JOURNAL OF ANIMAL BEHAVIOR

VOL. 5 SEPTEMBER-OCTOBER No. 5

THE BEHAVIOR OF FUNDULUS, WITH ESPECIAL REFERENCE TO OVERLAND ESCAPE FROM TIDE-POOLS AND LOCOMOTION ON LAND.[1]

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It is difficult for one not familiar with life in the sea to realize what a fierce struggle for existence many of the smaller fishes have to wage. Our common minnows, e. g. Fundulus, are beset on every side with danger. They are continuously hunted from below by many predaceous fishes and from above by various sea-birds. For these creatures the price of existence is indeed eternal vigilance. Owing to this price, no doubt, they are among the most wary of fishes. The least disturbance in the water from below or merely an approaching shadow from above sends them scurrying for places of safety.

For purposes of protection they are usually found in shallow water very near the shore-line. As the tide rises they continuously follow the water inland keeping quite near the edge, and as it ebbs they follow it out again. On the newly covered bottom they are frequently seen rooting in the sand, apparently feeding. Thus the movement in harmony with the tide probably serves them in securing food as well as in protection against enemies. But in following the tide aquatic animals are also exposed to danger, for with the incoming tide they are often directed into depressions in the beach which are of such a nature as to hold water for a considerable time after the tide recedes but not until it rises again. To linger at the shore-line in these pools waiting for the water to recede would mean certain death to most aquatic animals. How does it happen that Fundulus, which is so frequently found in such

[1] Published by permission of the Commissioner of Fisheries.

pools, and ordinarily does remain at the water's edge is rarely if ever caught in them.[2] It was this question that inspired the following experimental observations, all of which were made during the summer of 1914 on a sand beach at Beaufort, N. C.

I shall first give in a general way the results of these observations, all of which were repeated a considerable number of times; then I shall present a few experiments in some detail.

If Fundulus gets into a tide-pool while the tide is rising it usually swims about in a deliberate sort of way, stopping here and there to root in the sand and to play with its companions. This behavior continues until the tide turns or at any rate until it is very nearly high. After that the animals may still swim about much as they did before, but they invariably, every few moments, return to the outlet of the pool and swim out and in again. Thus they continue to test the depth of the water in the outlet, and as soon as it gets too shallow they leave the pool and do not return. This accounts for the fact that they are not caught in these pools under ordinary circumstances.

But what interested me primarily was the behavior observed in pools in which the outlet had been closed before the fishes had escaped. Under such conditions it was found that the behavior depends very largely upon whether the water is running in or out of the pool at the time it is closed.

If the water is running in, nothing phenomenal occurs. The animals may swim about rather rapidly for a few moments, but even if they do, they very soon become quiet and proceed to feed and play in their accustomed manner. This experiment was repeated many times and only in one case was the behavior essentially different from that described, and in this case the tide was very nearly high at the time the pool was closed. The response observed under these conditions lead to some important conclusions that will be stated later in connection with a detailed description of the experiment.

If the water is running out when the pool is closed the behavior of the fish is quite different from what it is if the water is running in. After the pool is closed under these conditions, they first swim about rapidly in various directions for a few

[2] I have again and again, during the ebbing tide, examined numerous tide-pools, but I have never found Fundulus in any of them after the water had stopped flowing out although in some instances they were still 40 to 50 meters long and contained water 20 to 30 cm. deep.

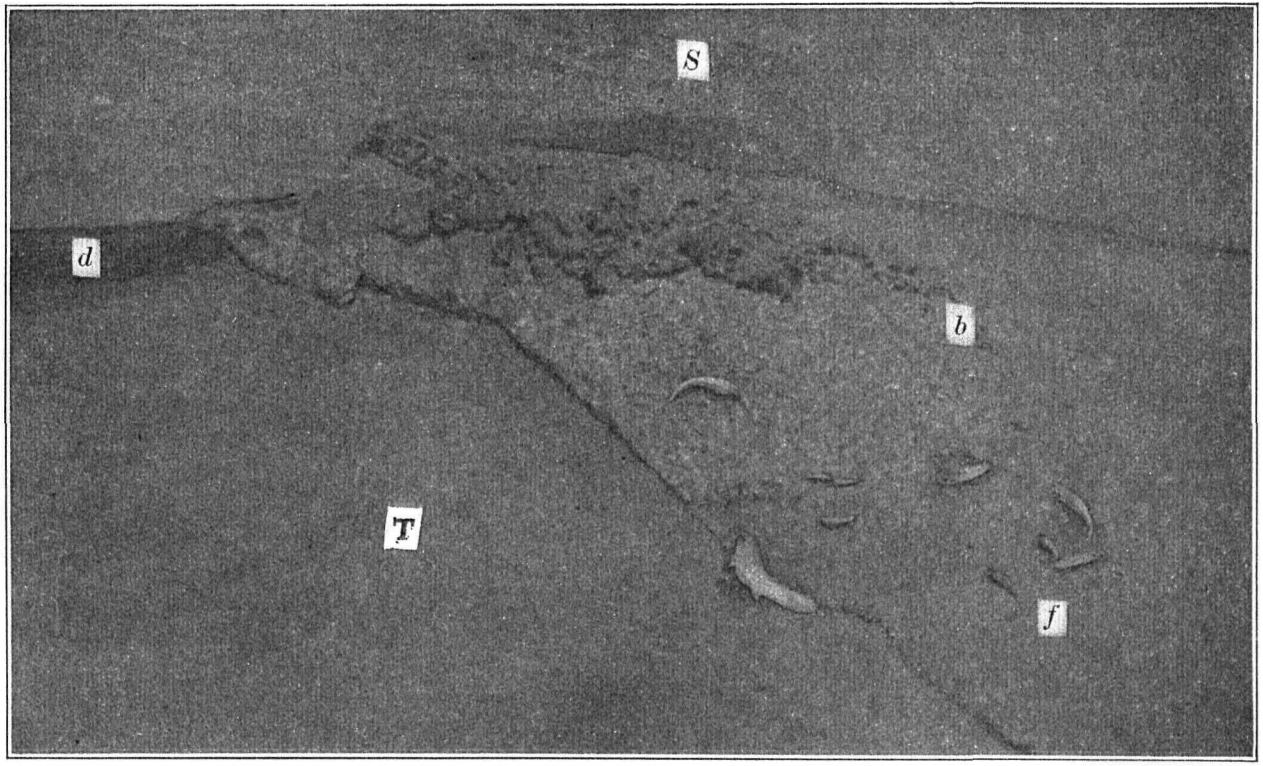

FIG. I. Instantaneous photograph showing a group of ten specimens of Fundulus shortly after they had left a tide-pool. They are traveling over a sand-bar about three meters wide to the sea. f, Fundulus majalis; T, tide-pool; d, dam; b, sand-bar; S, sea. Note that the animals were facing in all directions at the instant the photograph was taken. All were, however, proceeding toward the right.

I am indebted to my friend, W. P. Hay for this photograph.

moments, apparently very much excited; then they usually swim two or three times entirely around the pool keeping very close to the edge much as though they were looking for an outlet; after this a number of them ordinarily crowd together and wriggle well up on the beach into very shallow water. This

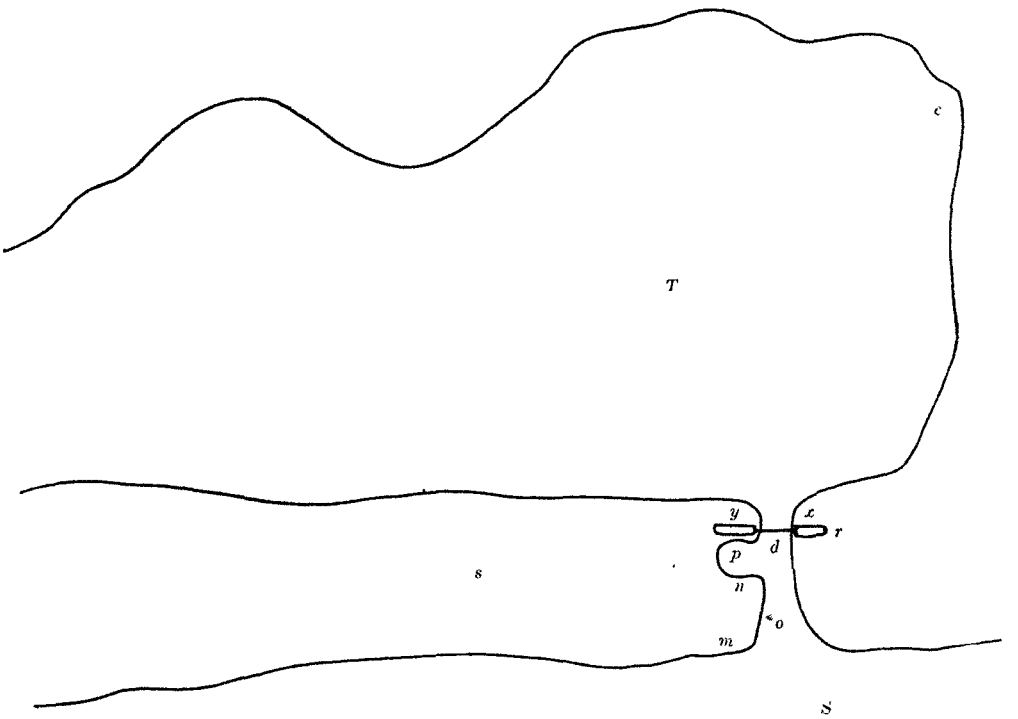

FIG. II. Outline of a portion of a tide-pool with the outlet closed by means of a board. This pool was 50 meters long, 13 meters wide and about 20 cm. deep. It contained approximately 300 specimens of Fundulus, all but 75 of which escaped to the sea by crossing a sand-bar 3 meters wide and fully 10 cm. high. T, tide-pool; o, outlet; S, sea; s, sand-bar; d, dam; r, ridge of sand; p, small pool; c, m, n, x, y, points mentioned in the description.

usually occurs in the original outlet at either end of the dam across it. Finally one flops entirely out of the water onto the sand. Others follow immediately much as sheep follow a leader. After they have left the water they continue flopping and proceed directly across the bar which separates the pool from the sea. (See Fig. I.) Those that are left ordinarily swim about again for a few moments then collect as before, after which more

escape. This is repeated, one group following another, until all or nearly all have escaped.

In this way I have seen more than 200 of these fishes leave a tide-pool 50 meters long, 13 meters wide and 30 cm. deep, and travel across a sand-bar more than 3 meters wide and 10 cm. high, all in the course of half an hour. And I have seen them proceed in a fairly direct course toward the sea even against a moderately strong wind. I have also seen them persistently attempt, continuously for at least a minute, to go overland to the sea against a wind so strong that they could make no headway. When I first saw this performance I was deeply impressed. I had often seen fishes, when thrown on the land, flop back into the water in a more or less aimless fashion, but I had never seen any voluntarily leave a body of water and travel in a coordinate way on land. Concerning the nature of this phenomenon and the regulation in direction of locomotion on land I shall have something to say presently.

The description given above is based upon numerous experimental observations among which the following are typical.

1. On August 30 a tide-pool containing numerous specimens of Fundulus majalis was discovered on a sandy beach. This pool, somewhat irregular in outline, had a maximum length and width of 50 and 13 meters respectively and the water in much of it was, in places, more than 20 cm. deep. A strong current about 3 cm. deep was running out through the outlet, and some of the specimens were continuously passing out or in through it. At 5 P. M. all in the immediate neighborhood were driven in and then the outlet was suddenly closed with a board which extended 5 cm. above the surface of the water. A ridge of sand 60 cm. long and 10 cm. high was thrown up at either end of the board. This ridge extending 16 cm. above the water in the pool, joined on one side of the outlet, a natural bar of sand of the same elevation, so that the pool was separated from the sea on this side by a continuous barrier having an elevation of 15 cm. On the other side however, the natural bar had an elevation of only 5 cm. On this side in the angle between the ridge and the outlet, there was a considerable depression containing a small pool of water connected with the outlet, as represented in figure 2. The sand-bar was at every point over three meters wide. The bank at the edge of the pool

on the sea-side was everywhere very steep, and the water became deep rapidly. On the opposite side the incline was very gradual, and the water was very shallow.

As soon as the pool was closed the fishes began to swim about rapidly in an aimless sort of way. They continued for a few moments, then they came very close to the edge of the water and swam several times up and down the side of the pool nearest to the sea. Finally a dense aggregation formed in the outlet near the dam and soon, three minutes after the outlet was closed, they began to come out in the angle between the outlet and the dam represented by y in figure 2. The first group that left the water consisted of about twelve individuals. All of these followed the ridge from y to its end, and then turned and went toward the sea. Other groups soon followed behaving in a similar way. Many attempted repeatedly to cross the ridge at y and three actually succeeded although the ridge was fully 10 cm. high and the incline over it formed an angle with the horizontal of more than 45 degrees. After passing the ridge some went directly across the sand-bar and entered the sea at m, but many of them got into the small pool p. All of these swam directly across this pool to the bank at n. Here three were seen to leave the water again, climb the relatively steep bank 9 cm. high and then proceed to the sea, although this pool had a free passage to the outlet through which nearly all escaped. This seems to indicate that after these creatures once start in a given direction toward the sea they have a strong tendency to continue in this direction.

About 25 individuals were seen to leave the tide-pool at c, but all returned A few of these reached a point nearly a meter from the edge of the water before they returned but most of them went only a few centimeters. Quite a number also left the pool at x but all of these returned after going a very short distance.

When the pool was closed there were approximately 300 specimens in it. The following morning 75 dead ones were found; consequently some 225 must have escaped.

2. In all of the experiments made during the falling tide behavior similar to that described above was observed. In some of them, there were, however, additional points of interest. A detailed description of one of these follows.

In this experiment a dam was thrown across a long narrow tide-pool running parallel with the coast-line as shown in figure 3. In this way approximately 150 specimens of Fundulus majalis of various sizes were enclosed. The sand-bar between the pool and the sea varied in height from 10 to 15 cm. This bar rose rapidly along the edge of the pool on the sea side, but on the opposite edge of the pool the inclines was very gradual: so that the elevation at the end of the dam on this side was only 3 cm., while on the sea side it was over 10 cm.

Observations were continued for 20 minutes. During this time nearly 50 specimens escaped by traveling overland around

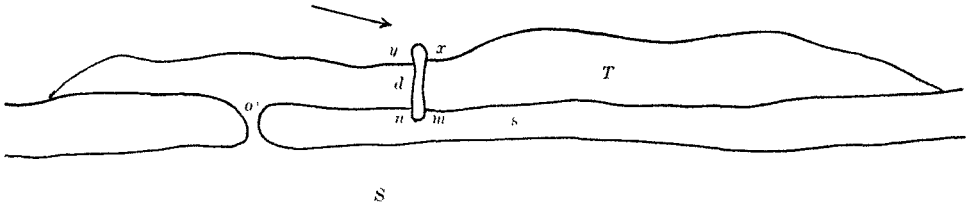

FIG. III. Outline of a long, narrow tide-pool with a dam thrown across near the middle This pool had a maximum width and length of 2 and 24 meters respectively. It contained approximately 150 funduli, most of which escaped by traveling overland, against a moderately strong wind, around the end of the dam on the land side, xy. T, tide-pool; o, outlet, S, sea; s, sand-bar; d, dam; m, n, x, y, points mentioned in the description. The arrow indicates the direction of the wind.

the end of the dam from x to y, i. e. on the land side where the elevation was least. These specimens were opposed in their locomotion on land by a fairly strong wind. A few escaped at the opposite end of the dam, going overland from m to n. And two crossed the sand-bar taking a direct course to the sea. A few also came out a short distance elsewhere but all of these returned to the pool.

The results obtained in these two experiments and others show that Fundulus tends to leave the tide-pools near the original outlet. Relatively few were seen to attempt to escape elsewhere in spite of the fact that the incline of the bottom was usually much more gradual in many other places. They also show that there is a tendency to select the lowest place near the outlet. This is particularly evident in experiment 2 Ordinarily these creatures leave the pools on the side of the outlet nearest the sea but in this case they left on the side nearest the land where the elevation was much less than on the opposite side.

The results show, moreover that after the fishes are out on the land they tend to go directly toward the sea. This is evident from the persistent attempts made in experiment 1, to cross the ridge at y, and from the direct course taken after passing the ridge, especially in the small pool p. They show, furthermore, that the tendency to go toward the sea is not a response to the light reflected from the water, for in experiment 1, the fishes, when they were behind the ridge, persistently attempted to go toward the sea, although in this position, the ridge effectively hid the sea from view while the pool was fully exposed. In experiment 2 they also proceeded toward the sea under similar conditions, or rather toward the original outlet of the pool.

3. As previously stated, if the tide flows in when the pool is closed, nothing out of the ordinary occurs in the reactions of Fundulus. Only in one experiment, that described below, was there an exception to this. Unfortunately, owing to other duties, I was unable to repeat this experiment under the same conditions.

On September 7, at 10.19 A. M. the outlet of a large tide-pool (12 by 30 m.) containing about 350 funduli was closed. At this time there was a strong current of water running into the pool indicating that the tide was still rising. Immediately after, the pool was closed, the fishes began to swim about rapidly being apparently very much excited, and two minutes later they began to come out of the water. In short, they behaved precisely as they ordinarily do when the tide is running out, not at all as they ordinarily do when it is running in. They continued to come out for some time, most of them, as usual near the original outlet, but nearly all of them returned to the pool; only a few succeeded in crossing the sand-bar which separated the pool from the sea. The sun was very hot at this time and the sand on the bar rather dry. This probably accounts for the fact that nearly all returned to the pool after proceeding a short distance toward the sea. At 10.40 the tide had unquestionably turned for the water outside the pool was already several centimeters lower than that inside. The tide was consequently very nearly high when the pool was first closed and this no doubt, was the cause of the unusual behavior. If this is true it must be assumed that in some way these animals know when the tide is about to turn, for their method of response

changes from that characteristic of the rising tide to that characteristic of the falling tide before the tide turns.

At 11.10, i. e. nearly an hour after the pool was closed, the fishes were much more quiet than they had been earlier, Most of them were swimming about in a leisurely fashion, some were feeding and none were coming out of the water. They were observed for some time after this, but at no time was there the slightest indication of an attempt to leave the water, although various methods were used in trying to make them leave, e. g., boards were thrown into the pool, the water was violently disturbed by running around in it and much of it was drawn off. Later the water in this pool together with the fishes was drained into a lower pool. In this pool the fishes swam about rapidly as though they were considerably excited but none of them left the pool, although a few at different times came out of the water a short distance. Their behavior in general was markedly different from that observed in animals suddenly shut in pools during the ebbing tide . This indicates strongly that the all-important factor involved in the behavior resulting in the overland escape of Fundulus from tide-pools is the sudden closing of the outlet through which it is accustomed to go. The location of this outlet they evidently remember for some time. The results of this experiment show also that Fundulus becomes very rapidly acclimated.

The movement of these fishes on land seems to be well coordinated. They travel in fairly direct courses. There is nothing in the nature of aimless tumbling about as is ordinarily seen in the behavior of fishes out of water. Locomotion consists of successive leaps due to sudden bending of the body. When the fish falls after a leap it may be directed toward any point of the compass, but the succeeding leap carries it on its course no matter in which direction it may be facing at the time of the response. Thus before each leap it may be headed in the direction in which it is traveling or in the opposite direction or in any other direction. It is really remarkable that the bending of the body is so regulated that the animal continues to move in a given direction regardless of its axial position at the beginning of the successive reactions. As to the mechanics of the process I am as yet quite in the dark. And I am also unable to say what factors in the environment serve to direct

these animals overland to the sea. Vision of the sea seems to play little or no part in this, for the fishes continue toward the sea if a screen is so placed that the water can not be seen; or if conditions are so arranged that the largest surface of water visible is in the tide-pool. The slope of the beach can also not serve to guide them, for in crossing the sand-bar they have to go up grade as well as down. Nor are there any other external features that seem capable of serving as a guide. The phenomenon is consequently probably very largely dependent upon internal factors.

SUMMARY

1. Fundulus is frequently found in temporary tide-pools, but rarely if ever after the water is so low that the outlet is closed. When the tide is falling it swims out and in at short intervals but as soon as the water in the outlet gets low it does not return. In this way it avoids being caught in these pools and killed when they dry during low tide.

2. If the outlet is closed while the tide is rising nothing out of the ordinary occurs, but if it is closed while the tide is falling the fishes swim about rapidly in various directions for a few moments. Then they come out of the water and travel overland to the sea. Many specimens have been seen thus to leave large tide-pools and travel across sand-bars more than 3 m. wide and 10 cm. high.

3. Fundulus nearly always leaves the pools on the sea side near the original outlet. It apparently remembers the location of the outlet, and it is the sudden closing of this that constitutes the principal factor causing these fishes to leave the pools.

4. On land they never travel in the wrong direction any considerable distance. It is not known how they are guided in the right direction, but it is known that light reflected from the water is not a significant factor in the process.

5. Locomotion on land is brought about by successive leaps due to rapid bending of the body. The course taken is fairly direct. Every leap carries the animal in the right direction, although the axial position at the beginning of the successive leaps varies greatly; the fish, at this time, may be headed in the direction of locomotion or in the opposite direction or in any other direction. The movements appear to be well coordinated, but the process involved in thus regulating the direction of locomotion is not understood.