# The Duration of Schooling Among Fish Separated and Those Not Separated by Barriers

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## INTRODUCTION

Schooling fish must see in order to form schools (reviews by Morrow, 1948; Atz, 1953; Breder, 1959; and Shaw, in press). If vision is obliterated, occluded, or otherwise interfered with, schooling ceases, as it does in dim light and in total darkness (Shaw, 1961; John, 1964; and Hunter, 1968). Vision is the evident and essential element in the attraction and approach phase of schooling. Questions remain, however, as to the role of vision in the maintenance of the school and particularly in the maintenance of parallel orientation, and as to whether or not group cohesion can be sustained without added information from sensory systems other than the visual system. Examining that aspect of the problem, Keenleyside (1955) and Hemmings (1966) reported that freely swimming fish were attracted to and approached conspecies enclosed in a transparent chamber, a box, or jar, and, in addition, Keenleyside reported that the freely swimming fish gradually moved away. He suggested that the absence of other than visual cues finally caused the moving-away of the freely swimming fish. In 1960 Shaw observed that young *Menidia* approached a glass tube containing a conspecies, and that the freely swim-

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ming fish oriented parallel for approximately one minute. After that period the fish swam away and did not return. In the above experiments the constricted fish was unable to reorient readily its swimming direction. But when a separated fish was able to reorient and to readjust its position in relation to that of the other fish, another behavior occurred. Shlaifer (1942) found that a pair of mackerel (*Pneumatophorus grex*) remained near each other and swam parallel to each other "with sufficient frequency to be considered significant" when the pair was separated by a long glass plate. Cahn (1967), in a preliminary report, noted that in the tuna (*Euthynnus affinis*) parallel orientation was maintained for "several days" among fish separated from one another by long, transparent barriers if they did not need to make major swimming-speed adjustments. Under those conditions the behavior of restricted fish appeared qualitatively equivalent to that of unrestricted fish. Thus, although stimuli for orientation were perceived only by means of the visual system, fish remained nearby. Parallel orientation was possible if both fish had the opportunity to readjust spatial positions relative to each other. But, before we conclude that barriers do not affect schooling orientation (and concomitantly that vision is the only sensory modality involved in parallel orientation) it is essential to obtain quantitative results that show whether or not the duration of schooling is the same among fish that are separated by a barrier and among those that are not separated. Through such quantitative analyses it becomes possible to establish the relative importance of various sensory systems in schooling behavior.

The following experiments were carried out to see (1) if fish swim parallel to one another when separated by either transparent barriers or barriers that partly occlude vision, and (2) if the time that the fish remain in parallel orientation is equal whether or not they are separated.

## MATERIALS AND METHODS

Jacks (*Caranx hippos*), 5 to 6 inches long, were taken by hand lines from the waters around the Bermuda Biological Station, St. George's West, Bermuda. Fish were kept initially in large concrete aquariums and observed within the same day because they tended to weaken rapidly under laboratory conditions.

During the experiment, the fish swam in a shallow concrete tank, 12 feet long by 39 inches wide. Fresh sea water flowed in continually, maintaining the depth at 9 inches, which virtually eliminated the vertical component of the fish school.

The barriers were 12 feet long by 12 inches high; the transparent one

was made of optical quality Plexiglas, ¼ inch thick, and the partially
occluding barrier was made of gray Saran screening, the kind commonly
used in household screens. The barriers divided the concrete tank into
two parts of equal size (fig. 1). At one end of the tank, called the near
end, a Ciné-Kodak Special, 16-mm. movie camera, was mounted 6 feet
above water level, and with a wide-angle lens it covered a photographic
field of 4 square feet. Fish were introduced at the opposite end, called
the far end, and generally swam along the length of the tank to the near
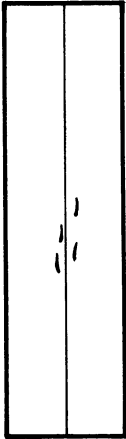end, where they were filmed. The filming, 24 frames per second, started



FIG. 1. Scale diagram of the experimental tank and the fish.

as the first fish entered the field of view of the camera and was terminated
after all the fish swam out of the field of view. Filmed sequences lasted
from 3.75 seconds to 15 seconds, the duration depending on the swim-
ming activity of the fish. Eighty-five sequences were recorded.

The fish were grouped into twos, threes, and fours, that is, two fish
were introduced into the tank, one on each side of the barrier; three fish,
two on one side and one on the other; and four fish, two on each side.
Figure 2 represents the arrangement of the groups and the number of
filmed sequences that were analyzed for each group. Each fish was
·numbered, relating to the analysis presented in the results. Once num-
bered, a fish retained the same number throughout the analysis.

The first requirement was to establish the criterion for the term "paral-
lel." This requirement was met by measuring fish to determine if they
ever were parallel and the degree to which they diverged from the paral-
lel during the course of normal swimming movements. Lines drawn
through the center of the snouts indicated that fish at any moment might
be parallel. Taking into account the natural divergences resulting from

swimming, we decided for the purpose of this experiment that fish were oriented parallel if their angular divergences or headings from one another were 26 degrees or less.[1]

Single frames from each filmed sequence were projected onto a drawing board, and the position of each fish in every sixth frame was outlined. For each sequence changes in orientation of any one fish appeared as a continuum on the drawing paper (figs. 3, 4).

Angular divergences or headings were obtained by giving the angular heading, 0 degrees, to the first fish entering the camera field. A line was drawn through the center of the snout and body. The tail, during normal swimming, was to the right or left of the line. Lines were drawn through the snouts and bodies of all other fish positions in that sequence. The initial heading of the first fish was used as the base against which to measure its own divergences in subsequent frames and the divergences of other fish in the first frame and in subsequent frames. Let me point out that one fish may have had a heading of 0 degrees, but that three other fish, for example, in the same frame may have had headings of 40 degrees, 45 degrees, and 50 degrees, respectively. The last three would be considered to be parallel to one another because their divergences relative to one another were less than 26 degrees, whereas the first diverged more than 26 degrees and would not be considered parallel. For clarification, see table 1. Cross-sectionally, in frame 1, fish 1 and 2 are not parallel, fish 2 and 3, 3 and 4, 2 and 4 are parallel. In frame 2, all the fish are parallel, since no divergences are greater than 26 degrees. Longitudinally, fish 1 diverged 20 degrees in frame 2 from its initial heading in frame 1, whereas the others diverged 5 or 10 degrees.

All angular divergences were established between every possible combination of two fish. As we have the time element recorded on film and the headings recorded from every sixth frame, it was possible to determine the amount of time any two fish in a sequence were oriented parallel (that is, had angular divergence of 26 degrees or less). The data were processed on a Recomp II computer, and the time each pair spent in parallel orientation was obtained.

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[1] This research was carried out during 1959 at the Bermuda Biological Station. Angular divergences were measured during 1960–1961, and the final computer analysis was made in 1963. Of particular pertinency, then, is a recent paper by Hunter (1968) who reported that jacks (*Trachurus symmetricus*) showed radical reorientation to one another as light was increased. At $6 \times 10^{-7}$ foot lamberts they showed angular divergences of 60 degrees or so, but at $6 \times 10^{-6}$ foot lamberts the divergences became 25 degrees or less and remained so during all further light increases.
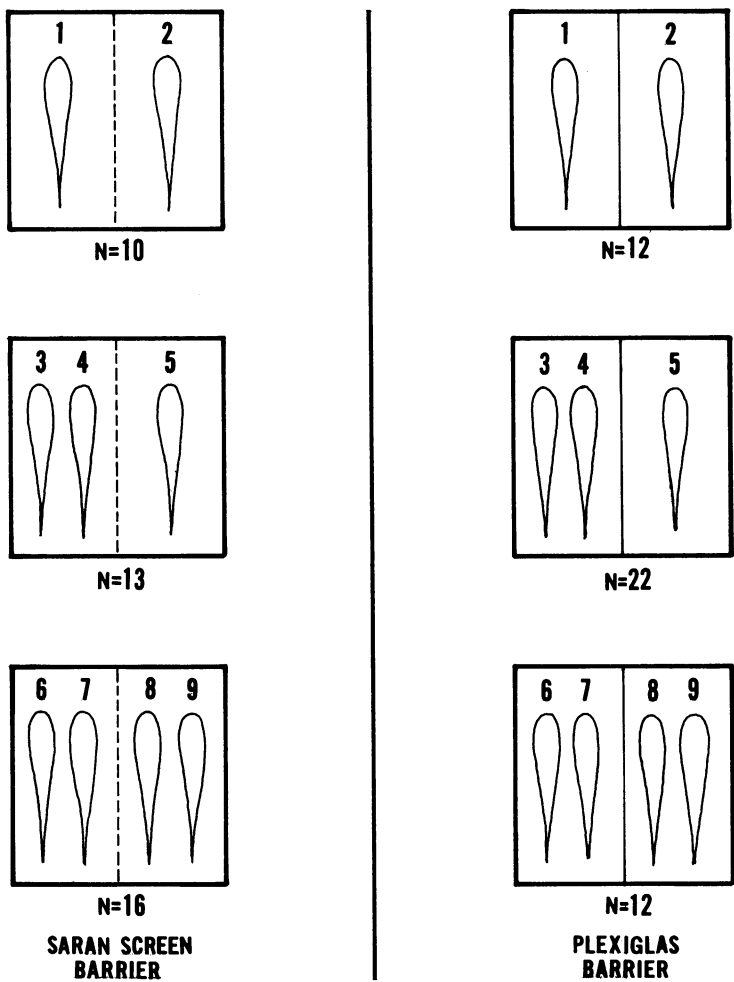
FIG. 2. Arrangement of the fish groupings. N represents the number of film sequences analyzed for each grouping. The numbers over each fish relate to the analysis of pairs (see text).

## RESULTS

Table 2 lists the mean percentage of time that two fish (pairs A through R) were oriented to one another, with headings showing angular divergences of 26 degrees or less. (Reference to fish number can be found in fig. 2.) The highest means of the time that two fish spent parallel to one another were obtained among pairs G, L, O, Q, when mean time
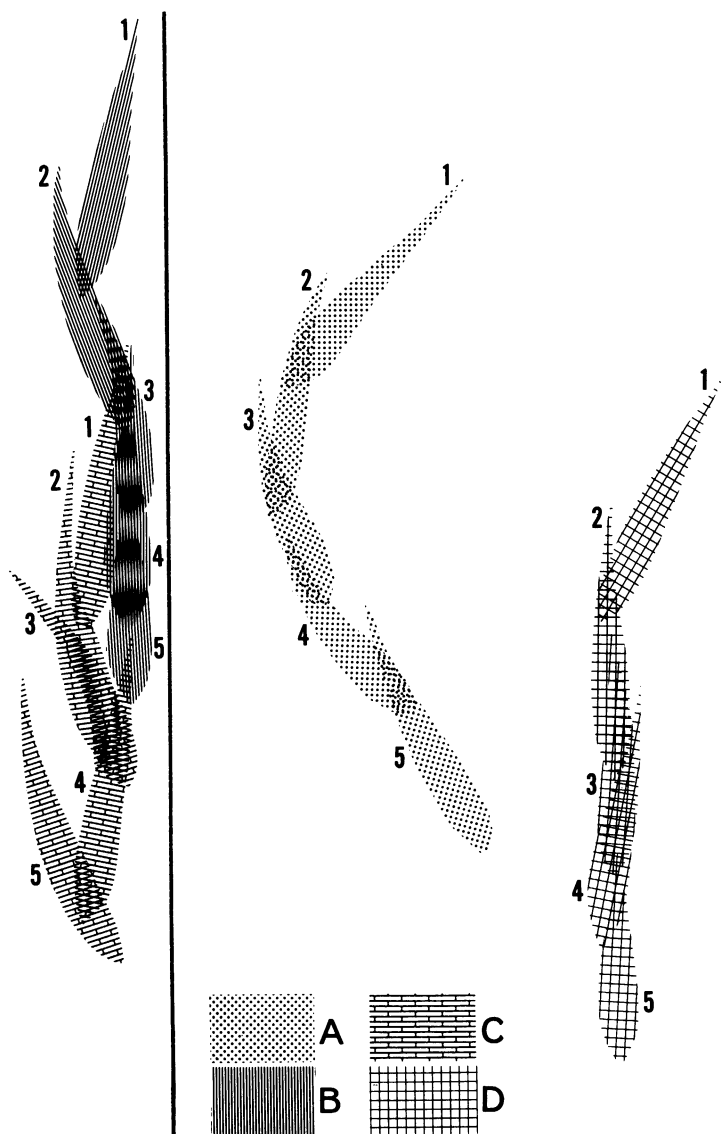
FIG. 3. Saran-screen barrier. A replication of the drawings used in measuring angular divergences. Each fish is in every sixth frame (24 f.p.s.). Individuals are designated by the specific patterns, and the numbers indicate corresponding frames. From left to right, the positions and sequential changes of all the fish in frame 3 are seen. Note that one pair swims away from the barrier and the other pair approaches it.
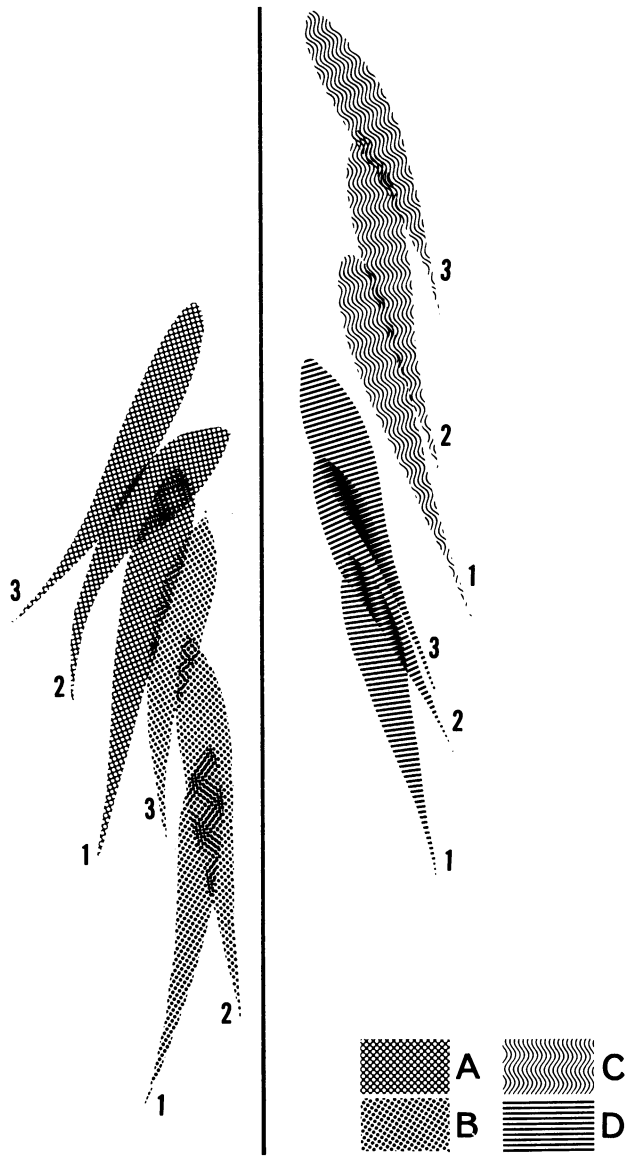
Fig. 4. Plexiglas barrier. Description as in figure 3. Note that the fish closely approach the barrier.

was more than 40 per cent of the sequence. Pairs B, E, and M showed more than 34 per cent and the remainder below 30 per cent.

Despite the fact that pairs A and K had low means, it was obvious to

TABLE 1

ANGULAR HEADINGS

| Frame Number | Fish Number | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| 1 | 0° | 35° | 25° | 10° |
| 2 | 20° | 45° | 25° | 20° |

TABLE 2

MEAN PERCENTAGE OF TIME THAT ANY PAIR OF FISH SPENT
ORIENTED IN ANGULAR DIVERGENCES OF LESS THAN 26 DEGREES[a]

| Fish Pair | Number of Sequences Evaluated | Mean | Standard Deviation |
|---|---|---|---|
| Plexiglas partition | | | |
| A (1, II) | 12 | 26.1 | 12.4 |
| B (3, 4) | 22 | 34.6 | 16.2 |
| C (4, V) | 22 | 27.8 | 17.3 |
| D (3, V) | 22 | 26.4 | 15.1 |
| E (6, 7) | 12 | 34.8 | 24.0 |
| F (7, VII) | 12 | 26.1 | 15.4 |
| G (8, 9) | 12 | 40.8 | 20.7 |
| Ha(6, VIII) and Hb (7, IX)[b] | 24 | 27.6 | 20.1 |
| J (6, IX) | 12 | 23.4 | 17.1 |
| Saran-screen partition | | | |
| K (1, II) | 10 | 28.9 | 13.1 |
| L (3, 4) | 13 | 43.2 | 14.9 |
| M (4, V) | 13 | 35.0 | 16.1 |
| N (3, V) | 13 | 26.8 | 18.8 |
| O (6, 7) | 16 | 46.4 | 18.8 |
| P (7, VIII) | 16 | 27.8 | 17.3 |
| Q (8, 9) | 16 | 44.0 | 19.4 |
| Ra (6, VIII) and Rb (7, IX)[b] | 32 | 28.6 | 18.4 |
| S (6, IX) | 16 | 23.1 | 18.6 |

[a] For immediate recognition, if a pair of fish were separated by a barrier, one member of the pair was given a Roman numeral and the other an Arabic numeral. A pair of fish that were on the same side of a barrier were given Arabic numerals. For convenience in comparison, each pair of fish was designated by a letter.

[b] Equivalent pairs.

TABLE 3

COMPARISON OF THE MEANS[a] OF ANY TWO PAIRS
THOSE FOR WHICH MEANS ARE SIGNIFICANTLY DIFFERENT

| Plexiglas Partition | Student's One-Tailed T-Test | Saran-Screen Partition | Student's One-Tailed-T Test |
|---|---|---|---|
| Pairs A and B | $p < .10$ | Pairs K and L | $p < .05$ |
| Pairs A and E | $p < .05$ | Pairs K and O | $p < .01$ |
| Pairs A and G | $p < .05$ | Pairs M and O | $p < .05$ |
| Pairs E and C | $p < .10$ | Pairs N and L | $p < .01$ |
| Pairs F and G | $p < .10$ | Pairs P and O | $p < .01$ |
| | | Pairs P and Q | $p < .01$ |

[a] See table 2.

the observer that the fish were attracted to one another. For example, if, after turning, one fish did not immediately return and swim along the partition, the opposing fish slowed down and the two fish faced each other. Often they remained at angular divergences of 45–60 degrees, but they gradually swam down the partition. Evidently there was strong inter-fish attraction, although parallel orientation did not occur.

In the sequences of three-fish groupings, the single fish reacted strongly to the changes in the movements of the two fish on the opposite side, and the condition found in the two-fish groupings occurred infrequently.

In the sequences of four-fish groupings, the behavior of the fish behind the Saran-screen partitions was noticeably different from that of

TABLE 4

COMPARISON OF THE MEANS[a] OF ANY TWO PAIRS
THOSE FOR WHICH MEANS ARE NOT SIGNIFICANTLY DIFFERENT

| Mixed Partition[b] | |
|---|---|
| Pairs A (P) with C (P) | Pairs G (P) with Q (S) |
| Pairs A (P) with F (P) | Pairs H (P) with R (S) |
| Pairs A (P) with K (S) | Pairs J (S) with S (S) |
| Pairs B (P) with C (P) | Pairs K (S) with M (S) |
| Pairs B (P) with E (P) | Pairs K (S) with P (S) |
| Pairs C (P) with M (S) | Pairs L (S) with M (S) |
| Pairs E (P) with O (S) | Pairs N (S) with D (P) |
| Pairs F (P) with C (P) | Pairs P (S) with F (P) |
| | Pairs P (M) with M (S) |

[a] See table 2.
[b] Plexiglas barrier; Saran-screen barrier.

the fish behind the Plexiglas partitions. A pair on one side of the Saran screening tended not to be distracted by changes in position of the pair on the opposite side. The two fish tended to readjust positions relative to each other. Not so in the Plexiglas partitions. For example, one fish of the pair on the same side could be distracted by a sudden change in behavior, that is, increased speed or turning, of a fish or of both fish on the opposite side of the partition. There appeared to be a brief attempt at reorientation to that change, then suddenly the fish stopped as if "aware" of its immediate neighbor to which it then reoriented. This kind of distractability would naturally lead to lower means of time spent parallel among fish in the Plexiglas partition tests, as was the case. It was noted, too, that the fish occasionally touched the partition (it may not have been visible) and that there was subsequent confusion.

It should be noted here that when fish were introduced into the tank they tended to retain the same position relative to one another until they turned around. In addition, the fish occasionally hugged the partition wall, which brought the fish on each side of the Plexiglas partition within a quarter of an inch of one another. They regularly swam along the partition rather than in the center or along the concrete walls. In addition, fish on each side remained together, never more than several inches apart, with one slightly behind and to one side of the other.

The means of each pair were compared to determine if there were significant differences (Student's one-tailed t test; level of significance set at $p = .10$ or less). Means of time that pairs spent in parallel orientation, which were significantly different as well as those not significantly different, are shown in table 3 and 4.

Thus, it is apparent that when the two fish are compared with the four-fish groupings the two fish not separated by a partition spend a significantly longer time in parallel orientation than do the two fish that are separated by a partition. An exception is found among the pairs in the three fish groupings, for when pair L was compared with M and pair B with C the time proved not to be significantly different, although the means were, respectively, 43.2 (L) and 35.0 (M), and 34.6 (B) and 27.8 (C).

## DISCUSSION

The results show that parallel orientation is achieved if two fish are separated by either a Plexiglas or a Saran-screen barrier. Had this experiment been carried out qualitatively, it could have been said that fish school equally well when separated by barriers, even if the barrier allows only reduced visual contact. However, by measuring the actual

time fish spend in parallel formation we found that there are quantitative differences, and that a pair of fish, when separated, are not oriented parallel for as long in time as a pair of fish that are not separated.

It is obvious that visual attraction occurs between fish. But visual attraction does not appear to be the only requisite for continual parallel orientation, and also distinct anatomical details are apparently not essential. In the two-fish groupings, the means were similar whether separated by Saran-screen or Plexiglas. With the Saran-screen barrier, information about anatomical detail was reduced or somehow modified, or both, and it could be inferred that sharp anatomical details are not imperative to parallel orientation. Perhaps of special importance are certain qualities of movement within a broad range of visual features (Shaw and Tucker, 1965).

What modifications occur to sensory information between fish when separated by the two kinds of barriers? Certainly visual stimuli are transmitted through the Plexiglas barrier. Not transmitted, however, are olfactory stimuli, and stimuli from water vibrations (water displacements). On the other hand, passing through the Saran barrier are visual, olfactory, and water-displacement stimuli. Visual stimuli, however, are modified, and the patterns of water flow are also altered as they pass through the tiny holes of the mesh screen. Olfactory stimuli could pass through it in unaltered condition. If olfactory stimuli served to intensify parallel orientation under these test conditions, then we have an explanation for the higher means obtained from the pairs tested in the Saran-screen barriers. It is unlikely that olfactory stimuli would operate in the actual spatial adjustments made by the fish. Rather, under the stressful conditions of the experiments, odors would tend to bring the fish together more intensely and serve to reinforce the attraction.

One point that should be mentioned is the observation that fish tended to move along the partition, very often abutting it. If the visual image on the retina was the critical determinant of fish-spacing (Parr, 1927) the fish would not have remained so near one another.

In sum, vision is clearly the primary attractive mechanism and obviously parallel orientation can continue via input from the visual system only. However, the fine spatial adjustments carried out during schooling and general group cohesion may well be enhanced by other sensory systems such as the lateralis system (Breder, 1965) and the olfactory system (Hemmings, 1966).

## SUMMARY

Experiments were carried out to determine whether or not the dura-

tion of schooling was equivalent among fish separated by barriers and those not separated by barriers. The barriers were either transparent or they partly occluded vision. The results showed that the time pairs of fish spent oriented parallel to one another when separated by barriers was significantly less than the time other pairs of fish spent oriented parallel when they were not separated by barriers.

## ACKNOWLEDGMENTS

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