The Role of Olfaction in Shark Predation[1]

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IT IS RECOGNIZED that most if not all species of sharks possess a keen sense of smell which is used in detecting dead and wounded prey or other edible material during their well-known scavenging operations. The early experiments of Parker (1910), Sheldon (1911), and Parker and Sheldon (1913) established the role of the paired nasal organs as olfactory receptors. Parker (1914) demonstrated directional response in the smooth dogfish (*Mustelus canis*) and provided a plausible explanation of how this was accomplished; he postulated that the two separated nostrils have the ability to detect small differences in the concentration of odorous materials enabling the shark to orient in the direction of equal stimulation and to head "upstream" to the source. This tracking ability is well recognized by skin divers and fishermen who have involuntarily attracted sharks by retaining speared fish or by discarding trash fish and offal from their boats.

It seems unlikely that any shark species could maintain itself entirely by scavenging operations, except perhaps in areas where man provides forage such as bait, fish offal, or other forms of edible garbage. Certainly the larger species are recognized as active predators which attack uninjured living prey, including man. Doubtless, vision plays a predominating role in locating and tracking normal living prey, and possibly other senses such as hearing are also involved. In considering olfaction, attention has focused largely on feeding activity induced by the release of attractive substances such as blood or other body fluids from the wounds of injured prey. The possible part played by olfaction in the detection and tracking of uninjured living prey has been largely overlooked.

In this paper I will present the results of experiments on the olfactory response of captive sharks to extracts of natural foods, to human materials, and to uninjured living fish in the hope of clarifying the role of olfaction in shark feeding activity. The results form part of an investigation of factors affecting the behavior of sharks sponsored by the Office of Naval Research (Contract Nonr 2756(00), Project NR 104503) over the period 1959–61. The work was undertaken at the Eniwetok Marine Biological Laboratory, Eniwetok Atoll, Marshall Islands, and at the Hawaii Marine Laboratory, Oahu, Hawaii. I am grateful to the respective directors, Dr. R. W. Hiatt and Dr. A. H. Banner, for laboratory facilities. I am indebted to personnel of the Atomic Energy Commission and the Pacific Missile Range Facility for logistic and other help. I am particularly indebted to those graduate students who have assisted in phases of the project: Edmond S. Hobson, Susumu Kato, Taylor A. Pryor, and Bori L. Olla.

FACILITIES, MATERIALS, AND METHODS

Eniwetok Marine Biological Station

At Eniwetok, small (18–36 inches) blacktip sharks (*Carcharhinus melanopterus*) and small (20–36 inches) grey sharks (*C. menisorrah*) were readily caught in shallow water by hook and line and established in captivity. Holding facilities consisted of two large concrete tanks housed in a building and illuminated by overhead fluorescent lighting (Fig. 1). The tanks were supplied with running sea water pumped

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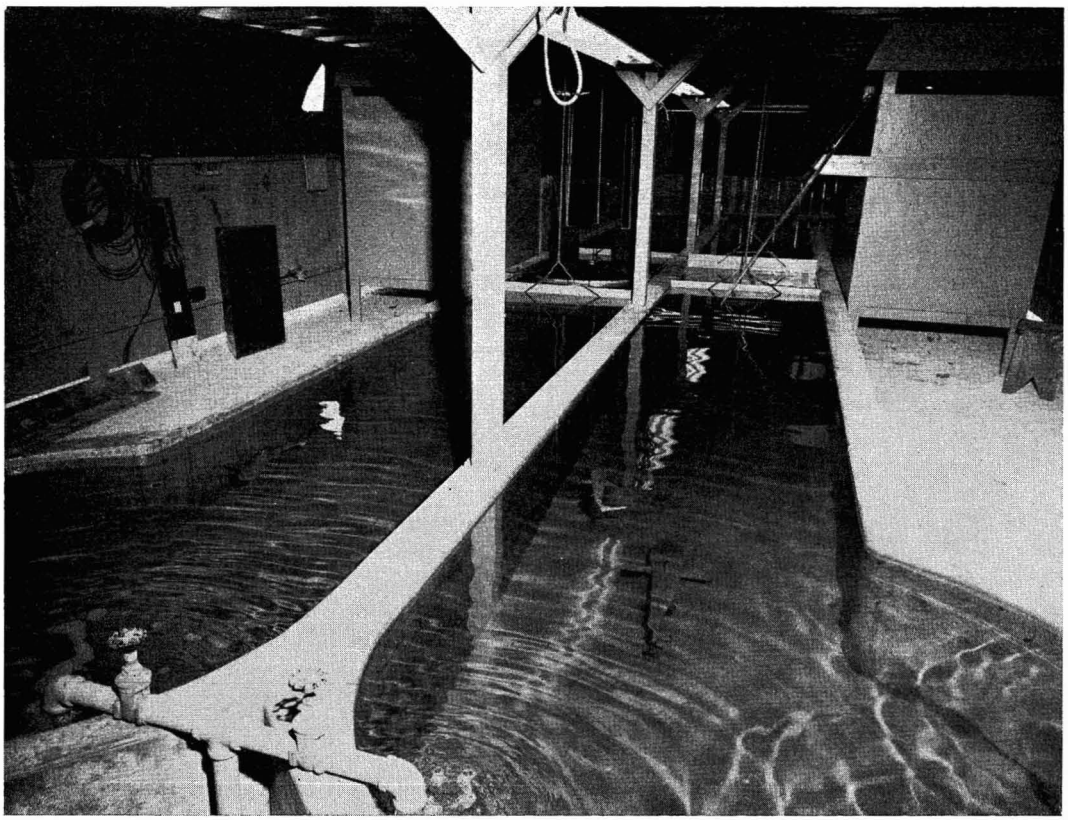

FIG. 1. View of shark tanks at Eniwetok Marine Biological Laboratory. (Photograph by Atomic Energy Commission.)

from the lagoon at a maximum rate of flow of about 10 gal per min. Lying side by side with a common middle wall, the tanks were 50 ft long, 4 ft wide and 3 ft deep with turning basins 6 ft in diameter at both ends (Fig. 2). The tanks could be divided into 5-ft sections by gates which slid in notches in the walls. Thus the sharks could be confined in a compartment consisting of one or several sections. Observation booths located midway along the tanks on both sides or blinds erected elsewhere effectively concealed the observer from the sharks.

Olfaction tests were conducted on both "normal" and blinded sharks. The sharks were blinded after anesthesia in a 1/1000 solution of MS 222- Sandoz (cf Gilbert and Wood, 1957) by coagulating the proteins of the aqueous humor with the diode probe of a "Hyfrecator" inserted through the cornea. Proof of blindness was lack of response to a hand waved close to the surface as they swam by or lack of response to the beam of a flashlight directed at their eyes. Within 1 hr after recovery from anesthesia the sharks circled their compartment, guided by the tip of the outstretched pectoral fin which touched the wall. Within a day they were able to circle the compartment without this tactile aide. They soon fed avidly on pieces of fish, squid, or other food which settled to the bottom before it was eaten. The sharks would detect the odor while swimming in mid-water and would spiral down, converging on the food by swimming in a figure-8 pattern on the bottom. Our attempts at blinding sharks with contact occluders (Mishkin, Gunkel, and Rosvold, 1959) were unsuccessful, perhaps because of faulty technique in molding plastic "lenses" and fitting them to the eyes. In general, the response of

the blinded sharks to olfactory substances was considerably less variable than that of sharks with normal vision.

Except during starvation experiments, the sharks were fed sparingly about once or twice a week; uneaten food was removed to avoid putrefaction and an unnecessary increase in olfactory level.

After investigating several different techniques during the early summer of 1959, a standard method of testing materials which could be dissolved or suspended in water was adopted. With natural foods such as fish flesh, usually 5 gm of material was macerated in a Waring blendor for 5 min with 250 ml of fresh water; sea water was not used because essential oils tended to accumulate in the froth. The material was then filtered and held in a refrigerator until used. Prior to an experiment a small quantity (usually 3.0 ml) of the clear solution was diluted with sea water to 25 ml in a test tube and then further diluted to 100 ml with sea water in a funnel. Substances other than natural foods were diluted to various concentrations before being tested.

Prior to testing, a glass funnel and tube leading from the observation booth to a point just below the surface in the center of a test area (e.g., Fig. 2, Tank 1, D) was filled with sea water to remove air bubbles; the contents were maintained by closing a pinchcock. The flow of sea water to the tanks was shut off at the inflow valve. Usually, five 2-min control periods were then run, during each of which the time (seconds) spent by one or more of the sharks in the test areas (e.g., Tank 1, C and D) was recorded by an electric timer activated by a foot switch. At the same time, observations were recorded of the behavior of the sharks and sometimes of the number of passes or turns in the test areas. The test material was then introduced silently while the sharks were at the far end of the compartment, and the activity of the sharks was again noted and recorded during five (or more) 2-min test periods. The nature of the response was then categorized as attraction, repulsion, etc. on the basis of the graphed data and the notes.

A similar technique was used in 1960 except that timing was abandoned in favor of counting the number of turns. Each of the two test areas was divided by an imaginary line into halves; turns in the four half-areas were given weights of 1 to 4, with the weights increasing toward the half-area of introduction (Fig. 2). The graphed "count index" of activity seemed to reflect our subjective impression of a response

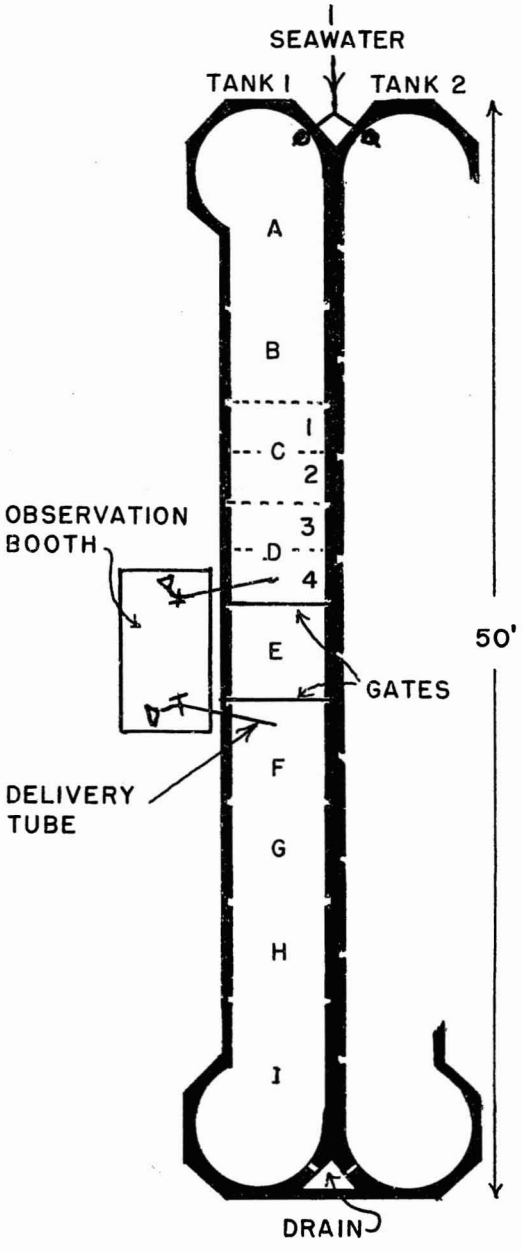

FIG. 2. Diagram of shark tanks at Eniwetok Marine Biological Laboratory.

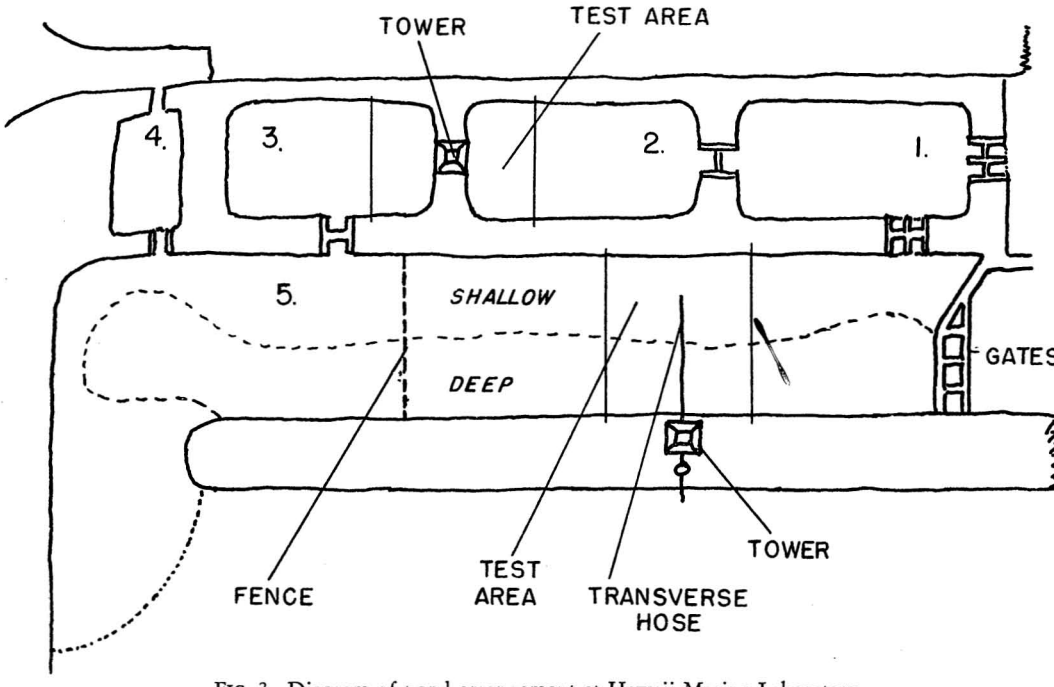

FIG. 3. Diagram of pond arrangement at Hawaii Marine Laboratory.

more realistically than the "time index." Special techniques used in studying the response of the sharks to living fish will be discussed later.

Hawaii Marine Laboratory

At the Hawaii laboratory several grey sharks of two species (*Carcharhinus* spp.), hammerhead sharks (*Sphyrna lewini*), and tiger sharks (*Galeocerdo cuvier*), all 5 to 7 ft in length, were readily caught by set line in the adjacent waters of Kaneohe Bay. They were established in large seminatural ponds (Fig. 3), screened by gates and flushed slowly by tidal action. Three grey sharks and one tiger shark were successfully maintained in captivity for 3 years and were still alive and healthy at the time of writing (October 1961). Hammerheads were successfully maintained in captivity for periods from 3 months to 1 year. It is suspected that their death was due either to injury caused by the other sharks or lack of food. They were unable to compete successfully with the fast, aggressive grey sharks; often our efforts at preferential hand-feeding failed when the food was taken persistently by the other species. The sharks were fed sparingly about once or twice a week on cut or whole fish.

Several experiments were undertaken on a tiger shark and a grey shark following their respective establishment in Ponds 2 and 3, both of which were about 100 ft long, 60 ft wide and 3–4 ft in maximum depth. Observations were conducted from a 16-ft tower between the ponds. By means of a pump and hose a continuous flow of water was taken from one pond, led to the top of the tower, and thence led into a test area of the other pond. Following a series of 3-min control periods, during which quantitative data were collected on the activity of the shark, notes were made of overt responses and the path of the shark was diagrammed. The material to be tested was then introduced into the stream of salt water after dilution in a suction funnel on top of the tower, and the observations were repeated during a series of 3-min test periods.

During the winter of 1959–60 both the grey and the tiger shark were transferred to Pond 5 (Fig. 4), a much larger enclosure about 360 ft long and 66 ft wide. Other grey and hammerhead sharks were added to this pond; eventually

they were confined in two-thirds of its length by a fence. Observations were conducted on the shark population from the 16-ft tower which had been moved to a central location along one side. Usually the sharks would swim back and forth along the length of the enclosure in a channel which averaged about 9 ft in depth. Occasionally the tiger shark and the hammerheads (but rarely the greys) would traverse the length of the pond in shallows 1–4 ft in depth along the side of the pond opposite to the tower. Two testing techniques were employed which are henceforth referred to as "point" and "curtain-funnel" or "curtain-drum" introduction. In both, activity was recorded during the usual control and test periods in a test area 50 ft in length and extending across the width of the pond. The area, centrally located in front of the tower, was marked off by cords which stretched across the pond and were several inches above the water surface at high tide.

In "point" introduction the material was contained in a 5-gal funnel on top of the tower and was introduced at a point either just below the surface or at a depth by means of a rubber tube suspended from a boom (Fig. 5). In "curtain-funnel" introduction the material passed from the funnel to a perforated hose running transversely across the bottom of the pond at the center of the test area and extending part way into the shallows. In a modification, used in the spring and summer of 1961 and called "curtain-drum" introduction, a continuous stream of salt water was pumped into the hose before and during control conditions; the stream was then switched to a 50 gal drum containing about 40 gal of sea water together with the test material. After introduction, which usually consumed about three 3-min test periods, the flow was again switched to salt water. With both methods care was taken to prevent the generation of air bubbles in the curtain for they produced a variable visual response. By using dye it was found that the curtain was fairly uniform and rela-

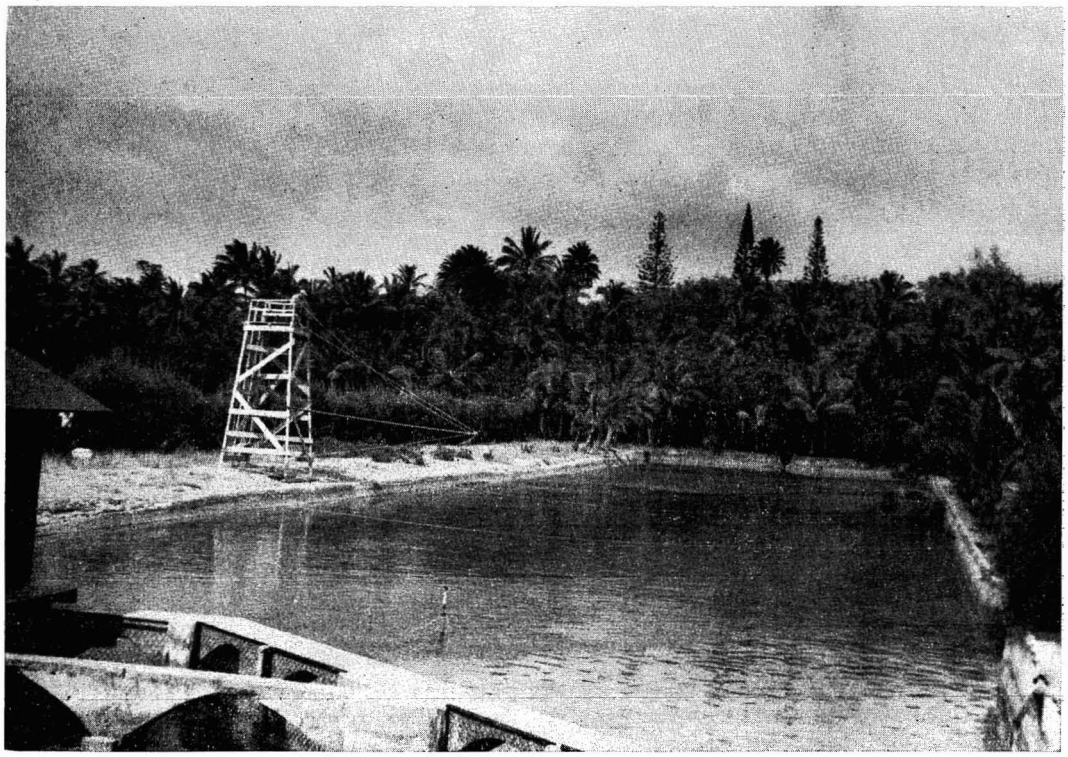

FIG. 4. View of Pond 5 at Hawaii Marine Laboratory showing the observation tower. (Photograph by E. S. Hobson.)

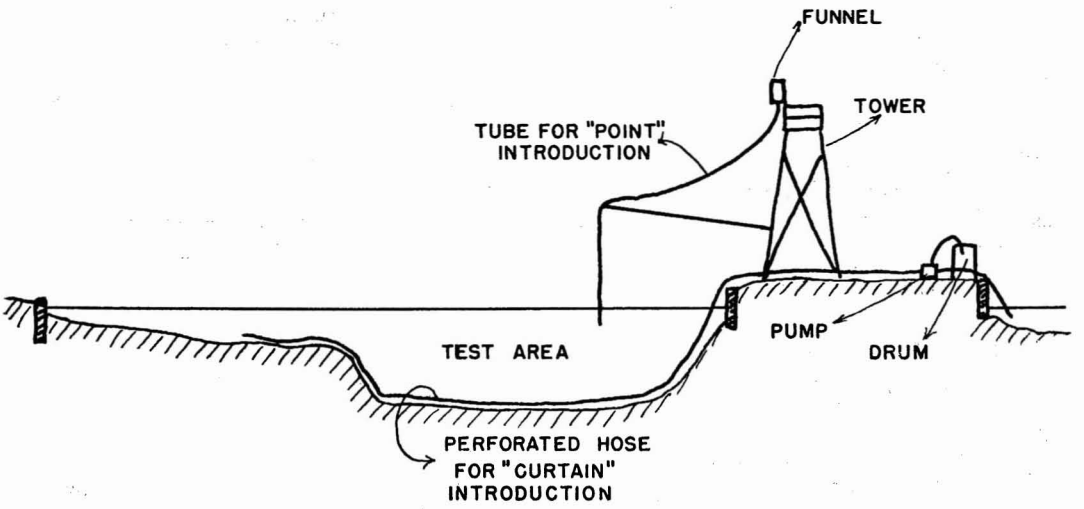

FIG. 5. Diagram of the arrangement of test apparatus in Pond 5 at Hawaii Marine Laboratory.

tively stable during periods at or near slack water. When there was a tidal current the curtain lacked uniformity in concentration and was irregular in shape; it slowly spread to one end or the other of the test area; sometimes it spread in one direction at the surface and in the opposite direction at or near the bottom. Normally the sharks would encounter the curtain of material during their passage along the deep channel. They could avoid it by swimming in the shallows.

Interpretation of a response

Based partly on quantitative data averaged as an index of activity or plotted in graphic form, partly on notes of overt responses, and, in the case of pond experiments, partly on diagrams of the swimming paths of the sharks in, out, or through the test area, the result of each experiment was classified as no noticeable response (O), sensing only (S), weak attraction (A), strong attraction (AA), weak repulsion (R), or strong repulsion (RR). Occasionally these were supplemented by other descriptions such as "startled reaction," "alarm reaction," "agitation," etc.

The category "no noticeable response" needs no further explanation. The category "sensing" was reserved for a response which consisted of a sudden start or turn on the part of the shark on first encountering the test material but with no other noticeable component suggestive of either attraction or repulsion. Sensing responses were obtained with a variety of materials including weak acids, bases, and salts. The response was interpreted merely as an awareness of any change in the composition of an otherwise uniform environment. An "attraction" response included an initial sensing followed by a more or less prolonged hunting response, usually with rapid swimming, circling at or near the surface, and occasionally with a "gulping" or flexing of the jaws as when feeding. The shark would usually make several excited circles in the test area on encountering the material, and would then dash down the tank, returning to the test area for further circling. Almost invariably the average index of activity during test conditions was higher than during control conditions. A "repulsion" response included an initial sensing, but this was followed usually by rapid departure from the test area, a slowing of swimming speed, and a "cautious" re-approach to the test area. Often in subsequent passes the sharks would turn short of the test area. A strong repulsion was often accompanied by shaking of the head or flexing of the gill slits. Almost invariably the average index of activity during test conditions was lower than during control conditions.

Unfortunately the response to a given material varied considerably in repeated testing and was often difficult to classify. The problems of bioassay should not be minimized. The responsiveness of the sharks both at Eniwetok and Hawaii seemed to vary from day to day for unknown reasons despite our attempts to maintain standard conditions of testing and feeding. Erratic behavior, frequently encountered during both control and test conditions, in some cases could be traced to obvious sources of disturbance, such as noise, but in other cases could not be explained. Particularly exasperating was an occasionally exhibited tendency to circle at one or the other end of the pond or tank for long periods of time so that tests could not be conducted. Even though an attempt was made to conduct tests only after some reasonable uniformity in swim pattern persisted throughout control periods, there was always the question of whether or not a subtle change in behavior pattern was related to the material being tested. In classifying a response, greater reliance was placed on overt signs such as sudden turns, circling, gills flexing, and head shaking than on the quantitative data. Unfortunately the location and concentration of the material being tested was not known precisely during tests and could only be estimated from the use of dyes after an experiment had been completed. Thus even overt responses could be related to the test material only by inference.

Our caution in interpretation is reflected in the large number of responses relegated to doubtful categories in the results which follow and the numerous tests which were conducted on materials of particular interest.

RESPONSE TO EXTRACTS OF NATURAL FOODS

Experiments were conducted on the response of the tiger shark to extracts of tuna flesh and decayed shark flesh and on the response of the blacktip and grey sharks to a wide variety of potential foods including tuna, eel, grouper, snapper, parrot fish, jack, giant clam, octopus, squid, lobster, fresh shark flesh and skin, and decomposed shark flesh and skin. In general, the extracts of all food substances tested could be classed as attractants, although because of variability in the response of the sharks sometimes several tests of the same substance were necessary to establish this conclusion. Because of this variability it was not possible to make rigorous comparisons between the attractiveness of extracts from equivalent quantities of the various foods. However, it seemed certain that extracts from moist- or oily-fleshed fish such as grouper, tuna, and eel generally resulted in greater activity than those from dry-fleshed fish such as snappers. In attempting to determine the response to nonfood substances, frequently standard extracts of grouper, tuna, or eel were used either before or after tests of the other substances to appraise the sharks' responsiveness.

From Table 1, summarizing the results of 169 tests, it will be noted that the response was classed as a strong attraction in 59, as a weak or doubtful attraction in 62, as nil or merely a sensing in 39, and as a weak or a doubtful repulsion in 9. The last, comprising 5% of the tests, warrants further comment.

The five instances of apparent repulsion in the 1959 tests at Eniwetok involved extracts of little tunny (*Euthynnus yaito*), yellowfin tuna (*Neothunnus macropterus*), and giant clam (*Tridacna*), and occurred early in the summer when testing techniques were being developed. Without doubt the response was related to either incipient pollution of the tanks or decomposition of the test materials. Excessive quantities of extracts were being used and excess food was not being removed from the tanks; one or both of these factors resulted in the death of several sharks in one compartment before the condition was rectified. Our notes state that the tunny extract, which had been kept for 9 days, smelt foul.

The four instances of apparent repulsion in the 1960 tests, involving standard extracts of eel, again took place early in the summer and involved not pollution of the tanks but decomposition of the extract even though it was held at ice-box temperature. The extract was prepared on July 7, 1960. On that and the following day tests of both greys and blacktips showed strong attraction (Figure 6*A*). On July 13, in seven tests the responses were indicated as weak or questionable attraction, sensing only, or nil. On July 16, the material produced erratic re-

TABLE 1

RESPONSE OF SHARKS TO EXTRACTS OF NATURAL FOOD AT HAWAII MARINE LABORATORY (HML) AND ENIWETOK MARINE LABORATORY (EMBL)

YEAR	SHARKS, LABORATORY, AND MATERIAL	RESPONSE*					
		RR	R-R?	O-S	A-A?	AA	Total
1959	Tiger, HML						
	Fresh tuna extract	–	–	3	2	2	7
	Aged shark extract	–	–	–	1	1	2
1959	Blacktips, EMBL						
	Various extracts	–	5	21	32	32	90
	Aged shark extract	–	–	7	8	3	18
1960	Blacktips and greys, EMBL						
	Fresh extracts	–	–	–	12	18	30
	Aged eel extract	–	4	8	6	2	20
	Aged shark extract	–	–	–	1	1	2
Total		–	9	39	62	59	169

* RR, strong repulsion; R-R?, weak or doubtful repulsion; O-S, no apparent response or sensing; A-A?, weak or doubtful attraction; AA, strong attraction.

sponses, some of which were classed as doubtful repulsion. The notes indicated that the material smelt foul. Similar results were obtained with the same material on July 18. The sharks were tested with freshly prepared standard eel extract on July 20 and both species showed a strong attraction response.

In direct contrast to the above results are those with extracts of decayed shark flesh, which after a week in the hot sun smelt particularly foul. Our material consisted of extract of decayed hammerhead and of decayed tiger shark tested on the tiger shark at the Hawaii Laboratory (two tests) and of extracts of decayed blacktip shark flesh and skin tested on blacktip sharks at Eniwetok (five tests). In addition, we tested blacktips at Eniwetok on an alleged shark repellent, supplied by a fisherman, which contained extract of decayed shark flesh as the principle component (six tests). We also tested fractions of extract of decomposed shark flesh which were supplied by Dr. M. A. Steinberg, Bureau of Commercial Fisheries Technological Laboratory, Gloucester, Mass. (11 tests). No repellent effects were noted in any of the tests. On the contrary, the majority yielded responses which were classed as either weak or strong attraction. Our results with the fractions of extract were in agreement with those reported by Steinberg (1960) when his material was later tested on the lemon shark (*Negaprion brevirostris*), the reef shark (*Carcharhinus falciformis*), and the bull shark (*Carcharhinus leucas*) at the Lerner Marine Laboratory, Bimini, Bahamas, B. W. I.

Our results with extracts of decomposed shark flesh seem to be at variance with those of Springer (1955), who found that the feeding of the dogshark (*Mustelus canis*) was consistently inhibited by the presence of decayed shark flesh. Although several hypotheses might be formulated to account for the difference in results, no convincing explanation can be made at the present time, particularly in view of the apparent repulsion noted with decomposed eel and other extracts noted in preceding paragraphs.

BEHAVIOR OF STARVED SHARKS

In considering shark predation, the questions arise as to how long a shark can exist without food and whether its olfactory response is modified by starvation. Some information on these points was obtained for small sharks at the Eniwetok laboratory.

In 1959, following the summer's work, AEC personnel at Eniwetok volunteered to keep track of the fate of four small blacktips under starvation conditions. Three of the sharks died after about 2 months in captivity. One survived for 3 months but it was not known to what extent it had maintained itself by feeding on the sharks which had died.

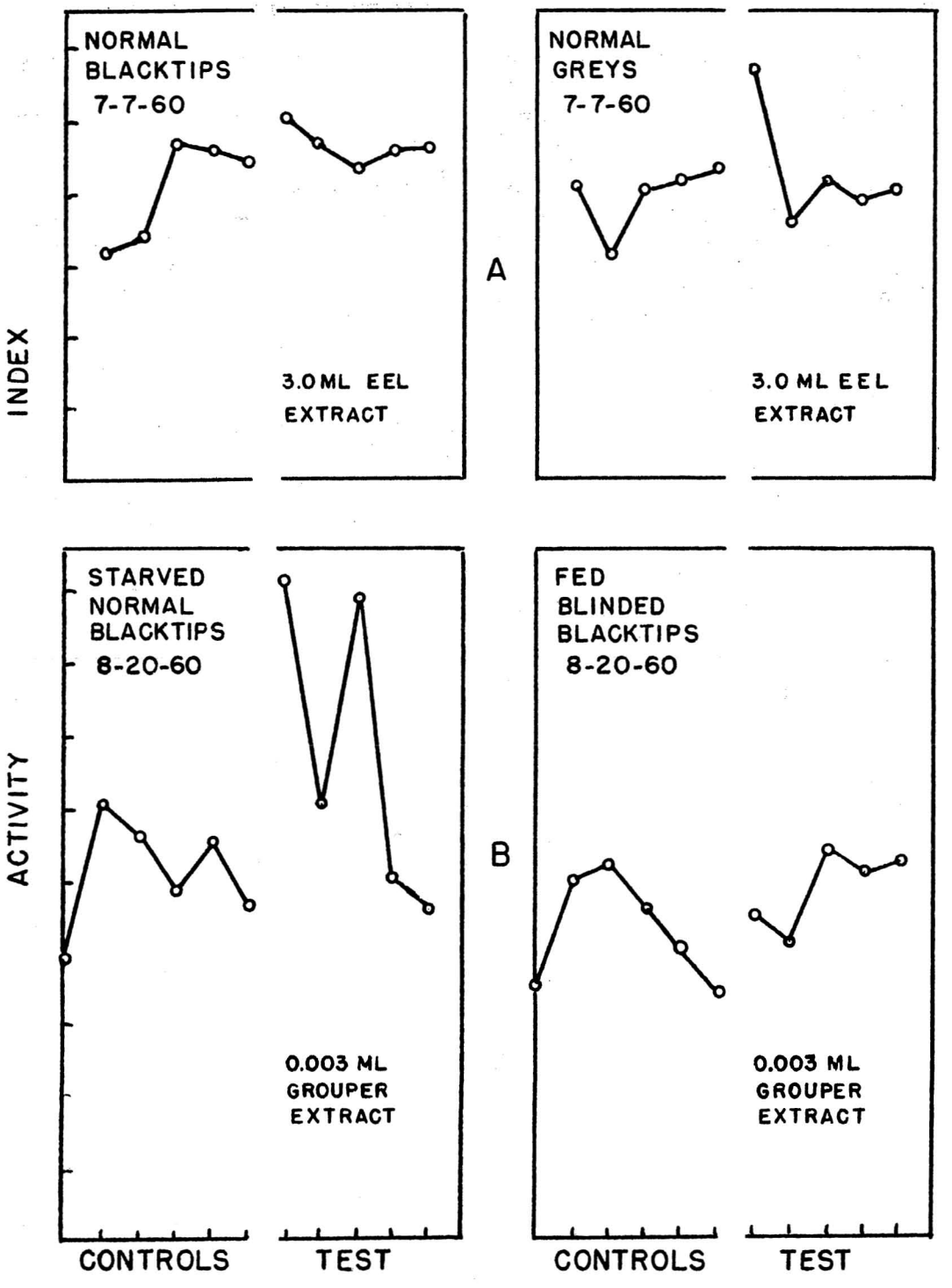

FIG. 6. Activity index during successive 2-min periods, illustrating (*A*) response of blacktip and grey sharks to standard eel extract, and (*B*) response of starved (normal) and fed (blinded) blacktip sharks to a 1/1000 dilution of standard grouper extract.

In 1960, four blacktip and four grey sharks were starved under close supervision. Of the blacktips, a 20-inch male died after 36 days, a 28-inch female died after 40 days, a 20-inch female died after 40 days and a 27-inch female survived for 43 days and was then fed. Of the greys, a 28-inch female died after 32 days and a 36-inch male died after 40 days. Two 30-inch females were starved respectively for 34 and 46 days and were then fed. During starvation, the sharks became very thin. Those which died had difficulty in maintaining their equilibrium for several hours before death; they could not be revived by forced feeding. These experiments show that small blacktip and grey sharks can survive for more than a month without food but that some will die after 5 or 6 weeks.

Using standard extract, tests were run at intervals to measure the response activity of both the starved blacktips and greys and, for comparison, that of four blinded blacktips which were fed two or three times a week. Activity data are given in Table 2.

The activity index for the fed sharks fluctuated from day to day but showed no trend. In contrast, the index for the starved sharks showed a more or less steady increase during both control and test conditions, particularly in the case of the blacktips. For the latter, the decrease in index on the last day is due to the moribund condition of two of the four sharks. As starvation proceeded, the sharks seemed to become increasingly restless and to respond with increasing vigor to the standard extract. Tests on the greys were discontinued after August 5, 1961 because of the death of one shark and the moribund condition of another (starvation began about 2 weeks earlier than with the blacktips).

Normally the blinded blacktips were more sensitive to odorous substances than the blacktips with normal vision. This situation was reversed when the latter sharks were starved. This is illustrated by one experiment (August 20, 1960) when both the blind, fed and the normal, starved sharks were tested with a 1/1000 dilution of standard extract (Fig. 6*B*). Using 0.003 ml (rather than the usual 3.0 ml) the fed sharks showed a weak attraction response which did not differ greatly from mere sensing. The starved blacktips on the other hand gave a strong attraction response which included the usual excited circling and hunting activity.

There is no doubt that hungry sharks are much more responsive than fed sharks to minute traces of odorous substances.

RESPONSE TO HUMAN MATERIALS

In this section are reported the results of tests on the response of normal and blinded blacktip sharks and normal grey sharks to human urine, blood and sweat, and to L-serine, a presumed component of human sweat. Other materials such as faeces and vomit were not investigated.

Urine

At Eniwetok, in both 1959 (eight tests) and 1960 (three tests) blacktip sharks were presented with human urine in quantities ranging from 3 to 80 ml of whole material. The urine was sensed, as indicated by a swirl or turn on encountering it, but there was no other consistent response.

TABLE 2

ACTIVITY INDEX OF FED (BLIND) AND STARVED (NORMAL) SHARKS TO STANDARD EXTRACT AT ENIWETOK MARINE BIOLOGICAL LABORATORY, 1960

DATE	FED BLACKTIPS		STARVED BLACKTIPS		STARVED GREYS	
	Controls	Test	Controls	Test	Controls	Test
7/20	29.2	41.2	31.0	40.4	33.8	60.4
7/23	21.2	32.0	31.8	44.2	23.8	38.6
7/29	34.8	37.6	57.4	76.8	52.6	74.2
8/5	29.6	54.0	50.6	71.2	86.3	96.8
8/18	27.2	36.2	56.0	97.0	—	—
8/25	23.4	32.2	36.4	49.2	—	—

TABLE 3

RESPONSE OF SHARKS AT ENIWETOK MARINE BIOLOGICAL LABORATORY TO HUMAN BLOOD

YEAR	MATERIAL AND SHARKS	RESPONSE*					
		RR	R-R?	O-S	A-A?	AA	Total
1959	Fresh or aged blood						
	Normal blacktips	–	4	4	1	–	9
	Blinded blacktips	1	4	2	2	–	9
	Total	1	8	6	3	–	18
1960	Aged blood (4–6 days)						
	Normal blacktips	1	2	1	–	–	4
	Blinded blacktips	–	2	3	–	–	5
	Normal greys	–	–	1	4	–	5
	Total	1	4	5	4	–	14
1960	Fresh blood (1–2 days)						
	Normal blacktips	–	–	2	2	2	6
	Blinded blacktips	–	–	2	2	3	7
	Normal greys	–	–	1	4	–	5
	Total	–	–	5	8	5	18

* RR, strong repulsion; R-R?, weak or doubtful repulsion; O-S, no apparent response or sensing; A-A?, weak or doubtful attraction; AA, strong attraction.

Blood

Most authors agree that blood in the water excites sharks. For example, Whitely (1940) notes that small blacktip sharks on the Great Barrier Reef would follow persons who had scratched their legs on coral and would dog their footsteps through slightly bloodied water. Bigelow and Schroeder (1948) remark that if persons in the water are bleeding from injuries the danger from shark attack may be imminent and the results may prove fatal. Moreover, they state that the more voracious of the larger sharks are excited by blood in the water to such a degree that they will make ferocious attacks whether the object be fish, whales, or man, dead or alive. In contrast, based on experience with releasing turtle and sheep blood while fishing for sharks, Wright (1948) concluded on admittedly weak evidence that blood alone, without the presence of some moving object, did not release the attack pattern. Steinberg (1961) reports that a captive lemon shark was not attracted by solution of dried beef blood.

The results of experiments with human blood in 1959 are included in Table 3. The responses were much more variable and erratic than those with food extract. A sensing was at times followed by an attraction response and at other times by an apparent flight reaction and a tendency to avoid the test area. The erratic behavior was unlikely related to a visual stimulus as it occurred in both the blinded sharks and those with normal vision. Moreover the quantities used, even when the techniques were being developed, were not sufficient to produce noticeable coloration in the water. It was suspected that the variability in response was related to the freshness of the blood.

In 1960, 32 experiments were conducted with human blood. The results are summarized in Table 3 and are given in detail in Table 7. Quantities ranged from 0.03 to 6.0 ml of a suspension of 5 ml of whole blood in 250 ml of sea water. With fresh blood tested within 1 or 2 days after collection, 3.0 ml of the suspension usually produced a moderate or strong attraction response with the usual behavior components: excited circling, swirling and hunting. An attraction response was obtained with 0.3 ml of the fresh suspension on several occasions and with as little as 0.03 ml in one test. By the use of dye it was estimated that the shark first encountered the material when it had mixed with ¼ to ½ of the volume of the test compartment. If this dilution is assumed, it may be estimated

that the sharks were attracted to human blood at a concentration of about 0.1 to 0.01 parts per million of sea water.

A blood suspension held under refrigeration for 4 days or longer usually underwent hemolysis and acquired a faint to strong putrid odor. The aged blood produced erratic results with blacktip sharks as had been suspected in the 1959 tests. At times there was only a sensing of the material, an avoidance of the area, or possibly a slight attraction. At other times there seemed to be a "startled" or "alarm" reaction with speeding from the area such as had been noticed the previous year. This was classed as repulsion. With grey sharks, on the other hand, the hemolyzed blood seemed more consistently attractive.

Our results prove that fresh blood excites blacktip and grey sharks and promotes a strong hunting response. They suggest that decomposed human blood contains a component which is repellent to blacktips.

Sweat

A large number of experiments were conducted at both the Eniwetok and the Hawaii laboratories on the response of sharks to human sweat. They were stimulated by the observation of Brett and McKinnon (1954) that water in which human hands had been rinsed retarded the upstream migration of salmon and induced an "alarm" response.

Sweat was collected initially by sponging the body and wringing the sponge in 500 ml of sea water. Later, at Eniwetok it was collected directly from the body as it ran down arms, chest and abdomen in the hot, humid atmosphere of the shark house, and at Hawaii it was collected in the same way by exercising and subjecting the body to heat lamps. The material was tested according to the standard procedures already described. Each sweat test was usually followed or preceded by standard extract to appraise the sharks' responsiveness to a known attractant.

The results of 29 tests conducted on normal and blinded blacktip sharks at Eniwetok are included in summary form in Table 4 and are given in detail in Table 8. The majority of the tests yielded results which were classed as repulsion. A weak repellent effect (R) was comprised of an initial sensing, followed by a slowing of swimming speed, an apparent wariness,

TABLE 4

RESPONSE OF SHARKS TO HUMAN SWEAT AT ENIWETOK MARINE BIOLOGICAL LABORATORY (EMBL) AND HAWAII MARINE LABORATORY (HML)

YEAR	LABORATORY AND SHARKS	RESPONSE*					
		RR	R-R?	O-S	A-A?	AA	Total
1959	EMBL, Normal blacktips	1	6	3	1	–	11
	Blinded blacktips	8	9	1	–	–	18
	Total	9	15	4	1	–	29
1960	EMBL, Normal blacktips	5	7	1	1	–	14
	Blinded blacktips	2	4	1	–	–	7
	EMBL, Normal greys	–	9	6	–	–	15
	Total	7	20	8	1	–	36
1959–60	HML, tiger, Pond 2	1	3	2	–	–	6
	HML, tiger, grey, hammerhead, Pond 5	–	8	7	–	–	15
	Total	1	11	9	–	–	21
1960–61	HML, tiger, greys, Pond 5	–	3	2	–	–	5
Total		17	49	23	2	–	91

* RR, strong repulsion; R-R?, weak or doubtful repulsion; O-S, no apparent response or sensing; A-A?, weak or doubtful attraction; AA, strong attraction.

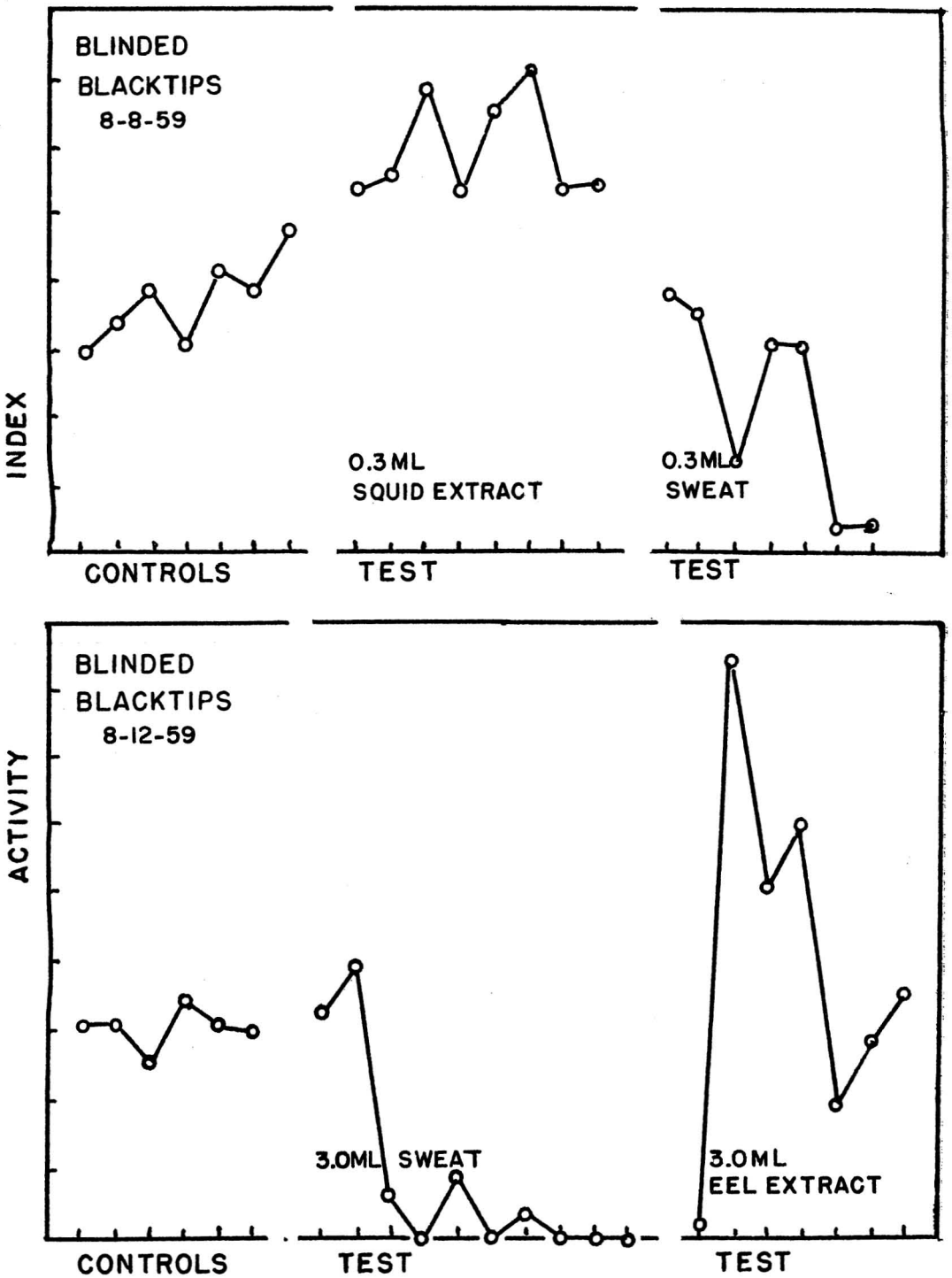

FIG. 7. Activity index during successive 2-min periods in two experiments, illustrating the difference in response of blinded blacktip sharks to human sweat and to food extract.

TABLE 5

INDEX OF ACTIVITY IN SUCCESSIVE RINGS (NO. 1, CENTER) OF A TARGET AREA FOR A HAMMERHEAD SHARK DURING SUCCESSIVE TESTS OF "TILAPIA WATER" AND HUMAN SWEAT IN POND 5, HAWAII MARINE LABORATORY, JUNE 16, 1960

TEST	RING NUMBER				AVERAGE
	1	2	3	4	
Controls, sea water	4.5	5.5	14.8	20.7	11.4
Tilapia water	27.3	29.3	22.0	11.8	22.6
Sweat	5.4	8.3	13.1	12.3	9.8
Tilapia water	28.4	36.8	29.4	20.6	28.8
Controls, sea water	15.0	19.1	16.9	20.0	17.7
Tilapia water plus sweat	15.1	30.0	21.2	16.9	20.8

and a tendency to avoid the test area. A strong repellent effect (RR) included in addition a rapid exit from the area following sensing, sometimes accompanied by head shaking. When no noticeable response occurred it was found usually that this was also the case with the known attractant. In the one case classed as doubtful attraction, the first sweat test which was conducted, it is likely that initial sensing was interpreted as attraction. The quantitative data of Table 8, illustrated for two experiments in Figure 7, give convincing evidence of a depression of shark activity following the introduction of sweat. In each of the 29 tests, the time spent in the test areas during test conditions was less than during control conditions; this is in striking contrast to the results with standard extract where the reverse is almost invariably encountered.

The apparent aversion to sweat was exhibited by both normal and blinded blacktips, possibly to a greater extent in the latter. The sweat of one donor (ALT) seemed to be effective at a roughly-calculated concentration of about 1 part per million. The sweat of a second donor (TAP) produced no obvious repellent effects in the two tests which were made.

Because of the possibility that the sharks in 1959 had become conditioned to associate sweat with punishment, e.g., from handling, the experiments were repeated during 1960, taking precautions against sweat dripping accidentally into the water and using fresh sharks, some of which had not been touched by hand. The results in 1960 were similar to those in 1959 (Tables 4, 9). With the blacktips the majority of the responses were classed as repulsion; in the one case of apparent attraction, again the first test of the season, the sharks had just been introduced and still exhibited erratic behavior. There was no noticeable difference in response between the blinded and normal blacktips. With the grey sharks an aversion to human sweat was present in the majority of the tests but it seemed less pronounced than with the blacktips. There were no obvious differences in response between the sweat of three donors. The sweat did not decrease in potency with aging at room temperature for several days; rather, its repellent properties seemed to increase but this could not be established with certainty.

In tests conducted during the winter of 1959–60 on the tiger, hammerhead, and grey sharks at the Hawaii laboratory, larger quantities of sweat (10–40 ml) were used because of the greater volume of the ponds compared with the Eniwetok tanks. In most cases the results, summarized in Table 4, showed vague repellent effects following the introduction of sweat. For the most part, the sharks displayed only a tendency to avoid the test area (R?), occasionally with a sharp veering from the presumed location of the material and rapid swimming through or away from the test area (R). Apart from these latter overt responses which were displayed on occasion by all three species, the only strong repulsion concerned the tiger shark in one test and consisted of obvious "agitation" and head shaking. Repellent effects were noted with the sweat of all three donors (ALT, RJ, and ESH) but more consistently with that of the first two than the last.

A different technique was employed in tests with the hammerhead which was particularly responsive to attractants. The introduction hose running from the funnel on top of the tower was submerged just below the surface at the center of a bullseye target area 32 ft in diameter, the boundaries of which were judged by eye from reference points on the bottom. During control conditions, sea water was introduced from the funnel. During test conditions the following materials were used in varied sequence: (1) an attractant consisting of water from the funnel in which fish (*Tilapia*) were swimming, (2) 50 ml of sweat mixed with sea water in the funnel, and (3) a mixture of the attractant and sweat in sea water. Activity data on one test are given in Table 5. Based on records of the time spent and the path followed by the shark in the target area, activity was calculated as the distance swum in each of four rings of the target per unit of time. It is apparent that, in general, activity was greatest with the attractant, intermediate with the mixture of sweat and attractant, and least (less than controls) with sweat alone. The sweat depressed but did not eliminate the response to the attractant.

By tracing the spread of materials in the pond with the use of dye and calculating the volume of sea water involved, it was concluded that the actual sea water concentration of sweat in the pond experiments at the Hawaii laboratory were still considerably less than those used in the tank experiments at Eniwetok. Additional experiments were undertaken during the early summer of 1961 using much larger quantities of sweat (100–400 ml per test) and the improved "curtain-drum" method of introduction. The results are summarized in Table 4. Despite the larger quantities of sweat which were used no strong repulsion was noted. In the five tests, there was weak or doubtful repulsion in three and sensing only in two. In those tests indicating repulsion, all three species of sharks, especially the tiger, showed definite signs of aversion including veering from the curtain and gill flexing. The sweat of one donor (SK) seemed to be more active than that of the other (BLO).

From the above experiments on blacktip, grey, tiger, and hammerhead sharks one cannot conclude that human sweat, per se, is an active shark repellent. On the other hand, it is certain that human sweat does contain, at least at times, a component which is aversive to sharks. Occasionally this induces overt signs of repulsion such as head shaking, gill flexing, veering, and rapid retreat; more frequently it induces only a subtle wariness manifested chiefly by avoidance of the area of introduction. The response is highly variable. This is unfortunate but almost inevitable when one considers the uncontrolled environmental conditions and the many factors which could contribute to both the variability of shark behavior and variability of sweat composition.

Steinberg (1961) found no evidence of repellent properties in either human sweat or pure compounds forming constituents of human sweat in tests with a captive lemon shark at the Lerner Marine Laboratory. Unfortunately he gives no information on the concentrations of material used. Moreover, he reports that the lemon shark was not responsive to solutions of dried beef blood nor would it eat chunks of fresh shark liver which, at other times, had been particularly attractive to captive sharks. His negative results are understandable. It has been our experience that sharks which have not yet fed in captivity do not respond to either highly attractive substances such as eel extract or fresh human blood, nor do they respond to subtle repellent substances such as human sweat.

In view of the results of this series of tests, it seems safe to assume that shark attack on humans is not motivated by the smell of human sweat.

L-serine

Following the discovery by Brett and McKinnon (1954) that human hand rinse retarded the migration of salmon, Idler, Fagerlund, and Mayoh (1956) undertook an analysis of hand rinse to determine the repellent component(s). By employing various fractionation techniques and testing the fractions on migrating salmon, they were able to identify the active fractions as amino acids of which serine was a major component. In further tests, the L-isomer of serine was found to induce the alarm response whereas D-isomer did not. They stated "L-serine definitely elicited a typical alarm reaction but the effects were neither so dramatic nor so long a duration as the response obtained by hand

rinse." As hand rinse doubtless contained sweat and as sweat produced a repellent effect on sharks, it was decided to investigate their response to L-serine.

Three tests were conducted at the Hawaii laboratory on the tiger shark in Pond 2, during the winter of 1959–60, using 1.0 gm of L-serine per test. In the first, there was no overt response except an obvious sensing on encountering the material. In the second, the shark showed a sensing of the material, followed by rapid exits from the area and violent head shaking. In the third test, there was no noticeable response. In all three, however, the time spent in the test area during test conditions was less than during controls, as had also been the case with sweat.

Three tests were conducted on blacktip sharks at the Eniwetok laboratory in 1960, using 6 ml of a solution containing 1.0 gm of L-serine (i.e., 0.12 gm per test). No repellent effects were noted other than a "wariness" in one test. Again, however, the time spent in the test area during test conditions was less than during controls.

As definite repellent results had been noted in one test with the tiger shark, it was decided to run a third series at the Hawaii laboratory during the summer of 1961, using much larger quantities of L-serine despite its high cost. Three tests were conducted on the tiger and grey sharks co-inhabiting Pond 5, using the "curtain-drum" technique.

In all three tests the tiger shark displayed an aversion to the chemical but only after introduction of the material had been completed. Introduction required about 10 min (three to four 3-min periods). It seemed either that the response occurred after a threshold concentration of the material had been reached, or that there was a latent period between exposure to the material and response. The overt response was a violent head shaking either while in or while leaving the area of concentration. At times this took place at the surface and caused considerable splashing. However, in only the first test (25 gm L-serine) was there frequent rapid exit from the area on encountering the material. In the second test (50 gm L-serine) there was swerving and head shaking after encountering the material, but no turning-back on initial encounter. The response was less pronounced than in the first test even though twice the quantity of material had been used. This may have been due to a higher tide and thus a larger volume of water and greater dilution of the material despite the larger quantity used. The shark frequently avoided the material by swimming in the shallows on the far side of the pond. In the third test (25 gm L-serine plus 10 ml of a 99% nicotine solution), the tiger shark again displayed agitation and head shaking. The response, however, occurred less frequently than in the other two experiments. The nicotine had been added in the hope of a synergistic effect; it had been our impression that the sweat of smokers was more repellent to the sharks than that of nonsmokers. Possibly it tended to inhibit rather than increase the effect of L-serine.

The grey sharks, in contrast to the tiger shark, were not obviously agitated by L-serine; no head shaking or gill flexing was observed. In the first test, two grey sharks of the same species veered sharply on first encountering the material and returned to the end of the pond. Thereafter all three grey sharks circled in the end zone for the duration of the experiment. In the second test no veering was noted but there was repeated circling in the end zone. It was uncertain whether this could be interpreted as a repellent effect, for the same habit was noted occasionally during control periods. In the third test, all three grey sharks passed through the test area without signs of awareness, agitation, or repulsion.

Although there is no doubt that the tiger shark was actively repelled by L-serine, the physiological mechanism producing the response is unknown. We can offer no satisfactory explanation of the difference in response of the tiger and the greys to L-serine. It may have involved species differences in physiological effect or differences in the concentration of materials to which they were subjected. The latter is possible even though the tests were conductd simultaneously on the tiger and the greys, for uneven curtains of material were formed by tidal currents in all three tests and the shallow-swimming tiger shark may have encountered different concentrations than the deep-swimming grey sharks. It may be added, however, that directly opposite results were obtained with a highly irritating lachrimator which is presently

FIG. 8. View of a tiger shark attempting to swallow a spiny puffer. (Photograph by E. S. Hobson.)

being tested as a potential shark repellent. With this substance, the greys responded violently with gill flexing, head shaking, and definite avoidance of the curtain. The tiger shark, on the other hand, was not noticeably affected until the concentration of the material had been doubled.

In the foregoing sections it has been shown that certain species of sharks have an aversion to and at times are repelled by aged food extracts, aged human blood, fresh or aged human sweat, and finally L-serine. Serine, presumably the D-isomer, is a common amino acid in both foodstuffs and blood. It may by hypothesized that at least one of the repelling substances in all of the above materials is L-serine, which is presumably present as the L-isomer in human sweat, but which may be formed in foodstuffs and blood from the nonrepellent D-isomer during decomposition.

It has *not* been demonstrated that L-serine has sufficiently active repellent properties to deter shark attack on prey, including man. However its repellent properties, its presence in human sweat, and its possible generation during the decomposition of foodstuffs and blood warrant further investigation.

RESPONSE TO LIVING FISH

Although at times sharks may obtain a large portion of their food by scavenging dead materials, they also feed on living prey. When the prey is wounded, the sharks are doubtless attracted by the odor of body juices as well as by visual and possibly by other stimuli. It is

reasonably certain that most species also attack healthy, undamaged, living prey, although apart from attack on man, observations of feeding activity are singularly lacking in the literature.

In the summer of 1959, a group of biologists from the Hawaii Marine Laboratory witnessed the persistent attack of a tiger shark on a spiny puffer which had inflated itself and was floating at the surface in Kaneohe Bay. The shark's attempts to swallow the puffer (Fig. 8) lasted for about 10 min despite the presence of the observers who circled in an outboard motor boat. During the shark's slow, awkward passes at the puffer the sound of its jaws clamping together as it missed the prey could be heard.

Other species of sharks are capable of catching fast moving prey. For example, Eibl-Eibesfeldt and Hass (1959) observed both the grey shark (*Carcharhinus menisorrah*) and the blacktip (*C. melanopterus*) actively feeding on healthy fish in the Indian Ocean, and even herding them against the shoreline to facilitate capture.

Although vision is doubtless the predominating sense which is used by sharks on converging on living undamaged prey, it is possible that olfaction may also be involved. I have found only one observation in the literature which supports this possibility, that reported by Sheldon (1911) and again by Parker and Sheldon (1913), who found that the dogshark (*Mustelus canis*) was able to locate undamaged living crabs concealed in a wrapping of eelgrass. The response of sharks to living, presumably undamaged fish was investigated at both the Eniwetok and the Hawaii laboratories.

Results

In one series of experiments at Eniwetok in 1959, an empty wire cage (about 6 × 6 × 12 inches) was silently lowered to the bottom of a test area at the upstream end of a compartment containing four blinded blacktip sharks. After the usual series of control periods during which activity was recorded, the cage was removed, a living fish was added, and it was again lowered into the test area when the sharks were at the far end of the compartment. Activity was again observed during a series of test periods. The water flow was maintained during both control and test conditions.

The results are included in Table 6. In most of the experiments attraction responses were obtained with a 12-inch grouper (*Epinephalus fuscoguttatus*), an 8-inch squirrel fish (Holocentridae), and an 8-inch stone fish (*Synancaja verrucosa*). Although probably excited by confinement in the cage, the fish did not move about much after the cage had been lowered. There was often a delay of several test periods before the sharks showed any response. Then, in most of the experiments, one or more sharks suddenly

TABLE 6

RESPONSE OF SHARKS AT ENIWETOK MARINE BIOLOGICAL LABORATORY TO LIVING FISH, 1959

SHARKS AND FISH	RESPONSE*					
	RR	R-R?	O-S	A-A?	AA	Total
Blinded blacktips						
Caged grouper	–	–	1	3	1	5
Caged squirrel fish	–	–	1	1	2	4
Caged stonefish	–	–	–	2	–	2
Total	–	–	2	6	3	11
Blinded blacktips						
Grouper water, grouper present	–	–	1	2	2	5
Grouper water, grouper absent	–	–	2	–	1	3
Eel water, eel present	–	–	–	1	–	1
Blacktip water, blacktip absent	–	–	2	–	–	2
Total	–	–	5	3	3	11

* RR, strong repulsion; R-R?, weak or doubtful repulsion; O-S, no apparent response or sensing; A-A?, weak or doubtful attraction; AA, strong attraction.

TABLE 7

RESPONSE OF NORMAL BLACKTIP SHARKS (NB), BLINDED BLACKTIP SHARKS (BB), AND NORMAL GREY SHARKS (NG) TO HUMAN BLOOD AT ENIWETOK LABORATORY, 1960

DATE (1960)	TIME	TANK	SHARKS	BLOOD (ML)	DONOR, DATE	ACTIVITY INDEX		RESPONSE*
						Controls	Test	
7/12	0954	I (F-I)	2BB	3.0	JK 7/8	26.0	9.0	R
	1040	II (A-C)	2NG	3.0	JK 7/8	13.0	20.2	A
	1108	I (A-D)	2NB	3.0	JK 7/8	57.8	39.0	R
	1445	I (F-I)	2BB	6.0	JK 7/8	21.6	6.6	R
	1515	II (A-C)	2NG	6.0	JK 7/8	19.8	24.6	A
	1540	I (A-D)	2NB	6.0	JK 7/8	15.6	13.2	R?
7/18	1529	I (F-I)	2BB	3.0	JK 7/8	21.6	24.6	O?
	1552	I (A-D)	2NB	3.0	JK 7/8	37.2	17.8	RR
	1645	II (A-C)	2NG	3.0	JK 7/8	11.0	10.0	O?
7/21	1015	I (F-I)	4BB	3.0	ALT 7/20	22.8	35.6	AA
	1045	I(A-D)	4NB	3.0	ALT 7/20	27.7	26.4	O?
	1135	II (A-C)	4NG	3.0	ALT 7/20	37.4	49.8	A
	1350	I (F-I)	4BB	3.0	ALT 7/20	30.4	39.2	AA
	1415	I (A-D)	4NB	3.0	ALT 7/20	21.8	28.0	A
	1450	II (A-C)	4NG	3.0	ALT 7/20	33.7	44.2	A
7/22	1015	I (F-I)	4BB	0.3	ALT 7/20	26.4	41.6	AA
	1045	I (A-D)	4NB	0.3	ALT 7/20	31.6	40.0	AA
	1135	II (A-C)	4NG	0.3	ALT 7/20	24.6	35.2	A
	1405	I (F-I)	4BB	0.03	ALT 7/20	30.6	35.0	A
7/26	0910	I (F-I)	4BB	3.0	ALT 7/20	22.8	25.0	O?
	1000	I (A-D)	4NB	3.0	ALT 7/20	51.0	46.4	O?
	1135	II (A-C)	4NG	3.0	ALT 7/20	28.9	40.8	A
	2035	I (F-I)	4BB	3.0	ALT 7/20	34.6	36.8	O
	2150	II (A-C)	4NG	3.0	ALT 7/20	31.0	36.8	A
7/27	0925	I (F-I)	4BB	0.3	SK 7/26	23.6	27.6	O
				1.0	SK 7/26	—	22.6	O
				3.0	SK 7/26	—	31.8	A
	1045	I (A-D)	4NB	0.3	SK 7/26	45.6	46.2	O
				1.0	SK 7/26	—	56.0	A
				3.0	SK 7/26	—	57.2	AA
	1500	II (A-C)	4NG	1.0	SK 7/27	46.8	53.2	O
				3.0	SK 7/27	—	52.2	A

* RR, strong repulsion; R, weak repulsion; O, no apparent response except sensing; A, weak attraction; AA, strong attraction.

became excited and engaged in the typical hunting response. It is assumed that they were stimulated by odors emanating from the fish. In view of the delayed response, it seems unlikely that the blinded sharks were attracted by vibrations or sounds that may have been made by the fish although this possibility could not be ruled out in these rather crude experiments.

In another series of experiments at Eniwetok in 1959, an uninjured fish was held in a bucket of saltwater for 15 to 20 min prior to an experiment. The bucket was slapped or agitated

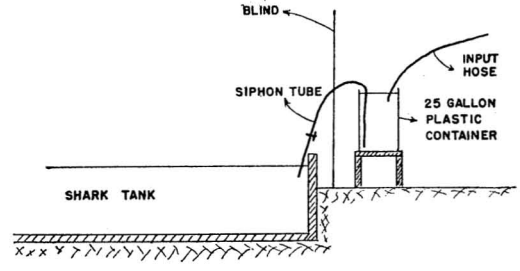

FIG. 9. Diagram of apparatus used at Eniwetok Marine Biological Laboratory for investigating response of sharks to living fish.

to keep the fish in an excited state. During control conditions, water from another bucket of sea water was siphoned into the test area of the compartment containing the four blinded blacktip sharks. The siphon was then switched to the bucket of water which either contained the fish or from which the fish had been removed. The usual observations were made during a series of control and test periods.

The results are included in Table 6. The blinded blacktip sharks showed an attraction response in most of the experiments with the "grouper water" and in the one experiment with "eel water" (*Gymnothorax*). It was concluded that the water in which these fish had been confined contained some substance which was attractive to the sharks. The blinded blacktips did not show a noticeable attraction response to "blacktip water."

During the winter of 1959–60 similar ex-

TABLE 8

RESPONSE OF NORMAL BLACKTIP SHARKS (NB) AND BLINDED BLACKTIP SHARKS (BB) TO HUMAN SWEAT AT ENIWETOK LABORATORY, 1959

DATE (1959)	TIME	TANK	SHARKS	SWEAT (ML)	DONOR, DATE	ACTIVITY INDEX		RESPONSE*
						Controls	Test	
8/8	1905	I (A-D)	3NB	0.3	ALT 8/8†	97.7	65.9	A?
	1930	I (A-D)	3NB	0.3	ALT 8/8†	—	73.7	R
	2115	I (F-I)	3BB	0.3	ALT 8/8†	67.6	52.7	R
8/9	1800	I (F-I)	2BB	3.0	ALT 8/8†	29.4	14.1	RR
	1945	I (A-D)	2NB	3.0	ALT 8/8†	54.4	41.7	R
8/10	0845	I (A-D)	2NB	3.0	ALT 8/8†	54.0	52.2	O
	0925	I (F-I)	2BB	3.0	ALT 8/8†	45.0	26.8	R
8/11	2322	I (F-I)	2BB	2–3	TAP 8/11	39.4	25.0	O?
8/12	0035	I (A-D)	2NB	2–3	TAP 8/11	70.0	58.8	O?
	1910	I (F-I)	2BB	3.0	ALT 8/8†	29.5	9.3	RR
	2010	I (A-D)	2NB	3.0	ALT 8/8†	73.6	61.9	R
8/13	1553	I (F-I)	2BB	3.0	ALT 8/8†	33.0	5.9	RR
	1710	I (A-D)	2NB	3.0	ALT 8/8†	68.2	58.5	R
8/14	1905	I (F-I)	2BB	3.0	ALT 8/14	54.0	35.3	RR
	2025	I (A-D)	2NB	3.0	ALT 8/14	67.0	57.7	R
8/16	1900	I (A-D)	2NB	0.06	ALT 8/14	80.8	77.8	O
	1930	I (A-D)	2NB	3.0	ALT 8/14	—	74.2	R?
	2010	I (F-I)	2BB	3.0	ALT 8/14	9.2	5.7	R
8/18	1355	I (A-D)	2NB	50.0	ALT 8/8†	34.8	17.5	RR
8/24	2010	II (G-I)	4BB	10.0	ALT 8/8†	85.7	56.3	RR
8/25	1515	II (G-I)	1BB	10.0	ALT 8/8†	24.2	1.9	RR
8/31	1930	I (F-I)	2BB	3.0	ALT 8/31	26.9	12.2	RR
9/1	2155	I (F-I)	2BB	3.0	ALT 8/31	37.0	32.0	R
9/3	1450	I (F-I)	3BB	3.0	ALT 8/8†	38.6	13.5	RR
	1900	I (F-I)	3BB	3.0	ALT 8/8†	53.0	36.0	R
	2145	I (F-I)	3BB	3.0	ALT 8/8†	49.6	35.2	R
9/4	1930	I (F-I)	2BB	3.0	ALT 9/4	37.0	24.2	R
	2145	I (F-I)	2BB	3.0	ALT 9/4	38.0	22.6	R
9/5	1400	I (F-I)	2BB	3.0	ALT 8/8†	21.6	12.2	R

* RR, strong repulsion; R, weak repulsion; O, no apparent response except sensing; A, weak attraction; AA, strong attraction.

† Sweat collected by sponge.

TABLE 9

RESPONSE OF NORMAL BLACKTIP SHARKS (NB), BLINDED BLACKTIP SHARKS (BB), AND NORMAL SHARKS (NG) TO HUMAN SWEAT AT ENIWETOK LABORATORY, 1960

DATE (1960)	TIME	TANK	SHARKS	SWEAT (ML)	DONOR, DATE	ACTIVITY INDEX		RESPONSE*
						Controls	Test	
6/30	1250	I (A-D)	2NG	3.0	ALT 6/29	14.6	13.2	R
	1340	I (A-D)	2NG	3.0	ALT 6/29	12.2	8.0	R
	1350	I (A-D)	2NG	5.0	ALT 6/30	—	7.4	R
	1530	I (A-D)	2NG	3.0	ALT 6/29	13.8	10.0	R
	1555	I (A-D)	2NG	6.0	ALT 6/29	8.7	8.6	O
7/1	1007	I (A-D)	2NG	3.0	ALT 6/29	17.0	18.0	O
	1035	I (A-D)	2NG	6.0	ALT 6/29	17.8	17.6	O
	1105	I (F-J)	2NG	3.0	ALT 7/1	13.2	7.0	R
	1130	I (F-J)	2NG	6.0	ALT 7/1	7.4	8.3	O
	1400	I (A-D)	2NG	6.0	ALT 7/1	13.6	8.8	R
	1422	I (F-I)	2NG	6.0	ALT 7/1	14.0	12.2	R
	1942	I (A-D)	2NG	6.0	ALT 7/1	22.4	17.8	R
7/2	0903	I (A-D)	2NG	6.0	ALT 7/1	18.4	18.6	O
	1140	I (F-I)	2NB	3.0	ALT 7/2	50.5	92.8	A?
	1430	I (F-I)	2NB	6.0	ALT 7/2	68.5	71.1	O
	1445	I (A-D)	2NG	9.0	ALT 7/2	18.4	15.6	R
7/6	1300	I (A-D)	2NB	5.0	SK-ALT 7/2	52.2	23.2	RR
	1400	I (F-I)	2BB	6.0	JK 7/6	31.4	31.0	R?
	1430	I (A-D)	2NB	6.0	SK 7/6	47.0	31.4	R
7/7	0905	I (A-D)	2NB	6.0	JK 7/6	40.8	33.8	R?
7/9	1010	I (A-D)	2NB	3.0	SK 7/6	20.0	7.0	RR
	1500	I (A-D)	2NB	3.0	JK 7/6	22.6	5.4	RR
7/11	0839	I (A-D)	2NB	3.0	SK 7/6	33.0	29.0	R
	1549	I (A-D)	2NB	3.0	JK 7/6	31.4	10.4	RR
7/19	1055	I (F-I)	2BB	3.0	SK 7/6	24.6	14.2	RR
	1120	I (A-D)	2NB	3.0	SK 7/6	31.4	31.6	R?
	1145	II (A-C)	2NG	3.0	SK 7/6	7.8	10.0	O
7/20	1505	I (F-I)	4BB	3.0	JK 7/6	25.4	18.6	RR
	1530	I (A-D)	4NB	3.0	JK 7/6	15.4	15.2	R
7/23	1243	I (F-I)	4BB	3.0	SK 7/11	20.4	24.8	O
7/24	1450	I (F-I)	4BB	3.0	ALT 7/23	23.8	22.6	R
	1655	I (A-D)	4NB	3.0	ALT 7/23	28.8	13.2	RR
7/25	0940	I (F-I)	4BB	3.0	ALT 7/23	25.2	18.4	R
	1020	I (A-D)	4NB	3.0	ALT 7/23	33.8	25.4	R
8/25	1230	I (F-I)	4BB	3.0	ALT 8/25	28.0	26.2	R
	1300	I (A-D)	4NB	3.0	ALT 8/25	34.0	32.2	R

* RR, strong repulsion; R, weak repulsion; O, no apparent response except sensing; A, weak attraction; AA, strong attraction.

periments were conducted at the Hawaii laboratory on the population of sharks in Pond 5, which at that time consisted of a tiger, a hammerhead, and a grey shark. The method of "point introduction" was used. During tests, three or four uninjured fish (*Tilapia mosambique*) were confined in the 5-gal funnel of sea water on top of the tower. During tests, the water from the funnel containing the fish was introduced through the hose. This produced a strong hunting response in the hammerhead. The response of the tiger shark and the grey

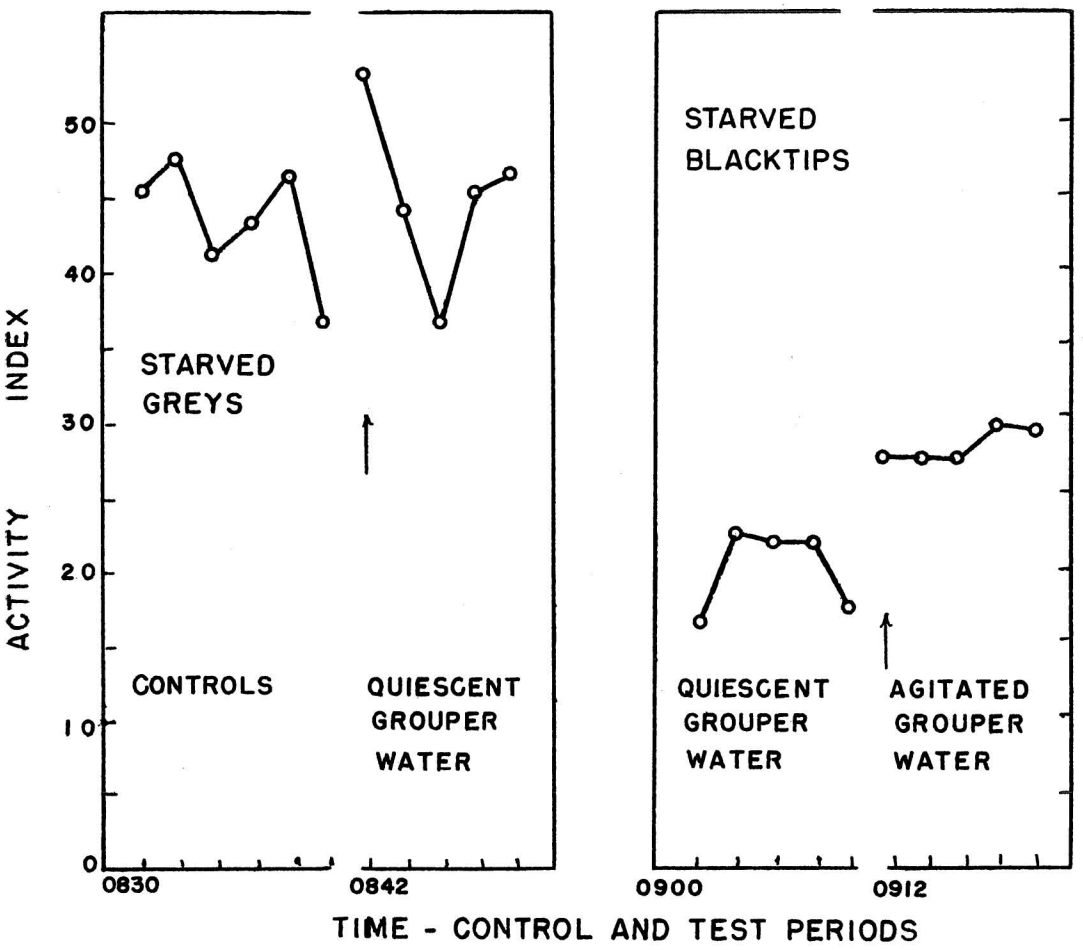

FIG. 10. Activity index during successive 2-min periods, illustrating response of starved grey sharks to "quiescent grouper water" and of starved blacktip sharks to "agitated grouper water."

shark was positive but less intense. "Tilapia water" was the attractant used in the experiment involving human sweat which was described earlier.

Several, more definitive experiments were conducted at Eniwetok during the summer of 1960 using an experimental arrangement illustrated in Figure 9. Living fish were placed in a 25-gal plastic container into which sea water was flowing. The sea water could be siphoned from the container into the test area of either Tank 1 or Tank 2, or it could be spilled to the ground. The compartment of Tank 1 contained four starved blacktip sharks and that of Tank 2 held four starved grey sharks, all with normal vision. One observer, manipulating the siphons and living "prey" fish, was concealed from the sharks by a blind; a second observer, recording data on shark behavior, was concealed in the observation booth.

Only two of several experiments will be described in detail. In one (Fig. 10), four groupers (*Epinephelus merra*) had been placed in the container the previous night, with the water siphoning into the blacktip compartment. In the morning, following a series of control periods which started at 0830 (timed on a 24-hr clock), the "quiescent grouper water" was siphoned into the grey shark compartment. In the first test period (at 0842) the grey sharks

showed obvious awareness and mild attraction, with one shark biting the siphon tube, but the response quickly subsided. Siphoning into the blacktip compartment was then resumed (at 0900) with no noticeable response from the sharks; this was anticipated as the water had been siphoning into this compartment all night. The groupers were then frightened and excited by threatening them with a moving stick. There followed a noticeable hunting reaction by the blacktips (at 0912), stimulated by the "agitated" grouper water. Similar results were obtained with both starved blacktip and grey sharks using quiescent and agitated surgeon fish and mullet in place of the groupers.

In the second experiment to be described in detail (Fig. 11), the grey sharks showed a normal behavior pattern during control periods which started at 1600. When "quiescent grouper water" was introduced (at 1612) they responded, as above, with a mild hunting reaction; one bit the tube and others milled near it. In the meantime, a small grouper had been removed from the aquarium and held in a dip net in air for 30 min, at which time it was still alive and apparently undamaged. Wth the water from the quiescent groupers still flowing into the grey shark compartment, the "distressed" grouper was quietly lowered into the container (at 1622) by a string tied around its body; it was removed after the third test period (1628). The sharks displayed a violent hunting reaction with circling and biting of the tube. The "quiescent grouper water" continued to siphon into the compartment for about 1 hr, at which time (1730) the sharks exhibited normal activity during control conditions. The small grouper which had been returned to the dip net and was still alive after 74 min, was again lowered into the container (at 1740) for three test periods.

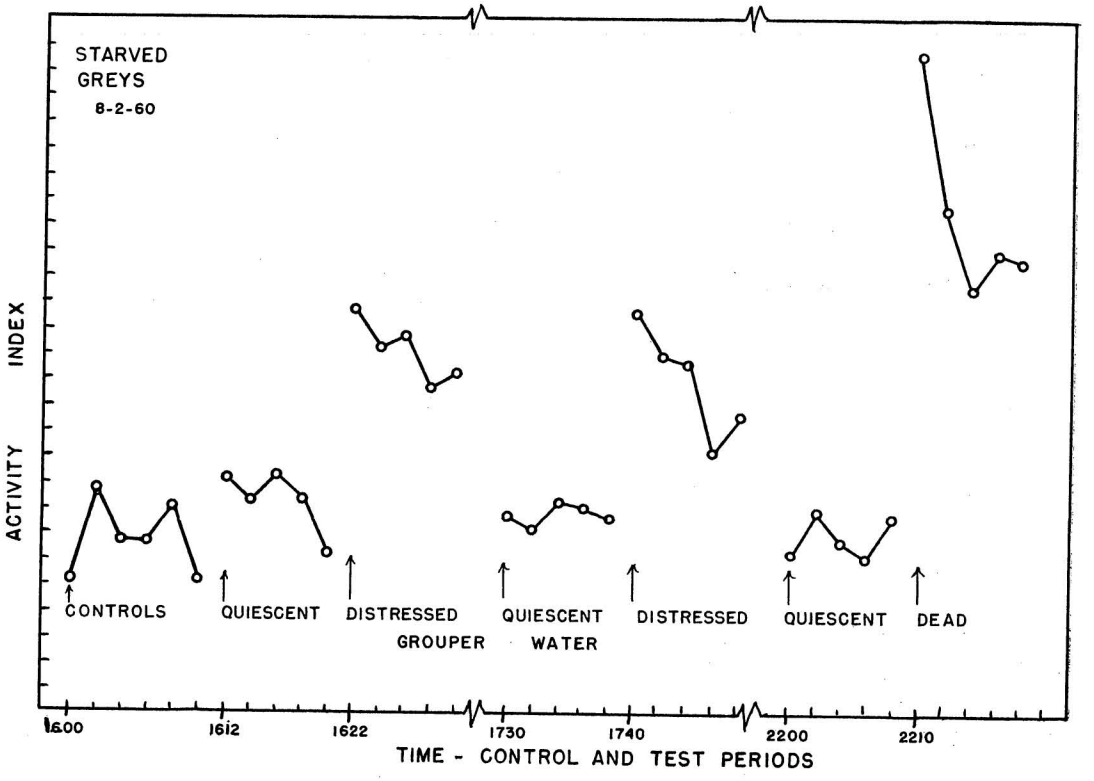

FIG. 11. Activity index during successive 2-min periods, illustrating response of starved grey sharks to "quiescent grouper water," to "distressed grouper water," and to "dead grouper water."

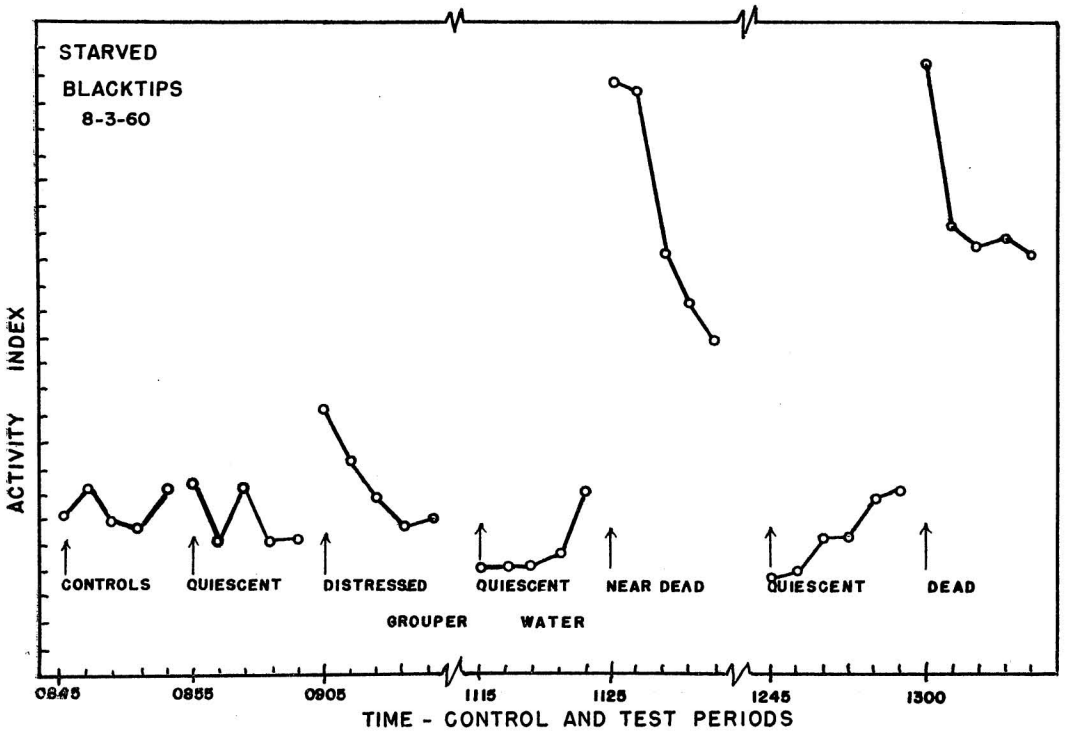

FIG. 12. Activity index during successive 2-min periods, illustrating response of starved blacktip sharks to "quiescent grouper water," to "distressed grouper water," and to "dead grouper water."

The sharks again responded with a violent hunting response and tube biting. The procedure was repeated after an additional 4 hrs (at 2200) during which time the quiescent grouper water had been flowing into the compartment and the sharks were responding normally. The small grouper in the dip net, however, had died. After the dead fish was lowered into the container (at 2210), there was a spectacular hunting reaction by the sharks. Only the string was recovered from the container at the end of the third period: the small dead grouper had been swallowed by one of the larger "quiescent" groupers. The water in the container was clear indicating that the fish had been engulfed whole without the escape of body juices.

The above experiment was repeated on the starved blacktip sharks, using the same four "quiescent" groupers and another "distressed" grouper. In this case the "distressed" grouper was not eaten after it had died. The results (Fig. 12) were almost identical to those obtained with the starved grey sharks. A similar test using four "quiescent" and one "distressed" mullet gave similar results (Fig. 13). The sharks even responded to a small "distressed" blacktip shark which was held in a dip net for a few minutes and then, still alive, was lowered into the container, in this case in the absence of any "quiescent" fish.

Discussion

These experiments show that "quiescent" prey give off an odor which can be detected by sharks when it is first introduced into their environment but to which they soon become habituated. There is still the question, of course, as to whether the "quiescent" fish were still under stress because of the artificial environment of the plastic container. Regardless of this, the experiments demonstrate that when the prey becomes frightened and excited it gives off an additional or a new odor which again stimulates the habituated sharks, provoking the typical

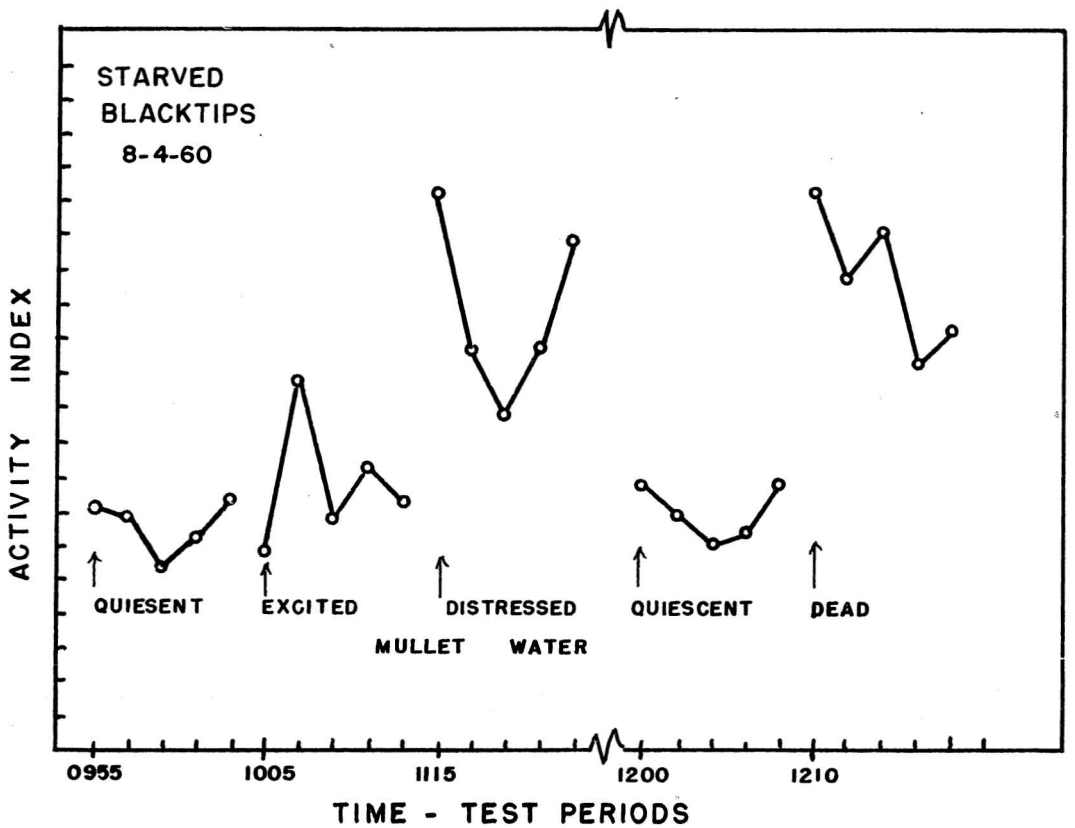

FIG. 13. Activity index during successive 2-min periods, illustrating response of starved blacktip sharks to "quiescent mullet water," "excited mullet water," "distressed mullet water," and "dead mullet water."

hunting response. Moreover it seems that shark activity, and thus presumably the amount of odorous material released, increases with increased agitation of the prey.

It seems unlikely that the odorous material is associated with body juices released by direct injury to the prey on the part of the observer. The fish used were healthy aquarium specimens which in some cases, e.g., groupers, were used over and over again and yet suffered no obvious ill-effects from being repeatedly "agitated." It is unlikely they would be damaged by rubbing against the sides of the smooth plastic container. They could, of course, rub against each other when excited. This may possibly have removed part of their mucous coating and enabled body juices to escape through the skin.

That the results were not induced by the artificial environment of the shark tanks was demonstrated in follow-up experiments with sharks in the natural environment of Eniwetok lagoon by Hobson (1963). Water siphoned into the lagoon from a plastic container in which large, living, agitated but apparently undamaged groupers had been placed, attracted both whitetip (*Triaenodon obesus*) and grey (*C. menisorrah*) sharks. They detected the "grouper water" from a distance and followed its path upstream to the source—a concealed plastic tube.

If the substance which attracts the sharks is released by some subtle damage to the skin of the prey it might be similar to that demonstrated by von Frisch (1941) in the injured skin of the minnow (*Phoxinus laevis*). As with von Frisch's material, identified as a purine- or pterin-like substance by Hüttel (1941), it might produce an alarm reaction among the prey but still be attractive to the sharks. On the other

hand it is tempting to postulate that the substance is some metabolite which is released from gill, vent, or skin by excitement rather than by injury of the prey.

Whatever may be the source and nature of the attractant, we have presented evidence that olfaction is involved in the predation of sharks on normal, healthy fish. It is suggested that in the natural environment, fish give off odors to which the sharks are conditioned. It is further suggested that when the fish become frightened or excited, and certainly if they rub against each other or against a coral head, they give off additional or new odors which stimulate the hunting response in sharks. This hypothesis is consistent not only with our experimental data but also with our observations of the behavior of the sharks in their natural environment. For the most part they display a complete disregard for the myriad of normal, healthy fish which surround them. However they are able to track down and converge on a distressed fish (such as a live fish suspended from a hook through the jawbone but otherwise uninjured) with uncanny speed and accuracy.

REFERENCES

BIGELOW, H., and W. C. SCHROEDER. 1948. Sharks. In, Fishes of the western north Atlantic. Sears Found. Mar. Res. Mem. 1, Pt. 1:59–546.

BRETT, J. R., and D. MCKINNON. 1954. Some aspects of olfactory perception in migrating adult coho and spring salmon. J. Fish. Res. Bd., Canada 11(3):310–318.

EIBL-EIBESFELDT, I., and H. HASS. 1959. Erfahrungen mit Haien. Zeit. Tierpsych. 16(6): 733–746.

GILBERT, P. W., and F. G. WOOD, JR. 1957. Method of anesthetizing large sharks and rays safely and rapidly. Science 126:212–213.

HOBSON, E. S., JR. 1963. Feeding behavior in three species of sharks. Pacif. Sci. 17(2).

HÜTTEL, RUDOLF. 1941. Die chemische Untersuchung des Schreckstoffes aus Elritzenhaut. Naturwiss. 29:333–334.

IDLER, D. R., U. H. M. FAGERLUND, and HELEN MAYOH. 1956. Olfactory perception in migrating salmon, 1. L-serine, a salmon repellent in mammalian skin. J. Gen. Physiol. 39(6): 889–892.

MISHKIN, M., R. D. GUNKEL, and H. E. ROSVOLD. 1959. Contact occluders: a method for restricting vision in animals. Science 129: 1220–1221.

PARKER, G. H. 1910. Olfactory reactions in fishes. J. Exper. Zool. 8:535–542.

——— 1914. The directive influence of the sense of smell in the dogfish. Bull. U. S. Bur. Fish. 33:61–68.

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

SHELDON, R. E. 1911. The sense of smell in selachians. J. Exper. Zool. 10:51–62.

SPRINGER, STEWART. 1955. Laboratory experiments with shark repellents. Proc. Gulf, Caribbean Fisheries Inst. 1954:159–163.

STEINBERG, M. A. 1960. Report on progress on contract NR 104-525, chemical analysis of shark repelling substances. (Mimeo.)

——— 1961. Final report on contract NR 104-525, chemical analysis of shark repelling substances. (Mimeo.)

VON FRISCH, K. 1941. Ueber eine Schreckstoff der Fischhaut und seine biologische Bedeutung. Zeit. vergl. Physiol. 29:46–145.

WHITELY, G. P. 1940. The Fishes of Australia: Part 1, Sharks. Royal Zoological Society of New South Wales.

WRIGHT, B. S. 1948. Releasers of attack behavior pattern in shark and barracuda. J. Wildlife Mgt. 12(2):117–123.