THE DIRECTIVE INFLUENCE OF THE SENSE OF SMELL IN THE DOGFISH

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The object of the professional fisherman is to bring fish within his reach. In some instances this is accomplished by direct attack, as in such primitive operations as harpooning and spearing, or by circumvention, as in most forms of seining. But in many cases some deceptive device is set up whereby the fish is lured to its fate. These deceptions are practiced on the fish through some of its various sense organs. Noises are made by the slapping of oars or other such implements on the water and thus fish are driven into gill nets or entangled in trammels. Such influences probably affect the fish through the ear, the sense organs of the lateral line system, or the skin, thus involving hearing and touch. Lights are often carried on boats at night and small fish are thus attracted in sufficient numbers to be easily caught by hand nets, a procedure dependent upon the organs of sight. But fishing in the ordinary acceptation of the term implies the use of some deceptive attraction in the form of bait, which, as originally used, depends on the feeding habits of the fish and has to do with its senses of smell and of taste.

The sense of taste has been almost universally attributed to fish, and most fishermen, naturalists, and even anatomists have assumed that fishes possessed a sense of smell. Of recent years some comparative physiologists have denied this sense to fishes. In their opinion the nasal organ of the fish acts more as an organ of taste than an organ of smell. This conclusion was thrown in question by the observations of Aronsohn (1884) and of Baglioni (1909), and was refuted by the experiments of Parker (1910, 1911), Sheldon (1911), and Copeland (1912). By these studies it was shown that fishes scent their food in essentially the same manner that air-inhabiting vertebrates do and with the corresponding sense organ, the nasal organ.

The following investigation has been carried out with the view of ascertaining the exact method by which a fish finds its food or may be caught by a bait. The work has been done on the smooth dogfish of the Woods Hole region, *Mustelus canis* (Mitchell). The gustatory, chemical, and olfactory senses of this fish have already been studied by Sheldon (1909, 1911), and it was therefore an unusually favorable subject for the investigation of those activities which depend upon the sense organs named.

The experiments were carried out for the most part in a small pen, 24 feet long by 6 feet wide, in one of the pools of the Woods Hole station. The pen was bounded partly by the walls of the pool and partly by chicken wire attached to poles driven into the bed. It was freely open to the changes of tide. Fish from an adjacent pool were transferred to it from time to time for experiment and observation.

When three or four dogfish were liberated in the pen, they swam leisurely up and down its length in a mid depth of water, occasionally resting on the bottom. If, during their swimming, some crushed crabs wrapped in cheesecloth were thrown into the pen, they quickly changed their method of locomotion. When a fish in the course of its ordinary swimming approached to within a few feet of the packet of crab meat, it usually made a sudden movement to one side with its head, swam at once to the bottom, and in quick circuitous turns, often in the form of a figure eight, swept the bed of the pen. In a short time it narrowed its search to the immediate vicinity of the packet and when at last its mouth was brought close to the bait, this was seized, shaken, and carried off. Occasionally the packet was not found and the fish then resumed its ordinary method of locomotion until again by accident it came close to the packet, when it would repeat the movements already described. The crab meat used in these experiments was always wrapped in cheesecloth to exclude the possibility of the recognition of the meat by sight. The dogfish, as is well known (Sheldon, 1911), has extremely poor vision, at least in daylight, and seldom responds to an object until the latter is within a foot of it.

If the nostrils of a set of fishes to be experimented upon are filled with cotton wool before the animals are liberated in the pen, no attention whatever is paid to the packets of crab meat, though the characteristic reactions return shortly after the removal of the cotton. These experiments, first tried by Sheldon (1911), show that the dogfish is excited by food through the stimulation of its nasal organs and that it subsequently locates the food by the same means; in other words, the dogfish scents its food as air-inhabiting vertebrates do.

The question that I set to decide was that of the precise method by which the dogfish reached its food. After the initial excitement, does the fish move aimlessly about till, by accident, it runs upon the packet of crab meat, or is it directed toward this packet by some special form of stimulation? In working on this problem it proved important to observe two conditions. First, it was found that dogfish of medium size were more favorable for these experiments than larger or smaller ones. In general, fishes about 2 feet in length were found to be most satisfactory, and these were used in most of the experiments. Secondly, the dogfish reacted well only when in companies. A single dogfish in the pen seemed to suffer an inhibition of its activities excepting those directed toward returning it to the school. It swam about with incessant efforts at escape and paid very little if any attention to baits or food. It was therefore found best to work with several fish at once, and usually a set was chosen in which the individuals differed enough in size and markings to make them severally distinguishable. Often in a given set the larger ones were prepared in such a way that they showed no response to the packet of crab meat, and the smallest one of all was made the subject of the special experiment. This one individual was provided with a favorable environment for its own reactions without being subjected to disturbances from others.

If the substances emanating from the packet of crab meat exert a directive influence on the dogfish through the sense of smell, evidence of this might be discovered by interfering with one or other of the nasal organs. This might be accomplished by cutting the olfactory tracts of one side or by temporarily occluding one of the nasal apertures. Fish in which the olfactory tracts have been cut rarely live more than a few days after the operation. They are apparently very susceptible to infection from cuts made in the vicinity of the brain. I therefore abandoned this method of procedure and adopted that of filling the nostrils with cotton wool. But even this method is not without its defects. If a single nostril cavity is plugged tightly with cotton the fish will often fail to respond to the presence of food precisely as it does when both are filled. On removing the cotton from such cavities they are generally found to be inflamed, if not suppurated, showing that their surfaces are decidedly delicate. None of these complications arise when the nasal cavity is only lightly filled with cotton and yet this method seems to be effective in checking the currents of water through the nose. I therefore adopted a light plug of cotton wool as a means of excluding the action of a given nasal organ.

To ascertain the state of the normal dogfish, records were taken of the direction of the head movements, to the right and to the left, in response to the presence of bait, and of the time consumed between the moment when the packet of crab meat was first scented by the dogfish and when it was finally seized and carried off. These records served as a basis for comparison with the reactions of fish especially prepared for tests. The records of the normal fish are given in table 1.

TABLE 1.—RECORDS FROM FIVE NORMAL DOGFISH.

Number of fish.	Movements of the head.		Time in seconds to secure bait.
	To left.	To right.	
1	14	16	186
2	22	20	135
3	27	28	108
4	17	22	161
5	21	18	67
Averages	20.2	20.8	131.4

From table 1 it will be seen that the dogfish tested found the bait in a little over an average of two minutes and that they accomplished this operation by making about as many right-handed as left-handed movements. Many of their movements were combined and resulted in more or less continuous and characteristic courses in the form of a figure eight.

In a second series of tests dogfish in which the left nostrils had been lightly filled with cotton were subjected to the same conditions as were the normal fish whose reactions are recorded in the preceding table. The records of five of the fish with the left nostrils occluded are given in table 2.

TABLE 2.—RECORDS FROM FIVE DOGFISH WITH LEFT NOSTRIL OCCLUDED.

Number of fish.	Movements of the head.		Time in seconds to secure bait.
	To left.	To right.	
1	3	26	132
2	6	32	116
3	0	24	110
4	2	16	121
5	4	32	141
Averages	3	26	124

As table 2 shows, the five dogfish with their left nostrils occluded consumed on the average about the same length of time to find the bait that the normal dogfish did, but they accomplished this by a predominance of right-handed movements rather than by an almost equal number of right and left handed turns. Their movements were essentially circular and seldom, if ever, in the form of a figure eight.

A third series of dogfish were prepared by filling their right nostrils lightly with cotton wool. As might have been expected from the results already recorded these fish found the bait in about the same time as those with the left nostrils occluded, but by means of left-handed movements chiefly. The records of this set are given in table 3.

TABLE 3.—RECORDS FROM FIVE DOGFISH WITH RIGHT NOSTRIL OCCLUDED.

Number of fish.	Movements of the head.		Time in seconds to secure bait.
	To left.	To right.	
1	31	2	123
2	34	1	92
3	21	2	111
4	17	5	116
5	19	3	131
Average	24.4	2.6	114.6

As tables 2 and 3 show, dogfish with one occluded nostril each tend to seek their food by moving over a more or less circular path and in such a way that the open nostril is toward the center of the circle.

Having ascertained that in seeking food or a bait normal dogfish turn about as much to the right as to the left, and that those with an occluded nostril turn predominantly toward the side of the open nostril, I attempted as a check series to repeat all the experiments thus far described on one set of fish. The plan of this series was to test five dogfish, first as normal individuals, then with their left nostrils occluded, next with their right nostrils occluded, and finally with both nostrils free. The fish were allowed to rest one day after each trial with occluded nostrils, so that the whole series of experiments covered a period of about three days. Unfortunately, during this period two of the fish made their escape and the series was completed with only three fish. The records of these three fish throughout the whole set of tests are given in table 4.

TABLE 4.—RECORDS FROM THREE DOGFISH UNDER SUCCESSIVE CONDITIONS, NORMAL, LEFT NOSTRIL OCCLUDED, AND BOTH NOSTRILS OPEN.

State of fish.	Number of fish.	Movements of the head.	
		To left.	To right.
Normal	1	21	26
	2	18	16
	3	31	28
Average	....	23.3	23.3
Left nostril occluded	1	3	24
	2	4	31
	3	3	30
Average	....	3.3	28.3
Right nostril occluded	1	26	3
	2	28	0
	3	19	4
Average	....	24.3	2.3
Both nostrils open	1	19	18
	2	21	17
	3	16	27
Average	....	18.7	24

It is quite evident from an inspection of table 4 that the conditions recorded in the preceding tables are not due to individual peculiarities on the part of the fish used; that a given fish, which in finding its food normally turns as much to the right as to the left, can be forced to assume either a predominantly right-handed or left-handed course by occluding the appropriate nostril, and that after this treatment the same fish can recover its normal methods of search by the liberation of both nostrils. It must also be evident from the whole series of records that the dogfish does not run upon its food by accident, but finds it in response to an influence more less directive in character.

The consistent and striking circular courses that these fishes can be forced to assume have, in my opinion, more than a superficial resemblance to the so-called circus movements of the invertebrates. These movements are dependent on the differences of intensity of stimulation on the two sides of the body and this explanation holds, I believe, for the circular movements of the dogfish. When a dogfish first enters water permeated with odorous material from its food, it invariably makes a quick turn with its head which, if the conditions of the water have been disturbed by currents, is always toward the bait. This movement is followed by other movements of a like kind whereby the fish eventually reaches the bait. When the normal conditions of the fish are disturbed by the complete occlusion of one nostril, the fish swims as though it were in water that was highly charged with odorous particles on the side of its body corresponding to the open nostril and devoid of these particles on the opposite side. The fish therefore turns toward the side of the open nostril, but since, under the artificial conditions of the experiments, this turn does not equalize the stimulus, the motion is continued and a circular form of locomotion results. Thus, in my opinion, the more or less circular movements induced in a dogfish with an occluded nostril by an odorous bait are to be explained upon the same basis as the circus movements of such invertebrates as crustaceans, insects, etc.

The movements of a dogfish differ from the movements of these lower animals, however, in that they are not pure circus movements. A dogfish with a fully occluded left nostril not only turns to the right but sometimes to the left, and a normal dogfish so often exhibits movements in the form of a figure eight that it is quite clear that the whole figure is a single response rather than two separate acts due to alternate excessive stimulation first on one side and then on the other. Thus, though the responses of the dogfish to the odors of food may be based predominantly on the principle of symmetrical stimulation, it is also clear that odorous material calls forth from this animal what are essentially random movements.

In consequence, the finding of food or of a bait by a dogfish may, therefore, be described as brought about by a combination of movements, partly random and partly directed, which have resulted from stimulations due to the varying concentrations of odorous materials in the surrounding sea water. The dogfish, like other elasmobranchs, has a structure especially favorable for this form of stimulation in that its nostrils are wide apart, a condition which is immensely exaggerated in the hammerhead shark, whose nostrils as well as eyes are lodged at the extreme ends of the transversely extended processes of its head. These conditions make it clear why chumming is so effective with mackerel and other fishes. When a fisherman spreads bait to attract such fishes from a distance the response is undoubtedly directive, especially on the part of sharks, which have been seen to come up to food against the tide from as great a distance as a quarter of a mile. Such fish must keep within the stream of odorous substance in the water by responding to the stimulation of their nasal organs in much the same way as the dogfish was found to do in seeking a bait.

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