

STUDIES ON THE STRUCTURE OF THE FISH SCHOOL

C. M. BREDER, JR.

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INTRODUCTION

CONSIDERABLE LITERATURE on the influences affecting the aggregating tendency in fishes has grown up in the last 25 years. In contrast to this are the relatively few papers attempting to analyze the much more striking phenomenon of the fish school. The first paper presenting critical treatment of the subject is that of Parr (1927). This scarcity of published work is evidently due to the fact that truly schooling fishes are notoriously difficult laboratory materials, as has been clearly indicated by Breder and Halpern (1946). The present author made some preliminary observations (Breder, 1929) on the schooling behavior of *Jenkinsia lamprotaenia* (Linnaeus) at the Tortugas Laboratory of the Carnegie Institution of Washington and considered them excellent material for such studies. It was not until the establishment of the Lerner Marine Laboratory at Bimini, Bahamas, that he was able to resume studies on *Jenkinsia*.

The present contribution, based on work carried out at this place, is the first report of the resumption of this study. Although *Jenkinsia* is as delicate to handle as most similar schooling fishes, if not more so, its abundance, permanent small size, and strong schooling tendency make it an extremely useful form for such studies, when it is possible to carry these out at a place where long transportation of the living fish is unnecessary.

In these studies the intention has been to determine as many as possible of the various influences that bear both on the form of a school and the location in which it will occur. We have as yet far too little data to make any worthwhile forecasts of behavior of schooling fish, but the various details that

are brought out in the present contribution are basically necessary, with many more yet to be explored, to any foundation of data that could eventually lead to prognostications on fish-school behavior.

Three kinds of data must be obtained, at least, on each item bearing on the formation of such schools: 1, does the item being investigated bear on the school formation in a purely qualitative sense; 2, how strong is the influence in a quantitative sense; and 3, how does it interact with other influences at work on the school? With such questions in mind all the possible factors affecting the formation, maintenance, and disintegration of the fish school, both extrinsic and intrinsic, should be studied.

Although it is fully realized that a school of a given species of fish may bear a resemblance to one of another species, each may be molded by very different factors in spite of a superficial similarity. This paper is concerned entirely with the structure of the schools of one species, largely because it was considered best to attempt to find out as much as possible of one available form rather than to scatter effort, at this time, superficially through a wide variety of forms. This work has been carried forward as far as both the imagination of the author and the laboratory equipment available to him at this time permitted.

Miss Priscilla Rasquin and Miss Libby Rosenbloom assisted in various aspects of the field work involved in this study. Their help is herewith gratefully acknowledged, as is that of Mr. J. W. Atz for reading the manuscript critically.

EXPERIMENTS AND OBSERVATIONS

THE EXPERIMENTAL AND OBSERVATIONAL parts of this study are treated together because in most cases they are closely interlocked, generally observations of wild fish from the laboratory dock being carried out simultaneously with experimental procedures on captive schools. The various items investigated are treated separately for convenience under their respective heads.

LIGHT AND DARKNESS

It has been abundantly shown that all known fish schools, or for that matter close aggregations, are mediated through the eye, resulting in dispersion on either blinding or on the coming of darkness. This has been demonstrated for the following species by the respective authors.

- Clupea harangus* Linnaeus; Newman (1876)
Mugil chelo Cuvier (= *M. septentrionalis* Günther?); Bateson (1889)
Pneumatophorus grex (Mitchill); Parr (1927), Schlaifer (1942)
Jenkinsia stolifera (Jordan and Gilbert) [= *J. lamprotaenia* (Gosse)]; Breder (1929)
Morone labrax Linnaeus; Spooner (1931)
Ameiurus melas (Rafinesque); Bowen (1931, 1932)
Lepomis auritus (Linnaeus); Breder and Nigrelli (1935)
Carassius auratus (Linnaeus); Breder and Nigrelli (1938)
Upeneoides spilurus Bleeker; Sato (1938a)
Plotosus anguillaris (Lacépède); Sato (1938b)

The optical control of a school of *Jenkinsia* can easily be demonstrated. If a light is suddenly turned on in a darkened aquarium room, the fish are seen momentarily to be scattered uniformly throughout the aquarium. Immediately they will rush together to form a school in the middle of the tank.

Plate 1 illustrates the appearance of such aggregations in the light and their dispersal in the dark. These photographs were made in an aquarium 2 feet by 1 foot by 1 foot. The area covered by the photograph in each case is 12 inches by 7 inches. The upper photograph (pl. 1, fig. 1) was taken in a lighted room, and the small school is in the center of the aquarium, every fish in it being in the photograph. The lower photograph (pl. 1, fig. 2) is of the same group of fish but taken by flashlight in a dark room. Here the fish

are moving at random throughout the aquarium and are not all in the picture.

It was of interest to determine whether schooling ceased at a point of light reduction where human vision was still possible or at a point beyond that. To accomplish this an aquarium of the fish was established in a dark room. A preliminary series of tests were made by flashing the light on and off merely to confirm the conditions already noted in the aquarium room. The results were identical. A dull red photographic dark room light was arranged so that it could be moved towards or away from the aquarium. When it was moved off so that it was just impossible to see the fish, the school broke up. This was checked by snapping on a white light. On the other hand so long as the fish could be distinguished in the red light they were seen to be in a compact school. This behavior was independent of the length of time that the fish were kept in darkness. Consequently it can be only inferred that the visual limit of the fish and the observer was nearly identical and also that the adaptation of the eyes of both fish and man to low illumination was also nearly equivalent.

Strangely this similarity of reaction to long wave length did not apply under starlight in a large outdoor pool. Here, not infrequently, the fishes could be seen not to be schooling, but to be still easily visible to the human eye.

The presence of moving shadows usually causes a "shock wave" to pass through the school, but at times in a yet not understood fashion the fishes pay no attention to such shadows. On the other hand a "permanent shadow," such as that of a dock or a moored boat, may have very definite effects. Sometimes an entire school will avoid the shadow, and others will avoid the lighted places. In one case in a rectangular concrete tank the entire school occupied the shaded portion only, which gave the school an L-shaped form. Passage from either light or shadow was sometimes made very hesitatingly, generally the more so when the contrast between light and shade was greatest. This behavior would seem to be borne upon by the features brought out by Breder and Rasquin (1950) in reference to the exposure of the pineal area

in *Jenkinsia*. It is probably related closely also to the hesitancy of other fishes to pass from a dark to a light background, or vice versa, as discussed by Breder (1947) and Breder and Rasquin (1950).

APPROACH TO BACKGROUNDS

It has been noted by both Gudger (1929) and Breder (1929) that a school of *Jenkinsia* will approach only to within a definite distance of a solid object such as a pile or a rock. Experiments were undertaken to determine the amount of this distance in terms of length of the fish and to determine whether this distance was invariable or varied with the color of the object. Superficial observation suggested that it was a constant distance. For this and other studies, a circular concrete pool was constructed which measured 12 feet in diameter and 1 foot deep. Schools of small size, 1000 or fewer individuals, took form and occupied only a small portion of the 113 square feet that this pool provided, in contrast to the constant deflection from tank sides that smaller containers provided. Algae grew on the sides of the concrete tank, darkening the surface so that it was rather similar in this respect to the piles and rocks in the adjacent sea. Under such conditions the fish regularly approached the sides as near as two and one-half times the length of the fish, actually very close to 6 inches.

A strip of cardboard 6 feet long and a little over 1 foot wide was prepared, 3 feet of which was white and 3 black. This was set in an arc from the sides so that it enclosed part of a school, which immediately moved to the center of the available area. When the fish had settled down it was observed that they approached definitely closer to the white than to the black vertical wall. The distance maintained from the black wall was about the same as that from the algae-covered concrete wall, while the distance from the white wall was maintained at about half that, or approximately 3 inches.

Although there was a space of easy passage between the concrete wall and the ends of the cardboard, this was less than 6 inches. It was thus sufficient to confine these fishes, as they refused to approach closer to the concrete than the specified distance.

Some of the fishes not within the enclosure

approached the white card but avoided the black, even in some cases "scratching" themselves on it. Those within did not do this, but apparently this is merely a mechanical circumstance, since the surface was convex to the first group and concave to the second. On the second day the cardboard collapsed, and many of the *Jenkinsia* gathered over the white portion but avoided the black.

FORMATION OF A MILL

Mill formation was of common occurrence under the conditions described in the preceding section, although a true mill has not yet been observed in the open sea in this species. This phenomenon has been referred to extrinsic factors, turning a school back on itself, by Parr (1927). This clearly occurs, but in addition, so far as observations show, mill formation sometimes seems to be initiated by purely intrinsic factors within the school itself. A mill about 3 feet in diameter will be formed by a school of about 500 fish. This pool, carefully designed so that not even inlets and outlets, which were recessed in the wall, formed obstructions, presented slight external physical reasons for mill formation. Actually the formation of at least 50 mills was witnessed. Some of these occurred when the school was near a wall and sometimes when it was as remote as possible from it, i.e., when the school was at the center of the tank, with the nearest fish $4\frac{1}{2}$ feet from the wall. Sometimes the shadow of a flying bird would deflect the "leaders," and they would pick up the "trailers," leading to mill formation in classic fashion. At other times when no detectable event whatever occurred, the fish simply reorientated themselves and passed rapidly from a forward-moving school to a mill. In these cases the leaders turned back on themselves, immediately after which a wave of "confusion" passed through the group, leaving a well-formed mill. It was difficult to see just what happened in that short period of "confusion" in which the school was temporarily disrupted, with fishes pointing in all directions, and which was followed by a smoothly turning mill. That the bottom was uniform and no external event associated with this activity occurred led to the supposition that such mills may in truth be formed from purely intrinsic causes. The influences

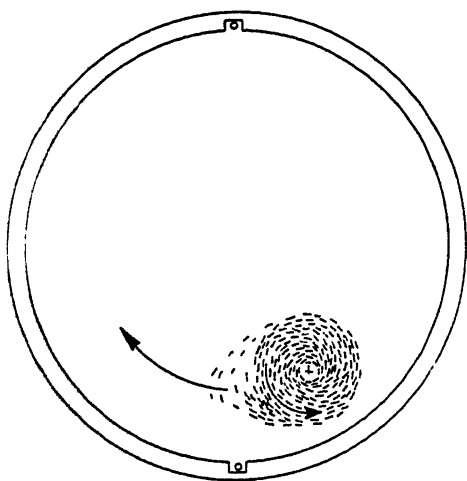


FIG. 1. Schematic representation of the behavior of a mill of *Jenkinsia* in a circular pool. The inside diameter is 12 feet. In this and all similar figures the inlet is at the top of the drawing and the outlet at the bottom.

at work here are far from clear, and much more study must be undertaken before the full mechanism involved can be understood.

The behavior of a mill of about 500 individuals was studied in detail. When such a mill was established and came in contact with the wall of the circular tank it tended to rotate as a wheel rolling along the inner circumference of a circle, as shown in figure 1. The reason for this appears to lie in the behavior

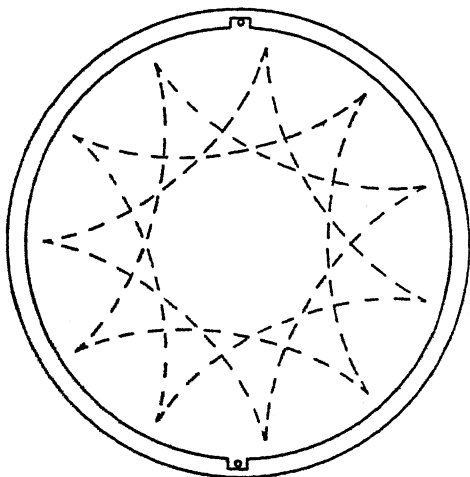


FIG. 2. The hypocycloid resulting from the dimensions and calculations of table 1.

of the individuals in the periphery away from the wall, i.e., their tendency to spread out. The rest of the fishes, in tending to crowd towards them, had the effect of advancing the mill in the direction of the larger arrow in figure 1.

Measurements were made of the speed of movement of the fishes themselves and of the mill as a unit and are given in table 1. Although each fish moved about with a certain amount of freedom, as previously indicated, the mean movements of a theoretically "average fish" can be estimated by the following means. Peripheral members of the mill were "clocked" for a complete journey around it, and this was considered to be representative of the motion at that place. The

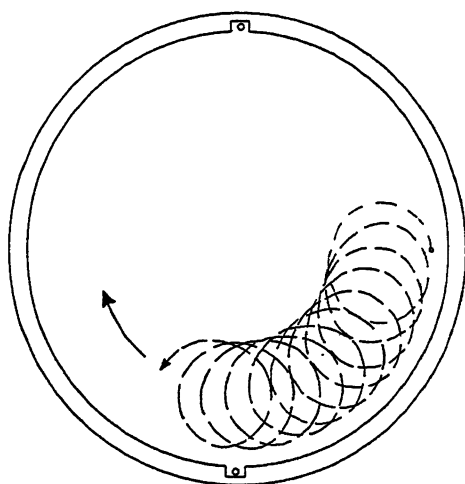


FIG. 3. The actual trajectory of an "ideal" fish based on the dimensions and calculations of table 1.

peculiarities of movement of the inner members of the mill are discussed below, for the mass of fishes does not move as a solid wheel. Such measurements were made only when the mill was in good, nearly circular form, which maintained at such times a remarkably uniform size and, as already noted, held a fixed distance from the wall of the pool. The superficial resemblance of such a mill in a circular pool to the tracing of a hypocycloid is obvious. With the dimensions obtained, a hypocycloid would be formed as one of 11 cusps, as shown in figure 2. Under such conditions an "ideal" fish would travel around

the mill three and two-thirds times while the mill moved around the pool once. It was obvious that the fishes were making many more circuits of the mill in the course of its travel around the pool. It was as though the generating circle kept slipping as it rolled around the fixed circle. The amount of this slippage can be calculated from the data of table 1. The mean revolutions per circuit calculate to 38.2+, or 10.4+ as many revolutions as the comparable hypocycloid. A portion of this trajectory is shown in figure 3. Because of the small variation in the behavior of a well-formed mill the extreme values are only plus 2.7+ and minus 3.9-.

Perhaps a more satisfactory way to look at this comparison would be to consider the figure in reference to a prolate hypocycloid in which the generating circle is small in comparison with the extension of its radius to the tracing point. It can be easily shown that a generating circle located as above must have a radius of a little more than $1\frac{1}{2}$ inches and, with this extended to 18 inches to the tracing point, it is possible to construct such a figure as shown in figure 3. It is interesting but probably merely accidental that the diameter of the generating circle happens to be

very close to the mean lengths of the fish forming the mill and close to one-half of the diameter of the vacant space these mills leave at their centers.

Under such conditions a few individuals were always found scattered about the tank, in no way taking part in the school itself. The apparent "erratic" behavior evidently indicates that some influence acted on one or a few individuals only. This type of behavior is generally, if not exclusively, based on intrinsic influences, as should be expected. Sometimes their nature is obvious; at other times, completely hidden. Probably at least half of the obscure cases are rooted in some pathological condition of the individuals involved.

EFFECTS OF WEATHER

Various elements in the weather definitely affect the schooling of these fishes. The amount of sunshine, the grayness of the sky, the presence of scattered clouds, and the rippling of the surface of the water by the wind all have an influence on the nature of the school. The most perfect schools are formed on brilliantly clear days with no wind, as observed both in the circular tank and in

TABLE 1
DATA ON THE MECHANICS OF A MILL OF 500 *Jenkinsia*, BASED ON OBSERVATIONS
OF TWO SEPARATE SCHOOLS^a

OBSERVATIONS				
Items Observed	Number of Cases	Maximum	Mean	Minimum
Rotation of mill in seconds	7	44	39.3-	35
Circuit of tank, in minutes	10	30	25	20
Diameter of mill, in feet	12	3.5	3.0-	2.4
Distance from wall, in inches	8	6.4	6.0+	5.5
CALCULATIONS ^b				
Items Calculated		Maximum	Mean	Minimum
Peripheral speed of mill, in feet per second		0.27-	0.24-	0.21-
Speed of translation, in feet per minute		1.7+	1.4-	1.2-
Revolutions per circuit		40.9+	38.2+	34.3-
Comparable hypocycloid		—	3 $\frac{1}{2}$	—

^a Water temperatures varied from 22.0° to 27.0° C. during these experiments. Its significance is considered under Discussion.

^b Taking the diameter of the mill as 3 and that of the circle within which it rolled as 11, then the following data may be calculated.

the open sea. The other influences mentioned all tend to break up the schooling behavior to a greater or lesser extent.

A strongly rippled surface was always found to be accompanied by a loosening of the compactness of the school, so that in some cases it could no longer be considered a school, but merely a loose aggregation. In extreme cases, the groups resembled the situation figured by Gudger (1929). No mills were ever formed except when the surface was calm, evidently a loosely compacted group being unsuitable to initiate the formation of a mill, which can be looked upon as only a special form of a definite school. Plates 2 and 3 illustrate the appearance of schools of *Jenkinsia* in the open sea on a calm day as seen through the surface of the water. These photographs also clearly indicate the extreme clearness of the water in this region. They were taken with no polaroid filter or other special device, and the prints were made "straight" with no "dodging" whatever. It can be seen that the edge of the dock at the left of each photograph is not over-exposed. The water shown in plate 2 is about 4 feet deep in the background and about 2 feet deep in the extreme foreground, and that in plate 3 very nearly 3 feet deep throughout.

Both these photographs were taken on a day when the fishes tended to keep over dark bottoms as much as they could, and the extent to which they were able to do so is clearly indicated and is responsible to a con-

havior of any one individual fish. It is as though any given fish were acting individually, but because of the large numbers of others present, each with its sphere of influence, that individual is continually thrown back from what would have been an independent course of action, giving the whole group the appearance of unit action. The spacing of individuals is also not so regular as might be supposed. In a well-established mill, the fishes near the center are considerably more closely spaced than are those near its periphery, and this occurs in a regular graded sequence. The exact center of the mill is usually occupied by a few individuals, pointed more or less radially, and turning with the whole mill. These are clearly under the influence of the fishes on either side, going in opposite directions and exerting about equal effect.

SIZE OF INDIVIDUALS

Casual examination of such a school of fish seems to indicate that the individuals are of a remarkably uniform size. This frequently is the case, but on the other hand in some instances there is a remarkably large amount of variation which is not evident until a collection and actual measurement is made of a representative sample. A random sample of 100 *Jenkinsia*, taken shortly after these experiments were terminated, showed the following characteristics concerned with the total length of the fish, in millimeters:

N	Max.	Mean	Min.	σ_m	Smallest as Per Cent of Largest
100	66	57.98	40	0.4504	60+

siderable degree for the form of the schools. On other days schools in this vicinity just as clearly avoided the dark areas and stayed over the lighter-colored bottoms as much as possible.

SPACING OF INDIVIDUALS

While the superficial aspect of a school is of a group of fish each performing as its fellow, a detailed examination of such a group shows that this appearance is merely an unconscious formation of a "mean" of a dynamic phenomenon in the mind of an observer. A second-to-second check shows that there is a considerable variation in the be-

Figure 4, which presents these data graphically, clearly indicates the nature of the underlying biological causes for this condition. The histogram is obviously made up of a mixed group of fishes, evidently small numbers of at least two groups smaller than the largest. Actually in such a school of somewhat mixed sizes, the fish tend to associate in groups of nearly equal-sized individuals, with a rather small amount of mixing. This could be interpreted to mean that there is continual self-sorting in such a school, or that the group simply represents the merging of several schools that never did mix thoroughly. The latter, however, seems to be unlikely, since

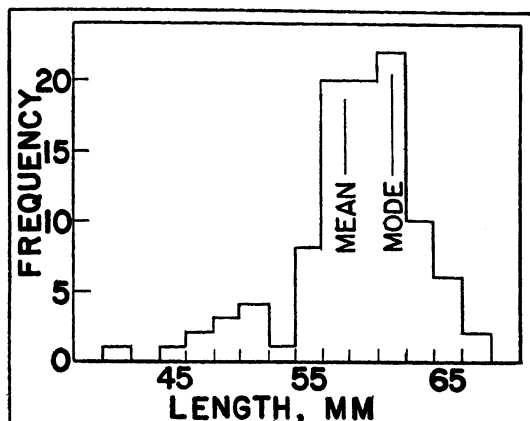


FIG. 4. Histogram of the total lengths of a random sample of *Jenkinsia* from a single school. Measurements were made to the nearest millimeter. The length values shown represent the highest of the group frequency, which covers 2 mm., e.g., 45 is to be read 44-45 mm.

on every dark night these schools break up and reform with the coming of dawn. Schaefer (1948), in discussing the composition of schools of *Neothunnus*, showed comparable variations in size, five schools out of 10 showing a slightly greater range in size, up to about 73 per cent, and five with a smaller range, down to 50 per cent.

EFFECTS OF ISOLATION

The effect of isolating one or even a few *Jenkinsia* and then placing in the tank a small school is that there is great hesitancy on the part of the isolates to join the group. This follows on periods of isolation of as little as a week and is evidently identical in principle with similar observations made on *Brachydanio rerio* (Hamilton-Buchanan) by Breder and Halpern (1946).

The introduction of other species of fishes into the circular tank led to a general loosening of the school, and after a number of *Cyprinodon* were added no further formation of a mill was found. This change in behavior is complicated by the fact that the longer these fishes were kept under conditions of captivity the weaker became the schooling instinct. This seems to be associated with general aquarium observations on the changes of fish behavior when long kept in aquaria, recently indicated for *Gobius flavescens* Fabricius by Wilson (1949). They seem to become

accommodated to the new conditions and less reactive to the fewer external stimuli usually obtaining under these conditions. For example, the absence of predatory forms may have an influence, since schooling can be induced temporarily by any unusual disturbance. Predation on *Jenkinsia* by *Strongylura*, for example, is continually taking place in the open ocean.

The presence of small *Mugil* in such a tank leads to another kind of confusion. Although the mullets tend to form small schools of their own, as they do in the open sea, they also try to school with both *Jenkinsia* and *Cyprinodon*. Although these attempts are transitory, they lead to a confused social status in each of the three species involved. Originally there was a single *Mugil* present, and it was thought that the behavior was based on simple specific isolation as described by Breder (1949) in connection with *Canthigaster*. However, when more mullet were added, they did not form a tight cohesive group, as is generally seen in the sea, but attempted schooling with the other species present as well. With about two dozen mullet so occupied, their behavior destroyed to a considerable extent the previous behavior pattern of both *Jenkinsia* and *Cyprinodon*.

EFFECTS OF TEMPERATURE

Although it should be clear from the preceding remarks and data that a wide variety of factors influence the schooling behavior of the fishes under study, we have as yet no answer as to why a school takes on any particular form and why it is at a given place and not at some other apparently just as suitable. Even in the circular tank, the reason for the specific location of a school was far from clear, until it could be demonstrated that, far beyond any other environmental factor, the actual temperature of the water in fractions of a degree determined just where the fish stationed themselves and limited the area of activity at their disposal. Certain temperature gradients acted to confine these fish as well as would a solid wall. No amount of frightening caused them to pass this temperature barrier.

As the water entering the circular pool was naturally cooler than that near the outlet of the pool, because of the heating effect of the

sunshine on the shallow basin of water, a nice gradient occurred across the tank. The critical temperature appears to be about 30°C ., the fish consistently refusing to enter water of this temperature. A typical case is illustrated in figure 5, with the temperatures indicated. In this case the school passed back and forth, as indicated, in water of lower

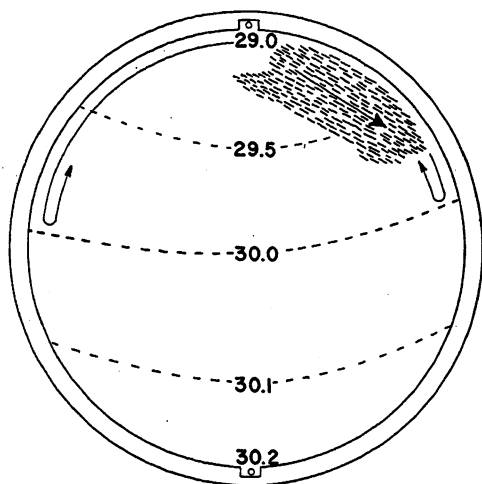


FIG. 5. Diagram of the effects of a temperature gradient on a school of *Jenkinsia*. Isothermal lines are represented by dashed lines and their value is given in degrees Centigrade. The solid line with an arrow at each end indicates the extent of travel of the school which moved back and forth regularly from one 30° limit to the other.

than 30°C . They simply could not be driven by nets or shadows from the area of tolerance. This is in close agreement with what Shelford and Powers (1915) found to be the case with *Clupea pallasii* Cuvier and Valenciennes by means of studies in a gradient trough. They were able to establish that this herring reacted to a thermal difference of as little as 0.2°C . Bull (1936) was able to show even finer discrimination by a system of conditioning feeding responses to temperature change. He demonstrated, in a wide variety of species, none of which were clupeids, that an increase of temperature of from 0.03° to 0.10°C . was adequate to elicit the response after sufficient training. He thought that the lower temperature was probably sufficient for the purpose and that the higher ones were caused by various experimental difficulties. Of course sensitivity of this degree, demon-

strated by a conditioning technique, is more than ample for the present results. Furthermore it does not follow that any fish would turn back from a temperature change approaching its limit of sensibility. Such a value might in fact be considerably higher than one on the basis of which a fish could learn to associate the opportunity to feed. That it is not vastly higher is borne out by the present experiments.

It should not be thought that the temperatures causing reactions are lethal for these fishes. They are entirely able to stand water temperatures up to the middle thirties before showing signs of distress. In one case the incoming water temperature rose to 30.8°C . The school then hung near the inlet in a mill, i.e., in the area of lowest temperature available to it (fig. 6). The asymmetry of the school about the inlet was due to a light breeze, which deflected the incoming water.

These two examples illustrate how schools are molded by the peculiarities of water temperature. Thus these schools may be influenced by very slight temperature differences, and the fishes are responding clearly to microthermal conditions. Since there was

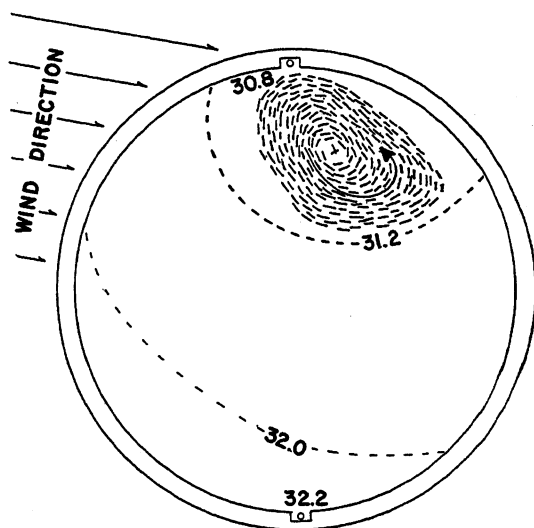
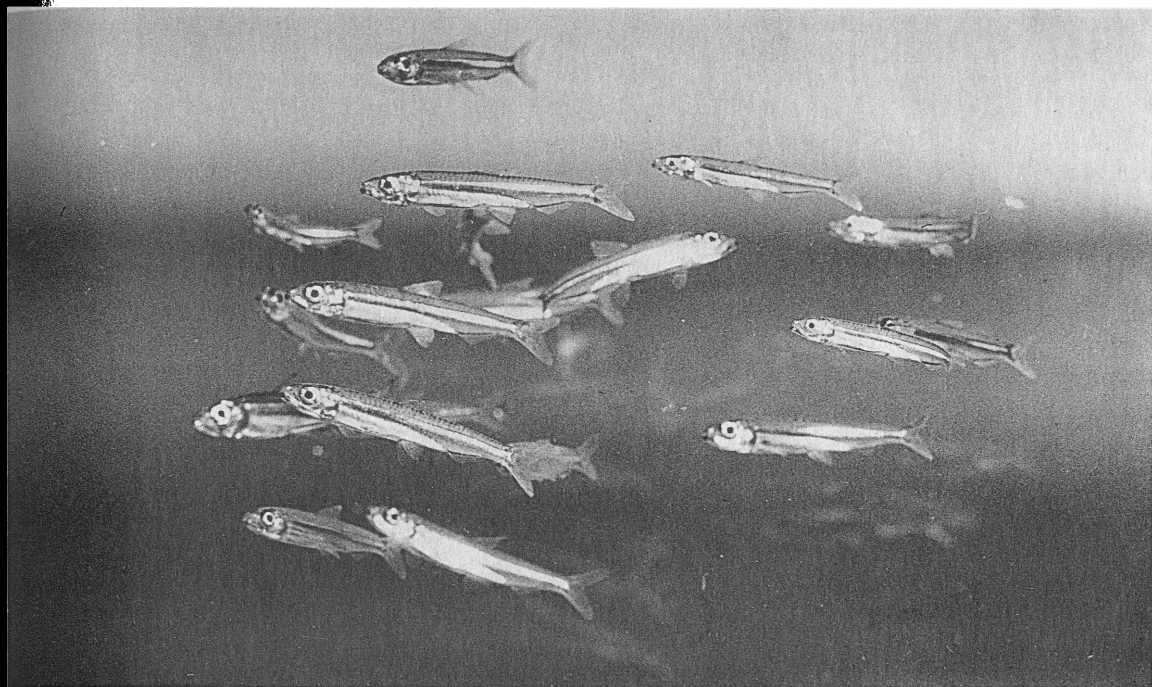
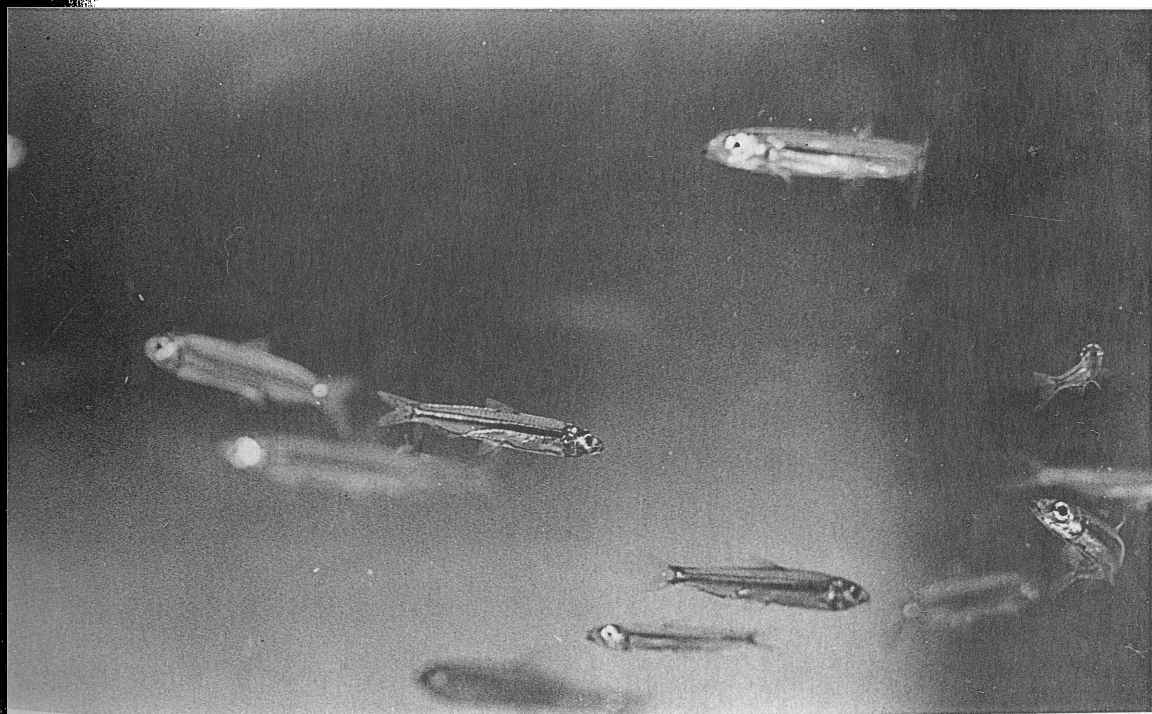


FIG. 6. Diagram of the effects of a temperature gradient and wind on a school of *Jenkinsia*. The temperature was higher than in the case shown in figure 5 and the flow a little slower. The asymmetry of the isothermal lines is caused by the deflection by the wind of most of the incoming water to the right.

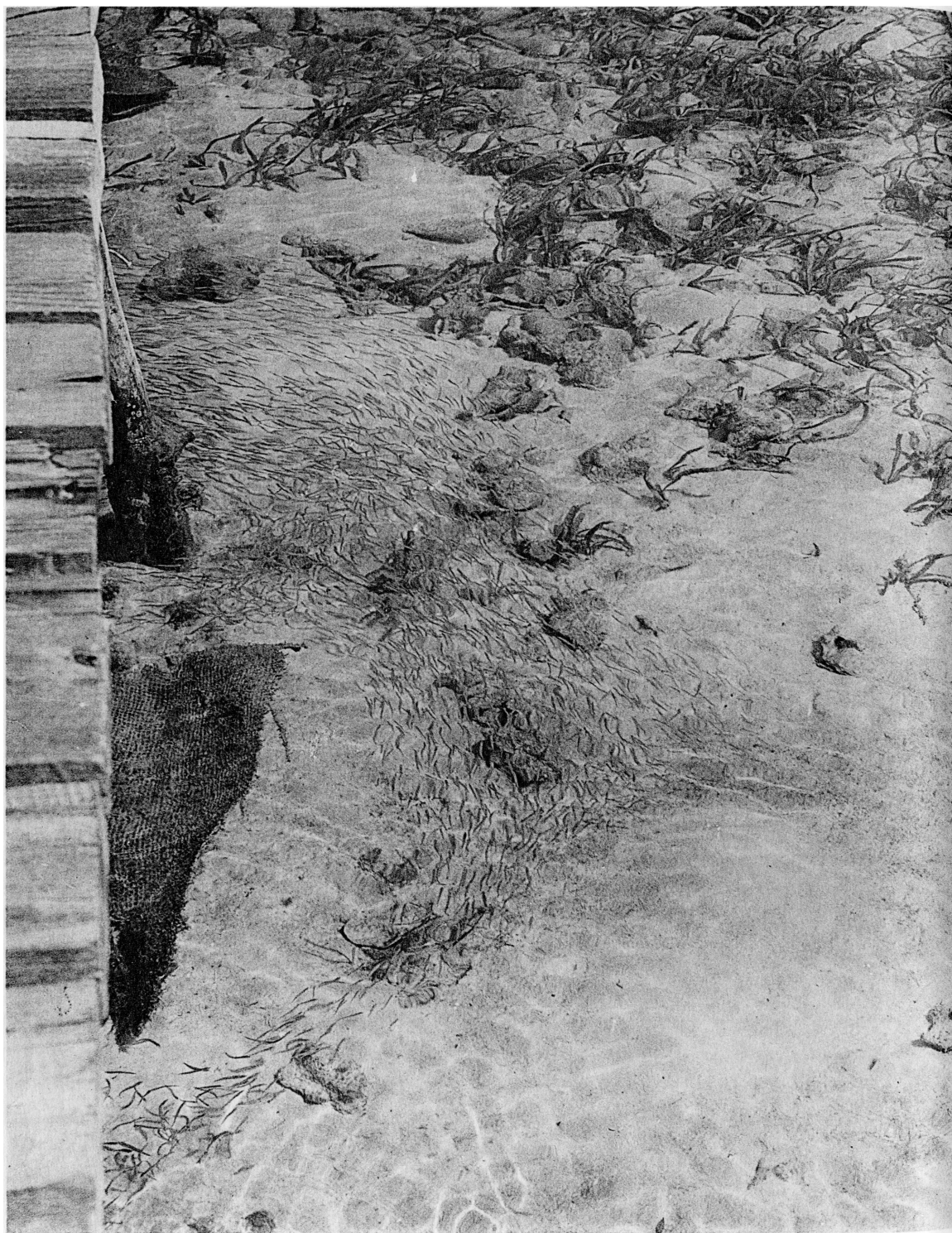


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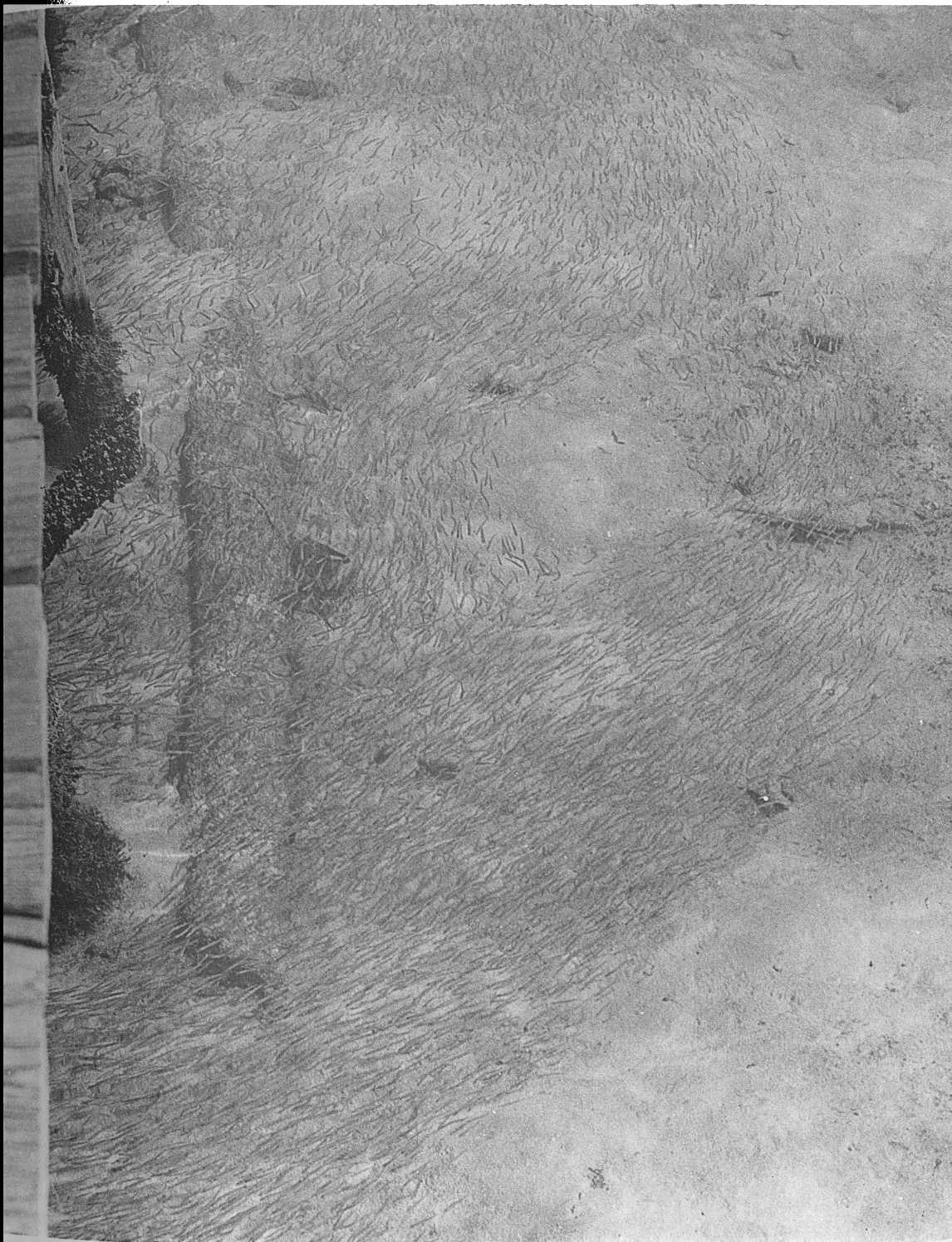


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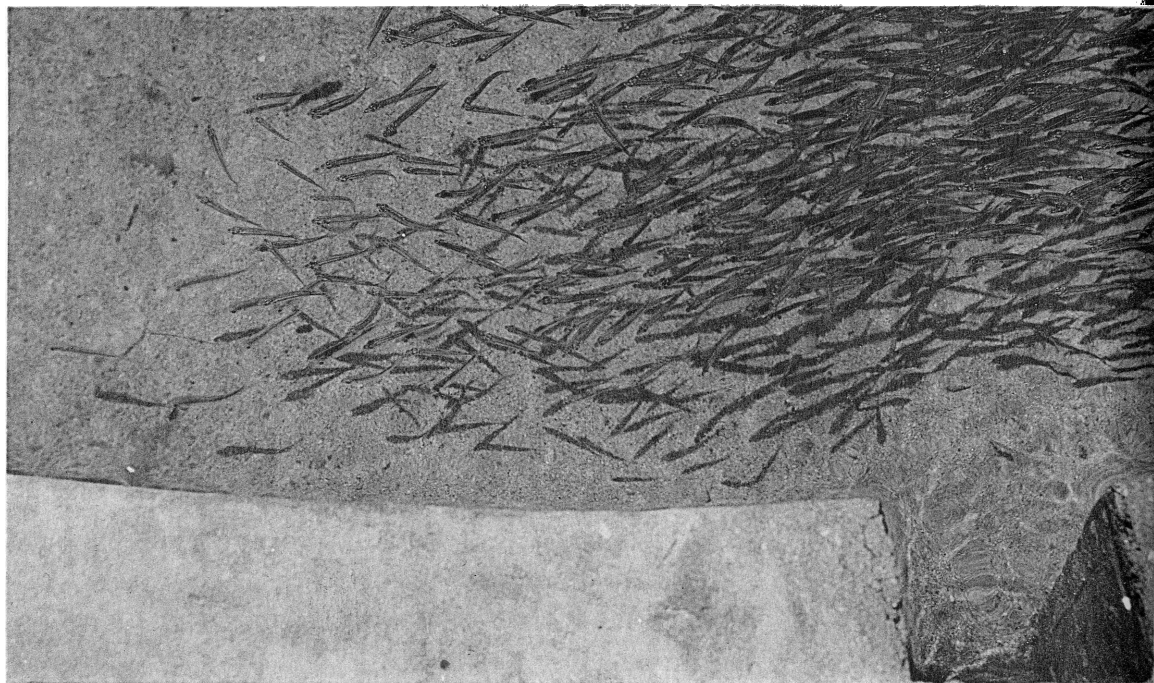
insia in a small aquarium. 1. Photograph taken in a lighted room. 2. The same group of fish photo-
graphed in a darkened room by synchronized photographic flash bulb



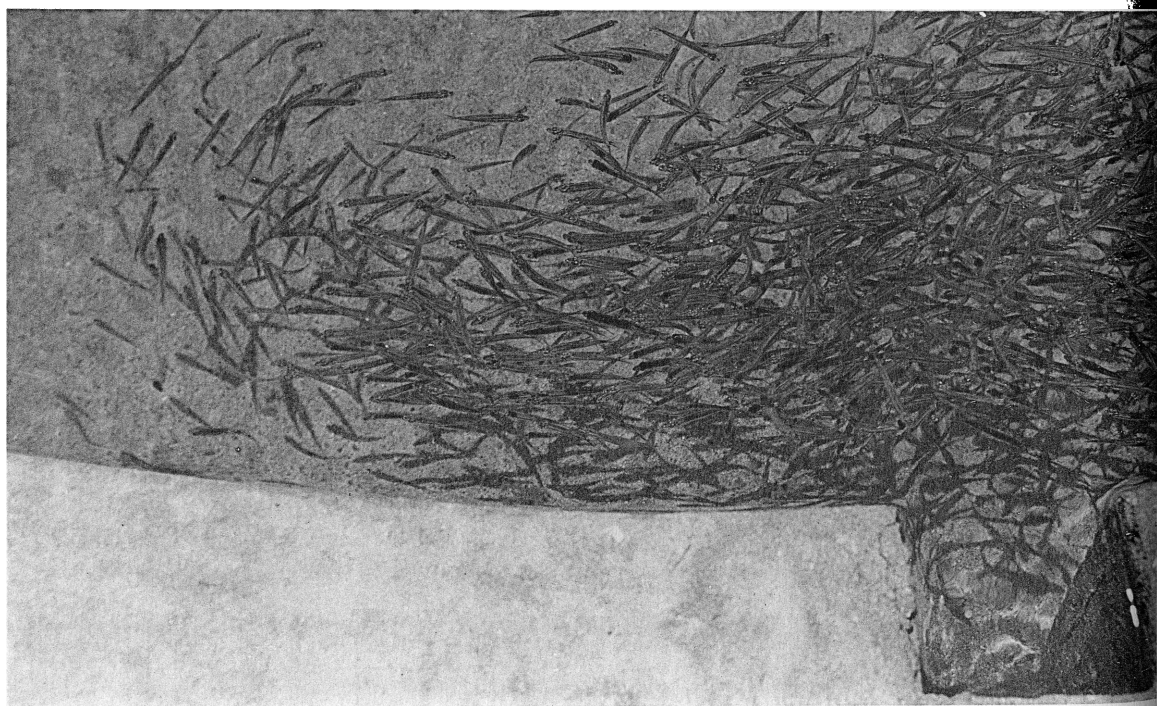
A typical school of *Jenkinsia* as seen from the laboratory dock on a day of exceptionally smooth water



of *Jenkinsia* at the dock side, showing one of the vacuities that are sometimes formed over a clear area



1



2

Jenkinsia in the circular pool. 1. A smooth-flowing school just before reaching a thermal "wall." 2. same school a few moments later, as it is turned back on itself

TABLE 2

THE EFFECTS OF SPECIFIC WATER TEMPERATURES (IN DEGREES CENTIGRADE) ON THE REACTIONS OF *Jenkinsia* TO A TEMPERATURE GRADIENT
(Data above 25° C. taken in June, data below taken during November, December, and January, all arranged in order of magnitude.)

Temperature of Inlet	Increase	Reactions of Fish
33.6°	1.40°	Would not enter water above 31.20°
31.4°	1.20°	Would not enter water above 30.00°
30.6°	0.60°	Would not enter water above 30.00°
29.0°	0.50°	Indifferent
24.85°	0.45°	Would not enter water below 24.75°
24.75°	0.20°	Indifferent
24.60°	0.32°	Indifferent
23.85°	0.30°	Indifferent
23.70°	0.10°	Indifferent
23.60°	0.35°	Would not enter water below 23.90°
23.50°	1.00°	Reaction complex, see text
23.36°	0.26°	Indifferent
23.30°	0.00°	Indifferent
23.05°	0.15°	Indifferent
23.00°	0.50°	Indifferent
22.50°	-0.40°	Would not enter water below 22.50°
22.15°	0.25°	Indifferent
20.40°	0.30°	Would not enter water below 20.70°
20.20°	0.00°	Indifferent
19.90°	0.10°	Would not enter water below 20.00°
18.90°	-0.60°	Indifferent
18.90°	0.00°	Indifferent
18.30°	0.00°	Indifferent
18.00°	-0.20°	Indifferent
17.40°	-0.30°	Indifferent
17.40°	-0.35°	Indifferent
16.20°	-1.00°	Indifferent
15.61°	0.00°	Indifferent

no microthermographic equipment available at the time the observations were made, further work was suspended until instruments adequate for pursuing this aspect of schooling could be provided.

Plate 4 illustrates another instance of this kind of thermal control and shows how abruptly it acts in turning a school back on itself. The recessed inlet can be seen in the lower right-hand corner of these pictures. The upper picture (pl. 4, fig. 1) shows the normal distance the schools keep from the concrete sides, which is temporarily shortened as the fish turn at the thermal "wall" and those following crowd into them before either reversing their direction or forming a mill. These thermally modified schools and mills, when compared with the data of Schneirla

(1944) on army ant mills that are modified by rain falling on a portion of the group, strongly suggest that despite the vast differences between ants and herring there is a basic similarity of response.

At the lower end of the thermal scale under which these fishes live there exists a similar "wall." Some of these effects are indicated in table 2. In contrast to conditions at the upper limit, here matters are complicated by the fact that the fishes on reaching a certain low temperature behave in a manner quite unlike their ordinary activity. When the temperature declines to about 20° C., it is as though the fishes' reactivity was numbed by the cold. There is very little activity, and schooling, and sometimes even all tendency to aggregate, are absent. Most no-

table, however, is the complete failure below this temperature to heed a gradient of a magnitude which at higher temperatures acts as a solid, wall-like barrier. This condition is clearly indicated in tables 2 and 3 and in figure 7. Under higher temperatures these fishes react to a thermal difference not greater than 0.10°C . and probably considerably less. However, below 20°C . differences as great as 1.00°C . fail to elicit any response.

It can be clearly seen both from tables and

do so they had to endure the water a full degree below that in which the others disappeared. This is evidently only a matter of two drives interfering with each other and working out differentially for different individuals, i.e., hunger versus warmth. It had been evident that there had been no noticeable amount of feeding during the preceding days.

It should be noted in connection with this discussion of thermal effects that in this pool

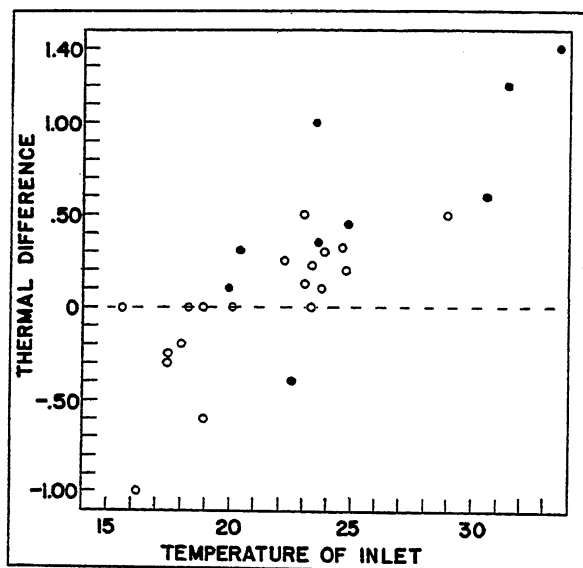


FIG. 7. Comparison of temperature at inlet of pool to amount and sign of difference at outlet. Black circles represent cases where fishes reacted to gradients, and white circles represent cases where they were indifferent. Both scales in degrees Centigrade.

from the graph that there are many other influences at work on these schools which make it impossible to establish a clear-cut band of temperature within which these fishes react uniformly. As an illustration of the difficulties here, the item in table 2 noted "reaction complex, see text" might be used. In this case, which occurred on a warm sunny day following several days of cloudy and cool weather with the water temperature below 22°C . during which time the fish were inactivated by the cold, the following took place. The bulk of the fish formed a school near the warm outlet water of 24.5°C ., but a considerable group not in the school were individually feeding on plankton. In order to

the water enters at the bottom and leaves diametrically across the pool at the top. There is naturally a vertical gradient in the 11-inch depth at which the water is carried. Usually the first half inch at the surface is considerably different from the rest, which from there on, in any one place, is nearly uniform to the bottom. In all cases the temperatures were taken where the fish actually were, or at the level at which they refused to pass a thermal barrier.

EFFECTS OF DEPTH OF WATER

As would be expected, the shallower the water the greater the reluctance to change from one background to another. This may

be merely that the background is optically closer, for obviously, even in the extremely clear waters of the Bahamas, the bottom under 10 feet of water can scarcely be of much import to a one-inch fish at the surface. *Jenkinsia* spend most of their time in water less than 10 feet in depth, seldom entering water as little as 6 inches deep, carefully avoiding water shallower than that. When forced into shallower water, their behavior changes sharply, as has been noted at various

dozen *Jenkinsia* were placed in an aquarium 20 by 40 inches and 4 inches deep. Water was at a depth of $3\frac{1}{2}$ inches, and the behavior of the fish was quiet. Water was withdrawn slowly by means of a small siphon. Some "nervousness" was evident when the water was only 2 inches deep, and a well-developed "panic" was established when it was only $\frac{3}{4}$ of an inch. As water was returned there was evidence of subsidence of the "panic" when the water reached 1 inch, and as more and

TABLE 3
CALCULATIONS BASED ON THE DATA OF TABLE 2, DEPARTURES FROM ZERO TEMPERATURE
DIFFERENTIAL BOTH PLUS AND MINUS

	Greatest	Mean	Least
Fish reacting (9)	1.40	0.61	0.10
Fish indifferent (19)	1.00	0.27—	0.00
Temperatures at inlet			
Fish reacting (9)	33.60	25.59+	19.90
Fish indifferent (19)	29.00	21.11—	15.61
The 20° point	Below		20° and Above
Fish reacting (9)	0		9
Fish indifferent (19)	8		10
The 30° point	Below		30° and Above
Fish reacting (9)	6		3
Fish indifferent (19)	19		0

times in the field and is borne out by the following experiments.

A group of about 500 *Jenkinsia* were introduced into the circular pool already mentioned, with the water level adjusted to a depth of $1\frac{1}{2}$ inches. Immediately the fish began swimming at what is evidently top pace for this form, in what can only be likened to a condition of "panic." Unusually close approach of the individual fish to one another was noted in these schools which kept breaking into numerous parts and reforming. Detached bands of 100 or more fish circled the pool at top speed and approached more closely than normal to the tank walls, nearly touching them. Groups such as this also dashed across the pool in curious serpentine paths slightly resembling a regular sine curve of low amplitude. This behavior continued until the pool had been filled to a depth of 3 inches. At this time the fish returned to the pattern that is "normal," as seen at other times in the pool as well as in the wild.

As further confirmation of the above, a

more water was introduced the "panic" subsided rapidly.

That this behavior is associated with water depth and not mere confinement is attested by the fact that such reactions are not encountered when *Jenkinsia* is placed in small aquaria with more adequate depth. They have been regularly kept in aquaria measuring 2 feet by 1 foot by 1 foot and occasionally in aquaria 10 by 6 by 8 inches deep.

In the above-described experiments in the shallow aquarium the impression was received that, in addition to the depth of water in absolute terms, the influence of an inflowing current had a quieting effect on the fishes. That this was noticeable in the smaller aquaria and not the large pool should be expected, for on a size basis the current was much stronger and exerted a more widespread influence in the smaller tank.

It seems entirely plausible that this "panic" behavior on the shallowing of water may have a utilitarian effect for *Jenkinsia* in that it may help to insure their not being

trapped by receding tidal waters. Because of their normal site of activity they would seem to be especially prone to such trapping, were it not for some satisfactorily operating mechanism to prevent it. Actually only one case of a few individuals of this species being so trapped has been observed. This was reported by Breder (1948) who had been es-

pecially studying tide-pool contents. It seems reasonable to suppose that under conditions of retreating water the fast swimming, closer approach to solids, and the breaking up of the group into small "exploratory" parties using a serpentine motion would tend to insure that at least some of the group would escape to open water.

DISCUSSION

THE VARIOUS FACTORS discussed in the main body of the present study are in general agreement with prior work, but extend further into finer details of the mechanical construction of the fish school than has been hitherto attempted. Although much further study and analysis must be made to gain an adequate understanding of this behavior, certain features already permit a certain amount of interpretation.

There is little in the literature bearing on the observation that these fishes will approach closer to a light than to a dark object, except perhaps that of Mookherji (1934). He confined goldfish in a tank with four windows which were, respectively, red, yellow, green, and blue. By various statistical methods of analysis he was able to show that the fish stayed close to the blue most frequently and least to the red. Although he developed this no further, on a basis of his data it is possible to do so. If his arbitrary values are arranged in order of magnitude and placed opposite some value within each of the colors he used in Ångström units (he gave no values), a relationship can be seen. As there is no way of knowing how close these guesses are to the principal wave lengths he was using, units of equality can be used—all of which is indicated in the following tabulation. In the column marked Approximate Å, values are given near the midpoint of each spectral color, and in the column marked Unitary Equality, values equidistant from each other are given:

UNITS OF APPROACH	COLOR
2	Red
3	Yellow
5	Green
8	Blue

If these values are plotted against each other, using either set of light values, an exceptionally smooth curve is formed which, when plotted with log values for the units of approach, transforms to a straight line. It would seem from this that there is some exponential relationship between intensity, wave length, and the light's attractiveness. This work should clearly be repeated, employing light of known spectral content.

More recently Kawamoto and Takeda (1950) approached the problem from a different standpoint. They noted the relative effectiveness of various colored lights of known spectra in attracting a variety of marine fishes. They found that there were two types of behavior. In one group the greatest effectiveness was found in the blue and green spectral areas. Fishes that found such wave lengths most attractive include *Sphyræna*, *Cybius*, *Oplegnathus*, *Monocanthus*, and *Spheroides*. These findings agree well with the work of Mookherji mentioned above. The other group of these authors, which was attracted to violet and red, included only *Anguilla*. Since the design of their experiment gave the animals the choice of only seven colors and one white chamber, it may be that the eel was merely showing its known photonegative response as well as it was able under such conditions. According to the spectral intensities given by these workers the violet and red were lower than elsewhere. If the eel has visual limits roughly equivalent to those of man, as has been shown for various other teleost fishes, the region of low intensity would presumably be the least repellent; thus the chambers in question might in fact appear relatively dark. A paper by Whitley (1946) contains an interesting aerial photograph showing the clear space left around two sharks by a large school of *Aripis*; and one by Sheard (1950), several photographs of a variety of schooling species as seen from above.

APPROXIMATE Å	UNITARY EQUALITY
6500	6500
5800	5833½
5100	5166½
4500	4500

The work of Fry and Hart (1947) has shown that under compulsive drives *Carassius auratus* (4.37 grams) can maintain a constant cruising speed of nearly 100 feet per minute at temperatures between 21° and 30° C. It happens that the temperatures at which the experiments on times of travel here reported were made are just nicely within that range, i.e., 22° to 27° C. The fish *Jenkinsia* were of much less mass, weighing

an average of 1.4 grams. These fish, not under strong compulsion but only under whatever social and biological compulsion there is inherent in the forward travel of a schooling fish, maintained a schooling speed of considerably less than the hard-driven goldfish, i.e., 14.4 feet per minute. Under strong compulsion, as when driven by a net, they can and do regularly travel much faster, their evident top speed being much greater than their normal schooling speed. Whether or not these smaller but more perfectly streamlined fish can do as well as, or better than, the larger, more clumsy goldfish under the conditions imposed by Fry and Hart is yet to be determined, but from general observations it would seem that the differences would not be great. This speed is much less than that found for *Scomber scombrus* Linnaeus by Sette (1950) for juvenile fish presumably between 50 and 100 mm. long, which he indi-

schools in the sea as well as the routes the schools follow in moving from place to place will be surveyed, in order to determine the significance of the temperature factor in delimiting both the form of the school and its path. It is indeed possible that what has been considered the spontaneous formation of a mill from intrinsic factors may eventually prove to be an extrinsic factor in the form of a micrometric thermal wall which turns the fish back on themselves.

This influence of temperature is evidently distinctly different from the effects of temperature and flow described by Breder and Nigrelli (1935) in which hibernating sunfish took up positions in reference to flow when the temperature became lowered to a certain value. Perhaps it is simplest to compare these two cases point by point in the following tabulation which indicates both similarities and differences:

FACTOR	<i>Jenkinsia</i>	<i>Lepomis</i>
Flow	Intrinsic	Extrinsic
Temperature threshold	Upper	Lower
Social attitude	Persistent schooler	Highly varied with season and age

cated at 600 feet per minute. There is every reason to suppose that mackerel are much more vigorous swimmers than *Jenkinsia* at comparable sizes.

While detailed statistics could not be kept under the conditions of these experiments, it became apparent that the mills that formed moved in a counterclockwise direction just about twice as often as in a clockwise one. Whether this represents something inherent in the fish or is referable to some peculiarity of the tank and its approaches must be studied separately at another time.

At higher temperatures than those at which the preceding work was carried out, there becomes apparent a great restriction of free movement on a thermal basis so that the fish will not enter water above 30° C., nor can they be driven into it. While it is clearly a morphogenic agent so far as the shape of the school is concerned, further work on this structural aspect of the fish school has been deferred until suitable microthermographic equipment can be provided. When such equipment is available, the outlines of such

The differences between these cases, and what at first might be thought to be different aspects of a single behavioral reaction, should be clear from the above table except for what is termed "flow," which requires some amplification. Flow can be thought of as extrinsic if a fish is holding a position in a stream and intrinsic if it is swimming actively in relatively still water. In the first case the flow is independent of the fish and in the second is caused by the fish. The utility of this usage becomes apparent when it is realized that thus in one word we can contrast the stationary school of sunfish, molded to its particular form by the characteristics of the current which influence it, with a moving school, or even a mill, of herring, which is in a flow only because of the forward movement of the fish, where whatever features that mold the school, intrinsic or extrinsic, are not a rheomorphic influence imposed from without.

Schneirla (1949) found it necessary to discuss at length the fact that a peck-order or social hierarchy must be established on a basis of some aggregating tendency and that

peck-order relationships, while conveniently handled experimentally, can be considered as only a fragment of a much larger total pattern of reaction. With this there can be no argument, and if the present knowledge of fish aggregation be considered in this light, certain pertinent items become clearly outlined.

If a graph similar to the one developed by Breder (1949) and here shown as figure 8, in which X equals the dispersive influence of aggressive activity within the group and Y

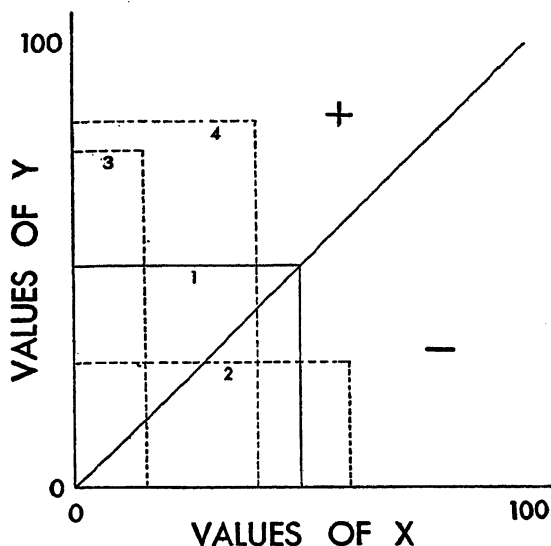


FIG. 8. Relationship of two factors that oppose each other; in this case X equals the dispersive influence of aggressive activity and Y equals the cohesive influence of the aggregating tendency. 1. Influences exactly balance and the organism is socially neutral. 2. Aggressive behavior greatly exceeds aggregating tendency and the organism is of solitary habit, as would be all cases below the diagonal line of equality. 3. Aggregating influence much stronger than aggressive tendency, the organism being extremely social, nearing, in fact, the extreme form found in schooling fishes. 4. Aggregating influence even stronger than in 3 but with the aggressive tendency more than twice as great, the organism being strongly social but the aggregation being one in which an active peck-order is prominent. Figure after Breder (1949).

the cohesive influence of the aggregating tendency be used, certain concepts would appear that can be tested experimentally. Along the line of equality the two influences cancel each other exactly; above it the cohesive influences

are greater and are represented by various types of aggregating species, while below it the dispersive influences are greater and are represented by the solitary forms. If a mathematical measure could be established to express these two complex factors, then species could be plotted on this framework as a true graph. The methods of Breder and Halpern (1946) and Breder and Roemhild (1947) can be further developed for employment in some such fashion. Perhaps eventually methods similar to those developed by Zipf (1947) and Stewart (1947, 1948), which appropriately apply in present connections, may be devised.

The above concept implies the following assumptions, the truth of which can be tested by experiments. True schooling fish have very little or no peck-order. Aggregating fishes have some, the looser the aggregation the stronger the pecking antagonism. This is tantamount to saying that aggregating forms would all school if it were not for the dispersive influence of the aggressive behavior, which leads to the establishment of a measurable peck-order. Viewed this way the "fright school" is merely the suspension of the peck-order under the duress of a strong extroceptive influence. Solitary fishes have peck-orders too vigorous to permit the group to remain intact or an aggregating tendency too weak to hold them together. There would thus be two kinds of solitary fish, those in which the relative values of the two influences are such that the group disperses and these values all lie below the diagonal line of figure 8, and those exhibiting neither aggregating nor dispersing tendencies in which the values lie on this line, the line of equality. Above it, of course, are the aggregating and schooling forms. The solitary forms lying on the line of equality would actually be socially neutral animals. This may explain why Breder (1949) could not find a representative species in nature that was socially neutral, for if there are in truth any, they would be masquerading as solitary species, and only careful study and experimentation could be expected to determine whether a given species was actually indifferent or hostile to its fellows.

Graham (1931) in an interesting paper on the nature of herring schools, actually based

primarily on the "schooling habits" of herring fishermen's boats, arrives at a rather curious conclusion. He indicates that the herring are able to see the drifting nets and generally to avoid them except when under conditions of panic, sexual excitement, or migratory impulse, when they are "... more or less unable to see the net." There is of course no reason to suppose there is any impairment of vision under conditions of excitement unless the author is using the word in a poetical sense. Mesiatsov (1937), who quite evidently had not seen much of the recent literature on social behavior of fishes, states that the form of certain schools is correlated with the activity of the moment. Thus a fast movement is correlated with a racket-like outline, a slow one with a crescent, and stopping breaks up the school. While there certainly is a strong tendency for a school to string out into a more or less oval or even ribbon-like form when moving along through open water, in no fish known to the author is there any high degree of association of shape of school with particular behavior. The impression given by most schools observed by the author is more that of a huge amoeba moving along, including the out-thrusting of heavy and bluntish pseudopodia.

Casual observation has shown that separate schools of fishes exert influences on one another, as shown by their tendencies to merge, and that in the merging of a small with a large, the former appears to speed up to some extent. No experimental work of a quantitative nature has been done with this, although there are plans to pursue this study when it is possible. Since there may be a considerable delay, it was thought best to note here one approach which should be productive in the field of separating the purely biological aspects of this matter from the purely physical considerations. The above remarks naturally suggest at once the possible applicability of the common gravitational formula, which in addition is equally useful in studies of magnetism and electrostatics as well as a variety of other less well known fields. This equation in its general form states:

$$f = k \frac{m_1 m_2}{r^2}$$

where f equals force, k equals a constant, depending on the units used, and m_1 and m_2 equal two particles or masses separated by distance r .

For the purposes of this discussion it could be conceived that it might be used directly, in the sense that m_1 and m_2 would represent the number of fishes in the two schools, respectively, eliminating k . The reaction could then be measured by the speed of approach, of the smaller school compared with that of the larger, or by the amount of shift of the school centers as the schools merge. In the case of gravity, the speed of approach of two unlike masses is the same *in vacuo* but not in the air. In the case of such psychogenic moieties as are here considered, the problem might be settled as to whether or not there is a faster approach towards a larger group. While it is clear that various technical difficulties would arise in such a study, they would seem to be not insurmountable, and an understanding of the relationship of one school to another on such a basis would unquestionably have considerable value in any further studies along these lines. On the basis of such an approach, initially a school of fish might even be looked upon as though it were a cluster of iron filings in a magnetic field. The whorls and other orientations would then indicate environmental influences, equivalent to a complex and dynamic magnetic field, the algebraic sum of which should be resolvable by vector analysis, once the nature and magnitudes were fully understood. For the present, however, they must remain for the most part as indications of the non-uniformity of the influences that mold the school.

If it is in truth legitimate to discuss the attraction of fish to fish in terms of gravitational formulas, one basic reason for the very existence of schools and aggregations on a purely physical level follows. Since a uniform distribution of mutually attractive items is gravitationally unstable, it should follow that a uniform distribution of fishes attractive to one another would not so remain under any conditions but would form "clots" of fishes in dense masses, with large vacant spaces between. The density, cohesiveness, and stability of such groups should be proportional to the strength of the force. Such a condition is not a "biological" matter in itself but is

equivalent to any similar physical situation. Selection would then operate on the elements (fishes in this case), modifying the basic homotropic attitude in a manner concordant with the survival of the groups of elements. As can be observed and should be expected on such a basis, many "answers" that are obviously adequate to long-continued survival have been made by differing social groups of fishes.

A rigorous mathematical approach to this problem was attempted by Gordon (1939) on a fully theoretical level but as yet has not been applied to actual material. As is evident from the preceding remarks, such application would at present be difficult, and it seems necessary to understand better what is taking place within aggregations before such methods could be expected to produce the important progress that their application implies.

The published work most pertinent to some of the preceding discussion on the structure of the fish school is that of M. Tauti and his associates. Tauti and Miyosi (1929) showed that carp, when moving along the wall of a confining tank in a group and encountering an obstruction such as an out-thrust wall, behaved in a definite manner on coming to the end of the wall. The group curved either inward or outward, most often the former. In this case the angle that the out-thrust wall formed with the tank wall, θ , determined the angle between the path on which the school moved off and a projection of the out-thrust wall, β , as is indicated in figure 9. Tauti and Miyosi were able to show that β varied inversely with θ , but that the length of the wall within the small limits at their disposal had no influence. This seems to indicate that the fish tending to keep on in the same direction, going around obstructions for mechanical reasons alone, would cause β to vary inversely with θ . If this is sound reasoning, then the wall, to have influence on the school, would have to be long enough to enable them to "forget" or otherwise disrupt the tendency of their path. The groups that curved away from the wall were not studied, but surely should be analyzed.

Tauti and Hudino (1929) confirmed the above on *Leuciscus hakuensis* Günther. By placing other aggregations of the same species

in the tank so that they appeared to the group under study as it passed the end of the wall, these authors were able to show that the attractive power of a group decreased with distance, that a moving aggregation was more attractive than a static one, and that a large group had more attractive influence than a small one.

Working with carp, rainbow trout, *Leuciscus hakuensis*, and *Oryzias latipes*, and using a net for an obstruction instead of an opaque

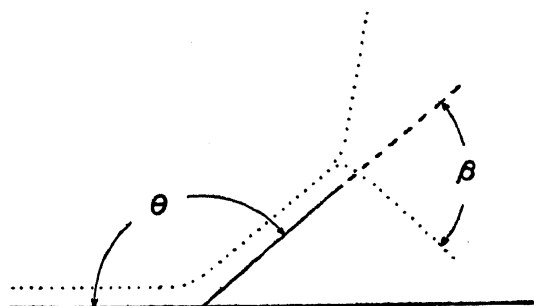


FIG. 9. Diagram of certain features in the case of a school passing an obstruction. Based on Tauti and Miyosi (1929). θ equals the angle of obstruction to tank wall; β equals the angle of inward-turning school with projection of obstruction. See text for explanation.

wall, Tauti and Yasuda (1929) found that β was always relatively larger except for the last-named. Also the relations between θ and β were the same in all except *Oryzias* in which there is a greater difference. This suggests that being able to see ahead through the meshes of the net caused the fishes to swerve more sharply back to the original direction in which they were moving than when the view ahead was blocked off. Tauti and Yasuda (1930, 1933) used these data to go on to a consideration of fish-trap construction and the influence of the angle of the bottom on the direction taken by a school of meeting the net.

With these various approaches to the problem of the structure and behavior of the fish at hand, it should be possible to move forward to a proper integration of them, which should be of value to both theoretical biology and practical matters.

The presumed biological utility or significance of the fish school continues to concern

students. Since Breder and Halpern (1946) expressed certain views on the subject, Morrow (1948), Sette (1950), and Baerends and Baerends-Van Roon (1950) have discussed similar and related matters. The latter two, evidently without knowledge of the earlier publications, cover similar ground and arrive at differing opinions. While Breder and Halpern wrote, "It would seem that schooling confers no direct advantage to the obtaining of nourishment," Sette believes that there may be an advantage in feeding on plankton by a school. Considering each mackerel as a very small "tow-net," Sette wrote, "If it be supposed that copepods (the principal element in their diet) are capable of darting 1 or several centimeters at a time through the water, as observation indicates they do, they might elude one such miniature tow-net; but with a group of miniature tow-nets as closely spaced as these, the success of a copepod in eluding one of them would frequently only put it in the path of another. Thus mackerel, acting in concert probably would average more copepods each than if they acted individually." This problem seems to be nearly identical, in its mathematics, with the one discussed by Breder and Halpern which was concerned not with the prey of the schooling fishes but with them as the prey of larger fish. With both, the solution is probably to be found in a comparison of mathematical models showing "the rates of collision" of closely packed prey or predators as against their being spread out widely. Such a study of course would involve considerable labor.

Baerends and Baerends-Van Roon (1950) seem to consider social facilitation and the con-

fusion effect more likely to be important. Unfortunately they make no clear distinction between the school proper and the simple, more or less loose aggregation of various diverse species of fishes.

In connection with any attempt to evaluate the biological significance of the fish school, it must be borne in mind that schooling and non-schooling appear at very diverse times in the ontogeny of different species. For example, certain fishes that are not extreme schoolers or even markedly aggregational as adults, such as *Amia*, *Ameiurus*, *Micropterus*, and *Aequidens*, pass through a close-schooling larval stage which they enter as soon as they are able to swim. Other fishes, such as *Danio*, as has been indicated by Breder and Halpern (1946), which form close aggregates or even temporary schools as adults, do not attempt to school as young until a certain stage of development has been attained.

It should be clear that the varied and sometimes apparently unrelated items mentioned in the foregoing discussion are actually all various facets of the complex phenomena which interact to determine the social behavior of a group of fishes. The school, then, can be looked upon as merely the algebraic sum of numerous items of behavior. In this view the addition or subtraction of various items would change the equation, so that the sum would not equal a school but some other solitary condition or simple aggregation. Also implicit in this is the expectation that perhaps numerous and very different algebraic sums could equate to superficially identical groups in each category.

SUMMARY

1. THE ORGANIZATION of a school of *Jenkinsia* is based on visual cues which become inoperative at just about the visual limit in man under certain conditions or before it under others.

2. Normally a school of *Jenkinsia* maintains a specified distance from solid vertical objects such as piles, and approaches twice as close to light-colored ones as to dark-colored.

3. The formation of a mill in *Jenkinsia*, typically based on extrinsic factors, may evidently under certain conditions be based on strictly intrinsic factors.

4. A mill of 3 feet in diameter of about 500 fish had members at the periphery traveling at about 3 inches per second.

5. Such a mill traveling around the wall of a circular tank traveled at the rate of about 1.4 feet per minute.

6. Individual fish near the center of a mill are more closely spaced than are those at its periphery.

7. A mill passing along a wall moves in a direction that a wheel would in rolling along a similar surface but with many more revolutions than a wheel would show without slipping.

8. Isolation of an individual or a small group for as short a time as a week will cause them to show reluctance to join a larger group.

9. Effects of weather such as rippled surface of the water or passing clouds tend to loosen the school, so that it is found in its most striking cohesive form close to the surface on days of clear skies and no wind.

10. Small differences in water temperature control the form and location of a school to a marked extent, certain isothermal lines acting as an effective barrier to the passage of such schools.

11. Within a school of somewhat mixed sizes there appears to be continual self-sorting, resulting in fish of the most nearly similar sizes being found together.

12. Aggressive behavior and aggregating tendencies are considered in theoretical terms in reference to school formation, simple aggregation, and solitary habits.

13. Further analytical suggestions are indicated with reference to future work extending to greater refinement of method than has been possible up to the present.

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