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Modifiability of Schooling Behavior in Fishes: the Role of Early Experience [1]

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INTRODUCTION

Investigating the development of schooling behavior in the atherinid fish *Menidia menidia* (Linnaeus), Shaw (1960) described the characteristic developmental patterns that occurred during preschooling and schooling stages. In Shaw's 1961 study, in order to determine the effect of limited early social experience on schooling, several larval fish were reared under modified environmental conditions, namely, without contact with species mates. Schooling appeared among those fish. The researches presented below are an extension and elaboration of Shaw's 1960 and 1961 studies. In the present paper, however, many hundreds of fish were reared under various modified environmental conditions, and quantitative records were made of specific behaviors.

In a broader scope, the problem of schooling development is pertinent to general problems in behavioral development. In the schooling fish, behavior is essentially stereotyped, and there is a limited range for the expression of behavior (Shaw, 1970). Within the framework of the innate vs. acquired dichotomy, schooling could be classified as innate. But does

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such a classification have any usefulness? The classification only indicates that the behavior is universal for the species and that it appears even when the animal does not have social experience with species mates (Lorenz, 1965). Because of these qualities the behavior is assumed to be coded in the genes. We are left with the obvious; species have species typical behavior, and a particular behavior may be modified by rearing conditions. It is time to discard the dichotomy and to look at how behavior develops in environmental conditions closely approaching the species typical and in nontypical conditions.

It is only through observation of how behavior comes about, through examination of subtle changes and of modifications no matter how minor, that an understanding of the factors shaping behavior will also come about. Behavior is a result of the animal growing up in its environment; animal and environment are closely interwoven. To assume that behavior is a result of the inherited and the acquired, may be fallacious.

At all stages of development, animal and environment are a continuum of interacting processes. When an animal is reared in a species typical environment, species typical behavior emerges. If the animal is reared in a nontypical environment, for example, in isolation from conspecies, conspicuous or subtle modifications often occur and affect the entire expression of the so-called stereotyped behavior.

MATERIALS AND METHODS

Fish

Adults of the common Atlantic silversides, *Menidia menidia* (fig. 1), were collected during late May and early June, 1967, on the south shore of Long Island, New York. Batches of fertilized eggs were prepared by "stripping" the adults of their gametes which were extruded into small plastic containers filled with thoroughly aerated artificial sea water.[1] Fertilization was indicated by clustering of the eggs, a result of the extrusion of adhesive threads from the chorion. Obtained by this method for the experimental study were 1208 larval fish.

General Rearing Conditions

In order to reduce contamination from bacterial infection as well as to

[1] Instant Sea Salts, Aquarium Systems, Wickliffe, Ohio, and tap water filtered through an Eaton Water Filter. Throughout the experiments the fish were reared and tested in this medium which was always thoroughly aerated, maintained at a mean temperature of 20°C ± 1°C, and a mean specific gravity of 1.021.

provide sufficient aeration, the embryos were separated from one another either at the 64-cell, or blastula, stage by cutting their adhesive threads apart. The embryos were then placed into elongated sacks made of plankton netting which were suspended in a 50-gallon tank. Air stones oxygenated and circulated the water in the tanks.

The fish normally hatched inside the nets in nine days at the earliest and 12 days at the latest. Fish permitted to hatch in the nets were those designated as community-reared fry, those chosen for isolation were removed from the nets at seven days (post-fertilization), and each one hatched in its own isolation cup. At the time of removal the embryos

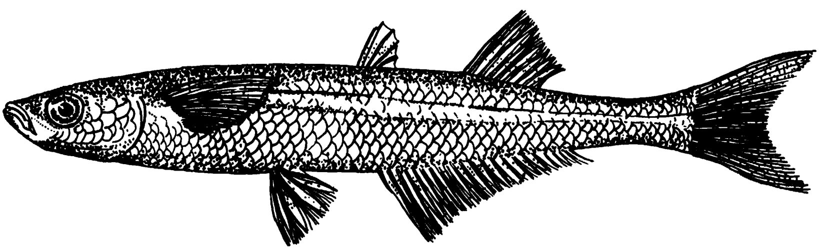

FIG. 1. Adult silverside, *Menidia menidia.*

were highly active and did considerable twisting and turning within the chorion. The isolation cups, composed of opaque white styrofoam, measured 7 cm. in diameter and 9 cm. high, and contained 200 cc. of sea water. The water was changed daily. All the newly hatched fish were fed large quantities of newly hatched *Artemia* nauplii, which was the continuous and steady diet throughout the experiment. Cups were replaced when a film of pigment from dead *Artemia* nauplii began to appear on the inner surface. The larval fish were reared and tested in a windowless laboratory with constant fluorescent lighting.

PROCEDURES

COMMUNITY-REARED FISH (C): One or two days after hatching in the plankton nets, 20 fish were placed in a 5-gallon tank. Many such tanks were set up. Once a fish was tested it was not returned to its community tank, assuring naiveté of the fish in regard to the tests. Community-reared fish were observed with their age peers on the first day after hatching, and at five-day intervals thereafter until the fifty-fifth day after hatching.

ISOLATES (I) AND RETESTED ISOLATES (RI): The isolates remained in their isolation chambers until testing time. As with the community-reared fish they were observed with age peers at five-day intervals until the fifty-fifth day after hatching. Each fish tested in this way was completely naive. However, instead of being discarded after the first test, the fish were returned to the isolation cups where they remained for 20 more days. At the end of the twentieth day, they were tested once more. On the first day after hatching, an isolate was given the opportunity to interact with species mates for the first time. The same isolates, 20 days later, were again given experience with age peers, although not necessarily with the same fish as before. Thus, the isolates (I) had no species experiences until the time of testing, whereas the retested isolates (RI) had a previous experience. Retesting did not occur in the one-day isolates until they reached the twenty-first day. Isolates tested initially on the fifth day were retested on the twenty-fifth day; those tested on the tenth day, initially, were retested on the thirtieth day. This procedure was carried out until the thirty-fifth day and the isolates were subsequently retested on the fifty-fifth day. As mentioned above, tests were continued with naive isolates (I) until the fifty-fifth day and isolates of 40, 45, 50, and 55 days were not retested.

TESTS

TESTING CHAMBER: Fry were observed in a circular tank, 48 cm. in diameter, with the water level maintained at a height of 6.0 cm. The tank was illuminated directly by a cold, circular, 10-watt fluorescent light 12 inches in diameter and suspended 38 cm. above the tank (fig. 2). Prior to each test the filtered and aerated sea water solution was changed.

TESTING PROCEDURE: Four fish of the same age and approximately the same total body length were used for each test. Measurement was obtained through a dissecting microscope as the fish swam over a grid. The decision to place four fish together was based on considerable previous experience, in which it was found that four generally formed a cohesive school. In addition, by observing only four fish, it was possible to keep records of individuals.

The test fish were individually and gently poured from a small cup into the testing tank at specific times. The first fish remained alone for three minutes, the second was introduced at the end of that period, the third three minutes later, and the fourth three minutes after that. The fish were introduced at the same location in the tank, with the exception of the one-day-old fry which was placed 5 to 8 cm. away from the fry already in the tank. During each three-minute period, continual records were made of the behavior of the newly introduced fry; that is, records

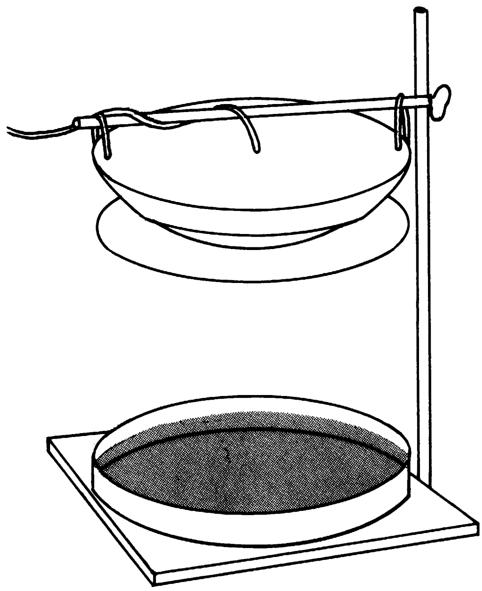

FIG. 2. Testing chamber.

were made of the reaction of fry no. 2 toward fry no. 1 during the fourth through the sixth minute of testing; of fry no. 3 toward no. 2 and no. 1 during the seventh through the ninth minute; of fry no. 4 toward no. 3, no. 2, and no. 1 during the tenth through the twelfth minute. At the beginning of the thirteenth minute through the twentieth minute, any interaction between any two, three, or all four fry was recorded. Afterward a one-minute observation was made at the twenty-fifth minute and at the thirtieth minute giving a total of nineteen minutes of recording time for the data presented. Several tests were extended to two hours to ascertain whether any differences in behavior appeared if the fish were together for longer periods. Data for the first 30 minutes are also presented for these tests.

RECORDING OF OBSERVATIONS

QUANTITATIVE: Records were made using the Esterline Angus operations recorder and the Aronson keyboard which give simultaneous readings of sequence, duration, and frequency of behavior (Tobach et al., 1962). Recordings were made of 1) frequency of approach-withdrawal (A-W): one fry approaches another to within 3 cm. or less and one or both immediately veer away from each other; 2) duration of orientation: one fry approaches another to within 3 cm. or less and both remain near each other; 3) duration of parallel orientation: two or more fry approach each other, orient into position parallel to each other and school; 4) duration of the longest persisting school made up of a minimum of two fry, during the thirteenth through twentieth minute (that is, when four fry were present in the testing chamber).

Statistically significant differences were determined by analysis of variance using the Newman-Keuls Multiple Comparisons Procedure (Winer, 1962). All comparisons of means were on a pair basis.

General observations were made of over-all schooling behavior, the patterns of approach leading to withdrawal or parallel orientation, and the general behavior of the resident fry in the test tank during the time that behavior of a test fry was being recorded. Behavioral observations were also made of the fry in their rearing environments.

RESULTS

The results show that although schooling behavior occurred in the fish reared under the altered environmental conditions, there were distinct modifications in the behavioral patterns and many of these modifications were statistically significant.

Behavioral interactions among the fish were examined every five days in the various groups. Highlights of the behaviors are presented below and the tables present data for each fifth day of observation. The most striking differences occurred in the approach-withdrawal behavior and in schooling formations.

Approach-Withdrawal Behavior (Fig. 3): In approach-withdrawal behavior an approach made by one fish to within 3 cm. of the other fish is followed by an almost immediate veering away of the two fish from each other. The approach is either head to head or head to lateral flank. It is usually the head to head approaches which are followed by withdrawal, although, in several tests, withdrawal followed head to lateral flank approaches.

Among the community-reared fish (C), head to head approaches, followed by withdrawals diminished as the fish grew, whereas the fish of I- and RI-groups showed a continuous high level of approach-withdrawal behavior. Among the I-group, only head to head approaches were followed by withdrawals, seen on the first, fifth, and tenth day of testing. On the fifteenth day, in addition to many head to head approach-withdrawals, a small number of head to lateral flank approaches were followed by withdrawals. However, on the twentieth day and subsequently, the majority of approaches were head to lateral flank and were

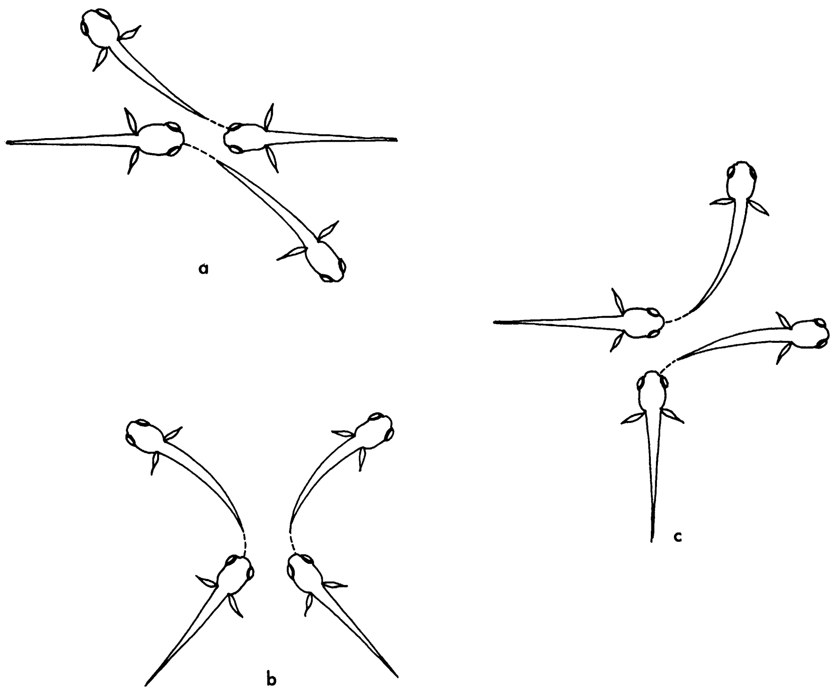

FIG. 3. Types of approach-withdrawal behavior. a. Head to tail. b. Heads oblique. c. Heads at right angles.

followed by withdrawals. Head to head approaches continued nonetheless.

Among RI fish, at the twentieth day, there were many head to head approaches followed by withdrawals and a few head to lateral flank approaches. On the twenty-fifth day, the majority of approaches were head to lateral flank, although head to head approaches continued at a high level. By the thirtieth day, the approaches were mainly head to lateral flank. It should be pointed out that the behavior of the RI-group fish at the twentieth day resembled that of the I-group of the fifteenth day and that the behavior of RI at the twenty-fifth day resembled that of the I-group of the twentieth day. By the thirtieth day, their behaviors were alike.

The mean frequencies of approach-withdrawal behavior are presented in table 1. Statistically significant differences are indicated in the table. The low number seen among the I-group on the first day reflects the fact that these fish tended to remain quiescent when introduced to the testing chamber. They simply did not move, in contrast to the actively swimming

TABLE 1
INTERGROUP COMPARISONS OF MEAN FREQUENCIES OF APPROACH-WITHDRAWAL BEHAVIOR[a]

Day of Test	C Group		I Group		RI Group	
	N	Mean	N	Mean	N	Mean
1	12	13.7[b]	14	5.6[b]		
5	12	8.1[c]	12	12.7[c]		
10	14	15.6	12	20.7		
15	14	20.4[c]	12	32.5[c]		
20	9	26.0[c]	12	48.1	7	56.0
25	12	9.3[b]	12	42.1[b]	6	79.8[b]
30	12	14.6[b]	12	39.0	7	42.3
35	12	5.7[b]	12	46.7	8	42.2
40	14	6.6[b]	12	39.6	8	38.2
45	14	3.5[b]	12	39.9	12	38.4
50	13	2.8[b]	13	41.4	12	41.7
55	14	2.0[b]	12	44.4	12	33.8

[a] Comparisons are on a pair basis and evaluated according to Newman-Keuls Multiple Comparisons Procedure.

[b] This group is significantly different from the other two groups; $p<0.01$.

[c] This group is significantly different from the other one or two groups; $p<0.05$.

Symbols: C, community reared; I, isolates; RI, retested isolates. N = number of groups of four fish each.

community-group fish of the same day. From the twenty-fifth through the fifty-fifth day, the approach-withdrawal frequencies between C and I and RI were strikingly different. The very high frequency shown by RI of the twenty-fifth day was particularly dramatic.

Frequencies of approach-withdrawal behavior are compared (fig. 4) for each of the groups, starting with the first day and ending at the fifty-fifth day. The trend is toward a reduction of this behavior among the C-group with tapering off beginning on the twenty-fifth day. In contrast, in the I-group, the frequency remains high. Aside from the one sharp spurt on the twenty-fifth day, the RI-group shows the same curve as the I-group.

In sum, a high frequency of approach-withdrawal behavior continues to be seen throughout the study among the isolates and among the community group fish.

Withdrawal occurred among C-group fish only after head to head approaches. Parallel swimming generally followed lateral flank approaches. Among I- and RI-group fish, withdrawals occurred after head to head approaches and also after head to lateral flank approaches.

LATERAL TURNING: Much of the withdrawal behavior seen among the

I and RI during later development was a component of lateral turning. This behavior was never seen among C-group fish.

Lateral turning is best seen in illustration. In figure 5, the sequential and repetitive events are diagrammatically presented, 1) a head to lateral flank approach, 2) momentary parallel swimming, 3) withdrawal, 4) head

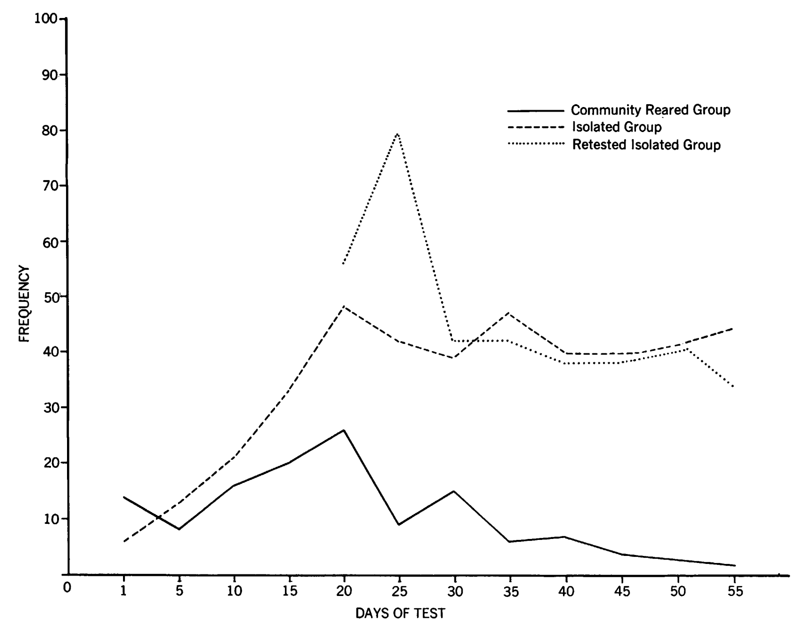

FIG. 4. Comparison of mean frequency of approach-withdrawals.

to lateral flank, etc. The parallel swimming lasted for a few moments and the fish were less than 1 cm. apart. Withdrawal was a simultaneous turning away of fish, at an angle of about 45°. Then each fish approached an adjacent one and went through the same maneuvers again. The activity was slow and pulsed rhythmically. Lateral turning generally occurred during the first 20 minutes of the test and was followed by sustained parallel swimming. The school moved in a zigzag path.

Sporadic lateral turning was first seen among the I-group of 15 days and consistently beginning on the twentieth day and thereafter. Among RI-group fish sporadic lateral turning was not seen until the twentieth day and consistently beginning on the twenty-fifth day and thereafter.

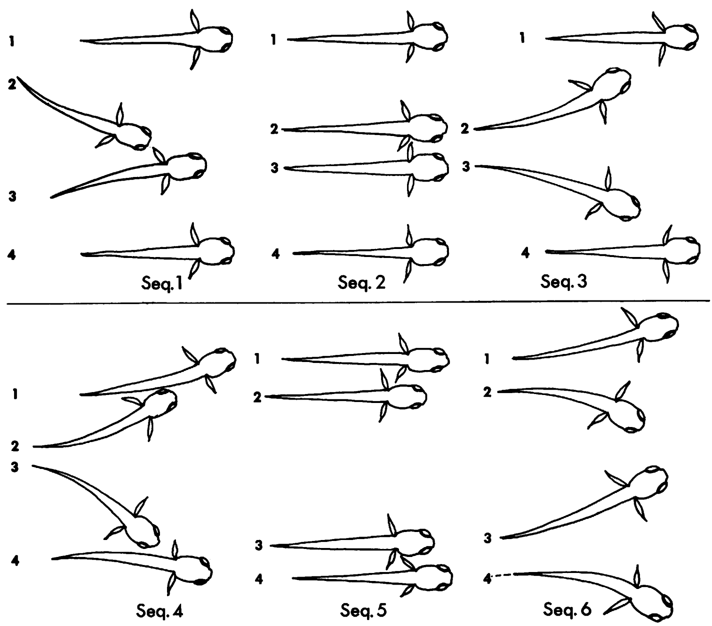

FIG. 5. Lateral turning. Sequence 1. Head to lateral flank approach of fry No. 2 to fry No. 3. Sequence 2. Momentary parallel orientation of fry No. 2 and fry No. 3. Sequence 3. Immediate withdrawal of fry No. 2 and fry No. 3 from each other at 45° angle. Sequence 4. Head to lateral flank approach of fry No. 2 to fry No. 1, and fry No. 3 to fry No. 4. Sequence 5. Momentary parallel orientation of fry No. 1 and No. 2, and of fry No. 3 and No. 4. Sequence 6. Immediate withdrawal of fry No. 1 and No. 2 from each other, and fry No. 3 and No. 4 from each other at 45° angle.

If lateral turning did not occur, as was the case in a total of nine tests throughout the study, parallel swimming never appeared.

The schooling pattern seen among the fish showing lateral turning will be discussed below.

DURATION OF PARALLEL ORIENTATION: Parallel orientation, or parallel swimming, did not occur with measurable frequency in any groups before the twentieth day of these tests. By the twentieth day, the average length of the fish was 10 mm. Parallel swimming occurred after a head to lateral flank or head to tail approach (fig. 6). The fish oriented parallel in a staggered formation and swam off together. A school could contain two, three, or four fish and the total duration of parallel swimming was measured for schools of two, three, or four fish.

The only significant differences among the groups in duration of paral-

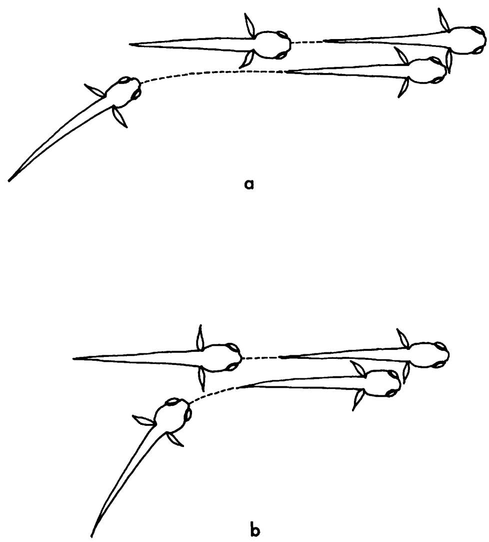

FIG. 6. Approach and parallel orientation. a. Head to tail approach. b. Head to lateral flank approach.

TABLE 2

INTERGROUP COMPARISONS OF DURATION (IN SECONDS) OF PARALLEL ORIENTATION[a]

Day of Test	C Group		I Group		RI Group	
	N	Mean[b]	N	Mean	N	Mean
20	9	418.8	12	307.1	7	142.6[c]
25	12	420.5	12	423.5	6	309.7
30	12	401.9	12	422.0	7	417.6
35	12	432.0	12	473.6	8	406.1
40	14	427.2	12	435.7	8	388.6
45	14	422.9	12	376.0	12	487.7
50	13	414.6	13	400.2	12	523.7
55	14	341.9	12	195.6	12	569.0[d]

[a] Comparisons are on a pair basis and evaluated according to the Newman-Keuls Multiple Comparisons Procedure.

[b] Means are expressed in seconds.

[c] This group is significantly different from the other two groups; $p < 0.05$.

[d] This group is significantly different from the other two groups; $p < 0.01$.

Symbols: C, community reared; I, isolates; RI, retested isolates. N = number of groups of four fish each.

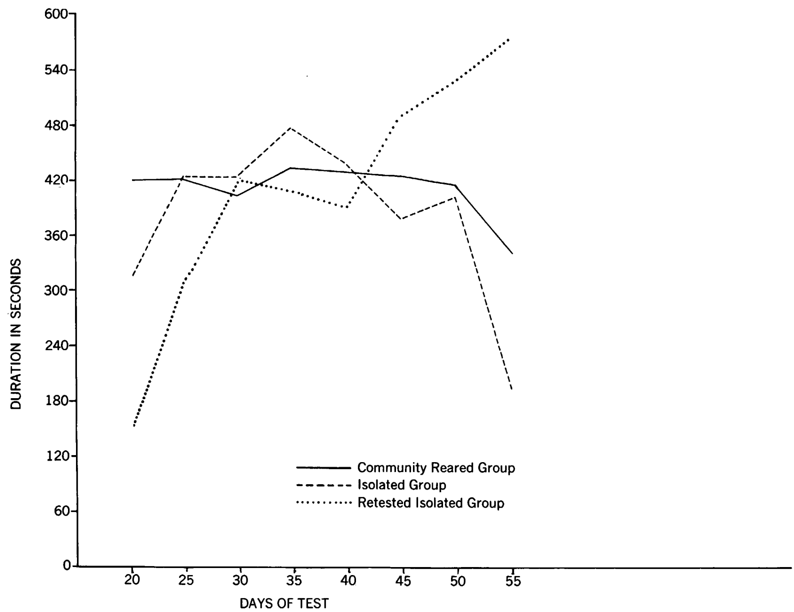

FIG. 7. Comparison of mean duration of parallel orientation.

lel swimming occurred on the twentieth and fifty-fifth day (table 2). On the twentieth day the duration among RI-group fish was lower than the others. On the fifty-fifth day the duration was higher than the others. The low figure on the twentieth day is reflected in the over-all activity of that group, resembling the I-group of the fifteenth day. As seen in figure 7, the trend among the RI-group is for parallel swimming of longer and longer duration as the fish grew; the C-group tended to remain the same, but the I-group showed a sharp decline on the fifty-fifth day.

Some interesting differences occurred in the number of fish that swam parallel in the measurements of duration of parallel orientation in schools composed of two, three, or four fry. It was found, at 20 days, RI schools occurred mainly between two fish, infrequently among three or four, with a concomitant and significantly low duration of parallel orientation. As this group of fish matured, schools composed of three and four fry became more stable and frequent in occurrence and especially so at 55 days, when mainly four-fry schools prevailed. At 45 and 50 days, the I-group fish exhibited long durations of parallel swimming between two fry and among three fry, but at 55 days schools composed of three fish were momentary, schools of four fry were non-existent, and most of the parallel swimming occurred between two fish. No such tendencies, on the other hand, were seen in C-group where schools of two, three, or four fish occurred randomly and regularly.

Description and Organization of Schools: The first tendencies toward parallel swimming occurred among the C-group fish on the fifteenth day when the fish were approximately 9.5 mm. in length. However, each time two or more fish lined up parallel they remained oriented for only several seconds with fish to fish distances variable, 1 to 3 cm. apart. Many such short-lived schools were formed and the general tone was of loosely organized schools. By the twentieth day, at the beginning of the tests, parallel swimming was seen but there was a great deal of position shifting, and variable fish to fish distances. When the fourth fish was added, the school acquired greater cohesion and the variability in fish to fish spacing and distances apart diminished. These schools cut a straight path as they swam (fig. 8). Clearly polarized, cohesive schools were seen among all the tested C-group fish from the twenty-fifth until the fifty-fifth day when some changes occurred. For example, no schooling occurred in two of the 14 tests. The fish, instead, chased each other. In four tests initially, schooling was uniform and good but in eight tests parallel swimming was sporadic during the first 20 minutes of testing, becoming cohesive and continuous later. Then the school was uniform, had close fry to fry distances, with less variations in swimming direction and position of the fish.

Schooling patterns among the I- and RI-groups were similar from the twentieth through the fiftieth day. Lateral turning, seen during the initial phases of the tests, diminished in intensity after the first 20 minutes of each test. Nevertheless, although the fish swam together in a coordinated fashion, the persistence of vestiges of lateral turning created a zigzag path, as seen in figure 8. Despite the zigzag path there was cohesion and consistency in the schools and the fish tended to stay 1 to 2 cm. apart.

By the fifty-fifth day, among I-group fish, no schooling occurred in three out of 12 tests. Interestingly, as mentioned above, when schools were not established, there was also no previous lateral turning.

On the fifty-fifth day, when the RI fish showed the highest duration of parallel orientation, their schooling was uniform and cohesive. Most of the schools zoomed along in a straight path with only occasional zigzag motions. The zigzag path had virtually disappeared.

Some other general observations about the various schools are worthy of mention. For example, among the C-group, if one of the members swam away from the school, attracted perhaps by a particle in the water,

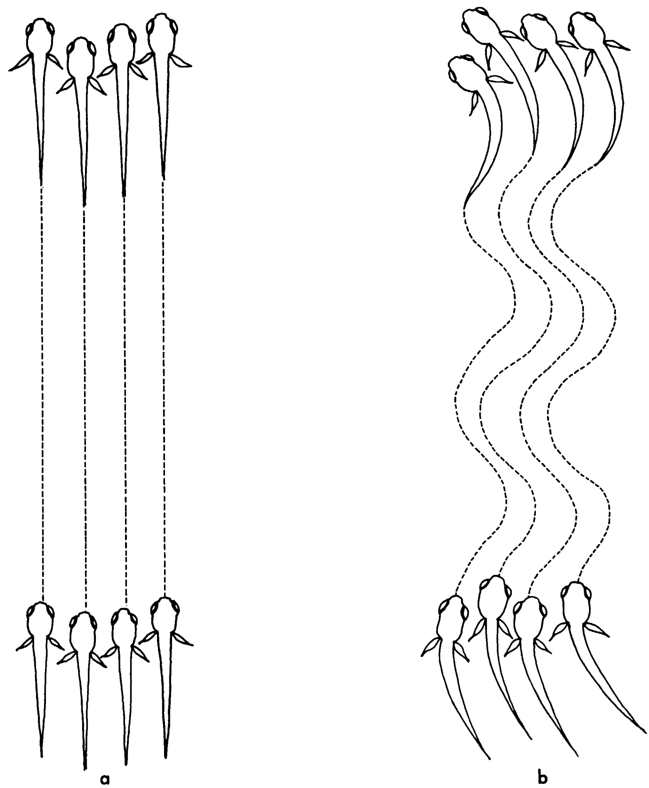

FIG. 8. Swimming paths of schools. a. C-group schools swimming in a straight path. b. I- and RI-group schools swimming in zigzag path.

this fish would rejoin the school very quickly. In contrast, a fish of the I- and RI-group under similar circumstances did not rejoin the school. Too, when a school of C fish changed direction or speed, all the fish seemed to execute the turn simultaneously and changed speed, if necessary, very rapidly. Not so with the I- and RI-group. These adjustments were slow and often gave rise to dispersal of the school for several seconds.

These observations are reflected in the analysis of the duration of longest persisting schools (fig. 9). It is quite clear that the C-group fish had much longer persisting schools than the I and RI. Statistically significant differences ($p < 0.05$) were found on the twentieth day, the fortieth day, and the fifty-fifth day, C differing from I and RI, C differing from RI but not from I, and C differing from I but not from RI, respectively.

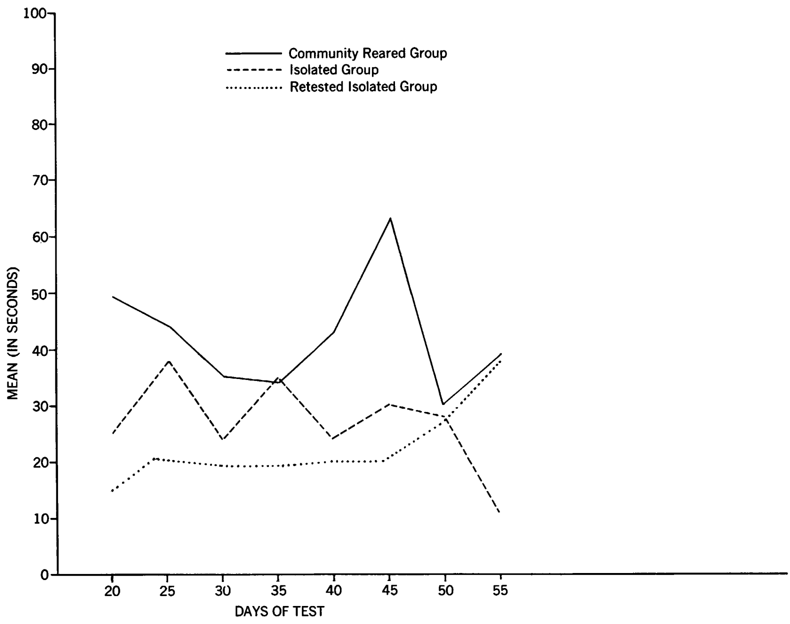

FIG. 9. Comparison of duration of longest persisting schools.

As mentioned earlier, records were made of the time fish spent near each other in a nonpolarized orientation. This occurred so infrequently that it is not reported here. The fish interacted by approaching and withdrawing or approaching and taking up parallel swimming.

In general, the fish were watched in their rearing chambers. Behavioral interactions among C-group fish in their home tanks appeared to be similar to those in the testing tank. The I- and RI-group fish were generally seen actively swimming along the periphery of their styrofoam rearing bowls. Considerable time was spent among all the groups in pursuit of the *Artemia* nauplii, their food supply.

DISCUSSION

This extension of Shaw's earlier work (1960, 1961), on the rearing of *Menidia menidia* under different environmental conditions, has resulted in a new finding: drastic modification of a species typical environment results in modification of species typical behavior among fish, animals considered to have stereotyped behavior essentially determined by genetic make-up and implicitly capable of minimal modifications. The fundamental behavioral characteristic, schooling, persisted, however. The modification occurred in the interaction between the fish and in the over-all schooling pattern. The results of these researches emphasize the point made by Schneirla (1966) when referring to the innate vs. acquired dichotomy. He stressed the point that characteristics often considered innate are results of the animal's having been reared in its species typical environment.

An environment other than species typical is a modified environment. In this experiment, all of the rearing conditions were environmental modifications. One environment, where fish were raised together in communities, more closely approached that typical of the species (Shaw, 1960). The other environment was a more drastic modification. The fish in the styrofoam cups either had no contact with species mates or a limited single experience. The isolated fish were confined to a small volume, the community-reared fish to a larger volume. The isolated fish, aside from their food supply, live *Artemia* nauplii, had a visually homogeneous environment. They could see upward, however, into the laboratory. The community-reared fish had a visually heterogeneous environment and considerable opportunity for interaction. The latter were not considered controls, but rather fish reared in environmental modification that more closely approached the species typical. In both conditions, the fish were fed the same food, probably experienced similar odors and similar laboratory sounds. Other vibratory stimuli, however, were different, particularly those sensed through the lateral line system. The community-reared fish had ample exposure to lateral line stimuli from species mates. But the isolates did not. Limited experience with lateral line stimuli among the isolates may have been a major factor in the development of lateral turning. For instance, as those inexperienced fish approached one another, the vibratory stimuli created by their movements could have represented a highly intense stimulus. This high intensity stimulus drove the fish apart, but the pull, or visual attraction, toward each other counteracted the withdrawal, and so the fish reapproached. Interestingly, if lateral turning did not occur, neither did schooling. Lateral turning may have been an orientation process for these inexperienced fish, which, once adjusted, could remain together. Lateral turning accounts for the high level of withdrawal behavior which continued well beyond the time that withdrawal behavior disappeared in the community-reared fish. It was as if the fish were ambivalent, having on the one hand, strong attraction and the schooling response, and on the other, withdrawal, a behavior tending to disrupt the school. The fish reared in isolation did not appear able to make the appropriate adjustments or to integrate completely the two opposing behaviors which left traces, like the zigzag pattern of swimming. Whether, in time, this pattern could have disappeared is at the moment conjectural, as the experiments terminated on the fifty-fifth day. However, that it might disappear is suggested by the results with the RI-group of the fifty-fifth day, on which lateral turning was minimal and the school swam in a relatively smooth, even path. Fish experienced one another on the thirty-fifth day, two weeks after the tendency to school had been established. Additional experiments would have to be carried out to test the hypothesis that single experiences at earlier stages of development tend to affect behavioral organization more readily than experiences at later stages.

Another provocative result is the finding that RI fish exposed to conspecies on the first and fifth days and retested on the twentieth and twenty-fifth days tended to show behavior comparable with that of younger counterparts, reared without exposure to species. The RI-group of 20 days resembled the I-group of 15 days and the RI-group of 25 days, the I-group of 20 days. Afterward their behaviors were comparable until the fifty-fifth day when changes again occurred, as mentioned above. Exposures to species mates on the tenth, fifteenth, twentieth, twenty-fifth, and thirtieth days did not have apparent effect on the RI-group when compared with the I-group of the same day.

In comparing these results with those of other workers and those of Shaw's earlier works, we find that Dambach (1963) and Jorné-Safriel and Shaw (1966) noted schooling among isolates of *Tilapia* sp. and *Atherina mochon* respectively. The data are not comparable, however, as they are concerned mainly with the gross appearance of schooling rather than any modifications. Shaw (1961) found that latencies in schooling appearance increased among fish that had conspecific experiences during the first seven days of life over fish that had no such experiences. Comparable latencies were not obtained in the current experiments because the measurement procedure was different. However, the important point is that short periods of exposure to conspecies (RI) affected the behavior and delayed its onset in these experiments as in Shaw's (1961) researches.

A question about the type of rearing chambers and their effect on behavior may be raised here. Would the fish, reared in styrofoam cups have behaved differently if they had been reared in another kind of chamber? Was it, in fact, isolation from species mates, per se, that produced the modifications or was it merely living in the small white cup? One avenue of evidence points up the social experiences, rather than the physical, as playing a critical role. The fish reared in styrofoam cups and given a single experience with conspecific fish behaved differently from those reared in the cups, but without the experience.

The experiments demonstrate that schooling behavior is modified to a significant degree when the fish are reared in atypical environmental conditions. They also demonstrate that behavior cannot be usefully categorized into innate or acquired qualities, but must be studied in terms of the totality of a developmental system.

SUMMARY

More than one thousand *Menidia menidia*, a schooling fish, were reared from the embryonic stage to the schooling stage under two environmental conditions, namely, together in aquarium tanks and separately in styrofoam cups. Many individually reared fish, the isolates, were given a single exposure with age peers at some point during their development. A number of individually reared fish that had contact showed behavioral modifications when compared with the isolates that were not given such an experience.

Schooling behavior was modified among the isolates. Withdrawal behavior, which normally decreases when the schooling tendency is established continued to be seen at a significantly high level during the schooling phase. A new behavior, named lateral turning, was observed. Apparently, as a consequence of the continued high withdrawal rate and the lateral turning, the schooling organization was different among the isolates when compared with the schooling organization of the fish reared together in aquarium tanks.

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