

Shark Behavior

Understanding Shark Behavior

Arthur A. Myrberg, Jr.
 Division of Biology and Living Resources
 Rosenstiel School of Marine and Atmospheric Science
 University of Miami
 4600 Rickenbacker Causeway
 Miami, FL 33149

Abstract: Of the many activities performed by animals, none draws more rapid and profound attention than predation. And, understandably, such an activity reaches its ultimate level when a given predator-prey relationship can force or has forced humans from their accustomed role as predators into the role of prey—in the sense of either self-survival or the survival of resources. One such relationship, probably better known than any other due often to sensationalism by the media, is that involving sharks. Although most of these predators are small and innocuous to humans, the simple word—**shark**—in any context often conjures up a vision of a marine monster driven as a machine solely by primeval instincts that serve only to reinforce its insatiable appetite. Such a perception is not only false, but its continued presence serves to hinder serious scientific inquiry. Unfortunately, it often occurs from a fatalistic bias that is based on information garnered through far more expedient means than that demanded by the scientific method. Ideas and feelings from knowledgeable persons can, at times, provide important speculations, but we must remember that such thoughts can in no way replace objective facts.

THE SHARK HAZARD PROBLEM

Shark lore has existed throughout history whenever sharks have directly influenced human endeavor. Tropical islanders, for example, have long been acquainted with the habits and movements of such animals so that they can predict where these predators may occur inshore. Interest in sharks was minimal, however, in the great population centers of the world even through the first third of the twentieth century. Human-shark interactions were not only rarely and sporadically reported over great expanses of coastlines but relatively little public news media existed to disseminate information rapidly to outlying regions. Ignorance about the ways of sharks extended even to supposedly knowledgeable scientists who questioned the impact of sharks upon any human interest.

Such blissful ignorance remained the norm except for one group of individuals, the coastal fishermen. Their interest in sharks was based not

only on reduced catches due to such predators but also on the reasonable prices paid for sharks in certain regions. That interest, in turn, generated (between the early 1920s and mid-1960s) sporadic investigations by fishery scientists from several countries, e.g. the United States, England, and Australia (Holden 1977). These studies provided important information on catch statistics for various commercially important species and numerous intriguing facts and ideas about the behavioral activities of the sharks concerned (e.g. rhythms of activities, migratory habits, sexual and size segregation of schools and aggregations). Many of these reports, as well as the personal knowledge gained as a shark fisherman and a shark fishery manager, have been admirably summarized by Stuart Springer (1967). This body of knowledge provided the initial insight into the importance of sharks as highly successful predators in marine ecosystems and a group highly vulnerable to human exploitation.

Progress in understanding the behavior of sharks accelerated following the establishment, in 1958, of the Shark Research Panel by the American Institute of Biological Sciences (Gilbert 1960). The Panel was concerned with all aspects of the biology of elasmobranch fishes, but emphasis was directed at the shark hazard problem. Although the problem had been long recognized in certain regions of the world prior to the Second World War (e.g. Eastern Australia, South Africa), little concern existed elsewhere until that war brought about global use of the world's oceans. The shark problem continued despite the end to hostilities because of the ever increasing awareness of the importance of the oceans for recreational purposes.

THE REMARKABLE SENSORY WORLD OF SHARKS

Information concerning the predictability and control of shark behavior was clearly central to solving or, at least, reducing the hazard problem. However, the lack of suitable laboratory facilities and the near impossibility of conducting field studies on such swift and wide-ranging animals with the equipment available at the time caused behavioral scientists to direct their attention at the sensory systems that influenced the behavior of these predators. The first major paper on the behavior of sharks actually centered on these systems (Gilbert 1962). These investigations, the majority of which were conducted between the mid-1950s and 1970s, demonstrated not only the high sensitivity of sharks for environmental stimuli of all sorts, but also limitations of the systems as well.

Chemoreception

Sharks and the other elasmobranchs have long been known to possess a particularly acute sense of smell (Tester 1963). In fact, the lemon shark (Negaprion brevirostris) and the nurse shark (Ginglymostoma cirratum) have been shown to be extremely sensitive (1 part/million) to many chemical compounds (particularly electrolytes, amino acids and amines) and can clearly distinguish waters of different salinity (Hodgson and Mathewson 1978). If coastal species, in general, possess this latter capability, it might be an important mechanism for the differential movements and the geographical

segregation often noted for different elements of populations at specific times of the year (e.g. nursery areas). Another important phenomenon was shown by the catshark (Scyliorhinus stellaris)--chemically-based recognition of tons-specific (Kleerekoper 1978). This, in turn, could constitute a mechanism for sexual segregation, as reported so often for sharks in fishery studies. Such a mechanism has been recently reiterated after direct observations of male grey reef sharks Carcharhinus amblyrhynchos moving along apparent odor trails produced by females of the same species (McKibben and Nelson, in press).

Vision

Physiological and anatomical studies of the visual systems of numerous species have shown, contrary to popular belief, that these systems are highly developed in many sharks (Gruber and Cohen 1978). The high sensitivity recorded for the lemon shark, for example (Fig. 1), and the rod-packed retinas of all the species examined point to the importance of night time (including twilight) habits for these animals. This has been corroborated repeatedly in both laboratory and field studies and particularly those involving field tracking by telemetry. In the latter cases, subjects predictably moved to specific areas apparently for purposes of feeding.

There is no question, however, that sharks will feed during the day if appropriately motivated and if given the opportunity. They are apparently highly attracted to brightly colored objects. McFadden and Johnson (in Gruber and Cohen 1978), for example, reported that survival gear painted yellow was highly attractive to free-ranging sharks while the same gear painted black was ignored. This does stand in contrast, however, to the results of a study reported by Gruber and Cohen (1978) in which silky sharks C. falciformis avoided bait on a fluorescent orange globe, but readily removed bait from a black globe and less frequently from a white globe. Meaningful field studies of visual ability and preference are extremely difficult to accomplish based on the variables which must be controlled. Nevertheless, such studies with sharks are badly needed to establish directly the importance of the visual modality to these animals.

Mechanoreception

Studies of mechanoreception by various elasmobranchs have included descriptions of at least two specialized nerve terminals located in the deep layers of the skin and in certain muscle masses as well as the sensory hair cells (neuromasts) of the extensive lateral line and those scattered over the head and body (free neuromasts or 'pit organs') and the inner ear. The neurophysiological and psychophysical bases of vibration sensitivity have also been examined in several species (Popper and Fay 1977; Roberts 1978; Corwin 1981). Present knowledge is still unclear as to the function of the lateral line and the free neuromasts, but there is no doubt that the neuromasts of both systems are sensitive to water movements (Roberts 1972). The systems probably play some role in coordination of swimming. This explanation is not totally satisfactory, however, as these fishes can swim normally even after

the appropriate nerves have been cut (Boord and Campbell 1977). Those species of sharks studied have a hearing range from 10 Hz (= 10 cycles per second) to about 800 Hz (extending from about 1.5 octaves below the fundamental frequency of the lowest key to that of G5 below high C on the piano, see Fig. 2). Since adult human hearing extends from about 25 Hz to around 16000 Hz, humans hear many sounds that sharks cannot hear. On the other hand, sharks can detect certain very low frequencies that humans cannot (Myrberg 1978). Numerous field investigations have demonstrated that sharks can rapidly move to specific sources of vibration (table 1). The animals usually approach the sound source between 30 sec and 1 min after the onset of transmission from distances beyond the limit of visibility (20 to 30 m in clear water). Such rapid reactions explain why nearby sharks can appear from any direction often shortly after a speared or hooked fish begins struggling. Low frequency vibrations which are irregularly pulsed are also produced by the strumming of cables and set lines and by humans when struggling in the water. Such actions are reasonable sources of attractive sounds to nearby sharks. It is equally important to realize, however, that another element of any attractive sound is its loudness or sound level. Probably most natural sounds of interest to sharks are produced such that no energy exists above the threshold of detection at distances much beyond 25-30 m. However, synthetic sources having exceptionally loud levels may well attract such predators from distances far beyond that limit. Sounds can also cause sharks to withdraw rapidly from a sound source under specific circumstances (Eibl-Eibesfeldt and Hass 1959; Myrberg et al. 1978; Klimley and Myrberg 1979). Although there are clear species differences regarding levels of arousal at such times and also differences based on individual size, members of at least three species (the lemon shark, the silky shark, *C. falciformis*, the oceanic whitetip shark, *C. longimanus*) have rapidly withdrawn from a nearby sound source when confronted with a sudden increase (20 dB or more) in the level of transmission. This response seems highly adaptive, since a successful predator when rapidly approaching a sound source might well change its behavior if the sound suddenly changes unexpectedly, i.e. the expected flow of information changes. Sharks cannot simply stop swimming and so withdrawal appears to be the appropriate response. Unfortunately, the level of such response decreases as the size of the predator increases. Also, sharks rapidly learn to ignore sudden increases in sound level. Nevertheless, understanding that qualitatively similar sound can produce both approach and withdrawal explains apparent contradictions in the literature where in one situation animals rapidly approached a source, while in another, they withdrew.

Electroreception

Electroreception constitutes still another dimension of the sensory world of sharks, but one that we cannot easily identify with, since humans possess no comparable system. When one considers the behavioral implications of the electrosensory system in elasmobranchs, one soon realizes that these border on the incredible. The significance of the electrical sensitivity of sharks and their relatives first became evident when members of the group were observed to "home in" on bioelectrical fields emanating from prey (Kalmijn 1966, 1974). Threshold gradients measuring 0.01 V/cm at the time have now reached

0.005 V/cm (Kalmijn 1981). Such sensitivity is unique in the animal kingdom and there can be no doubt these weak electrical fields have great meaning to these predators. The ampullae of Lorenzini located on the head of all elasmobranchs constitute the receptors for this remarkable system (Fig. 3) (Dijkgraaf and Kalmijn 1963; Murray 1974). Field experiments on the shallow water dogfish (Mustelus canis), the oceanic blue shark, (Prionace glauca) and the swell shark (Cephaloscyllium ventriosum) have all demonstrated that these animals indeed detect and take prey by the use of electroreception (Kalmijn 1978, Heyer et al. 1981; Tricas 1982). Fortunately for the prey of sharks, the magnitudes of bioelectrical fields fall off very steeply over distance and so even in the case of a human body, the gradient is below threshold sensitivity beyond a distance of about 1 m. Nevertheless, indications exist that attacks on humans and their equipment may be elicited or guided by electrical fields that resemble those of natural prey. Recent experiments conducted on the stingray (Dasyatis sabina) by Blonder (1985) have shown that although members of the species are electroreceptive, they did not discriminate between prey (shrimp--Penaeus sp.) and non-prey (tunicate--Molgula sp.) solely on the basis of emitted bioelectric fields. Also, galvanic currents produced by the close association of dissimilar metals are clearly within the sensitivity range of elasmobranch electroreceptors. Since testing has, as yet, not involved such currents, one cannot predict the nature of the response in their presence; they may inhibit attacks by providing unexpected change (see above) or they may even constitute "supernormal" stimuli. Only future research will provide us with the answer.

Other tiny voltage gradients, well within the dynamic range of elasmobranch electroreceptors, also exist in the world's oceans. Ocean currents, by flowing through the earth's magnetic field, create electrical fields through electromagnetic induction as does any body for that matter, e.g. a shark moving at a speed of 2 cm/sec (Fig. 4). Since such fields possess voltage gradients ranging from 0.05 to 0.5 V/cm and they are dependent on the direction of movement, sharks have all that is necessary to endow them with an electromagnetic compass sense. Accordingly, Kalmijn (1978, 1984), after initiating preliminary observations on the leopard shark (Triakis semifasciata), completed a series of exacting experiments which showed that the stingray (Urolophus halleri) was fully capable of geomagnetic orientation. Whenever consideration is given to long distance migrations, one often considers the possibility that animals are somehow directing their attention to the earth's magnetic field. Sharks certainly can attend to that field and we now know something about the mechanism involved. It is at least reasonable to assume that the long travels that have been documented for many species of sharks by John Casey and his co-workers over the years (The shark tagger...summaries. National Marine Fisheries Service, Narragansett, Rhode Island.) are the result not of lost and aimlessly wandering animals, but rather of well-oriented animals moving to other regions for unknown reasons. Actually, the well known migrations of so many elasmobranchs, as well as their often uncanny homing abilities (e.g. McLaughlin and O'Gower 1971, Klimley 1981) may well have as their basis the possession of a highly tuned geomagnetic compass--one component of their sophisticated electroreception system.

Learning Abilities

Studies of the sensory biology of elasmobranchs have provided great insight into the behavioral actions of such animals. They have also supplied us with direct evidence of learning capability. Psychophysical experiments have almost invariably employed learning procedures to determine threshold levels of sensitivity or discrimination. The success of such studies attests to the fact that elasmobranchs can rapidly learn a wide variety of tasks (Figs. 5 and 6) (Clark 1959; Wright and Jackson 1964; Aronson et al. 1967; Banner 1967; Gruber and Schneiderman 1975; Graeber and Ebbesson 1972). Habituation, a common form of simple learning, also has been shown by sharks during field tests of sensory function (figure 7) (e.g. Myrberg et al. 1969, 1978; Nelson et al. 1969; Nelson and Johnson 1972). No longer can such animals be viewed as creatures of primitive instincts with little or no capacity to learn through experience. Such knowledge aids in explaining certain behavioral differences often observed in the field, for example, those between juvenile and adult sharks. Juveniles are almost invariably more aggressive than adults. Their activity levels are also often higher and their actions often more erratic and unpredictable than those by adults of the same species. Reasons for such differences are unknown, but their nature reminds one of those observed in the young animals of many other species, in which behavioral modifications occur through learning experiences as individuals grow to maturity.

SHARKS IN CAPTIVITY

Clark (1963), while reviewing the distribution and longevity of sharks in captivity around the world, reported that more than 50 species had been held in aquaria for at least up to several months. Nevertheless, until recently only a relatively few hardy benthic species consistently survived under such conditions for long periods of time (e.g. more than one year). These include several hornsharks (*Heterodontus* spp.), certain leopard (*Triakis* spp.) and catsharks (*Scylliorhinus* spp.), the sand tiger shark (*Odontaspis taurus*) and the western Atlantic nurse shark (*Ginglymostoma cirratum*). Despite these successes, the consensus has been that most sharks are not only difficult to collect and transport but, once in captivity, they often refuse to feed and die shortly thereafter (Essapian 1962; Clark 1963; Gruber and Keyes 1981). Severe haematological changes can readily occur in sharks during and after capture and consequently critical research data may actually be based on abnormal animals (Martini 1974, 1978). Fortunately, the knowledge that has been gained over the last 15 years has provided ever greater success in maintaining captive sharks, including the larger and more pelagic species (e.g. those of the genus *Carcharhinus*). Proven techniques for transporting sharks to distant locations are now available, as are the means for maintaining high water quality during captivity. The requirement that sufficient space be provided for periods of unimpeded movement, prophylaxis (Keyes 1977; Herwig 1979), and the use of dietary supplements to correct deficiencies brought about by using certain food (table 2) (Gruber and Keyes 1981) are just a few of the practices that are now employed to maintain subjects at a level of health comparable to that found under natural conditions.

Although knowledge about the factors that control feeding behavior could perhaps be considered most critical for the health of sharks held in captivity, surprisingly few studies have been directed at this important field. Also, food is often used as the reinforcer for appropriate behavior in psychophysical tests of sensory capabilities. Such testing relies on the experimental control of motivation through an understanding of the ad libitum rate of food intake. Yet, until recently, little or nothing was known about ad libitum feeding by sharks under uncontrolled conditions, let alone under controlled conditions. Graeber (1974), using outdoor pools, suggested a 15-day peak in food intake for juvenile lemon sharks, while Longval et al. (1982), providing similar animals with a recirculating water system with precise control over light, temperature, salinity, and flow rate, found a consistent 3.5 to 4 day peak in food intake with additional but uncertain peaks at 7 and 28 days (lunar periodicity?). The four-day peak was generally preceded by a gradual 2-3 day rise in food intake and followed by a precipitous drop in intake. This suggested that after an animal is sated, it takes a few days for the appetite to become reestablished. Although the results of the two studies differ, they both clearly show that food deprivation and satiation are important in the food intake behavior of sharks. These and other studies (e.g. Graeber and Ebbesson 1972) leave no doubt that Springer (1967) wrongly believed that hunger motivation does not exist in sharks. It certainly does exist and it has been a most useful tool in discovering new facts about these animals.

The natural feeding behavior of sharks rarely has been observed, the one significant experimental study of such behavior in free-ranging sharks being that by Hobson (1963). Perhaps such rare occurrences of feeding during the day point to the period of darkness (including twilight) as the major time for that activity by most of these predators. If true, innovative techniques will be required to examine the behavior. Such rhythmic activity, if demonstrated, would not come as a surprise, since sharks are certainly no exception when it comes to demonstrating the universality of rhythms in biological systems (Fig. 8) (e.g. Hobson 1968; Standorra et al. 1972; Klimley and Nelson 1984). Controlled studies on locomotor rhythms in elasmobranchs have been confined, however, solely to the hornshark, (Heterodontus francisci) and the swellshark (Cephaloscyllium ventriosum) (Nelson and Johnson 1970; Finstad and Nelson 1975). In both cases, clear circadian rhythms with a strong endogenous component were evident (Fig. 9). Various diel rhythms as well as seasonal rhythms are also readily apparent from many studies and they certainly aid in predicting at least certain behavioral events. Although the significance of such rhythms remains unclear in many cases, the diel rhythms in locomotory activity appear directly related to feeding. And it is this activity that often is referred to in cases of human-shark interactions (Zahuranec 1975).

HUMAN-SHARK INTERACTIONS

Much has been written about the dangers posed to humans by sharks, with large sections of books being devoted to the subject (Gilbert 1963; Davies 1964; Budker 1971; Baldrige 1974; Ellis 1975; Hass and Eibl-Eibesfeldt 1977;

Walleit 1978; Sibley et al. 1985). A major assumption running through much of the early literature held that shark attacks on humans are motivated by hunger. Baldrige and Williams (1969) were the first to question this assumption based on a peculiar finding that consistently appeared in many of the cases listed in the International Shark Attack File (Baldrige, 1974). These cases involved apparent bite and run or slash-type wounds seemingly to inflict damage but not to remove flesh. In numerous cases, the resulting wounds, though severe, showed no loss of flesh. Often such attacks appeared as if only the teeth of the upper jaw made contact with the victim. The facts seemed inconsistent with the idea that hunger was the underlying motivation for the attack. As Baldrige and Williams pointed out, "If hunger motivated (such) attacks, then the shark or sharks involved were certainly inefficient feeders."

Other instances of attack apparently motivated by factors other than feeding have since come to light following the bold speculation by Baldrige and Williams. These particular cases have all involved the gray reef shark (*C. amblyrhynchos*). They are unique in that a highly stereotyped motor pattern termed "the exaggerated swimming display," preceded the attacks (Fig. 10) (instances are known, however, where no such display was seen prior to attack). The display, apparently signifying threat, varied in intensity depending upon the specific situation facing the animal at the time. Maximum intensity was shown when a shark was closely approached and especially if it was cornered, i.e. its avenues of escape were cut off. (Johnson and Nelson 1973; Nelson et al. in press). The display, though not seen during periods of feeding, resembles an exaggerated bite and it appears to have been derived from the feeding act. Although only the gray reef shark performs the full display, Hobson (1964) noted the early stages of the display in Galapagos shark (*C. galapagensis*), while Myrberg and Gruber (1974) noted a similar but far less intense display (the hunch) by captive bonnethead sharks (*Sphyrna tiburo*) (Fig. 11) and blacknose sharks (*C. acronotus*) and by free-ranging silky sharks (*C. falciformis*). In all instances, the display was seen in potentially agonistic situations, such as when a new shark was suddenly placed in the near vicinity of a group of residents (the first two cases) or when a diver approached individuals shortly after entering the water (the third case).

Since these displays have been found to be neither site-dependent nor related to feeding activity, their significance remains unclear. However, I do remember once reading a recommendation to swim rapidly toward an approaching shark, since such behavior on the part of potential prey (me) would likely confuse the onrushing predator (the shark), causing it to break off the attack and move away. Apparently the author who recommended such an action had not attempted such a maneuver at a gray reef shark. Further studies are needed to clarify the function of such displays, but the danger that exists for divers making direct observations of such actions forces extreme caution and innovative techniques to prevent harm to personnel. That gray reef sharks are so aggressive despite their relatively small size (usually 1 to 1.5 m long) stands in contrast to that observed in other species

both in waters where grays abound as well as elsewhere (Allee and Dickinson 1954; Hobson 1963; Myrberg and Gruber 1974; Clark 1981; Nelson 1981). One rarely sees overt aggression such as attacks, chasing or apparent threat. Even during active feeding, including the infamous "frenzies," sharks seem interested only in getting the food rather than competing with one another, such that access to the desired item(s) is earned by winning an aggressive interaction. Aggressive behavior could be expected if sharks, such as the gray reef, defended exclusive areas. No evidence exists, however, that members of any species are territorial. Perhaps such behavior is due to individuals attempting to maintain a position of relative dominance in specific areas. This is suggested by recent evidence that female gray reef sharks show elevated aggression and exaggerated swimming displays in pupping areas. However, males and females, far distant from such areas, show the same behavior. Perhaps such animals are simply defending themselves from possible predation by large moving objects in their vicinity. Defense of such a "personal sphere" has been suggested by several authors. The story appears even more complex, however. Although the display is extremely difficult to elicit in feeding situations, Johnson (1978) has observed it in a feeding interaction between a moray and an apparently frustrated gray reef shark. Thus, considering all the evidence to date, the heightened aggression in such sharks seems to be caused by several motivating factors, including competition and antipredation. Since gray reef sharks are often found in packs, feed opportunistically, and are known to feed on their own kind, any mechanism that can increase fitness through competitive and antipredatory tactics must have high selective advantage.

THE SOCIAL BEHAVIOR OF SHARKS

There exists for many the view that the typical shark moves as a solitary hunter throughout its domain. Although this is either true or probable for certain large species (e.g. basking, white and tiger sharks), many others move in groups. One of the most spectacular instances of such behavior is that of the scalloped hammerhead (*Sphyrna lewini*). Populations of this species form daytime schools offshore of several islands and seamounts in the Sea of Cortez (Klimley and Nelson 1981, 1984; Klimley 1985). These predators apparently possess mechanisms that provide them the means to reach and then remain at specific locations within their extensive feeding ranges during relatively inactive non-feeding periods. Recent evidence gained from the movements of lemon sharks in the waters of Bimini, Bahamas, also suggests the existence of similar but less spectacular refuging areas (Gruber 1982). That sharks, such as hammerheads, can somehow pinpoint specific geographical locations in waters of great depth seems astounding, but considering their elaborate sensory capacities, such a feat should not be surprising.

It is axiomatic that when animals congregate in groups, social interactions will follow. Unfortunately, relatively little information exists about the social behavior of sharks, since few instances of direct observation have been made under conditions in which such behavior might be expected. Instances of interspecific, social hierarchial associations have been

reported, but one must remember that such cases of apparent dominant-subordinate relationships may be reflecting subtle instances of antipredatory behavior on the part of the subordinates. Intraspecific social hierarchies have also been reported (Allee and Dickinson 1954; Myrberg and Gruber 1974) and in at least one instance (bonnethead sharks), females tended to shy away from males regardless of size (Fig. 12). Reasons for such shyness are unclear, but based on the physical damage that males apparently inflict upon females during the mating period, it is little wonder that females give them wide berth. The social hierarchies investigated to date have been shown to be size-dependent. Although this might suggest again that antipredatory mechanisms are operating, such an organization is also typical of those hierarchies examined thus far in other fishes, regardless of their feeding habits.

One might actually question why adult sharks would congregate in packs or schools at any time. One can understand why small sharks might do so, since a relatively tight aggregation would reduce the chance of predation upon any given individual. Such an argument wanes in importance, however, as individuals reach a size such that there exists a low risk of predation. Perhaps the answer rests with the fact that food often occurs in widely separated patches and an optimal strategy for any given individual might be to associate with others so that it can take advantage of the extended sensory capabilities of the group. Such an advantage could be extended even further if social facilitation occurs (i.e. enhancement of a given action by one individual in the presence of others showing the same action) and such a phenomenon is well known in sharks (Springer 1967; Myrberg et al. 1969, 1972; Johnson 1978).

The ultimate social activity in sexually reproducing animals constitutes mating behavior. The relative scarcity of observations of such behavior in sharks suggests that it occurs primarily during the nocturnal period. The few cases which have been observed during daylight show that despite the widely separate taxa involved, similarities exist among the behavioral actions shown by the pairs and in the orientation of members one to another (Scyliorhinus canicula Bolau 1881, Schensky, in Gilbert and Heath 1972; S. torazame Uchida 1982; Heterodontus francisci Dempster and Herald 1961; Carcharhinus melanopterus Johnson and Nelson 1978; Ginglymostoma cirratum Klimley 1980 (Fig. 13); Triaenodon obesus Uchida 1982; Tricas and LeFeuvre 1985). All instances of copulation have occurred on the substrate, save that reported by Clark (1963) for the lemon shark (N. brevirostris) (a presumed copulation). In most instances, the male maintains a bite-hold on one of the pectoral fins of the female during actual copulation, no doubt to maintain relatively consistent orientation as regards the placement and maintenance of the clasper (the intromittant organ) in the cloaca. Fresh wounds, often found on the dorsal surfaces of adult females, also strongly suggest that pre-mating activity includes harassment by males (Springer 1967; Clark 1981). Perhaps it is for that particular reason in blue sharks (Prionace glauca) the hides of mature females are more than twice as thick as those of males of the same size (Pratt, in Clark 1981).

THE BEHAVIORAL ECOLOGY OF SHARKS

One of the major ways to understand the activities of any animal is to understand its role in the ecology and the bio-economics of the community of which it is a part. This is particularly the case for predators, since they can exact both stabilizing and oscillatory influences on ecosystem dynamics. Thus, it is difficult to comprehend that except for ecologically related investigations conducted on catch-statistics by several federally directed fishery efforts, few detailed ecological studies of sharks exist (Clarke 1971; Waas 1971; O'Gower and Nash 1978; Gruber 1982). This is likely due to major limitations facing such studies. Many species are not only relatively rare in most areas, but are wide-ranging in their often turbid habitats, shy (in most instances) and fragile (re: capture and transport). Ways must be found to overcome these problems before important advancements can be made in the ecology and the behavioral ecology of these animals. One such way is the use of ultrasonic underwater telemetry (Thorson 1971; Nelson 1978; Gruber 1982; McKibbin and Nelson in press). The excellent information that already has been gathered about the activities of selected species points to a most profitable future for any behavioral or ecological study employing such instrumentation. Other tools include small 1- or 2-man submersibles (Nelson 1981), underwater television (Myrberg 1973), stereophotography (Klimley 1981), specially designed boats (Gruber 1982) and even tethered balloons (Ross Robertson, pers. comm.). Often such tools require a reasonable financial base for the research programs of which they are a part, but the rewards gained by their use can far outweigh their costs.

Analyses of the structural components of behavior, i.e. the stereotyped action patterns shown by animals in general, have provided insight into the underlying causes for various activities of sharks (Johnson and Nelson 1973; Barlow 1974; Myrberg and Gruber 1974; Tricas 1982, 1985; Klimley 1985). The methodologies and ideas inspired by the fields of ethology and behavioral ecology will surely provide continued growth of our knowledge about not only the causes of shark behavior but also about the function and evolution of the behavior. This is particularly the case when considering one major void in our knowledge about shark behavior. We are well aware that sharks can intercept a variety of signs (chemical, acoustical, electrical) from their prey and use them for their own purpose. However, we are totally ignorant about the ways that sharks use signals to communicate with one another. Is it possible that certain sharks might even attempt to communicate with their prey, using deceptive signals (see Myrberg 1981 and below)? If we knew something about the communication processes used by those predators, it might be just the means for controlling or at least directing important aspects of their behavior.

Body markings for example, are often used throughout the animal kingdom for purposes of communication (Sebeok 1977). Is it possible that the distinctive body markings of shark are used for such purposes? In certain cases, such markings may well be used as camouflage (e.g. disruptive coloration). However, many sharks show specific regions of pigmentation, such

as along the edges and the tips of fins, that do not suggest functional camouflage (Fig. 14). Do these marking patterns have a social function? Do they provide important cues for species recognition (see Bass 1978; Johnson 1978)? What other communicative functions might they serve?

As one of many who has dived among sharks, I have been intrigued by the variety of body markings shown by these animals. For the purpose of accelerating interest in this particular aspect of the behavioral ecology of sharks, I would like to advance an idea about the possible function for the white fin markings of one species, the oceanic whitetip shark C. longimanus (Fig. 15).

While conducting acoustical experiments on oceanic sharks over the deep waters of the Tongue of the Ocean, Bahamas, during the mid 1970s, we often encountered oceanic whitetips that had been attracted to underwater loudspeakers transmitting various sounds. After arrival, these sharks moved slowly, almost lethargically, about the area. Their movements appeared uncommonly effortless compared to the movements of other sharks that we had observed over the years. The slow movements were deceptive, however. Oceanic whitetips could move with astounding speed for distances exceeding 50 m. Rapid movements were seen in several instances, e.g. after biting the steel loudspeaker or immediately after a sudden, loud sound was transmitted from a nearby loudspeaker. Attaining such high speeds could explain, at least in part, something long known about this particular shark--their prey often include some of the fastest moving oceanic fishes (e.g. tunas, various scombroids, dolphinfish and even white marlin). It is highly likely, however, that this shark cannot simply overtake such rapid moving prey in a test of speed nor sneak up on them in the clear open waters. One hypothesis has already been advanced to answer this intriguing problem (Bullis 1961): oceanic whitetips move into the surface schools of small fishes at the time when these schools are being preyed upon by the larger high-speed fishes. As the latter leap about feeding on their prey, they literally jump into the open mouths of the sharks. Although the hypothesis is viable, I must admit skepticism based on the requirement that a shark must be precisely positioned at the end of the trajectory of a leaping fish to achieve capture.

My alternate hypothesis is based on a visual effect that I often experienced while observing oceanic whitetips as they ranged throughout the surveillance area. Upon questioning other divers at the time, they also confirmed the effect that I now relate. As long as such sharks remained close by, their form was unquestioned. However, as they moved to the limit of visibility, my eyes were constantly drawn to their white-tipped fins, with the concomitant result that the grayish, countershaded bodies became indistinct. Actually, the shark-form disappeared unless attention was riveted on it. Accordingly when that form became indistinct, attention became immediately focused on the white-tipped fins, clearly visible as three to five spots moving in close formation. Occasionally, when two whitetips moved closely together at such distances, a "school" of white spots was seen moving through the clear waters. The effect was particularly striking during periods of low

light when the spots stood out in far greater contrast than the darker body of the shark. Now comes the speculation--if the eyes of a human and those of several oceanic fishes are not too dissimilar as to general levels of sensitivity and acuity, the perceptual change that occurred (i.e. the white-tipped fins of a shark becoming a "school" of white spots) were considered, at a distance, to be a small school of appropriately sized prey, rapidly moving predaceous fishes might well move on a "bee-line" toward such "prey." Then, if such high-speed swimmers happened to reach a point where the sudden high-speed acceleration of the oceanic whitetip could overcome veering by the onrushing fish, the latter could become the unexpected prey of the "spots." I hypothesize that the above-mentioned scenario is true. The white spots of the oceanic whitetip shark might well be species-recognition marks. However, they appear also to possess another function as well--they are lures for attracting rapidly moving visual hunters into the near vicinity of their owners. Such a function explains also why the first dorsal and pectoral fins of the oceanic whitetip are so conspicuously large that they are often called "paddles." One way to improve the effectiveness of any lure is to increase its size so that it can be seen over a larger area. This would increase the probability of prey being attracted and thus provide the selective pressure necessary for increasing the size of the spots by increasing the size of the fins. One cannot disagree that the large pectoral "paddles" likely play an important role in the "gliding" movements of such sharks and that the large median dorsal fin likely adds stabilization to sudden, rapid forward movement (Weihs 1981). Nevertheless, apparently whatever forces initiated the increase in fin size, the spots benefited since their increasing size would lure prey from ever greater distances.

Thus, two hypotheses are now available to answer how oceanic whitetip sharks obtain their unlikely prey. Perhaps someone will come up with a truly neat experiment in the near future to test these and perhaps other hypotheses. Only by such means will this fascinating puzzle finally be answered.

FUNCTIONAL MORPHOLOGY OF THE SHARK BRAIN

Since we are now aware that sharks and their near relatives possess many of the attributes ascribed to the so-called "higher vertebrates," we, who study fish behavior, are pleased that yet another so-called "truth" about elasmobranchs has been recently debunked. Sharks and their relatives were long considered as primitive feeding machines. Thus, it was perhaps not unreasonable to accept the "fact" that such animals have pea-sized brains. Accordingly, when early anatomists looked at the brains of a few species, specifically those most commonly available, i.e. the spiny dogfish, Squalus acanthias (a member of the most primitive group of living sharks, the squalomorphs) and the spotted catshark, Scyliorhinus canicula (one of the most primitive members of the galeomorphs), they did indeed find small brains. Such results, plus typological thinking, resulted in the initiation and the perpetuation of the myth that all elasmobranchs had brains similar in size to these species.

We can thank Glen Northcutt and his associates for the demise of this myth (Northcutt 1977, 1978). They demonstrated in elegant fashion that many elasmobranchs possess brains fully comparable in size to those of many avian and mammalian species (Fig. 16). Although any elasmobranch might be "pleased" to have the true story finally be told, they, as a group, are now part of another fascinating problem—long known, but never solved. The allometric relationship between brain size and body size among vertebrates does reflect, in a rough sense, a phylogenetic sequence, but that relationship has no known biological significance (Gould 1966, 1971; Jerison 1973). Information provided by elasmobranchs could possibly aid in clearing up this mystery.

Those galeomorph species studied generally have a two-fold to six-fold increase in brain:body ratios over that shown by all squalomorphs examined thus far; and the most highly evolved galeomorphs possess the highest known ratios among sharks. In like fashion, among the batoids, the primitive rajiforms possess low brain:body ratios, while the more advanced myliobatiforms have far greater ratios. The latter even exceed those of any known shark (Fig. 17 and 18) (this may change as the sample size increases, G. Northcutt, pers. comm.). In conversation with Dr. Northcutt dealing with these facts, we considered the idea that the allometric relationship between brain size and body size is reflecting some process(es) related to metabolic activity. This provides a fascinating set of questions since differences in metabolic activity (or efficiency) are likely among different groups of elasmobranchs. For example, do egg-layers and placental types have different levels of metabolic activity and do these reflect differences in brain:body ratios? Do squalomorph and galeomorph sharks differ in metabolic rates? What about rajiform versus myliobatiforms? Is locomotor activity somehow reflected by the brain:body ratio? It will be astounding if any of these questions is answered by a simple yes or no, since the questions themselves are likely far too broad in scope. Nevertheless, the elasmobranchs seem to be a group that might well provide some extremely interesting answers to some long standing questions in biology.

CONCLUSIONS

Our knowledge about the behavior of sharks is still relatively sparse and it is based on information from precious few species. Yet, that knowledge is vastly greater than what was available only a few years ago. Many facts have replaced the speculations and myths that were so intimately associated with these animals for so many years. Fortunately, the field had a group of pioneering workers: Perry Gilbert, Albert Tester, David Davies, Otto Lowenstein, Sven Dijkgraaf, Stuart Springer, Leonard Schultz, Irenaus Eibl-Eibesfeldt, Eugenie Clark, Sidney Galler and others, whose interest and dedication provided the programs of research during the 1950s and 1960s that formed the groundwork for many of the studies mentioned in this report.

The number of scientists working around the world on behaviorally related studies of sharks has always been small, but even that number appears now to

be dwindling. This may well be the case because such studies are often fraught with serious difficulties, due largely to the nature of the animals themselves. Sharks are wide-ranging and inhabit a concealing medium. They are relatively swift swimmers and often move alone or in very small groups. Many species of interest are abundant only at remote geographical locations. Members of most species are fragile, requiring careful capture and transport, large holding facilities with highest water quality, and appropriate diet. Finally, many of the most interesting species, from the standpoint of human interest, are formidable and dangerous. When observers must enter the water in their vicinity, severe measures must be taken to assure their safety. These and other considerations, when taken together, often result in shark studies being long-term in nature, with data accumulating often too slowly for many of today's scrutineers and their associated funding agencies. Important advances in our knowledge of shark behavior will surely be made in the near future, so long as they are not deterred by the very processes that provided the means to reach our present level of understanding.

Table 1. Summary of experiments in which sharks were attracted to an underwater transducer (speaker) during playback of low-frequency, pulsed sounds^a (from Myrberg 1978).

Family and species	Common name	Sound ^b	Author(s)
Alopiidae <i>Alopias</i> sp.	Thresher	HF (N)	Nelson & Johnson (unpublished)
Carcharhinidae <i>Carcharhinus</i> sp.		FN (A) FN (A) FN, SqW (A)	Nelson & Gruber 1963 Richard 1968 Myrberg et al. 1969
<i>C. albimarginatus</i>	Silvertip	FN (A)	Nelson & Johnson 1972
<i>C. falciformis</i>	Silky	FN (A) SpF (N) FN (A)	Nelson et al. 1969 Evans & Gilbert 1971 Myrberg et al. 1972 Myrberg et al. 1975a Myrberg et al. 1975b Myrberg et al. 1976
<i>C. leucas</i>	Bull	FN (A)	Nelson & Gruber 1963
<i>C. longimanus</i>	Oceanic whitetip	FN (A)	Myrberg et al. 1975a Myrberg et al. 1975b Myrberg et al. 1976
<i>C. melanopterus</i>	Blacktip reef	FN (A) FN (A)	Nelson & Johnson 1970 Nelson & Johnson 1972
<i>C. menisorrh</i>	Gray reef	SpF (N) FN (A) FN (A)	Brown 1968 Nelson & Johnson 1970 Nelson & Johnson 1972
<i>C. springeri</i>	Reef	FN, SqW (A)	Myrberg et al. 1969
<i>Galeocerdo cuvieri</i>	Tiger	FN (A)	Nelson & Gruber 1963.
<i>Negaprion brevirostris</i>	Lemon	FN (A) BbN (A) FS (N)	Nelson & Gruber 1963 Banner 1968 Banner 1972
<i>Negaprion fosteri</i>	"Lemon"	FN (A)	Nelson & Johnson 1972
<i>Prionace glauca</i>	Blue	HF, StF (N) FN (A)	Nelson & Johnson (unpublished)
<i>Rhizoprionodon porosus</i>	Sharpnose	FN (A) FN, SqW (A)	Richard 1968 Myrberg et al. 1969
<i>Triaenodon obesus</i>	Reef whitetip	SpF (N) SpF, StF (N) FN (A) FN (A)	Brown 1968 Nelson & Johnson 1970 Nelson & Johnson 1972
Lamnidae <i>Isurus oxyrinchus</i>	Mako	HF, StF (N)	Nelson & Johnson (unpublished)
Orectolobidae <i>Ginglymostoma cirratum</i>	Nurse	FN (A) FN, SqW (A) FN (A)	Richard 1968 Myrberg et al. 1969 Nelson et al. 1969
Sphyrnidae <i>Sphyrna</i> sp.	Hammerhead	FN (A)	Nelson & Gruber 1963
<i>S. tiburo</i>	Bonnethead	FN (A)	Nelson et al. 1969

^a Taken in part from Nelson and Johnson 1972.

^b Types of artificially produced (A), and naturally recorded (N) pulsed sounds: FN, filtered random or white noise; BbN, broadband noise; SqW, square waves; SpF, speared struggling fish; HF, hooked struggling fish; StF, stampeded group of fish; and FS, fish sounds.

Table 2. Dietary supplements for captive sharks. Many of the vitamins and minerals are furnished in a single multivitamin tablet. Vitamins A, B₁, C, E and ferrous gluconate were separate tablets. These supplements have been used successfully for four years on lemon sharks and nurse sharks, and for two years on bull sharks and brown sharks (from Gruber and Keyes 1981).

Dietary addition	Dosage per kg animal weight per week
A	3570 I.U.
B ₁	210.0 mg
B ₂	0.39 mg
B ₆	0.23 mg
B ₁₂	0.9 mg
C	37.5 mg
Calcium pantothenate	0.6 mg
Choline	Trace
D	150 I.U.
E	37.5 I.U.
Ferrous gluconate	11.25 mg
Folic acid	Trace
Inositol	Trace
Kelp Iodine	18 μ g
Niacin	0.6 mg

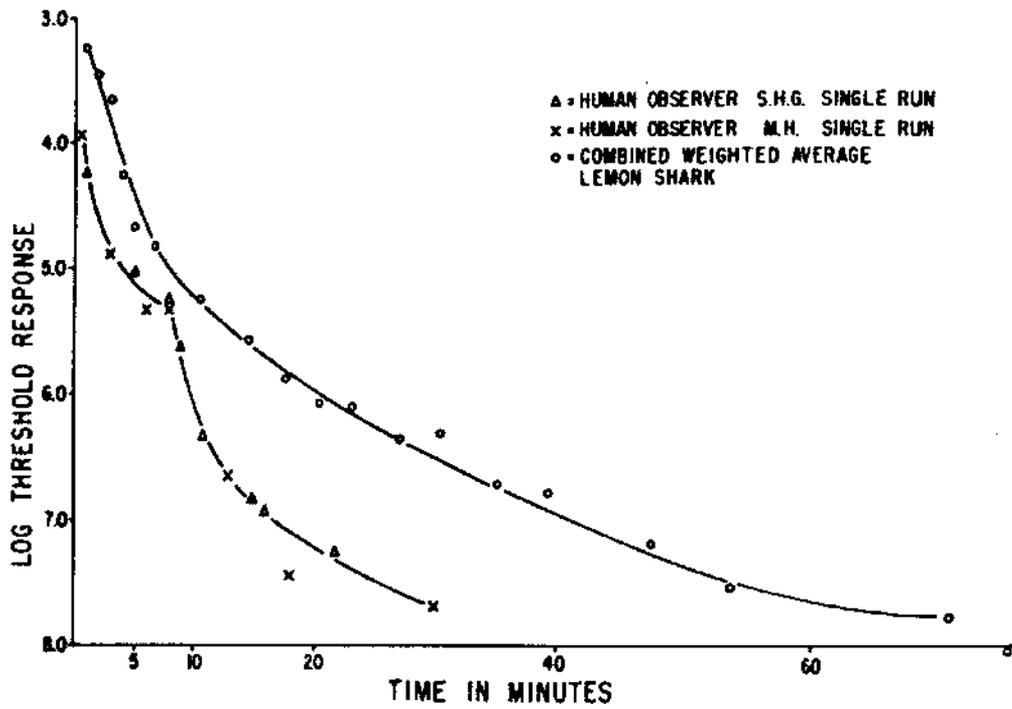


Figure 1. Comparison of the sensitivity to low light level and the time course of dark adaptation in the lemon shark *Negaprion brevirostris* with two human subjects. The points along the human curves represent single subjective thresholds obtained on the same apparatus used for testing the sharks. The single shark curve is an average of eleven curves (130 threshold determinations) obtained on five subjects. Note that the sensitivity shown by the sharks equals that attained by the human subjects; however, the sharks showed a slower time course of dark adaptation than that shown by the human subjects (from Gruber 1967).

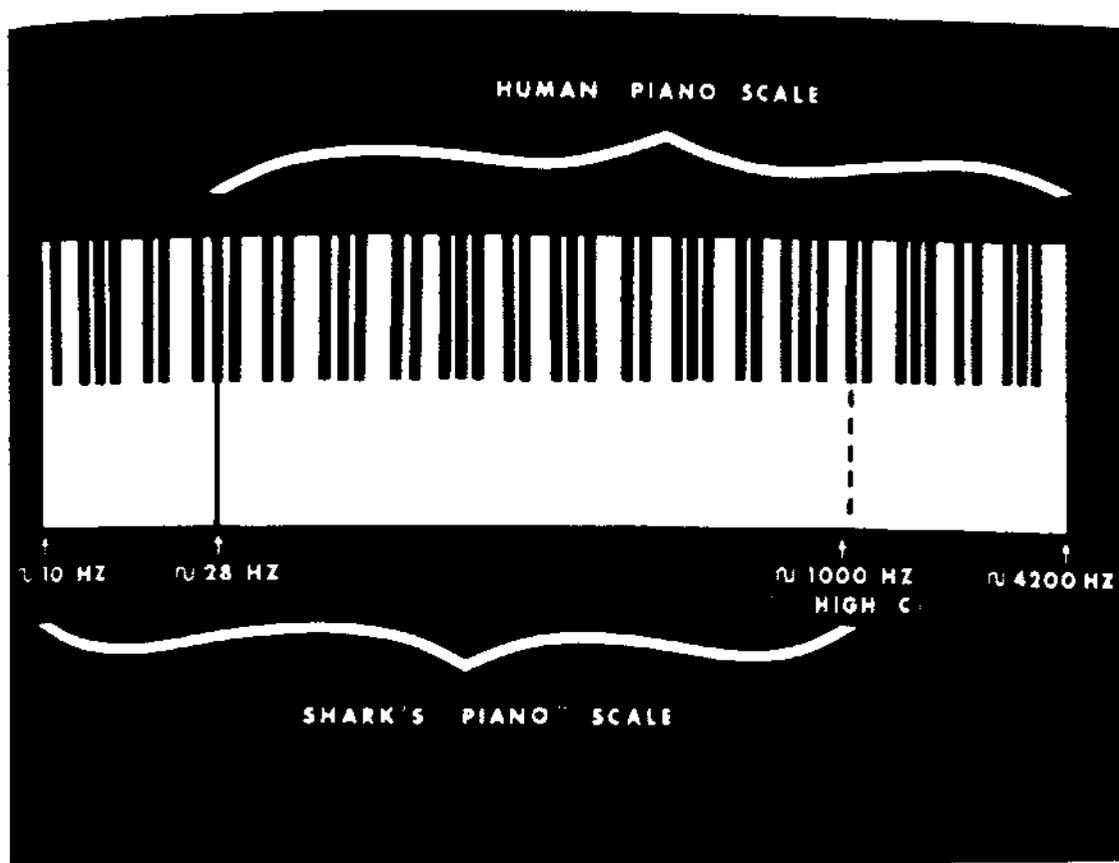


Figure 2. The extended range of low frequency hearing by sharks studied beyond that of human hearing is illustrated by the analogy to a piano scale. The frequencies shown are the approximate fundamental frequencies of the keys directed to by the arrows. Human hearing extends far beyond that of the highest fundamental frequency of the human piano scale; sharks probably do not hear frequencies higher than about 800 Hz.

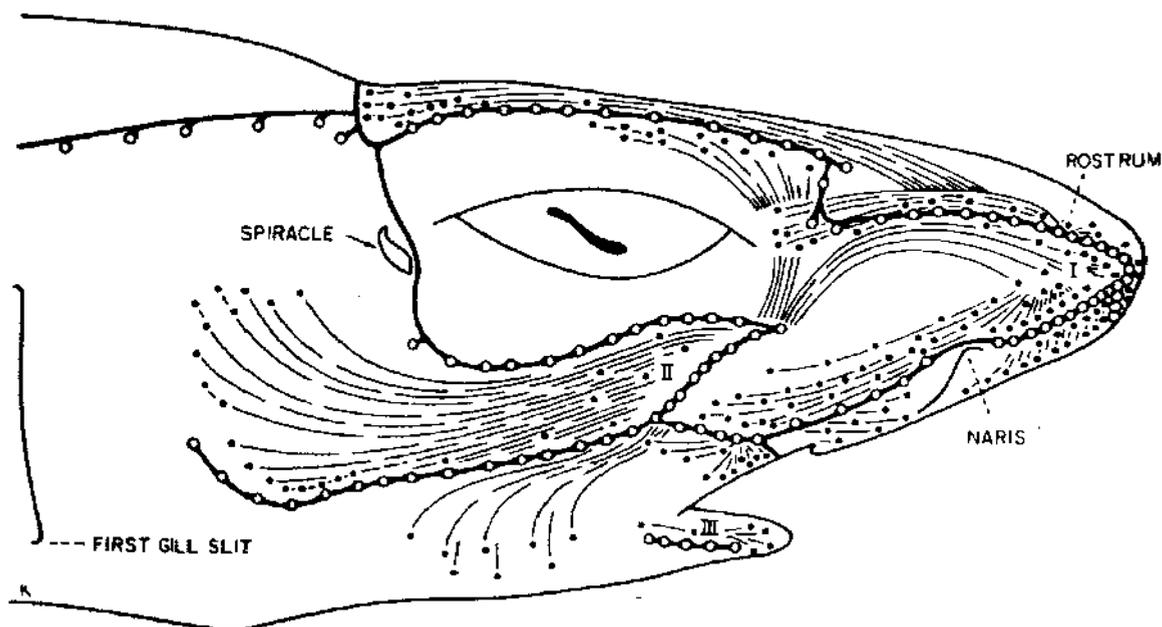


Figure 3. Ampullae of Lorenzini and lateral-line canals in the head of the dogfish shark *Scyliorhinus caniculus*. The opening of the Lorenzini ampullae (solid dots) form a dispersed pore pattern. Each gives access to an often long jelly-filled canal (broken lines) ending in a blind sensory swelling. The lateral-line canals (in heavy black) contain the mechanoreceptive neuromasts. They connect to the outside through laterally arranged skin pores (open circles) (from Kalmijn 1978).

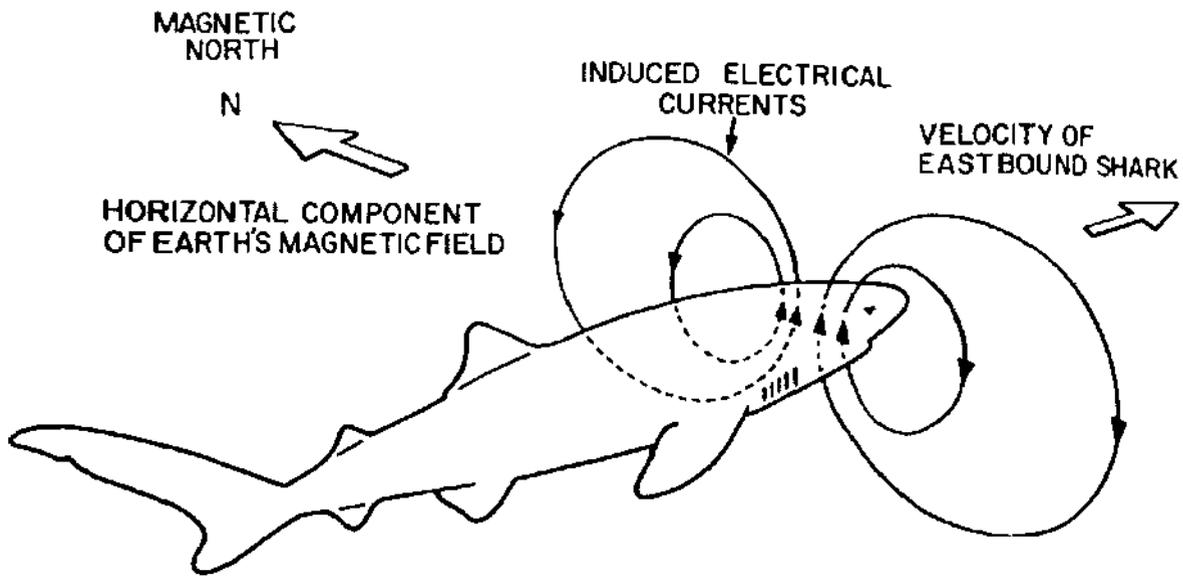


Figure 4. A shark swimming through the earth's magnetic field induces electric fields that provide the animal with the physical basis of an electromagnetic compass sense (from Kalwijn 1978).

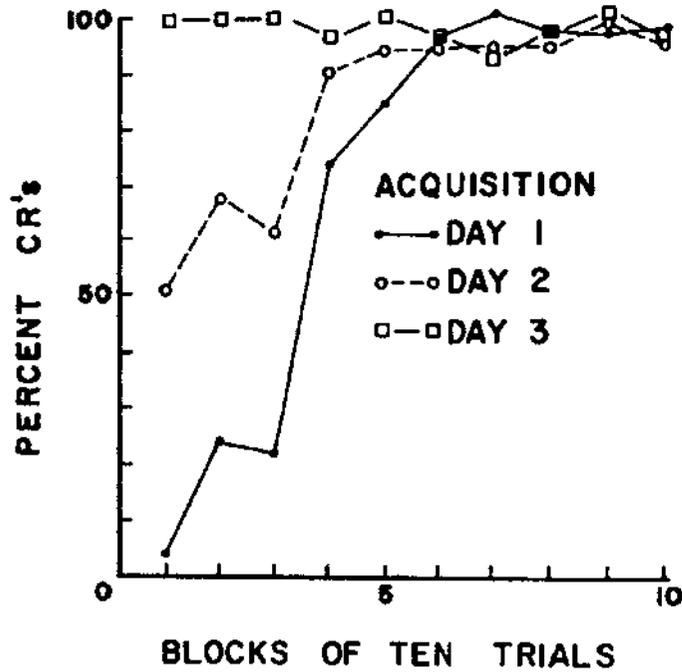


Figure 5. Course of acquisition of a classically conditioned movement of the eyelid (nictitating membrane) of the lemon shark (*Negraprion brevirostris*). Training consisted of pairing a flash of light with a low voltage electric shock 100 times a day (i.e. 10 blocks of 10 trials). Three days of training are shown. Note that the sharks reached nearly 100% conditioned responses by the 60th trial of the 1st day (from Gruber and Myrberg 1977).

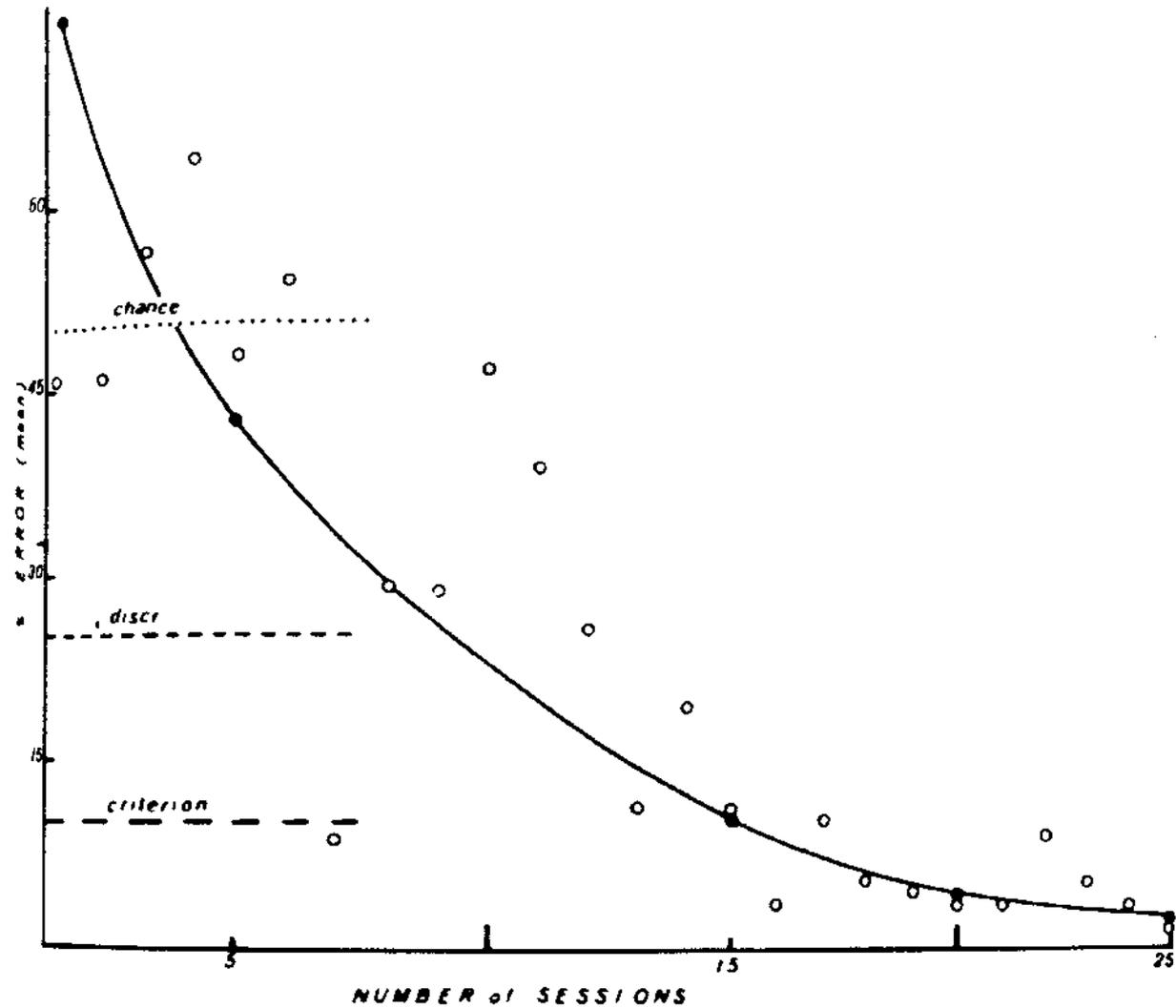


Figure 6. Instrumental learning curve of the lemon shark (*Negaprion brevirostris*) on a brightness discrimination task. Open circles represent mean % errors for six animals; closed circles were calculated from a standard curve-fitting procedure. Learning is signaled by the reduction in errors, i.e., choosing the dimmer of two lighted patches. Chance refers to random choice, i.e., the 50% correct level. Discr. refers to the 75% correct limit of discrimination usually acceptable in psychophysical testing while Criterion refers to the arbitrary 90% correct level chosen in the study (from Gruber and Myrberg 1977).

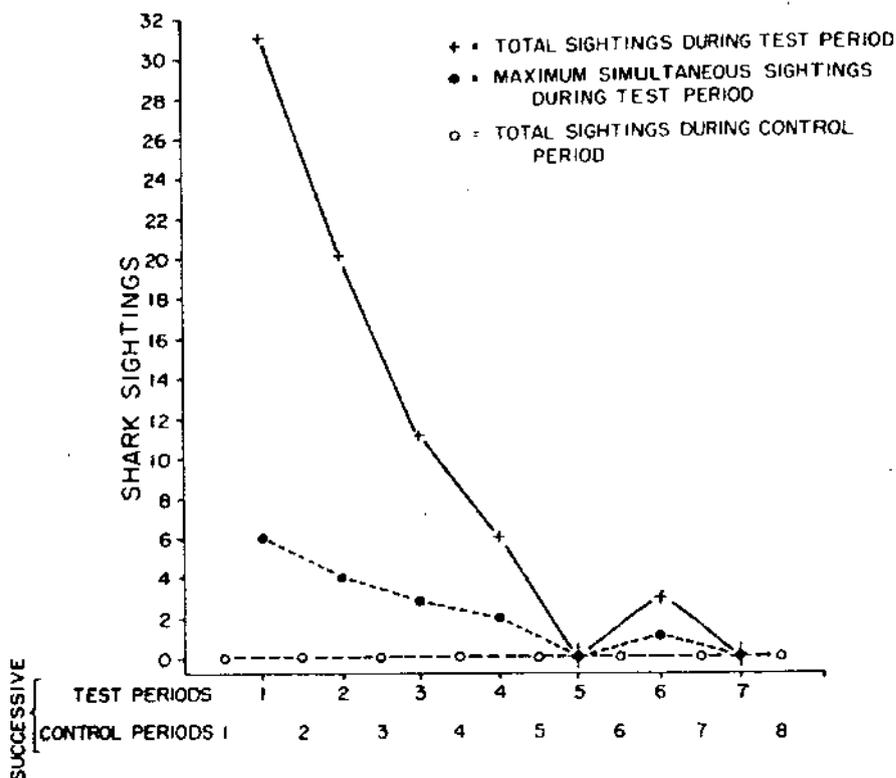


Figure 7. Decrease in sightings of free-ranging sharpnose sharks *Rhizoprionodon* sp. through successive test periods using sound as an attractant. Sound consisted of constant level, irregularly pulsed, overdriven 80 Hz sine waves (biphasic, symmetrical, and distorted square waves). Each test and control period—3 min. (from Myrberg et al. 1969).

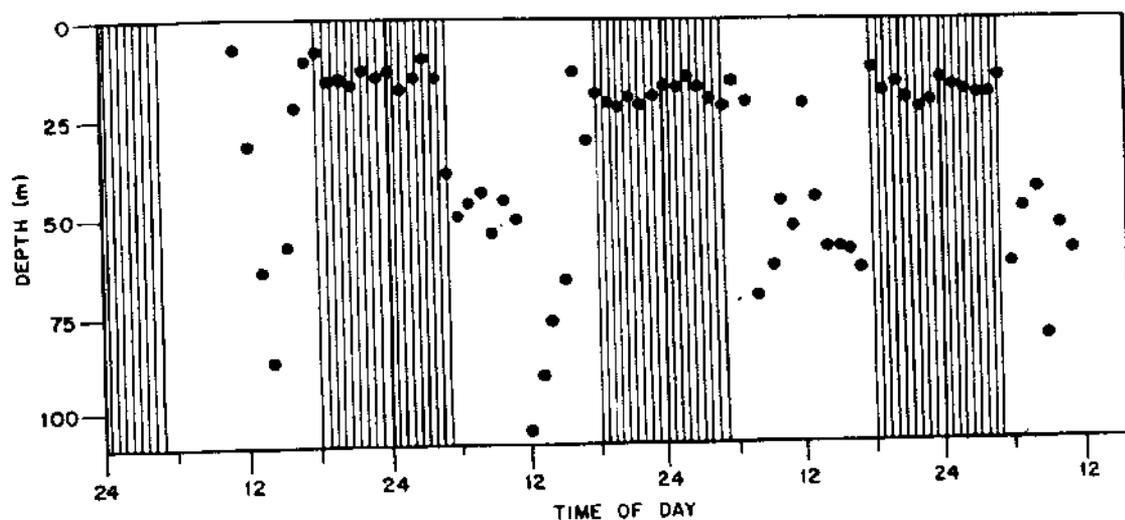


Figure 8. Rhythmic diurnal movements of one free-ranging, gray reef shark *Carcharhinus amblyrhynchos* tracked continuously for 72 hr. by acoustic telemetry (Rangiroa, French Polynesia). Shaded areas indicate times from sunset to sunrise. Note the distinct correlation between depth and time of day. First point is at the site of transmitter application (self-ingested in bait) in shallow water to which the shark was bait attracted (from Nelson 1978).

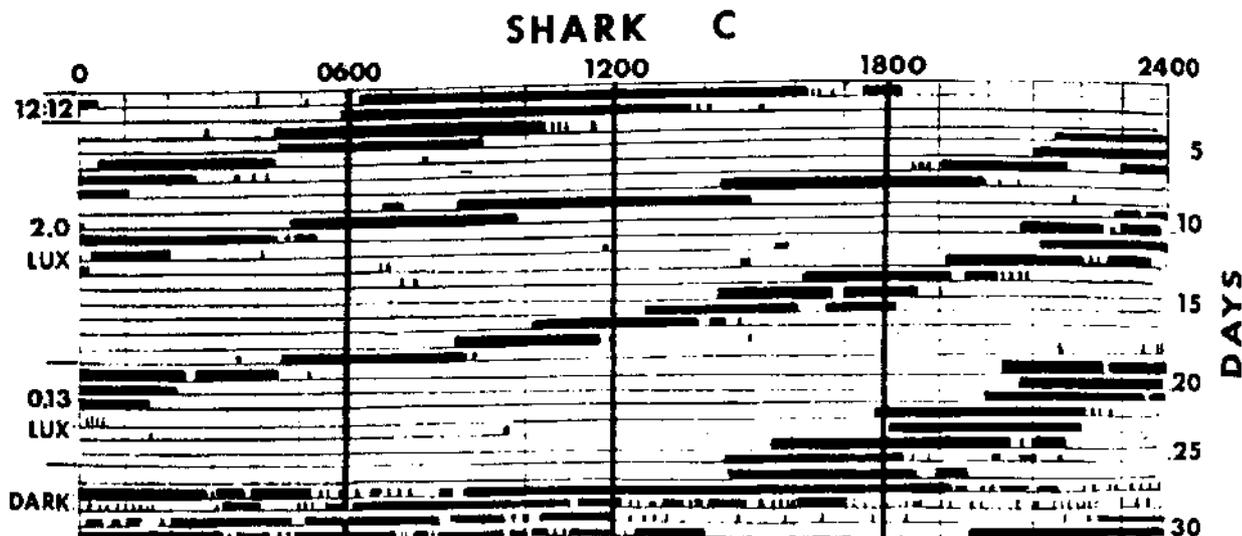


Figure 9. Laboratory demonstration of activity rhythms in a horn shark *Heterodontus francisci* as a function of light level. On day 5, the animal was placed in constant illumination of 2.0 lux (bright) and later in dim illumination of 0.13 lux. The solid bars across the graph represent motor activity steadily drifting out of phase with the time reference. Such drift is evidence favoring an endogenous circadian rhythm (from Finstad and Nelson 1975).

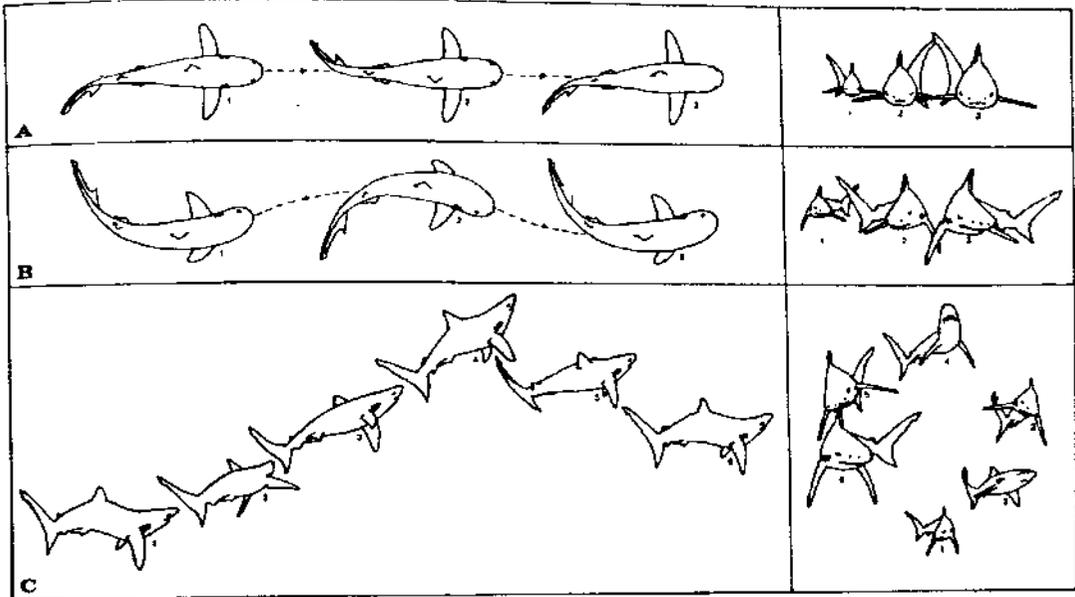


Figure 10. Comparison of normal and display swimming modes in the gray reef shark Carcharhinus amblyrychos: A. normal swimming; B. display, laterally Exaggerated Swimming and C. display, Rolling (1-2-1-2-1) and Spiral looping (1-6). Rolling, although similar to the initial phases of Spiral Looping, is distinct in that the shark returns to a level display attitude without entering into the up and down path seen in Spiral Looping (from Johnson and Nelson 1973).

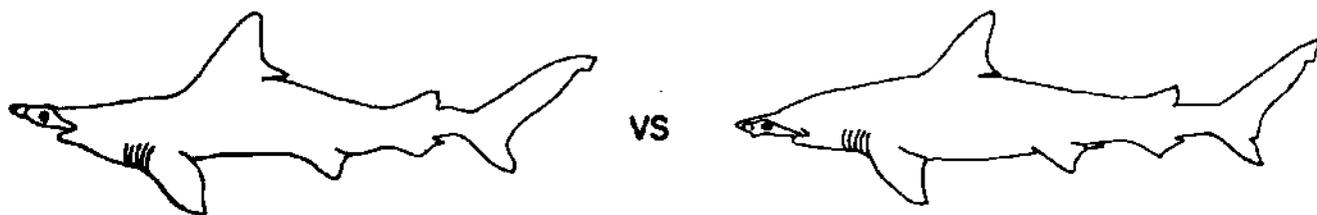


Figure 11. The agonistic display, Hunch (left figure), versus the normal posture (right figure) of a bonnethead shark Sphyrna tiburo. Note that the former consists of a raised head, lowered pectoral fins, raised back, and lowered tail fin. These same components are also seen in the Exaggerated Swimming display of the gray reef shark Carcharhinus amblyrhynchos, where they are more highly developed (modified from Myrberg and Gruber 1974).

April - July
40 Hrs Observations
Upper Tide Channel -
M. Seaquarium
N = 200 Giveaways

33 = % of times that a given shark giveaway to the shark to which the arrow points
4 = no. of giveaways by one shark to the shark to which the arrow points

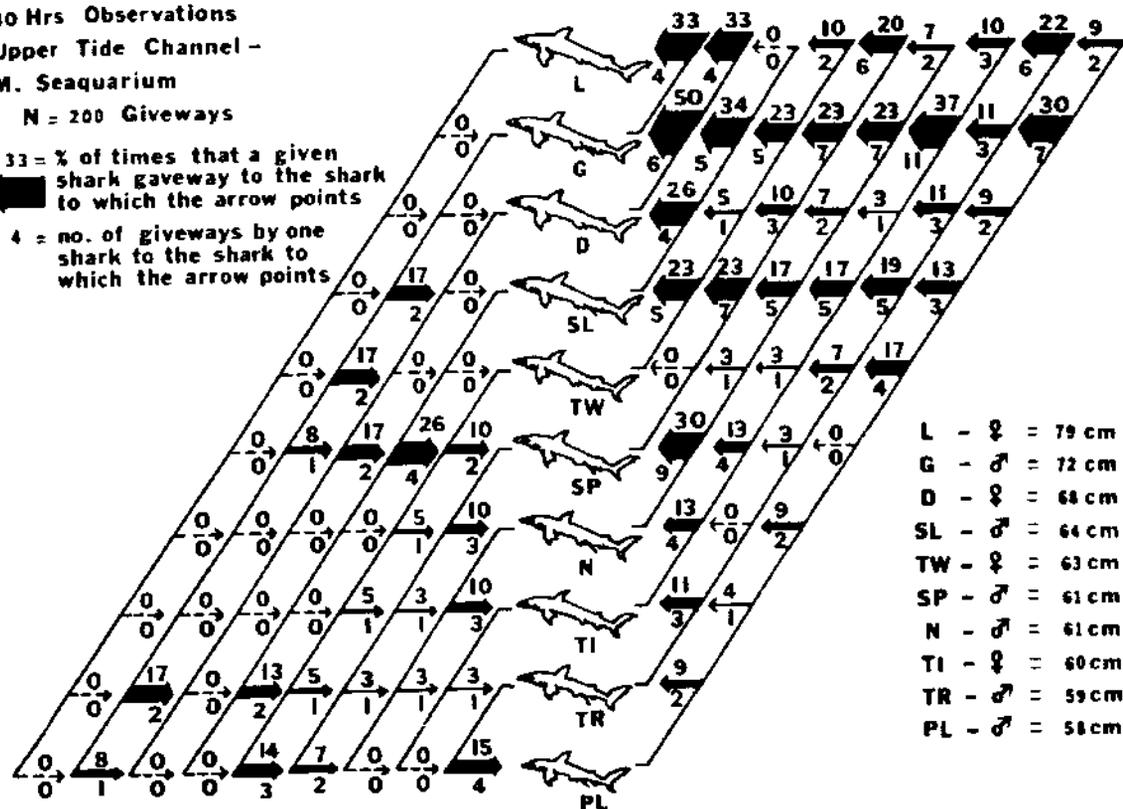


Figure 12. Social organization and dominance hierarchy in a captive colony of ten bonnethead sharks *Sphyrna tiburo*. In the diagram, sharks are ranked in order of descending size. Two diagonal lines are associated with each shark (except the largest and smallest). Each solid arrow points to the (dominant) shark that did not give way during a head-on encounter with another (subordinate) shark (source of the arrow). The thicker the arrow, the more frequently the former shark dominated the encounters with the latter shark. Sex also played a role in the hierarchy; note the consistently thicker arrows pointing to G, SL, and SP (i.e. the larger males) (from Myrberg and Gruber 1974).

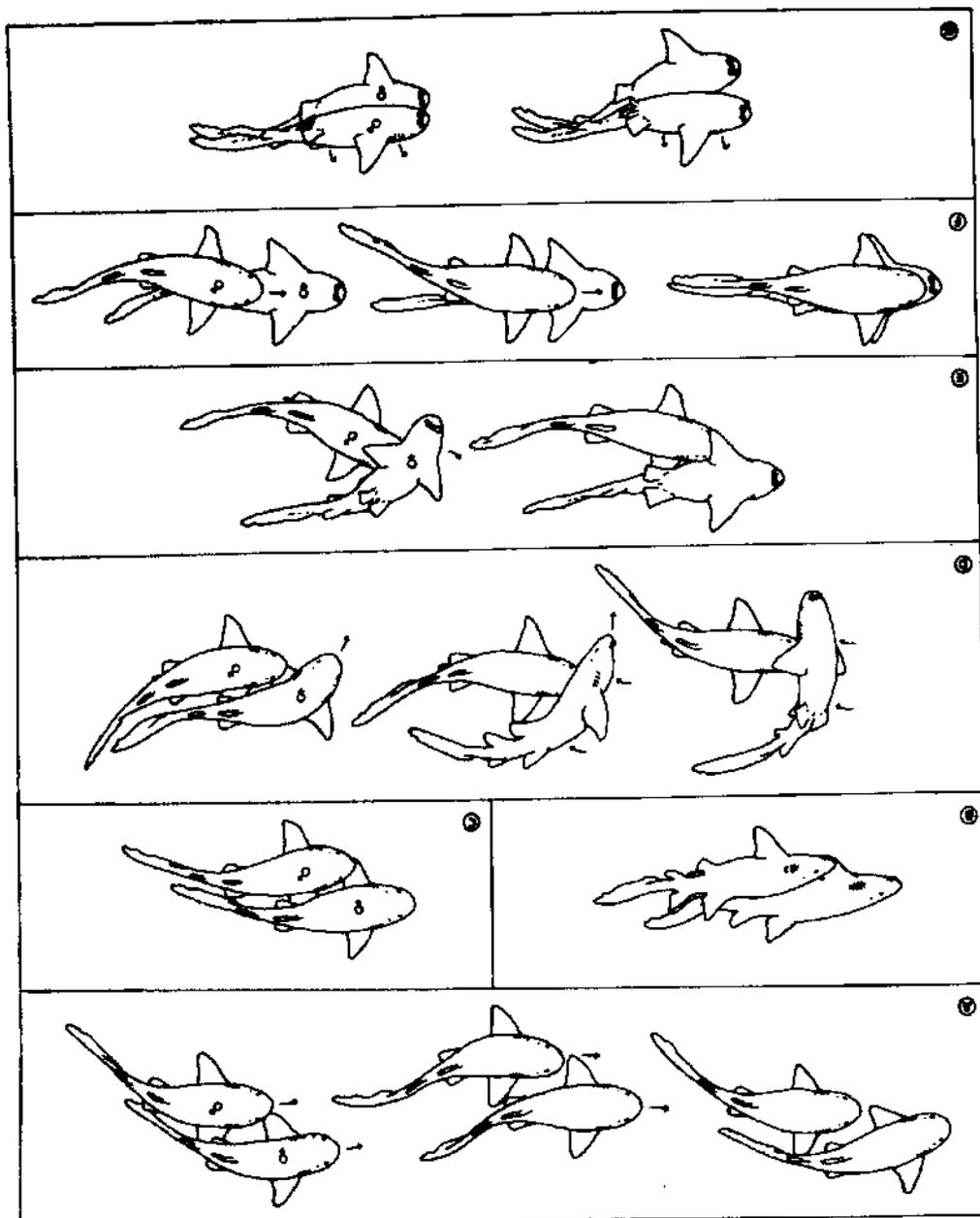


Figure 13. Courtship patterns and movements associated with copulation in the nurse shark *Ginglymostoma cirratum*: A) Paralled Swimming; B) Pectoral Biting (side view); C) Pectoral Biting (top view); D) Pivot and Roll; E) Nudging, Lying on Back (female); F) Male on Top (of female); G) Lying on Back (male, female). The actions are lettered in the order of their usual occurrence (from Klimley 1980).

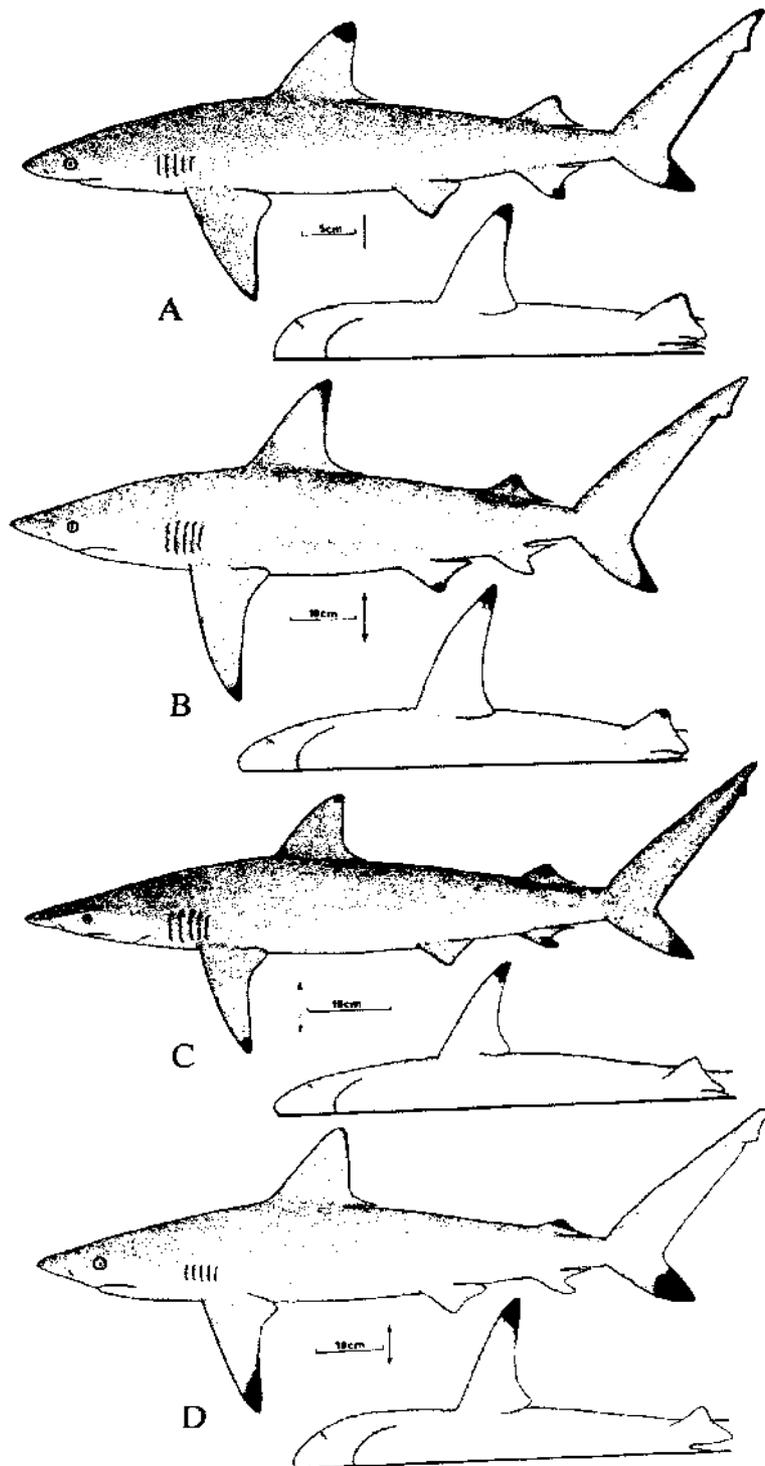


Figure 14. Comparison of the markings of four species of Carcharhinus from the southwest Indian Ocean: a. C. melanopterus; B. C. limbatus; C. C. brevipinna; D. C. sorrah (from Bass 1978).

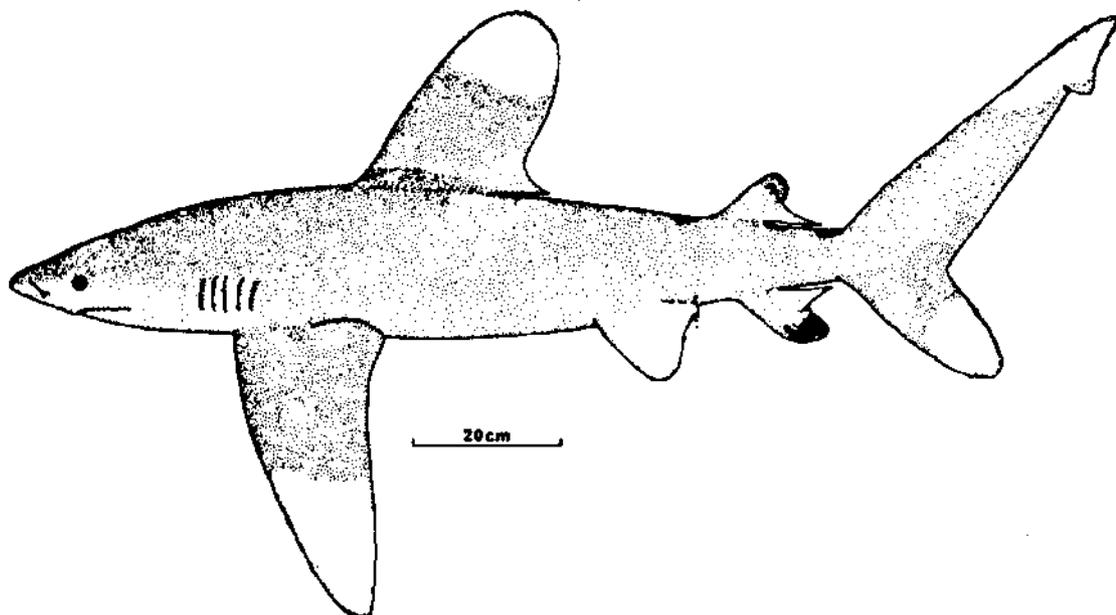


Figure 15. The oceanic white tip shark, *C. longimanus*). Note the large white regions of the fins and the large size of the first dorsal fin and the pectoral fin (compare with those shown in figure 14) (modified from Bass 1978, based on photos taken by the author).

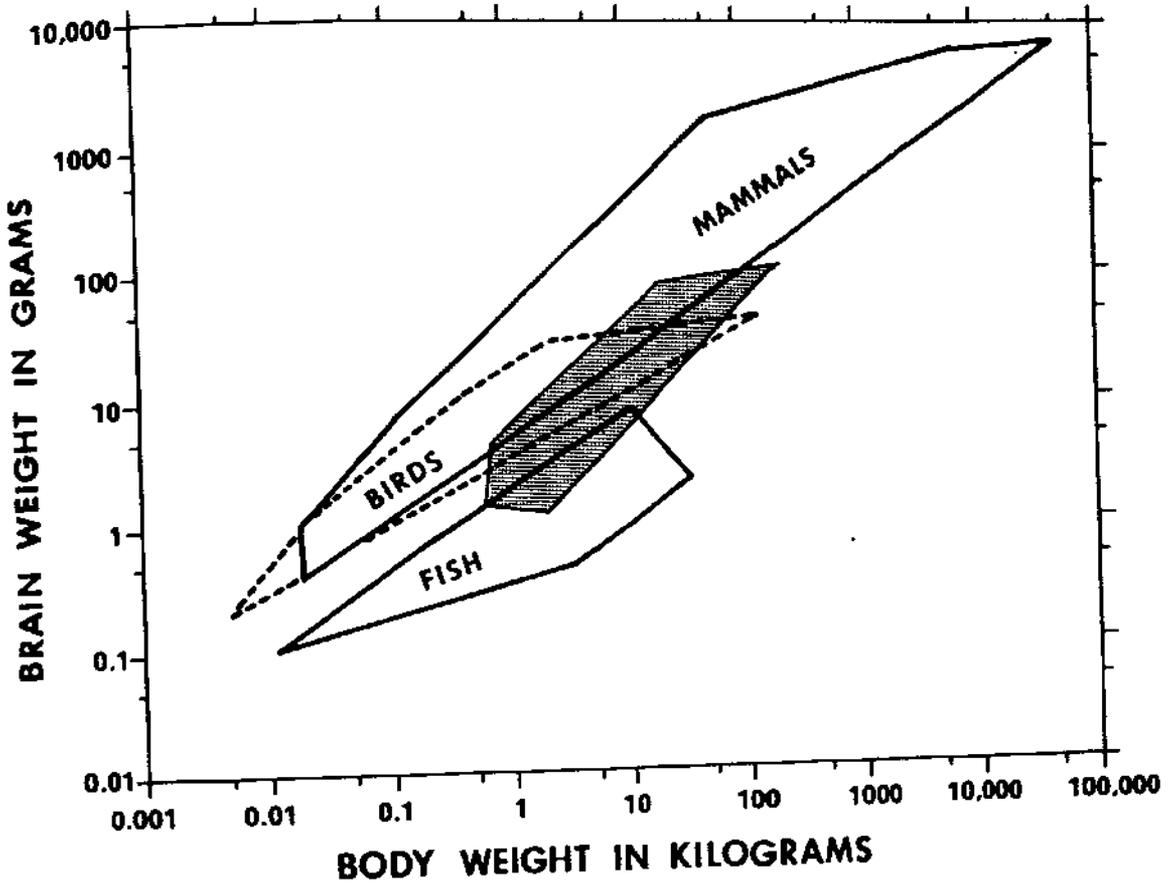


Figure 16. Brain and body weight for four vertebrate classes expressed as minimum convex polygons (each enclosing all ratios for a given class, see Jerison 1973; Northcutt 1978). Stippled polygon encloses elasmobranch brain-to-body ratios and overlaps polygons for bony fishes, birds, and mammals (from Northcutt 1978).

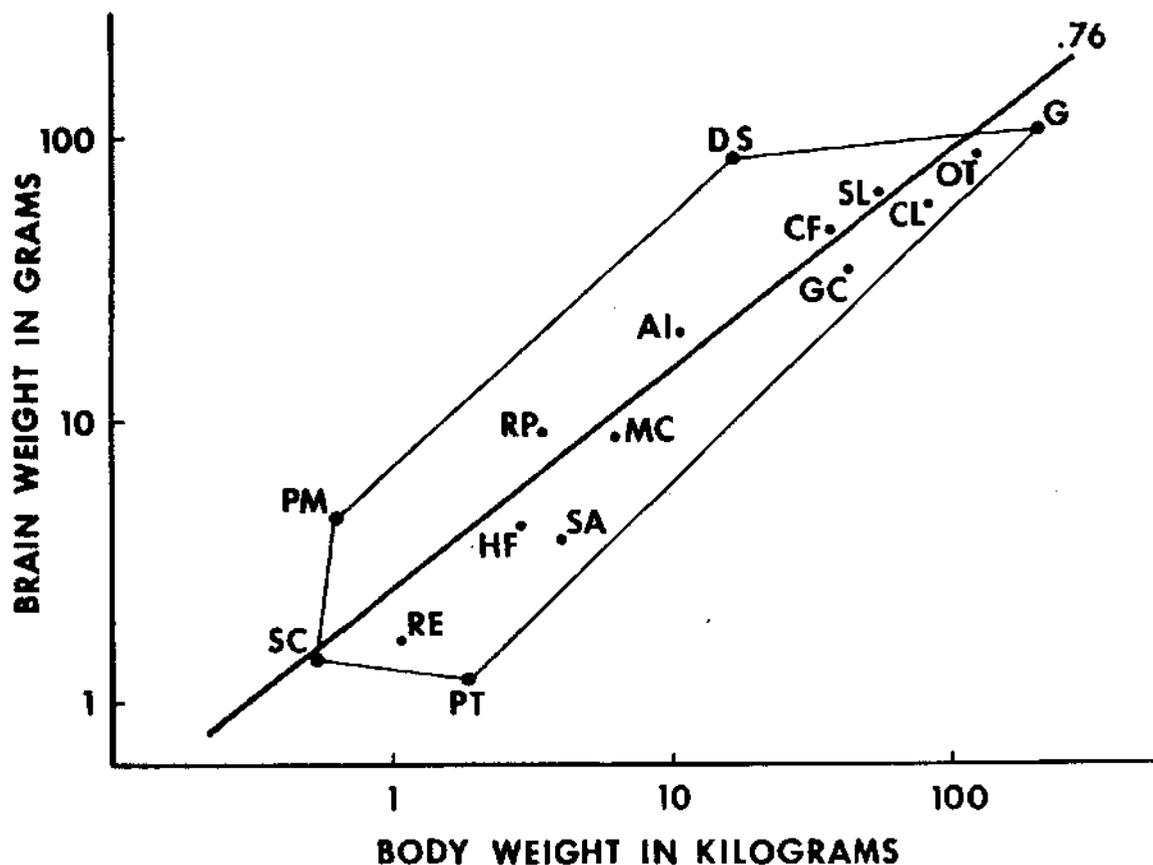
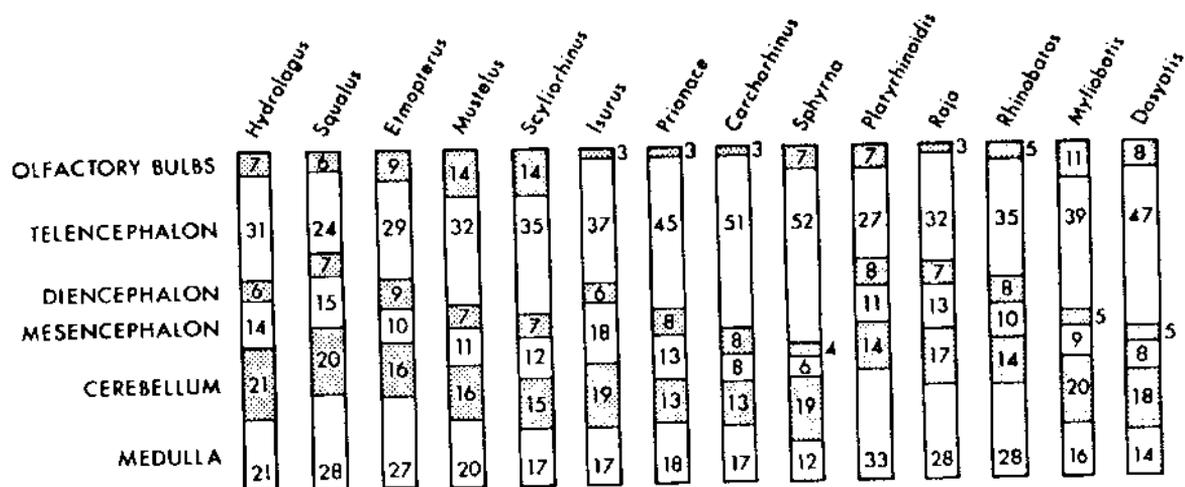


Figure 17. Detailed elasmobranch minimum convex polygon, illustrating positions of various taxa. Interspecific coefficient of allometry is 0.76 with a coefficient of determination of 0.86. AI, Aprionodon isodon; CF, Carcharhinus falciformis, CL, C. leucas; DS, Dasyatis sabina; G, Galeocerdo cuvieri; GC, Gluglymostoma cirratum; HF, Herterodontus francisci; MC, Mustelus canis; OT, Odontaspis taurus; PM, Potamotrygon motoro; PT, Platyrrhinoidis triseriata; RE, Raja elantera; RP, Rhinobatos productus; SA, Squalus acanthias; SC, Scylliorhinus caniculus; SL, Sphyrna lewini (from Northcutt 1978).



Weight of brain subdivisions as percent of total brain

Figure 18: Relative development of major brain divisions in a number of cartilaginous fishes: Hydrolagus colliei, Squalus acanthias, Etmopterus hillianus, Mustelus canis, Scyliorhinus retifer, Isurus oxyrinchus, Prionace glauca, Carcharhinus milberti, Sphyrna lewini, Platyrrhinoidis triseriata, Raja eglanteria, Rhinobatos productus, Myliobatis freminvillei, Dasyatis centroura (from Northcutt 1978).

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