to maximize cathodic protection of instrument cases or achieve electrical isolation of aluminum and stainless steel hardware (Morey, 1973). The importance of this requires further clarification. However, as discussed previously, those elasmobranchs investigated have demonstrated great sensitivity to weak electric fields.

c. Conclusions and Recommendations

1) Moored systems for the collection of oceanographic, meteorological, and surveillance data are susceptible to damage or loss owing to biting or slashing by fishes, including sharks.

2) The extent and seriousness of the problem cannot be determined from presently available evidence, although "fishbite" incidents are apparently more common in tropical Atlantic waters.

3) A central office (probably in the Naval Oceanographic Office) should be established for collection and study of reports of fishbite incidents, and users of moored systems should be informed of the existence of such an office. Information provided to such an office would permit determination of the identity of the perpetrators of such "attacks" as well as the geographical and seasonal occurrence of fishbite incidents.

4) Further investigations are needed to understand the reasons for the apparent attraction of sharks and other fishes to mooring lines and cables.

5) Information derived as a result of the above recommendations can be used to help develope more effective and practical mooring lines and cables.

CLOSING STATEMENT

In summary then, this workshop has attempted to review some of the main areas of shark research and to suggest those areas where efforts expended may give the most profitable results in the future. It is hoped that this report will prove useful not only for scientists but for planners, research managers, Navy personnel, and laymen interested in sharks and shark research.

In abbreviated form, these recommendations can be summarized as follows:

1. A proposed "Guide to the Sharks of the World" to be produced by a multiplicity of authors in a loose leaf format in order to insure wide dissemination of accurate and up-to-date information about the identification and biology of sharks.

2. A proposed "Systematic Catalogue of Sharks and Rays of the World" intended as a companion to the guide listed above but containing more technical information for specialists.

3. A proposed Shark Data Bank where potentially useful ecological data on sharks may be gathered and collated as contributed, perhaps much of it collected incidental to other marine research.

4. Concentrated ecological and behavioral studies on a variety of representative and preferably ubiquitous species of sharks such as the great white shark, tiger shark, bull shark, or oceanic whitetip.

5. Expansion of research using the most advanced ethological techniques for investigating social, rhythmic and feeding behavior, especially toward a quantification of the results.

6. Continuation of research: behavioral, physiological and anatomical; on shark sensory systems: acoustic, chemical, visual and electric; as well as on a number of other systems: central nervous system, orientation mechanisms and the osmoregulatory system.

7. The establishment and maintenance of an effective reporting system for shark incidents, perhaps within the framework of a re-established Shark Attack File with its attendant function of analysis and reporting.

8. Improved dissemination of information about sharks in relation to man including medical treatment for shark attack injuries and the reassessment of accurate and current information in training programs.

9. Discontinuance of the purchase of Shark Chaser by the Department of Defense along with the objective assessment of all proposed

deterrents especially in light of technical and operational requirements.

10. An accurate assessment and further investigation of the problem of sharks attacking and biting mooring lines and equipment, especially through the establishment of a central clearing house for the collection and study of fishbite incident reports.

BJZ

REFERENCES CITED

Allee, W.C. and J.C. Dickinson, 1954. Dominance and subordination in the smooth dogfish, _Mustelus canis_ (Mitchill). Physiol. Zool., 27: 356-364.

Ariens Kappers, C.U., G.C. Huber and E.C. Crosby, 1936. The Comparative Anatomy of the Nervous System of Vertebrates Including Man. Reprinted by Hafner, New York, 1965.

Aronov, M.P., 1959. The role of sensory organs in the search for food by the Black Sea whiting. Acad. Sci. USSR, Studies Sebastopol. Biol. Sta. 11: 229-237.

Aronson, L.R., 1963. The central nervous system of sharks and bony fishes with special reference to sensory and integrative mechanisms. pp 165-241, IN: P.W. Gilbert, (Ed.), Sharks and Survival. D.C. Health and Co., Boston.

————, F.R. Aronson and E. Clark, 1967. Instrumental conditioning and light-dark discrimination in young nurse sharks. Bull. Mar. Sci., 17: 249-256.

Baldridge, H.D., Jr., 1966. Reaction of sharks to a mammal in distress. Military Medicine, 131: 440-446.

————, 1969a. Kinetics of onset of responses by sharks to waterborne drugs. Bull. Mar. Sci., 19(4): 880-896.

————, 1969b. Analytical indication of the impracticality of incapacitating an attacking shark by exposure to waterborne drugs. Military Medicine, 134: 1450-1453.

————, 1971. Studies on physical and chemical factors influencing shark behavior. Final Report, ONR Contract No. 104-025. 7pp.

————, 1973. Shark attack against man. Report submitted to Office of Naval Research (Code 484) under Contract N00014-73-C-0252, 31 Oct. 1973, 66 pp. plus appendices.

————, 1974. Shark attack: a program of data reduction and analysis. Contributions from the Mote Marine Laboratory, 1(2): i-x; 1-98.

————, and J. Williams, 1969. Shark attack: feeding or fighting? Military Medicine, 34: 130-133.

Banner, A., 1967. Evidence of sensitivity of acoustic displacements in the lemon shark, _Negaprion brevirostris_ (Poey). pp. 265-273, IN: P. Cahn (Ed.), Lateral Line Detectors. Indiana Univ. Press, Bloomington.

————, 1968. Attraction of young lemon sharks, _Negaprion brevirostris_ (Poey) by sound. Copeia, (4): 871-872.

————, 1972. Use of sound in predation by young lemon sharks, _Negaprion_

brevirostris (Poey). Bull. Mar. Sci., 22(2): 251-283.

Bigelow, H.B. and W.C. Schroeder, 1948. Fishes of the Western North Atlantic. Part 1: Sharks. Mem. Sears Found. Mar. Res. I: 58-576.

Budker, P., 1938. Les cryptes sensoriels cutanes des plagiostomes. Ann. Inst. Oceanog., 18: 207-288.

Bullis, H.R., Jr., 1961. Observations on the feeding behavior of whitetip sharks on schooling fishes. Ecology, 42(1): 194-195.

Church, R., 1961. Shark attack. Skin Diver, June, pp. 30-31.

Clark, E., 1959. Instrumental conditioning of lemon sharks. Science, 136: 217-218.

———, 1963. The maintenance of sharks in captivity, with a report on their instrumental conditioning. IN: Sharks and Survival, P.W. Gilbert, (Ed.), D.C. Heath and Co., Boston, pp. 115-149.

———, 1974. The Red Sea's sharkproof fish. National Geographic, 146(5): 718-727.

———, and S. Chao, 1972. A toxic secretion from the Red Sea flatfish Pardachirus marmoratus. Scientific Newsletter NO. 2, Hebrew University, Jerusalem, Marine Biology Laboratory, Eilat.

———, and K. von Schmidt, 1965. Sharks of the central Gulf Coast of Florida. Bull. Mar. Sci., 15(1): 13-83.

Clarke, T.A., 1971. The ecology of the scalloped hammerhead shark, Sphyrna lewini, in Hawaii. Pacific Sci., 25(2): 133-144.

Collette, B.B. and F.H. Talbot, 1972. Activity patterns in coral reef fishes, with emphasis on nocturnal-diurnal change over. Nat. Hist. Mus. of Los Angeles County, Sci. Bull., 14: 98-124.

Davies, D.H., 1964. About sharks and shark attack. Routledg and Kegan Paul Ltd., London, 237 pp.

———, and G.D. Campbell, 1962. The aetiology, clinical treatment of shark attack. Jour. Royal Naval Medical Service, 48(3): 110-135.

———, J.P.A. Lochner and E.D. Smith, 1963. Preliminary investigations on the hearing of sharks. Oceanogr. Res. Inst. (South Africa), Investigational Rept. No. 7, 10 pp.

———, and L.S. Joubert, 1967. Tag evaluation and shark tagging in South African waters, 1964-1965, pp. 111-140, IN: P.W. Gilbert, R.F. Mathewson and D. Rall (Eds.), Sharks, Skates and Rays. Johns Hopkins Press, Baltimore.

DeGroot, J., 1967. Organization of hypothalamic feeding mechanisms. IN: Handbook of Physiology, The Alimentary Canal, Vol. 1, Amer. Physiol.

Demski, L.S., 1973. Feeding and aggressive behavior evoked by hypothalamic stimulation in a cichlid fish. Comp. Biochem. Physiol., 44: 685-692.

————, 1974. Structure of the inferior lobe of the teleost hypothalamus. Anat. Rec., 178:341.

————, and K.M. Knigge, 1971. The telencephalon and hypothalamus of the bluegill (Lepomis macrochirus): Evoked feeding, aggressive and reproductive behavior with representative frontal sections. J. Comp. Neurol., 143: 1-16.

Denton, E.J. and J.A. Nichol, 1964. The choroidal tapeta of some cartilaginous fishes, Jour. Mar. Biol. Assoc. U.K., 44: 219-258.

————, and T.I. Shaw, 1963. Visual pigments of some deep sea Elasmobranchs. Jour. Mar. Biol. Assoc. U.K., 43: 65-70.

Dijkgraaf, S., 1963. The functioning and significance of the laternal-line organs. Biol. Rev., 38: 51-105.

————, and A.J. Kalmijn, 1962. Verhaltungsversuche zur Funktion der Lorensinischen Ampullen. Naturwissenschaften, 49: 400.

———— and ————, 1963. Untersuchungen über die Funktion der Lorenzinischen Ampullen an Haifischen. Z. vergl. Physiol., 47: 438-456.

Dowling, J.E. and H. Ripps, 1970. Visual adaptation in the retina of the skates. J. Gen. Physiol., 56(4): 491-520.

————, 1971. S potentials in the skate retina. J. Gen. Physiol., 58(2): 163-189.

Ebbesson, S.O.E., 1970. The selective silver impregnation of degenerating axons and their synaptic endings in non-mammalian species. IN: Contemporary Research Methods in Neuroanatomy, W.J.H. Nauta and S.O.E. Ebbesson (Eds), Springer-Verlag: New York, pp. 132-161.

————, 1972. New insights into the organization of the shark brain. Comp. Biochem. Physiol., 42A: 121-129.

————, and L. Heimer, 1970. Projections of the olfactory tract fibers in the nurse shark (Ginglymostoma cirratum)Brain Res., 17: 47-55.

————, and J.S. Ramsey, 1968. The optic trructs of two species of sharks (Galeocerdo cuvieri and Ginglymostoma cirratum). Brain Res., 8:36-53

————, and D. Schroeder, 1971. M.S. Connections of the nurse shark's telencephalon. Science, 173: 254-256.

Eibl-Eibesfeldt, I. and H. Haas, 1959. Erfahrungen mit Maien. Zietschrift f. Tierpsychologie, 16: 733-746.

Evans, W.E. and P.W. Gilbert, 1971. The force of bites by the silky shark (Carcharhinus falciformis) measured under field conditions. Naval Undersea R and D Technical Report, NUC TN 575, 20 pp.

Faye, R.R., J.I. Kendall, A.N. Popper, and A.L. Tester, 1974. Vibration detection by the macula neglecta of sharks. Comp. Biochem Physiol. 47A: 1235-1240.

Fiedler, K., 1964. Versuche zur Neuroethologie von lippfischen and Sonnenbarschen. Verh. Dtsch. Zool. Ges. Kield. Zool. Anz. Supple., (1965) 28: 569-580.

Fischer, W. (Ed.), 1973. FAO species identification sheets for fishery purposes. Mediterranean and Black Sea (fishing area 37), 2 Vols. Incomplete pagination.

Ford, E., 1921. A contribution to our knowledge of the life histories of the dogfishes landed at Plymouth. Jour. Mar. Biol. Assoc. U.K., new series, 12(3): 468-505.

Franz, V., 1931. Die Akkommodation des Selachierauges and Seine Abbeldungsapparate, Nebst Befunden an der retina. Zool. Jahrb. Abt. allg. Zool. Physiol., 49: 323-462.

Gifford, J., 1973. Cruise Report, R/V Chain 107, 22 October - 10 November 1972. Woods Hole Oceanographic Institution Report WHOI-73-4. Appendix II, Summary of fouling, fishbite and corrosion data obtained on Chain 107.

Gilbert, P.W. (Ed.), 1963a. Sharks and Survival. xiv + 578 pp. D.C. Heath and Co., Boston.

————, 1963b. The visual apparatus of sharks. IN: P.W. Gilbert (Ed.), Sharks and Survival. D.C. Heath & Co., Boston. 578 pp.

————, 1966. Feeding and attack patterns of sharks. Proc. Eleventh Pacific Science Congress, Tokyo, Japan, 7: 32-33.

————, 1968. The shark: barbarian and benefactor, Bioscience, 18(10): 946-950.

————, 1970. Studies on the anatomy, physiology, and behavior of sharks. Final report to Office of Naval Research (Code 484) Contract No. NR 401 (33); Project NR 104-471.

————, and C. Gilbert, 1973. Sharks and shark deterrents, Underwater Journal 5(2): 69-79.

————, E.S. Hodgson and R.F. Mathewson, 1964. Electroencephalograms of sharks. Science, 145: 949-951.

————, R.F. Mathewson and D.P. Rall (Eds.), 1967. Sharks, Skates and Rays. xv + 624 pp. The Johns Hopkins Press, Baltimore, MD.

Goldstein, L., 1972. Elasmobranch Biology. Comp. Biochem. Physiol., 42A, Symposia held at Bar Harbor, Maine, 20-23June 1971.

Graeber, R.C., 1972. Visual discrimination learning and central nervous system lesions in lemon (Negaprion brevirostris) and nurse sharks

(Ginglymostoma cirratum). Unpubl. Doctoral Thesis, Univ. of Va.

————, 1974. Food intake patterns in captive juvenile lemon sharks,
Negaprion brevirostris. Copeia No. 2: 554-556.

————, and S.O.E. Ebbesson, 1972. Visual discrimination learning in normal
and tecta-ablated nurse sharks (Ginglymostoma cirratum). Comp. Bio-
chem. and Physiol., 42A: 131-139.

————, ————, and J.A. Jane, 1973. Visual discrimination in sharks without
optic tectum. Science, 180: 413-415.

————, D.M.S. Schroeder, J.A. Jane and S.O.E. Ebbesson, 1972. The importance
of telencephalic structures in visual discrimination learning in
nurse sharks. Soc. for Neurosci., Houston, TX.

Green, E.G. and I.M. Sigel, 1973. Duplex flicker fusion curves recorded
from the skate. Biol. Bull., 145(2): 43. Abstract only.

Grimm. R.J., 1960. Feeding behavior and electrical stimulation of the brain
of Carassius auratus. Science, 131: 162-163.

Gruber, S.H., 1967. A behavioral measurement of dark adaptation in the
lemon shark, Negaprion brevirostris. pp. 479-490, IN: P.W. Gilbert,
R. Mathewson and D. Rall (Eds.), Sharks, Skates and Rays. Johns
Hopkins Press, Baltimore, MD.

————, 1973. Purkinje shift in the lemon shark: behavioral and electro-
physiological findings. Publ. abstracts ARVO Meeting.

————, 1975. Duplex vision in Elasmobranchs: Histological, electrophysio-
logical and psychophysical evidence. IN: M.A. Ali (Ed.), New Approaches
to the study of Vision in Fishes. Plenum Press, New York.

————, R. Gulley, and J. Brandon, (in press). Photoreceptors in seven
elasmobranch species. Bull. Mar. Sci., 25(3).

————, D.I. Hamasaki and B.L. Davis, 1975. Window to the epiphysis in
sharks. Copeia, 1975(2): 378-380.

Hamasaki, D.I. and C.D. Bridges, 1965. Properties of the electroretinogram
in three elasmobranch species. Vision Res., 5: 483-496.

————, and S.H. Gruber, 1965. The photoreceptor of the nurse shark,
Ginglymostoma cirratum and the stingray, Dasyatis sayi. Bull. Mar.
Sci., 15(4): 1051-1059.

————, and P. Streck, 1971. Properties of the epiphysis cerebri of the
small-spotted dogfish shark, Scyliorhinus caniculus (L.) Vision
Research 11:189-198.

Hartman, P.J., 1972. Examination of sea lanes Mooring E after two years on
station. National Ocean Survey, National Data Buoy Center, NDBCM W6222
-2.

Herrick, C.J., 1905. The central gustatory paths in the brains of bony
    fishes. J. Comp. Neurol., 15: 375-456.

Herrnkind, W., 1974. Behavior: In Situ approach to marine behavioral
    research. pp. 55-98 IN: Experimental Marine Biology. Academic Press,N

Hickling, C.F., 1930. A contribution to the life history of the spiny
    dogfish. J. Mar. Biol. Assoc. U.K., 16(2): 529-576.

Hinde, R.A., 1970. Animal Behavior. McGraw-Hill, NY. 876 pp.

Hobson, E.S., 1963. Feeding behavior in three species of sharks. Pac.
    Sci., 17(2): 171-194.

————, 1965. Diurnal-nocturnal activities in some shore fishes in the Gulf
    of California. Copeia, 1965(3): 291-302.

————, 1968. Predatory behavior in some inshore fishes in the Gulf of
    California. U.S. Fish Wildlife Serv. Res. Rpt. 73. 92 pp.

————, 1972. Activities of Hawaiian reef fishes during the evening and
    morning transitions between daylight and darkness. Fishery Bull. 70(3):
    715-740.

Hodgson, E.S., 1971. An invasion of sharks. Natural History, 80(10): 92-
    101.

————, and R.F. Mathewson, 1971. Chemosensory orientation in sharks. Ann.
    N.Y. Acad. Sci., 188:175-182.

————, ————, and P.W. Gilbert, 1967. Electroencephalographic studies of
    chemoreception in sharks. pp. 491-501, IN: P.W. Gilbert, R.F. Mathewson
    and D. Rall (Eds.), Sharks, Skates and Rays. Johns Hopkins Press,
    Baltimore, MD.

Holland, G.A., 1957. Migration and growth of the dogfish shark of the
    eastern North Pacific. Fishery Research Papers, Washington Department
    of Fisheries, 2(1): 1-17.

Irvine, B., R.S. Wells, and P.W. Gilbert, 1973. Conditioning an Atlantic
    Bottle-nosed dolphin, Tursiops truncatus, to repel various species of
    sharks. Jour. Mammalogy, 54(2): 503-505.

Johnson, C.S., 1968. Countermeasures to dangerous sharks. American Society
    of Mechanical Engineers Publication 69-UNT-8.

————, and E. McFadden, 1971. Color and reflectivity of sea survival equip-
    ment, as related to shark attack. Aerospace Medical Meeting, Houston,
    Texas, 26 April.

Johnson, R.H. and D.R. Nelson, 1973. Agonistic display in the gray reef
    shark, Carcharhinus menisorrah, and its relationship to man. Copeia,
    (1): 76-84.

Kalmijn, A.J., 1966. Electro-perception in sharks and rays. Nature, London:
    187: 957.

————, 1971. The electric sense of sharks and rays. J. Exp. Biol.,
    55: 371-383.

————, 1972. Bioelectric fields in sea water and the function of the am-
    pullae of Lorenzini in elasmobranch fishes. Scripps Institution of
    Oceanography Reference Series, Contr. No. 72-83: 1-21.

————, 1973. Electro-orientation in sharks and rays: theory and experi-
    mental evidence. Scripps Institution of Oceanography Reference Series,
    Contr. no. 73-39: 1-22.

————, 1974. The detection of electric fields from inanimate and animate
    sources other than electric organs. IN: ∶A. Fessard, (Ed.), Handbook
    of Sensory Physiology, Vol. III/3: 147-200. Springer-Verlag.

Kato, S., 1962. Sharks Feeding Behavior (Film) U.S. Department of Interior,
    Southwest Fisheries Center, Tiburon Laboratory.

————, and A.H. Carvallo, 1967. Shark tagging in the Eastern Pacific Ocean.
    pp. 93-109, IN: P.W. Gilbert, R.F. Mathewson and D. Rall (Eds.),
    Sharks, Skates and Rays. Johns Hopkins Press, Baltimore, MD.

Katsuki, Y., T. Hashimoto, and J.I. Kendall, 1971. The chemoreception in
    the lateral line organ of teleosts. Jap. Jour. Physiol., 21: 99-118.

————, K. Yanagisawa, A.L. Tester and J. Kendall, 1969. Shark pit organs:
    responses to chemicals. Science, 163: 405-407.

Kleerekoper, H., 1963. The response to amine "F" by six species of marine
    fish. Am. Zoolog. 3(4): 169.

————, 1965. Olfaction and orientation in fishes. Am. Zoolog. 5(4): 382.

————, 1967a. Some effects of olfactory stimulation on locomotor patterns
    in fishes. pp. 625-645, IN: Proc. Second Int'l. Symposium - Olfaction
    and Taste II. Pergamon Press, N.Y.

————, 1967b. Some aspects of olfaction in fishes with special reference
    to orientation. Am. Zoolog. 7: 385-395.

————, 1969. Olfaction in fishes. Indiana Univ. Press. Bloomington, Ind.

————, D. Gruber and J. Matis, 1975. Accuracy of localization of a chemical
    stimulus in flowing and stagnant water by the nurse shark, Ginglymostoma
    cirratum. J. Comp. Physiol. 86: 27-31.

————, J.H. Matis, A.M. Timms, and P. Gensler, 1973. Locomotor response of
    the goldfish to polarized light and its e-vector. J. Comp. Physiol.
    86: 27-36.

Klimley, A.P., 1974. An inquiry into the causes of shark attack. Sea
    Frontiers, 20(2): 67-76.

Kobayashi, H., 1962. A comparative study on electroretinogram in fish with
    special reference to ecological aspects. J. Shimon. Coll. Fish.,
    11(3): 17-148.

Kuchnow, K.P. and P.W. Gilbert, 1967. Preliminary in vivo studies of pupillary and tapetal pigment responses in the lemon shark, Negaprion brevirostris. pp. 465-477, IN: P.W. Gilbert, R.F. Mathewson and D. Rall (Eds.), Sharks, Skates and Rays. Johns Hopkins Press, Baltimore, MD.

Langguth, A.F., 1972. Gas injection shark dart. Am. Sco. Mech. Eng. Pub. 72-WA/OCT. -10.

Liddicoat, J.D. and B.L. Roberts, 1972. The ionic composition of the lateral-line canal fluid of dogfish. J. Mar. Biol. Assoc. U.K., 52: 653-659.

Limbaugh, C., 1963. Field notes on sharks. pp. 63094, IN: P.W. Gilbert (Ed.), Sharks and Survival. D.C. Heath, Boston.

Lineaweaver, T.H. and R.H. Backus, 1970. The natural history of sharks. 256 pp. Lippincott, Philadelphia.

Lowenstein, O., H.P. Osborne and J. Wersall, 1964. Structure and innervation of the sensory epithelium in the labyrinth of the thornback ray (Raja clavata). Proc. Royal Soc. London B, 160: 1-12.

————, and T.D.M. Roberts, 1950. The equilibrium function of the otolith organs of the thornback ray (Raja clavata), J. Physiol., 110: 392-415.

————, and ————, 1951. The localization and analysis of the responses to vibration from the isolated elasmobranch labyrinth. A contribution to the problem of the evolution of hearing in the vertebrates. J. Physiol., 114: 471-489.

————, and A. Sand, 1940a. The mechanism of the semicircular canal. A study of the responses of single-fibre preparations to angular accelerations and to rotation at constant speed. Proc. Roy Soc. London, B: 256-275.

————, and ————, 1940b. The individual and integrated activity of the semicircular canals of the elasmobranch labyrinth. J. Physiol., 99: 89-101.

Marler, P. and W.J. Hamilton III, 1966. Mechanisms of Animal Behavior. Wiley and Sons, N.Y. 771 pp.

Mathewson, R.F., and E.S. Hodgson, 1972. Klinotaxis and rheotaxis in orientation of sharks toward chemical stimuli. Comp. Biochem. Physiol. 42A: 79-84.

Morey, R.L., 1973. Evaluation of long term sea effects on mooring line components. Massachusetts Institute of Technology Report E-2748, 75 pp.

Murray, R.W., 1974. The ampullae of Lorenzini. IN: A. Fessard (Ed.), Handbook of Sensory Physiology, Vol III/3: 125-146. Springer-Verlag.

Myrberg, A.A., Jr., 1969. Attraction of free-ranging sharks by acoustic signals. Proc. Gulf and Carib. Fish. Inst., p. 135.

————, 1972a.   Ethology of the bicolor damselfish, <u>Eupomacentrus partitus</u> (Pisces, Pomacentridae): a comparative analysis of laboratory and field behavior.   Anim. Behav. Monogr., 5: 197-283.

————, 1972b.   Using sound to influence the behavior of free-ranging marine animals.   pp. 435-468, <u>IN</u>: H.E. Winn and B.L. Olla (Eds.), Behavior of Marine Animals - Current Perspectives in Research, Vol. 2.   Plenum Press, N.Y.

————, 1973.   Underwater television - a tool for the marine biologist. Bull. Mar. Sci., 23(4): 824-836.

————, 1974.   The behavior and sensory physiology of sharks.   Ann. Rept. to ONR, Contract N00014-67-A-0201-0008, 17 pp.

————, and S.H. Gruber, 1974.   The behavior of the bonnethead shark, <u>Sphyrna</u> <u>tiburo</u>.   Copeia, (2): 358-374.

————, A. Banner and J.D. Richard, 1969a.   Shark attraction using a video-acoustic system.   Mar. Biol., 2:264-276.

————, ————, and ————, 1969b.   Bioacoustic studies on sharks.   ONR Tech. Report, Contract 4008(10).   16 pp.

————, S.J. Ha, S. Walewski and J.C. Banbury, 1972.   Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source.   Bull. Mar. Sci., 22(4): 926-949.

Naka, K.I. and P. Witkovsky, 1972.   Dogfish ganglion cell discharge resulting from extrinsic polarization of the horizontal cells.   J. Physiol. (London), <u>223</u>(2): 449-460.

Nelson, D.R. and S.H. Gruber, 1963.   Sharks: Attraction by low-frequency sounds.   Science, 142(3594): 975-977.

————, and R.H. Johnson, 1970.   Diel activity rhythms in the nocturnal, bottom dwelling sharks, <u>Heterodontus</u> <u>francisci</u> and <u>Cephaloscyllium</u> <u>ventriosum</u>.   Copeia, (4): 732-739.

————, and R.H. Johnson, 1972.   Acoustic attraction of Pacific reef sharks; effect of pulse intermittency and variability.   Comp. Biochem. Physiol., 42A: 85-95.

————, ————, and L.G. Waldrop, 1969.   Responses in Bahamian sharks and grouper to low-frequency, pulsed sounds.   Bull. Southern Calif. Acad. Sci., 68: 131-137.

Obara, S. and M.V.L. Bennett, 1972.   Mode of operation of Ampullae of Lorenzini of the skate, <u>Raja</u>.   J. Gen. Physiol. 60: 534-557.

Okado, Y., M. Aoki, Y. Sato and H. Masai, 1969.   The brain patterns of sharks in relation to habit.   J. für Hirnforschung, 11: 347-365.

Olsen, A.M., 1953.   Tagging the school shark, <u>Galeorhinus</u> <u>australis</u> (Macleay) (Carcharhinidae) in Southeastern Australian waters.   Aust. J. Mar.

Freshwater Res., 4(1): 95-104.

————, 1954. The biology, migration, and growth rate of the school shark, Galeorhinus australis (Macleay) (Carcharhinidae) in Southeastern Australian waters. Austral. J. Mar. Freshwater Res. 5: 353-410.

Onada, N. and Y. Katsuki, 1972. Chemoreception of the lateral-line organ of an aquatic amphibian, Xenopus laevis. Jap. Jour. Physiol., 22: 87-102.

Parker, G.H., 1910. Olfactory reactions in fishes. J. Exp. Zool. 8: 535-542.

————, 1922. Smell, Taste, and Allied Senses in the Vertebrates. J.P. Linnincott Company, Philadelphia, Penn.

————, and R.E. Sheldon, 1913. The sense of smell in fishes. Bull. U.S. Bur. Fish. 32: 33-46.

Pavlov, D.S., 1962. Some data on sense of smell of nalima (Gaidropsarus mediterraneus L.) and its significance in searching for food. Vopr. Ikhtiol. 2: 361-366.

Preston, J.R., J.A. Hassell, and M.M. Epstein, 1973. Summary report on the development of shark-bite resistant plastic armor for deepsea buoy cables - Phase 1. Prepared by Battelle Columbus Laboratories for Woods Hole Oceanographic Institution, 26 pp plus Appendix.

Quiring, D.F., 1930. Development of the ear in Acanthias vulgaris. J. Morphol., 50: 259-274.

Randall, J.E., 1963. Dangerous sharks of the western Atlantic. IN: Sharks and Survival, P.W. Gilbert, (Ed.), D.C. Heath and Co., Boston, pp. 339-361.

————, 1967. Food habits of reef fishes of the West Indies. pp. 665-847. IN: T. Bayer (Ed.), Studies in Tropical Oceanogr., No. 5. Univ. of Miami.

Rauchbach, E. and I.K. Arenberg, 1972. Comparative scanning electron microscopic study of inner ear sensory hair cell regions of the lemon shark. 30th Ann. Proc. Electron Microscopy Soc. Amer. C.J. Arceneaux, (Ed.).

————, and ————, 1973. Experimental endolymphatic hydrops: scanning electron microscopic observations of the inner ear of the lemon shark. Revue de Laryngologie 95 (5-6): 193-208.

Richard, J.D., 1968. Fish attraction with pulsed, low-frequency sound. J. Fish. Res. Bd., Canada, 25: 1441-1452.

Ripley, W.E., 1946. The soupfin shark and the fishery. California Fish and Game, Fishery Bulletin, 64: 7-37.

Roberts, B.L., 1969a. The co-ordination of the rhythmical fin movements of dogfish. J. Mar. Biol. Assoc. U.K., 49: 357-425.

————, 1969b. The response of a proprioceptor to the undulatory movements
of dogfish. J. Exp. Biol., 51: 775-785.

————, 1972. Activity of lateral-line sense organs in swimming dogfish.
J. Exp. Biol., 56: 105-118.

————, and I.J. Russell, 1970. Efferent activity in the lateral-line
nerve of the dogfish. J. Physiol. 208: 37 pp.

————, and ————, 1972. The activity of lateral line efferent neurones in
stationary and swimming dogfish. J. Exp. Biol., 57: 435-448.

————, and K.P. Ryan, 1971. The fine structure of the lateral line sense
organs of dogfish. Proc. Royal Society of London; Series B, Biological
Sci. 179(1055): 157-169.

Rüdeberg, C., 1969. Light and electron microscopic studies on the pineal
organ of the dogfish, Scyliorhinus caniculus (L.) Z. Zellforsch., 96:
548-581.

Schnitzlein, H.N., 1964. Correlation of habit and structure in the fish
brain. Am. Zool., 4: 21-32.

Schone, H., 1973. Raumorientierung, begriffe und Mechanismen. Fortschritte
der Zoologie 21(2/3): 1-18.

Sheldon, R.E., 1911. The sense of smell in Selachians. J. Exp. Zool.
10: 51-61.

Springer, S., 1950. A revision of North American sharks allied to the
genus Carcharhinus. Am. Museum Novitates; No. 1451 pp 1-13.

————, 1960. Natural history of the sandbar shark Eulamia milberti. U.S.
Fish & Wildl. Serv., Fishery Bull., 178: iv + 38 pp.

————, 1963. Field observations on large sharks of the Florida-Caribbean
region. pp. 95-114, IN: P.W. Gilbert (Ed.), Sharks and Survival. D.C.
Heath, Boston.

————, 1967. Social organization of shark populations. pp. 149-174, IN:
P.W. Gilbert, R.F. Mathewson and D. Rall (Eds.), Sharks, Skates and
Rays. Johns Hopkins Press, Baltimore.

Standora, E.A., Jr., T.C. Sciarrotta, D. Ferrel, H.C. Carter and D.R. Nelson,
1972. Development of a multi-channel, ultrasonic telemetry system for
the study of shark behavior at sea. ONR Tech. Rept. 5, Contract 00014-
68-C-0318, 69 pp.

Starkey, R.J., Jr., 1974. Vulnerability of Mooring and Submarine Cables to
attack by fish and other marine organisms. General Electric Technical
Information Series.

Stell, W.K., 1973. Structure and morphologic relations of rods and cones
in the retina of the spiny dogfish Squalus. Comp. Biochem. Physiol.
42A(1): 141-151.

Stimson, P.B. and B. Prindle, 1967. Armoring of synthetic-fiber deep-sea mooring lines in the vicinity of Bermuda. Woods Hole Oceanographic Institution Report WHOI-67-58, 7 pp.

Strasburg, D.W., 1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. U.S. Fish and Wildlife Service Fishery Bulletin 138, vol. 58, pp 335-361.

Suda, A., 1953. Ecological study on the blue shark. Contributions of Nankai Regional Fisheries Laboratory, no. 26. In Japanese with English captions.

Tamura, T. and H. Niwa, 1967. Spectral sensitivity and color vision of fish as indicated by S-potential. Comp. Biochem. Physiol., 22: 745-754.

Teichmann, H., and R. Teichmann, 1959. Untersuchungen über den Geruchssinn der Haifische. Pubbl. Stazione Zool. Napoli 31(1): 76-81.

Templeman, W., 1944. The life-history of the spiny dogfish (Squalus acanthias) and the vitamin A values of dogfish oil. Newfoundl. Dept. Nat. Res. Bull. (Fisheries), no. 15: 102 pp.

Tester, A.L., 1963. Olfaction, gustatation and the common chemical sense in sharks. pp 255-282, IN: P.W. Gilbert (Ed.), Sharks and Survival, D.C. Heath, Boston.

————, 1969. Cooperative shark research and control program. Final rept. 1967-1969. Univ. of Hawaii, Honolulu. 47 pp.

————, and S. Kato, 1966. Visual target discrimination in blacktip sharks (Carcharhinus melanopterus) and grey sharks (C. menisorrah). Pac. Sci., 20(4): 461-471.

————, and J.I. Kendall, 1967. Innervation of free and canal neuromasts in the sharks Carcharhinus menisorrah and Sphyrna lewini. IN: Lateral Line Detectors.

————, and ————, 1969. Morphology of the lateralis canal system in the shark genus Carcharhinus. Pac. Sci. 23(1): 1-16.

————, ————, and W.B. Milisen, 1972. Morphology of the ear of the shark genus Carcharhinus, with particular reference to the macula neglecta. Pac. Sci. 26(3): 264-274.

————, and G.J. Nelson, 1967. Free neuromasts (pit organs) in sharks. pp. 503-531, IN: P.W. Gilbert, R.F. Mathewson and D. Rall (Eds.), Sharks, Skates and Rays. Johns Hopkins Press, Baltimore, MD.

————, ————, and C.I. Daniels, 1968. Test of NUWC shark attack deterrent device, NUWC-TP-53. Naval Undersea Center, San Diego. 46 pp.

Tinbergen, N., 1952. The Study of Instinct. Oxford University Press, London, 228 pp.

Tuge, H., K. Uchinashi and H. Shimamura, 1968. An Atlas of the Brains of Fishes of Japan. Tsukiji Shokan Publ. Co., Tokyo.

Turner, H.J., Jr., 1965. Some characteristics of "fishbite" damage on deep sea mooring lines. Woods Hole Oceanographic Institution Report, WHOI-65-22, 9 pp.

————, and B. Prindle, 1967. The vertical distribution of fishbites on deep-sea mooring lines in the vicinity of Bermuda. Woods Hole Oceanographic Institution Report WHOI-72-75, pp.

Walden, R.G. and N.N. Panicker, 1973. Performance analysis of Woods Hole taut moorings. Woods Hole Oceanographic Institution Report WHOI-73-31, 47 pp.

Waltman, S., 1966. L. Electric properties of the ampullary canals of Lorenzini in Raia. II. Fine structure of the ampullary canals of Lorenzini in Raia. Acta Physiologia Scandinavica 66 Supp. 264:1-59.

Wang, C.J., 1969. The eye of fishes with special reference to pigment migration. Dissertation, Cornell University; 291 pp.

Waterman, T.H., 1973. Responses to polarized light: animals. Biology Data Book, Second Edition, IN: P.L. Altman and D.S. Dittmar (Eds.), Federation of American Societies for Experimental Biology, Bethesda, Maryland. 1272-1289 pp.

Wright, B., 1948. Releasers of attack behavior patterns in shark and barracuda. J. Wildlf. Magnt., 12(2): 117-123.

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