FISH SCHOOLS AS OPERATIONAL STRUCTURES

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ABSTRACT

The interaction of a space lattice, vortex trails, and the lubricity of fish surface mucus is shown to be important to the operation and structure of fish schools and significant in terms of locomotor efficiency. This is independent of the various interpretations of possible survival values, protection from predation, and similar ideas—all of which are extremely difficult to prove, even if valid.

A single type of space lattice is shown to approximate the arrangement of fishes in a school on the basis of geometrical reasoning. This is supported by empirical data.

The vortex trails left by each fish, when the fishes are deployed according to the "fish school" lattice, lead each following fish into a series of vortices at a point where the water flow is traveling in the direction in which they are swimming.

The lubricity of the mucus-water mixture that the fish ahead leaves in its vortices decreases the drag on the following fish.

The advantages of the regimented life in a school, as against the freedom of action common to the more or less solitary life, are evidently related to the effectiveness of the drag-reducing mucus in the vortices. The fishes with the least effective mucus appear to take advantage of the schooling life while those with the most effective mucus are more likely to be solitary.

The past decade has witnessed a considerable increase in output of papers addressed to a better understanding of the numerous phenomona presented by fish schools. These documents have covered a wide variety of the inherent problems. Nonetheless, there remain some basic questions that have proved peculiarly elusive, such as the nature of the evident regularity of the positional relationships of individuals in well organized schools and the nature of influences that hold the school members in their regular patterns. A fish school is considered here as a group of polarized individuals that operates as a unit between the times of its resolution and eventual dissolution. Initially, the activity of the fishes crowding together in their polarized pattern creates the structure of which they form components. Once established, the school efficiently regulates the locomotor activities and general comportment of the organized fishes.

The primary purpose of this paper is to show that both the geometrical pattern of the space lattice approximated by schooling fishes and the surface mucus on their bodies are mutually important elements in the formation and maintenance of fish schools. The physical bearing of these two elements is direct and important, each in its own right, to an understanding of any theory that attempts to explain the origin of schooling without recourse to theoretical interpretations.

How much of the schooling phenomenon observed in modern fishes is a result of interactions between the swimming capabilities of the fishes and the physical restrictions imposed by their environment, as compared with other biological needs, is not readily determined. However, the experiments described here are in some cases suggestive. These experiments, primarily undertaken to establish data relevant to the basic purposes of this study, in each case, have been carried only as far as was necessary to make a point. Many of them could be extended into much greater refinement with the promise of worthwhile further elucidation.

This work leads to a number of lines of possible approach to the problems of school organization. Some of the newer items discussed have had the benefit of recent studies—remote from schooling problems and in some instances remote from biology. This is especially marked in those studies that are dependent on developments in hydrodynamics during the last decade.

FISH SCHOOLS AS SPACE LATTICES

To further the understanding of the physical organization displayed by schools of fishes, a study

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of their geometrical characteristics has been undertaken. Much of the older literature on the distribution of individuals of a population, or smaller group, of animals or plants took for granted that the deployment is stochastic. Clark and Evans (1954) stated, "This assumption is no longer a tenable one and is probably even less applicable to animal populations." It is, of course, doubtful if creatures with well organized locomotor abilities and complex sensory systems are ever distributed in a fully random manner. The systems encountered in nature seem to be mostly those of ordered arrays variously distorted by processes of many kinds, sometimes obvious, but more often obscure or barely discernible. Attempts to measure the structure of assemblages of individuals have been predicated mostly on the idea of showing the extent of their departures from theoretical randomness. Since fully organized fish schools have very obvious structure, it is at least equally appropriate to compare them with mathematically organized patterns, especially where there are good theoretical reasons to expect the presence of some similarity.

Geometrical Models

The establishment of a geometrical model of a fish school is relatively simple, for whatever else a fish school[2] may be, it is essentially a closely packed group of very similar individuals united by their uniformity of orientation. A more explicit definition has been given by van Olst and Hunter (1970) who stated, "The principal characteristics of the organization of fish schools are that the individuals stay together, tend to head in the same direction, maintain even spacing, and the activities of the individuals tend to be synchronized." Because of the nature of fish locomotion it is necessary that a certain amount of swimming room be maintained by each fish (Breder 1965, van Olst and Hunter 1970). Thus each fish and a "shell" of water about it may be considered as a unit, and a school as a packing together of these units. Such structures can be handled by established mathematical procedures. The fact the fishes are all moving forward and, in many instances, often shifting their relative positions merely makes the

handling of such data a little tedious, but does not vitiate the basic propositions.

One approach to the analysis of the structure of a fish school, the empirical, can be made by measuring the distance, angle, or other parameter between a given fish and the other members of the school. The mathematical manipulation of such measurements can establish values that may serve as an index to the school's organization. One's imagination alone limits the selection of data. Papers that have employed this type of approach include Keenleyside (1955), Breder (1959, 1965), Cullen et al. (1965), Hunter (1966), van Olst and Hunter (1970), Symons (1971a, b), Healey and Prieston (1973), Weihs (1973a), and Pitcher (1973). Only Cullen et al., Symons, and Pitcher in the above list attempted complete tridimensional measurements. Pitcher's paper has important bearing on the approach developed here on the basis of abstract reasoning. It will be discussed in detail later.

A theoretical approach, equally valid, is based on tridimensional geometrical concepts and constructs for purposes of comparison with fish schools. Since there is an infinite variety of such constructs possible, only those of some conceivable application to this study are discussed here. Unlike the empirical approach, there are evidently no prior papers that have employed this theoretical one. The following treatment has been made especially explicit because of the complex relationships within both space lattices and space packings, as some biologists who might consult these pages may not have instant recall of such details.

It is necessary to introduce some elementary data on tridimensional lattices that are essential to an understanding of their bearing on fish schools.[3] The most readily visualized space lattice is that in which a cube is the element or cell (Figure 1A). It is not the closest possible packing of such points: a closer one can be obtained by figuratively pushing the cubic lattice askew (Figure 1B) so that the special case of cubes with their 90° angles become rhombohedrons with other angles. The dotted arrow in Figure 1B indicates the amount of travel of the point in the upper left front corner of the lattice in attaining

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[2]Definitions of this word as used here are given by Breder (1959, 1967). For an extended discussion of this and other usages see Shaw (1970).

[3]Support of all geometric statements made in this section may be found in any formal or informal geometry text covering the area concerned, such as Hilbert and Cohn-Vossen (1952) and Lines (1965).
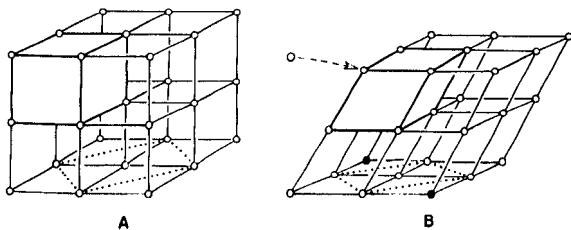
FIGURE 1.—Two space lattices in perspective, each with a single cell shown as a solid. A. The cubic lattice. B. The rhomboidal lattice. The arrow indicates the manner of transformation by which the cubic lattice becomes the rhomboidal lattice.

the transformation from cube to rhombohedron. All the angles in this rhombic lattice are either 60° or 120°, so transformed from the cubic lattice with only angles of 90°. On the floor of the cubic lattice in Figure 1A, the nearest points to the central one, in the same plane, are four in number. These are connected to each other by a dotted line. On the floor of the rhombohedron in Figure 1B, the sides of which have internal angles of 60° and 120°, the nearest points to the central point include four at the corners of the dotted parallelogram plus two more, indicated by the dark points. These define a regular hexagon because the parellelograms are composed of two equilateral triangles.

If models of identical fishes are stationed with their centers at each lattice point, and if all the models are in parallel orientation, the group superficially resembles a fish school. It becomes immediately apparent however that such a lattice of fishes has characteristics that are never seen in a school. If they had ever been seen in such a formation, their appearance would have been so striking that the details of the regimentation would have been recorded long ago. In such a school, viewed from above, fish would be seen in horizontal files and these files would be swimming ahead in rows transverse to their direction of travel. Viewed from the side, each fish within the school would have another directly above and another directly below it, forming columns, except the two fish marking the upper and lower limits of the school in each vertical column of fishes. These two would be without another fish above and below, respectively. Thus we can temporarily put this unschoollike lattice aside.

Fish models positioned at the points of the rhombic lattice do not show the peculiar features seen in the cubic lattice, but have a more distinct resemblance to fish schools. It is difficult to deny

that schooling fishes, in most situations, are indeed approximating this configuration, the details of which will be discussed later.

Turning now from space lattices to the packing of space, it is easy to arrive at the above rhombic lattice by a very different route. As a preliminary mathematical simplification, fishes and the immediately surrounding water that envelops each fish individually in a school shall be equated to spheres, the centers of which are located on the axis of the fish midway between the end of the snout and the tip of the tail. Here it is necessary to describe some of the less obvious geometrical features of a mass of spheres packed together as closely as possible. A single layer of identical spheres on a plane surface packed at maximum density may be represented on paper by an equivalent packing of circles (Figure 2). A hexagon may be circumscribed about each circle, one of which is shown in the lower left corner.
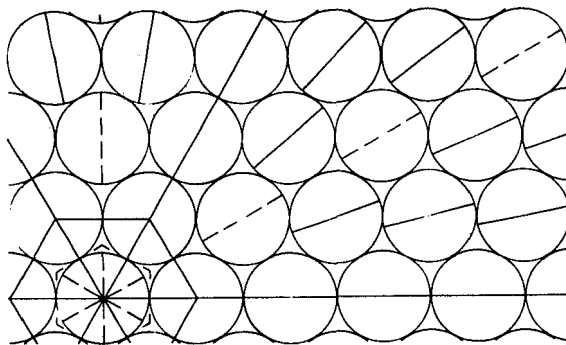

FIGURE 2.—The closest possible packing of a single layer of identical spheres or circles, showing the relationships to hexagons and their six equalateral triangles as well as the disposition of a single diameter in each circle when drawn radiating from the center of the circle with the circumscribed hexagon.

The individual diameters of each circle as shown in Figure 2 lie along radiating lines emanating from the common center of the hexagons.[4] Those lying on the radials passing through the apices of the larger hexagon are continuous lines (major axes), while those passing through the equivalent points on the smaller hexagon are dashed lines (minor axes). If these diameters are all permitted to become parallel to one another, a very different

[4]Although simple, this geometric treatment of transformations of related diameters of packed circles or spheres is evidently original here, or at least no approach to this treatment has been found. No formal proofs are necessary as the usage here is simple enough to be self-evident and would be irrelevant to present purposes.

situation appears. This may be conceptually treated as though the diameters were under some common influence, somewhat like iron filings in a rectilinear magnetic field. Figure 3 shows such an arrangement, where all diameters are in the first case at an angle of 30° to a major axis and 15° in the second case. Obviously the continuous lines of the major axes of Figure 2 are no longer possible except when the diameters are at one of the three angles of the major axes, where in each case such a drawing would show only a series of continuous parallel lines. In any of these parallel arrangements the distances of the diameters from end to end are constant throughout as are the distances from side to side. These two dimensions change only if the angle between the diameters and major axes is changed, as can be seen by comparing Figures 4 and 5 based on a square with Figures 2, 3A, and 3B based on a hexagon.

These two types of packing may now be considered in their more complex form in three dimensional space. The cubic space lattice is very simple and will be referred to later; the rhombic spatial array, more likely to be confusing, is

FIGURE 4.—Cubic packing of a single layer of spheres or circles, directly comparable with Figure 2.

FIGURE 5.—Parallel diameters drawn on the frame of Figure 4, based on diameters halfway between two consecutive axes, 45° from either. Directly comparable with Figure 3.

discussed in sufficient detail for present needs. Starting with the single layer of spheres of Figure 2, another layer may be placed upon it so that each sphere of the second layer rests in the hollow between three adjacent spheres of the first. The second layer automatically has a pattern identical to the first, but the centers of all the spheres of the upper layer are displaced so as to fall over the centers of an equilateral triangle connecting the centers of the supporting first layer spheres. This is shown in Figure 6 where the centers of the first layer spheres are indicated by large circles and those of the second by smaller dark circles. The dash-line hexagon of Figure 6 indicates the displacement of the second layer centers. It also shows that just three second layer sphere centers are within the solid-line hexagon. There are also shown three similar small open circles forming a similar pattern within the hexagon, which indicate the absence of spheres centered by them, and connected by dotted lines to form a hexagon of absences. In the upper left corner of this same
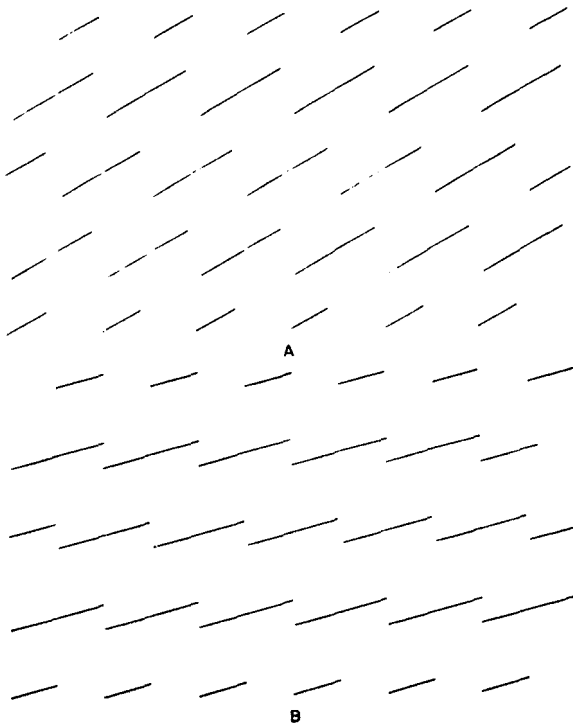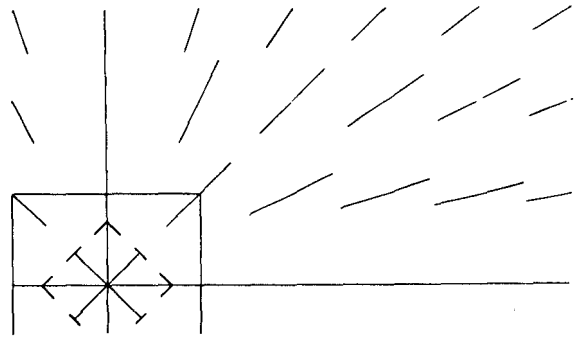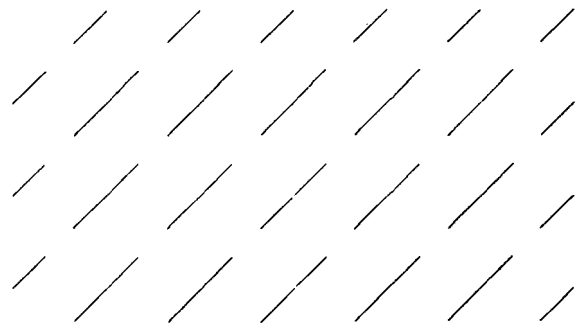

FIGURE 3.—Parallel diameters drawn on the form of Figure 2. A. Based on diameters halfway between two major axes, 30° from either. B. Based on half the angular distance used in A, 15°.
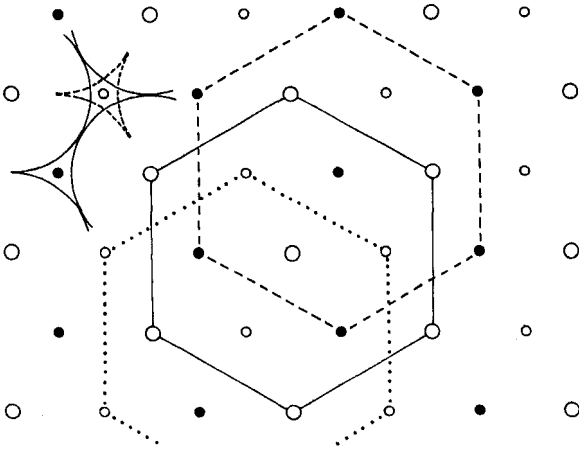
FIGURE 6.—The rhombohedral sphere pack of three layers as viewed from above. Based on Figures 1B and 2. See text for full description.

figure parts of the adjacent outlines of four spheres of the first layer are shown by solid lines. The dotted lines of three overlying spheres of the second layer are also shown. This indicates clear vertical passages through the overlying junctures that permit passage through the two layers of spheres (small open circles) while two are blocked by overlying spheres (small dark circles). The pattern is repeated throughout the system. A third layer of spheres may be identical with the first, a fourth layer identical with the second, and so on indefinitely. This pattern preserves the integrity of the vertical passages, but this need not be the case. If the second layer of sphere centers exchanges the position of the black and open small circles, the clear passages occur where the black circles are now shown and vice versa. As any layer may be so reversed the passages may be blocked in many complicated patterns. The shortest possible passage can be the vertical distance between the level of the centers of two adjacent layers of spheres, otherwise the passage may be indefinitely long.

As these planes, referred to above as layers, form the faces of the generating rhombohedron shown in Figure 1B, these passages run in three intersecting directions, as do the three planes of the lattice. The passages are all interrelated, as altering the relationships of the sphere centers in one plane automatically alters those in the two others.

The above may be simpler to visualize by referring to the perspective illustration of Figure 7.
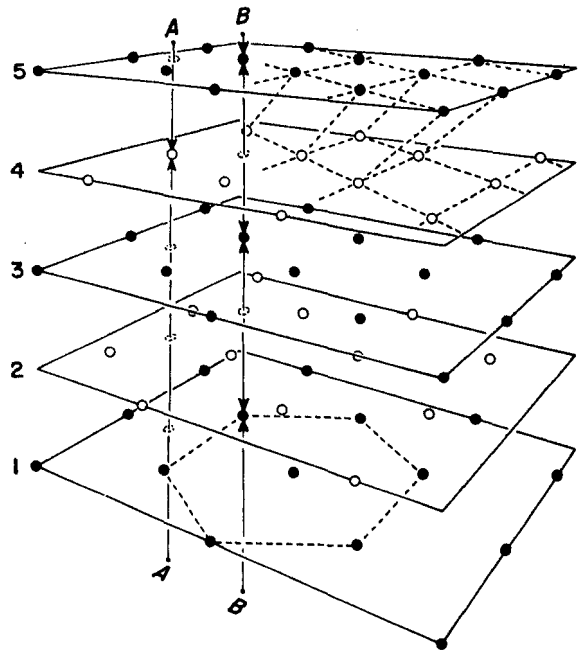

FIGURE 7.—The rhombohedral packing of spheres in perspective, showing only sphere centers. Two other sets of planes could be drawn through these centers at angles determined by the sides of the generating cell, two of which are shown between layers 4 and 5. See text for full explanation.

Here it has been necessary to completely alter the symbols used in Figure 6 owing to other needs. Plane 1 of Figure 7 is identical with the first layer of Figure 6. The hexagon of Figure 6 is shown in Figure 7 as one of dotted lines. Planes 1, 2, and 3 of Figure 7 represent the corresponding layers of Figure 6. The two added planes, 4 and 5, show more realistically the vertical passage running from A to A. It has clearance through the first three planes but is blocked at plane 4 and runs clear through 5. Note that plane 4 is "reversed" from 2, which is the reason for the blockage. The passage from B to B is blocked by planes 1, 3, and 5, but not by 2 and 4.

The indications of the rhombohedral cells by dotted lines between planes 4 and 5 clearly show how two additional sets of planes could be passed through the points.

A perspective view of the simpler cubic packing of spheres is shown in Figure 8 for comparison with Figures 1, 4, 5, and 7. Only four planes are shown, as more are unnecessary. It is evident that the cubic cell and consequent total right angled construction precludes any of the rhombic complications.

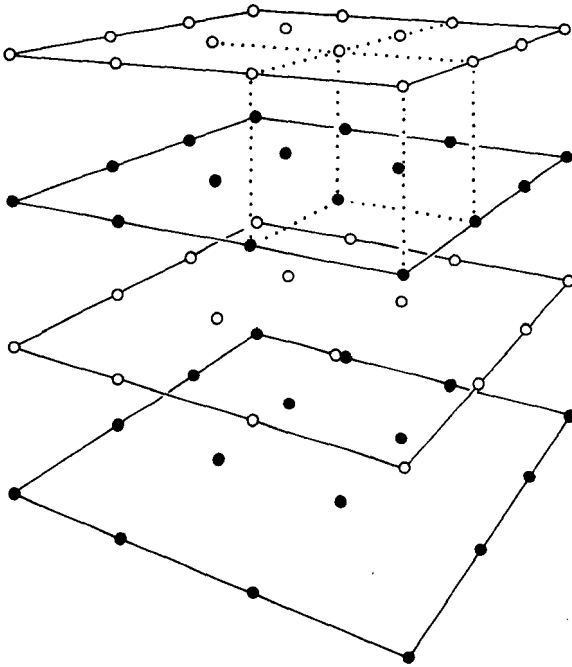These two systems of packing spheres are all

475

FIGURE 8.—The cubic packing of spheres, directly comparable with Figure 7. See text for full explanation.

that will be considered here, as all others are much looser and are not relevant to this study. The density of these two and the number of contacts that interior spheres have with others are given below.

Packing	Percent of volume occupied	Number of contacts of each sphere
Rhomboidal	0.740	12
Cubic	0.513	6

The number of contacts indicated here are identical with the number of "nearest neighbors" mentioned in reference to the equivalent space lattices.

Pitcher's (1973) data on clusters of spheres presented another way of explaining the complications of close sphere packing. It emphasizes the measurements from center to center, with which he was working, rather than the overall pattern of a larger group, which emphasizes the layering effect of polarized parallel diameters discussed here.

Structure and Functioning of Natural Schools

The series of diagrams in the preceding section is virtually a key to determining what, if any,

space lattice a given school of fishes could approximate and it clearly indicates what types of space lattices do not find their embodiment in fish schools. Reason and observation also indicate that school-forming fishes establish their schools rapidly with great unanimity of action. The schools come to stability only after each individual has the common orientation, all normally as close together as the spatial requirements of their individual propulsive acts permit. The organization is strictly one formed in this manner and without any of the differential behavior that more complex lattices would require.

Pitcher (1973), by purely empirical means, arrived at the geometrical relationships of a school of *Phoxinus phoxinus* (Linnaeus) identical with the present formal lattice reached by theory. His fishes fit our theoretical operations even better than any of the fishes checked for this study. Our material all showed some attenuation of the lattice along the axis of travel, which also was the case in Weihs (1973a). This may simply mean that *Phoxinus* keeps a tighter school than any species we checked, or that there is some small effect here that relates to speed of fish and their absolute size. Possibly, however, it may be related to a difference in behavior between a school swimming ahead in quiet water and one holding a stationary position in flowing water, as did Pitcher's fish. In the latter, optical fixation on fellow fishes and some background feature is possible, but in the former, fixation is only possible on other members of the school as the background apparently drifts backward. If this effect does modify the spacing of the fishes, stationary schools in fast flowing rivers where backgrounds are visible should more closely approach the theoretical.

Spacing of Fishes

Using the preceding examination of lattices and the packing of spheres, a preliminary comparison with fish schools may start by continuing the equating of fishes in a school to the diameters of the packed spheres. Schooling fishes should not be expected to space themselves exactly as spheres and they do not do so in precise detail, see Pitcher (1973), but a basic resemblance exists.

If the rigid sphere of geometry be mentally replaced by a soft rubber ball, the approximation comes closer to that of a fish embedded in a school of its fellows. Thus a group of such balls, when packed together, are subjected to slight flattening

and to other minor distortions where contacts are made with other balls, all proportional to the amount of pressure and its direction. The pattern of lattice considered here as closest to the spatial distribution commonly shown by schooling fishes can be reached by very simple transformations.

The calculations that equated the diameters of the spheres to the fishes' lengths can be altered. Here the lengths are changed but the positions of fishes in space remain the same.

A change that evidently does occur regularly involves altering the angles in the quadrilateral mesh composed of two triangles as illustrated in Figure 9, where A and B represent the quadrilaterals in Figure 1, and C represents a quadrilateral that has been used by Weihs (1973a) in connection with his studies on vortex streets. It is called simply a "diamond" by that author. His model resulted from considerations of energy saving requirements. The Weihs (1973a) diamond can be used as a very convenient basic unit or cell[5] characteristic of the fish school lattices, without altering any of concepts discussed here. At this writing, all known changes from the conditions of regular geometrical figures are on the side of increased differences between the two pairs of angles of the diamond. No instances have been found in real fish schools that would lie between case A and B of Figures 1 and 9, unless the widespread separations which have been considered as degenerating schools are included. All other variations found are on the far side of B except for the data of Pitcher (1973), which is precisely at B. In Figure 9, A shows the square pattern with 90°, B shows the 60°, 120° rhombus, and C shows a rhombus with 30°, 150° which depicts a condition frequently seen in fish schools and is, as already indicated, the Weihs (1973a) diamond. Carrying this angular reduction further, the end is reached as the side to side distance between fishes is reduced to zero, so that the total length of the figure becomes a single line equal to twice the length of a side of the diamond. At the other end of this series of quadrilaterals, an increase beyond 90° produces another series. In
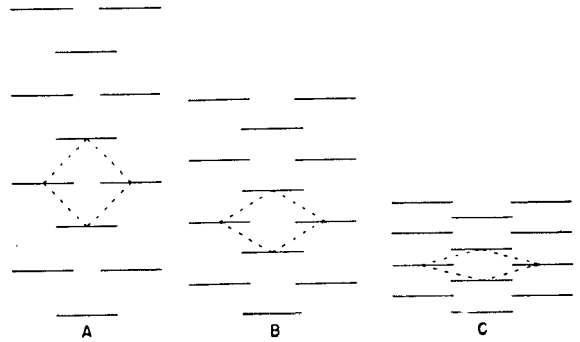

FIGURE 9.—Three quadrilaterals (lattice elements) as related to "diameters" or "fish lengths." See text for full explanation.

this case the final result is also a single line, equal to twice the length of a side but at right angles to the one reached at the other extreme of the series, as described above.

Figure 10 shows how these matters relate to the hexagons and how the quadrilaterals relate to an entire school. Each small circle in the upper row of three diagrams represents the midpoint of each fish. The four fishes, each on a diamond point, are represented by heavy horizontal lines representing the fish lengths. The direction of swimming is understood to be from left to right. All the others, shown only by the small circles, are moving parallel to and in the same common direction as the four indicated. Starting at A with a square and passing to B composed of two equilateral triangles, the series terminates at C with acute angles of 30°,
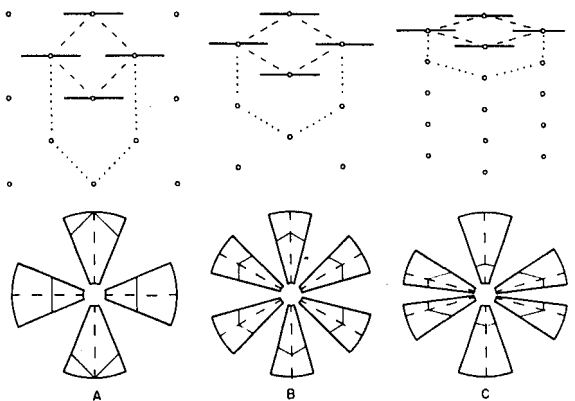
FIGURE 10.—The relations of the three quadrilaterals shown in Figure 9 to the station points in a school and to the corresponding hexagons (upper row). The clear turning sectors and those requiring a too close mutual approach are shown in the lower row. The latter are marked by their two radii and arc by a heavy solid line. Their axes, the lines of contact, are marked by dashed radii. See text for full explanation.

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[5]In most schooling fishes two individuals, if isolated from the others, will swim together side by side or with one diagonally ahead of the other. If three fish are so isolated, they will normally form a pattern of three points of a diamond. In this case there is usually much more shifting around than in the case of two, while four fish tend to form a diamond. It has been a common practice for workers in this field to consider these cases of very small schools. From groups of less than four, it is impossible to make any reasonable estimate of the shape of the diamond. Some judgment can normally be obtained from a group of four, although even that might vary somewhat from a school.

which is the most compressed of the three. Also shown are the relations between the quadrilaterals and the corresponding hexagons, as well as the number of fishes in a given area.

Continuing with Figure 10, it is obvious that the direction of travel could be in any other horizontal direction of swimming, than the one shown here. It should be noted however, that the lattice of each shows that if the fish turned so as to be parallel with any edge of their parallelogram, the fishes would all be brought to the nose to tail position, something which does not occur.

In the lower row of three corresponding diagrams in Figure 10 the dashed radial lines show the directions of swimming that would place the fish in contact. The clear spaces indicate where the passages are unobstructed. The enclosed areas, which surround the dotted lines of contact, meet the clear areas at a point halfway between that line and the centers of the clear areas, except in C which is not based on a regular quadrilateral or hexagon. This will be further discussed under Problems of a School Turning.

In any school, a certain minimum distance from the nose of a following fish to the tail of a leading fish is maintained. The evident need for this separation is natatorial. Requirements differ with the various types of fishes that form schools. Although fishes do not leave wakes behind, as does a motor-propelled ship, there is still the matter of dying vortices (Rosen 1959; Breder 1965). This alone could account for the need of a spatial lead. Conceptually, fishes could swim satisfactorily on any of the diameters shown in Figures 2 and 3, except those on the major axial lines. The minimum distances between these diameters (fishes) in a line occur halfway between these axes as in Figure 2. It is to be noted also that the horizontal rows of diameters tend to line up so that the diameters are not all the same distance from each other as in Figure 3A. This change continues with angles less than 15° so that when these diameters become horizontal they are in end-to-end contact, producing a series of parallel lines. This is merely a matter of the geometry of the uniform rotation of the diameters. No schooling fishes would tolerate this condition, but would adjust their positions to lie near midway between the positions of those lateral to them, as shown in the diagrams of Figure 9. Compare Figure 3B with Figure 9C. The apparent differences between the two are entirely owing to the fact that the first diagram is based on

rigid circles, or spheres, and the second does not have that heavy stricture. The three quadrilaterals in Figure 9 can be considered as making a closed curvilinear figure, where Figure 9A would be circumscribed by a circle while Figures 9B and 9C would both be circumscribed by ellipses, Figure 9C being much narrower than Figure 9B. This transformation can be brought about by increasing the head-to-tail distances of the fishes in a single file and decreasing the distances between adjacent files.

The greatest width between the tracks of fishes swimming parallel is also at the halfway angle between two successive axes, as shown in Figure 3A. As long as all the fishes are swimming in parallel courses the distance need not vary, as seen in Figure 3A. The closer this angle approaches an axis, the smaller becomes the distance between the parallel tracks, indicated in Figure 3B. The distance between fishes, head to tail, varies inversely as an axis is approached.

Still photographs cannot give the sense of a regular pattern of fishes that is evident on viewing a school or a motion picture. Because of these conditions, in those photographs shown here sufficiently open to see the fishes distinctly, they appear as rather ragged groups. Thus in Figure 11 of *Katsuwonus pelamis* (Linnaeus), only fragments of some regularity of pattern can be seen. Those on the left of center show the pattern of a loose school while those on the right are breaking ranks for feeding. This picture, however, indicates several lines of fish alignment, some running from top downwards to the right and others to the left, from which the relationship to the diagram in Figure 7 can be seen within the limits of a still picture.

Species attaining very large size, such as *Thunnus thynnus* (Linnaeus), tend to have disproportionally greater distances between individuals when large, as compared to their younger and smaller sizes (see Breder 1965). Contrary to this, van Olst and Hunter (1970) showed that other smaller fishes (*Scomber, Engraulis, Trachurus,* and *Atherinops*) tighten their ranks as they grow from larvae to near adult size, some abruptly and others gradually.

Hunter (1966) presented some data on the organization of fish schools for purposes that do not concern present interests. However these data, based on motion picture analysis shown in his figure 2, have a distinct bearing on some features
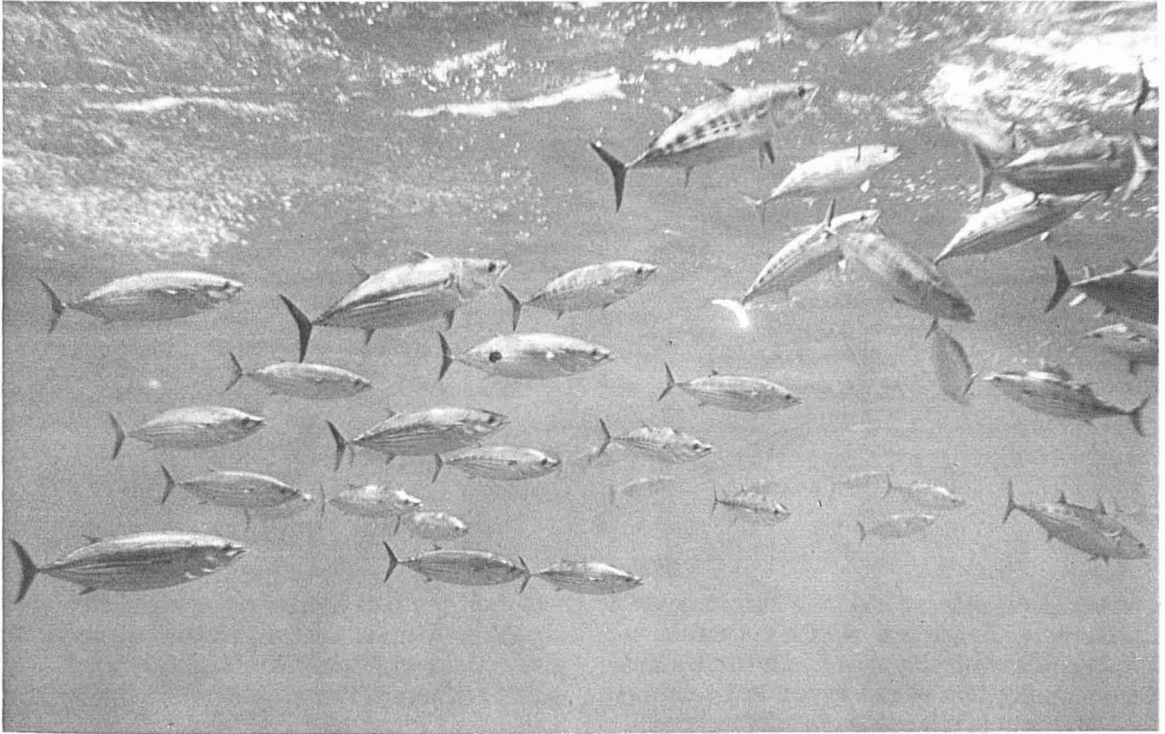
FIGURE 11.—A school of *Katsuwonus pelamis* off the Hawaiian Islands, breaking up for surface feeding. Courtesy of the National Marine Fisheries Service, Honolulu Laboratory, Honolulu, Hawaii.

of this study. Figure 12 is based on Hunter's figure, modified appropriately for this analysis. Although the small group used, six captive in-
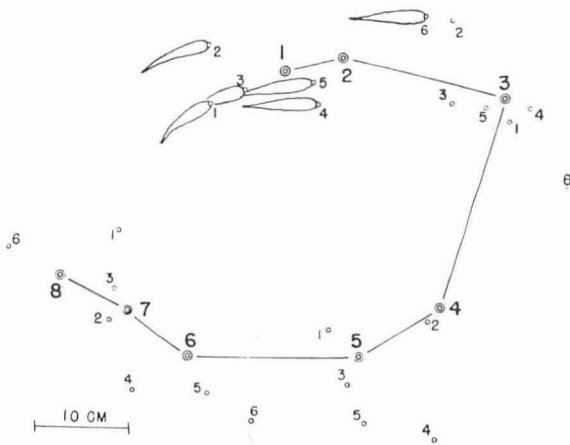

FIGURE 12.—Analysis of the location of six *Trachurus symmetricus* in a school, shown by successive eight steps in their travel. Based on data of Hunter (1966) and his figure 2. Only the odd-numbered positions have the individual fish positions indicated. To show them all would confuse rather than clarify.

dividuals of *Trachurus symmetricus* (Ayres), is not large enough to form a well organized school and even has members that do not always stay precisely at the same level as the others, it is exceptionally interesting in that it does display items pertinent to school structure.

Figure 12 represents the progress of the six fish covering 8⅓ s shown on 100 frames of motion picture film exposed at a rate of 12 frames/s. The larger circles indicate the mean values of the eight positions of the snouts of each of the six fish. These means are connected serially by straight lines.[6] The small circles indicate the patterns of positions of the six fish's snouts for four of the eight means. Every other one has been omitted because adjacent patterns overlap enough to be confusing.

Figure 13 indicates the manner in which the values are related to the trajectory of the group.

[6]Hunter (1966) recognized three turns in his figure 2. For present purposes the sequence is given six turns, as indicated in Figure 12 and Table 1. His three indices, mean separation, distance to nearest neighbor, and angular deviation represent other measures of the same activity, all of which relate to the differences of the mathematical approaches involved.
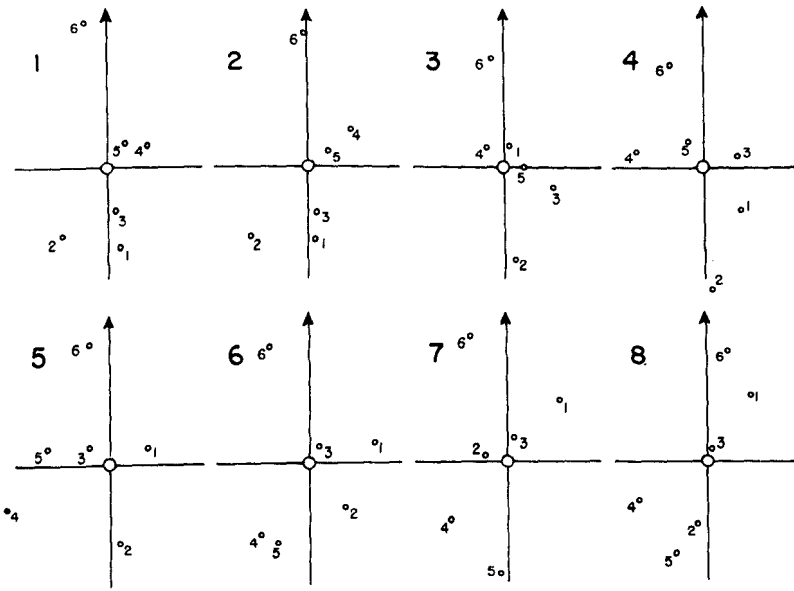
479

FIGURE 13.—The positions of each of the six fishes (small circles) and their means (large circles). The arrowheads indicate the directions of travel of the group. These lines pass through the means and the transverse lines intersect to divide the field into quadrants.

Also shown is the pattern of each fish's distribution, together with the means,[7] the momentary swimming direction of the school, and a line at right angles to it intersecting at the mean position. This device divides the area in which the fishes occur into quadrants. The data for this are given in the first part of Table 1. The precise positions of the fishes were picked from Hunter's (1966) figure 2 and have been handled by graphic methods in the construction of the diagrams shown in Figures 13 and 14. The numerals attend-

ing the positions of the fishes, actually the tips of their snouts, in Figures 12, 13, and 14 are those used by Hunter (1966) to differentiate the individuals and they have no other significance here.

It is immediately apparent that fish number 6 is in the front quadrants continuously. Replotting this data according to the total number of each fish separately as in Figure 14A, other features appear. Figure 14B, which shows the means of Figure 14A, does indeed approximate the Weihs (1973a) diamond.

Considering the manner in which the data have been assembled—captive fishes in a tank, the curvature of their paths, the difficulties in estimating the path of the school, and its generally

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[7]These means were obtained by separately spreading each of the eight positions of the six fishes on Cartesian graph paper and determining their X and Y values and the means.
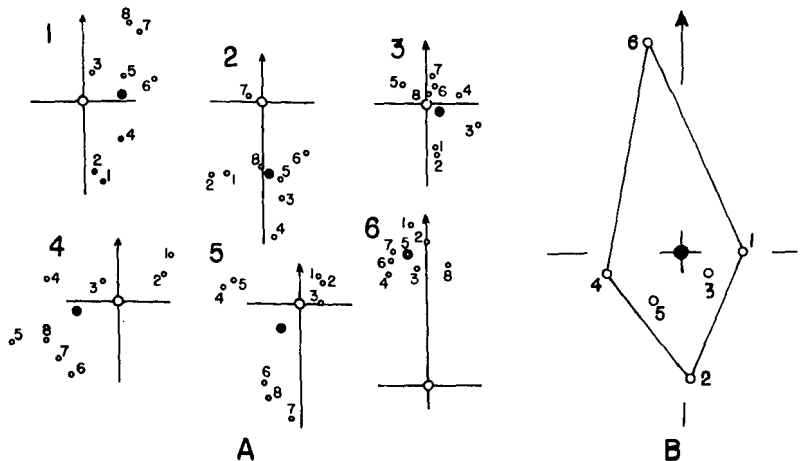
FIGURE 14.—The location of each of the six fishes (small circles) at each of the eight positions. A. The larger light circles with the intersecting lines passing through them are those shown in Figure 13. The large dark circles show the locations of the mean positions of each of the six fishes. B. The large light circles represent the means of the six in A. The small circles show the mean position of each fish (the dark circles of A).

A

B

TABLE 1.—Location of individual fishes (*Trachurus*) by quadrants and by halves. Data based on figure 2 of Hunter (1966). (First letters, L and R = left and right. Second letters, F and R = front and rear.)

	Location of each fish (See Figure 13)					
School's position	By quadrants				By halves	
	LF	RF	LR	RR	F	R
1	6	4 5	2	1 3	4 5 6	1 2 3
2	6	4 5	2	1 3	4 5 6	1 2 3
3	4 6	1		2 3 5	1 4 6	2 3 5
4	4 5 6	3		1 2	3 4 5 6	1 2
5	3 5 6	1	4	2	1 3 5 6	2 4
6	6	1 3	4 5	2	1 3 6	2 4 5
7	2 6	1 3	4 5		1 2 3 6	4 5
8		1 3 6	2 4 5		1 3 6	2 4 5

	Quadrants and halves occupied by individual fishes (See Figure 14)					
Fish no.	By quadrants				By halves	
	LF	RF	LR	RR	F	R
1		3 5 6 7 8		1 2 4	3 5 6 7 8	1 2 4
2	7		1 2 8	3 4 5 6	7	1 2 3 4 5 6 8
3	5	4 6 7 8		1 2 3	4 5 6 7 8	1 2 3
4	4 3	1 2	5 6 7 8		1 2 3 4	5 6 7 8
5	4 5	1 2 3	6 7 8		1 2 3 4 5	6 7 8
6	1-7	8			1-8	

loose nature—it is remarkable that any such approximation to a regular figure could be found. This material indicates that the influence tending to hold schooling fishes to approximating figures this close to geometrical regularity is effective even in assemblages of fishes barely coming within our definition of the word.

Healey and Prieston (1973) brought out a very interesting feature of schools by the application of multivariate analysis. This is evidently closely related to the preceding geometrical study on the data presented by Hunter (1966). The problem of the origins or the reasons for the existence of these individual variations in fish movements within a school is not yet susceptible to a general solution. Clearly some are caused by extrinsic stimuli and some by intrinsic causes, such as the physiological state of the individual. Healey and Prieston (1973) wrote that their data suggested, ". . . that there may be a short-term and a long-term organization within the school." Possibly this could eventually be referred to equivalently short- or long-enduring stimuli, not grossly evident to the observer. The data of McFarland and Moss (1967) and Moss and McFarland (1970) may represent an intrinsic short-term event, in this case being a reduction in oxygen tension. Alekseeva (1963) showed that various fishes have a greater oxygen consumption when visually isolated from their fellows. Such individuals, if able to see the others, do not. Schuett (1934), Escobar et al. (1936), and Breder and Nigrelli (1938) indicated that individuals of *Carassius auratus* (Linnaeus) swam faster when alone and when crowded, but slower when with a few companions. This should be reflected in their oxygen demand and may account for the results of Alekseeva (1963).

The very short duration of the Hunter (1966) data suggests that the details here might be based on intrinsic sources, as in the case of the fish that kept the leadership of the school and of the one that brought up the rear. It is conceivable that these may be the consequences of the individual physiological states.

In agreement with Bowen (1931, 1932) and Radakov (1972), there is no convincing evidence that the superficial appearance of "leadership," to be seen occasionally, supports such a view. Hunter's (1966) data covered only 8⅓ s. Breder (1959) suggested that "white" *Carassius auratus* (Linnaeus) seem to take the leadership in schools otherwise composed only of "yellow" individuals. This finding of white fishes in leading positions is apparently related to the greater conspicuousness of the white fish as compared with the yellow in a lily pond environment and is not an indication of leadership by any individual.

Radakov's (1972) data, which was extensive and important, considered "leadership" in a rather different sense than the others. He considered numbers of leaders up to 40% of the number of fishes comprising a school. The front fishes, with no other fishes ahead of them, are considered here as leaders. These fishes are in a different physical category as they have none of the advantages of being a following fish.

481

An exceedingly interesting and simple exper-
iment was undertaken by Radakov (1972) with
21 young *Pollachius virens* (Linnaeus) of 8 to 9
cm. These were placed in a tank measuring
$1.6 \times 7 \times 0.3$ m. It was divided into two equal com-
partments by a clear glass partition. All the fish
were placed in one compartment. The experiment
consisted of transferring the fishes, one at a time,
to the other compartment. With 20% or less of the
fishes transferred, the smaller group tried contin-
uously to swim through the glass partition in their
efforts to rejoin the others. Above that percent-
age, the two larger groups, between 30 and 40% of
the fish on both sides tried to form a common
school with the glass partition cutting through it.
Continuing the transferring, a reverse series of
the attitudes described above was obtained.

Movements of Individuals

The study of travel by individual fishes within a
school has difficult and tedious aspects, as is
evident from the preceding. The subject has not
attracted many investigators as witness the
paucity of comments on it in earlier papers. An
examination of Figure 12 shows quickly that such
internal traveling is neither negligible nor slight,
at least in very loosely organized schools, but is
probably much less so in very tight schools.
Because of this, the geometrical properties of
schools have been considered chiefly in a single
layer of fishes, i.e., in terms of plane geometry.
Schools of greater depth present special difficulties
in obtaining adequate field data, as it is necessary
to invoke the complications of the third dimension
while the fishes are often so closely packed that
visual perception within the school is severely
restricted. In addition, there are further problems
incident to the fishes' continual activity. This is
particularly difficult in efforts to recognize the
rhombohedron of Figure 1B. The present efforts
have yielded some hints that suggest support to
our thesis.

The vertical structure of schools and vertical
mixing within them is much more difficult to
handle. This is evidently owing partly to the
greater inherent difficulties in three dimensional
plotting and partly in the nature of fish mor-
phology and methods of propulsion. The influences
of each fish on the others in the same horizontal
plane are greater than in any other direction
because both vision and locomotor mechanics
operate primarily in that plane. That is, optical

axes of schooling fishes lie in that plane and the
propulsive mechanism produces forces operating
in it.[8]

It is consequently less difficult to compare the
relative amount of shifting about in the horizontal
plane as compared with that in the vertical.
Although we have no clear observations or photo-
graphs of a fish sinking to the layer below it or
rising up from one below, there are many in-
stances of evidently "uncertain" fishes seen
between distinct layers or ones dropping slightly
below, as in Hunter's (1966) figure 2.

Shape and Size of Schools

The closed figure that forms the outline of a
school is a remarkably flexible boundary subject to
continual transformation. These changes are
produced by a large variety of influences both
intrinsic and, by a vastly greater number, extrin-
sic. Obviously, the most important intrinsic factor
in holding a school together is the impulse that
causes fishes of one kind to assemble, respecting
each others necessary swimming room and ac-
cepting a common polarization.

The fishes that are outermost along the sides of
a school do not form a special boundary layer any
more than do those at the front form "leaders."
Those at the side surfaces differ from the rest only
in that they lack fellows on one side. Like those at
the front, they are continually changing as their
aggregating tendency apparently moves them
toward a more central position.

Aside from temporary weakening of the bonds
by such things as vigorous feeding, reproduction,
the coming of a sufficiently dark night, or a
particularly violent disturbance, the basic school
structure is continuous in obligate schoolers. In
facultative schoolers, the school is periodic or of
occasional occurrence. True semipermanent inter-
mediates between these two ordinarily distinct
modes are not easy to find and are uncertain at
best.

The intrinsic influences divide naturally into
two groups, the first being those of nonorganic
elements. Common examples of these are light,
water currents, shoreline, sharply mottled bottom
patterns, and obstructions. Sharp discontinuities
of any of these are especially influential. Organic

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[8] A comparison of fish schools with those of cetaceans should be
illuminating because the propulsive efforts of the latter operate
in the vertical plane.

factors include other schools, large predatory fishes, fish-catching birds, and rich plankton streaks.

Theoretically at least, fish schools could take any shape. Considered as three dimensional "blobs," they have been described and photographed in a wide variety of shapes, including even the nearly spherical (Breder 1959). The latter mostly occurs in open water some distance from the influence of the water's surface and the bottom of the body of water. These are rare and suggest almost exactly balanced forces. Under such conditions the school formation in the ordinary sense breaks down[9] The form of organization within such near-spheres has not been analyzed, nor has their manner of formation or eventual dissolution. Other shapes not

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[9]There is in this case a question as to the propriety of including this assemblage as a school in any sense. At least the fishes that form this ball are in a solid school formation as they rush in to form these structures.

readily described in simple geometrical terms, as that shown in Figure 15, seem to illustrate the presence of either spiral arms or "smoke ring" formations.

Much more frequently encountered are schools close to the water's surface or the bottom. These often show a more or less oblate spheroidal form from which a portion has apparently been planed off, where near contact with surface or bottom necessarily caused flattening. Otherwise, the opposite side follows the contour of the flattened side so that the school takes the form of a flattened sheet of rather uniform thickness. These often take the form of a sheet one-fish deep, the school practically reducing to a nearly two-dimensional figure. These all may occur in open water, either near the surface or bottom. They are, however, more usually seen in very shallow water where both surface and bottom influences impinge on the school. These schools in which the horizontal dimensions greatly exceed the small vertical one
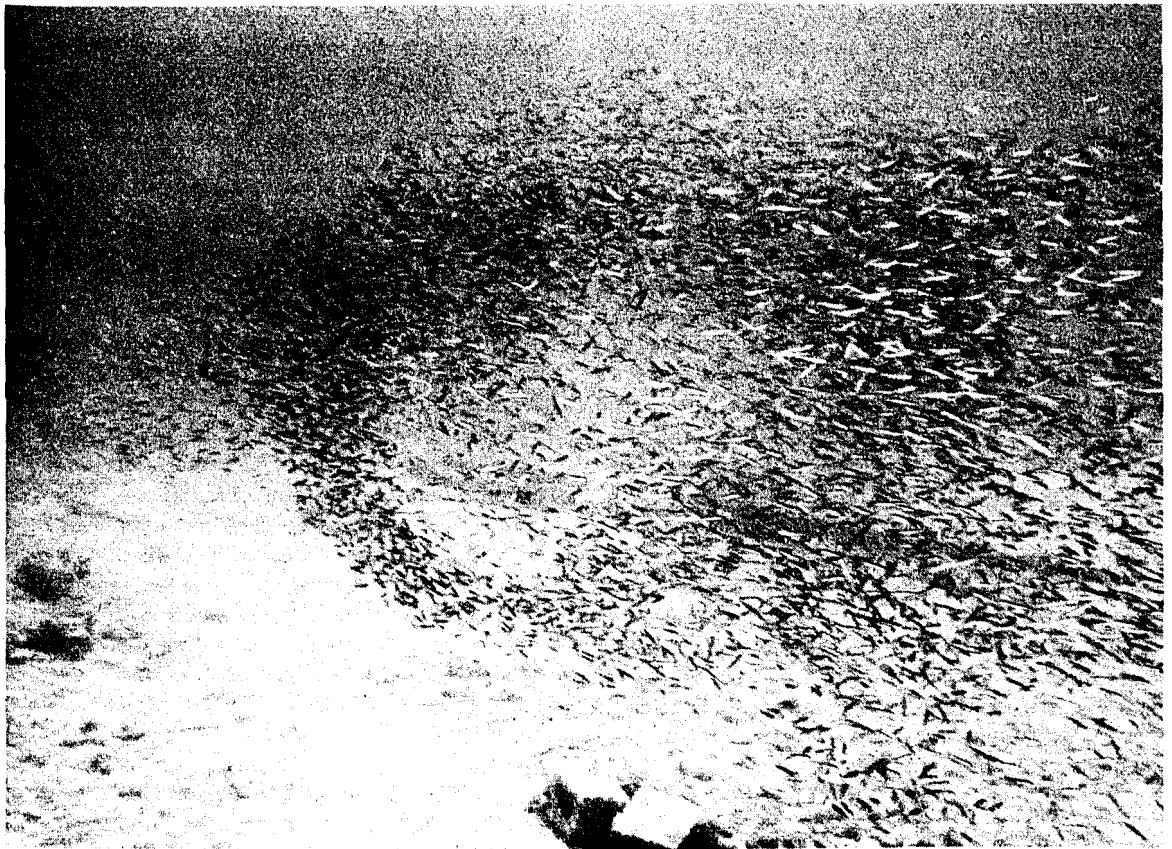

FIGURE 15.—An unusual and not readily explicable maneuver of *Jenkensia stolifera*, seen at Grand Cayman from scuba gear under very calm conditions.

are more accessible for study and the data obtained from them is readily handled by much simpler geometrical methods. Most of the present knowledge of schools is based on observations and analyses of these sheetlike schools, treated as a geometrical surface.

Unless there is mention to the contrary, all statements in this study refer to small or moderate schools. When schools attain huge dimensions, some of these statements require modification. A fish in the central part of such a school, that may have thousands of others between it and open water in any direction, is locked in a position that permits practically no freedom of movement. Such fish are forced to swerve and swim almost as a single block. Thus the turns discussed in the section Problems of a School Turning are not possible. The section Sizes of Fishes in a School discusses conditions involving the amount of size variation of the individuals found in a school. This reaches its maximum in huge schools where size variations are often large enough to break up a lesser school.

Problems of a School Turning

A solitary fish obviously can alter its path from that of a straight line and swim off in any direction. The presence of objects, such as neutrally disposed fishes of the same or other species and same general size, may make little difference except for appropriate course altering. Problems loom as a significant influence only when the density factor becomes relatively large, as in a loose unpolarized aggregation. When fishes become even more crowded by each other, the ability to swim in any direction is severely restricted by the mere presence of the bodies of other fishes. In a dense school this manner of restriction becomes intense. Such closely packed and regimented fish can swim serenely, parallel to each other, in a straight line or in large swinging arcs of a radius down to a value of about as little as five to ten lengths of the fishes involved as shown in Table 2A. If, however, a sharp curve of shorter radius is attempted, complications arise (Table 2B). Such turns are commonly made by small schools up to sizes that are too large to act as a completely cohesive unit.[10] The data shown in Table 2 refer only to these small cohesive groups.

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[10]See Breder (1967) for a discussion of the vastly greater complexities inherent in the behavior of enormous schools.

TABLE 2.—Data on two types of turns made by fish schools.

A. Radii of broad curves in *Selar crumenophthalmus*

Radius in fish lengths	Fish lengths in cm			No. of fishes
	Max	Mean	Min	
5.5	30.5	25.4	22.6	11
9.3	25.9	25.4	22.8	9

B. Measurements of sharp curves

Species	Angles of turn in °	Remarks
Menidia berylina	41.5	
Selar crumenophthalmus	135.5	Shown in Figure 17.
	148.0	
	158.0	
	160.0	
	163.0	
	175.±	Turns as in Figure 18.
	177.0	
Trachurus symmetricus	94.0	Note: The 11 numbers
	40.5	not set in boldface
	33.0	refer to Figure 16
	31.5	
	25.0	

Here some disturbance ahead frequently can set off an activity among the leading fishes in which they turn sharply left or right. These are then followed by the others, making their turns in substantially the same place. Normally the maneuver is accomplished with a scarcely apparent and transient slowing of pace. The hydrodynamics of how sharp turns are made by fishes with a minimum of deceleration was discussed in detail by Weihs (1972).

Some of the angles between the initial and subsequent paths of schools making these sharp turns are given in Table 2B, picked from motion picture sequences. Figure 16A indicates that turning at a certain angle could cause following fishes to approach the tail tips of those just ahead, an accident that appears never to happen.

There is nothing inherent in the situation of a school swimming ahead that concerns angles of turning. The features of the diagram in Figure 16A are meaningless to the fishes until they begin to turn. Let the school swim in a straight line and turn 30° to the right at the center of the diagram. Each fish will come out in an occluded sector and find it being brushed by the tail of the fish ahead. If the Weihs (1973a) diamond is elongate along the axis of travel, the fishes will fall a little short of contact but will swim into the wrong side of the vortices shed by the preceding individual. This is evidently sufficient to initiate avoidance reactions.

If they turn at 60°, there will be no problem as they will be well separated by the amount indicated in Figure 3A. The fishes in turning evidently do so only where there is no danger of
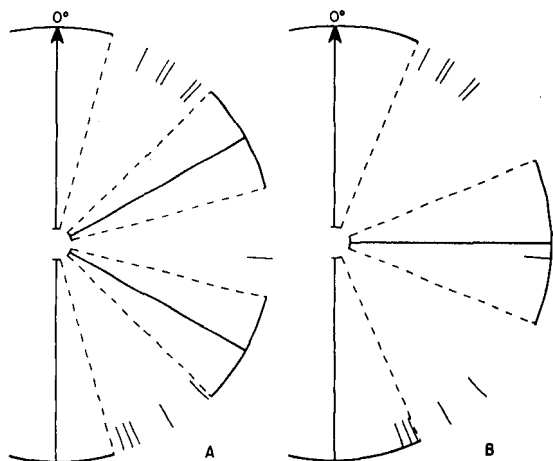
FIGURE 16.—Angles of sharp-turning fish schools. A. Angles compared with the rhomboidal lattice. The four solid radial lines represent the collision paths of turns if the original path is represented by the vertical line marked 0°. This direction of a fish's path is indicated by the arrowhead. The dashed radials marking the end of each arc separate the clear sectors, without arcs, from the occluded. The 11 short radial line segments represent the new path of the fishes after they have made their sharp turn. The numerical values of the angles are given in Table 2B. The same fish turns compared with the cubic lattice. Here the fish paths are not limited to the clear sectors. See text for full explanation.

interfering with each other's swimming. Actual turns of various species keep well away from the critical angle. Which particular clear space is selected is evidently determined, at least in part, by the strength of the deflection-causing stimulus. As such a turn is completed, the fish again start to swim in an essentially straight line while they regain the positions that were somewhat disturbed in turning and the Weihs (1973a) diamond appears again. Thus the outlined sectors in Figure 16A become "forbidden" paths. Since the diagram in this figure is purely a geometrical construction with the occluded and clear sections having equal areas, this is not to say that some intrusion into the outlined sectors is impossible. The axis of the occluded sectors is the worst position for turning and that of the clear sector the best, the areas between grading gradually from one condition to the other. The dotted radii are halfway between the center lines of the clear and the occluded areas. The turns made by real fish schools, measured by motion picture analysis, and shown in Figure 16A and Table 2A indicate the absence of intrusion into the enclosed areas.

This examination of the sharp turnings of fish

schools would not have shown these features if they had been organized on some pattern other than that of the hexagonal lattice. If they had been organized on the square lattice, shown in Figure 4, there would have been at least some in the "forbidden" sectors, as is shown in Figure 16B where the same data on turning angles have been placed on a diagram based on the square mesh. Here the same data show less preferential behavior on the part of the fishes toward the clear sectors. All the schools, in the hexagonal case, stayed within the boundaries of the clear sectors (Figure 16A) while only 64+% did in the square case (Figure 16B). Also the intrusion into the occluded sections increased with the increasing angle between the initial course and the new one. These two items are additional reasons for considering the lattice to be basically hexagonal.

A typical turn of the sort discussed is shown in Figure 17 and in Table 2B. This drawing is based on a series of seven motion picture frames (0.44 s). The sequences are of a tight school, the angles between the straight paths, before and after the turn, are based on the mean paths of the fishes. Only a few of the individual fishes are shown in Figure 17 to indicate the nature of the turn at that point. Not shown are the many fishes constituting the bulk of the school.

There is also another type of sharp turn that is not mentioned in the preceding description. It can lead to considerable confusion because superficially it is readily confounded with the foregoing type. It differs primarily in not being concerned with angular limitations, which apparently can be ignored only at the expense of making the turn
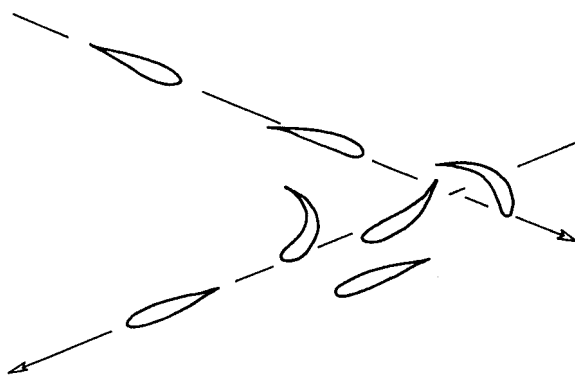

FIGURE 17.—A sharp turn of *Selar crumenophthalmus*. Only the paths before and after the turn are indicated and a few of the turning fishes. The directions of the two paths are indicated by arrowheads. See text for full explanation.

with considerably less alacrity. Once the behavioral differences between the two types of turn are understood, they can be seen in the field if one happens to be looking directly at the point of turning before it begins. This is easier to see in a relatively large school than in a small one because the larger the number of individuals involved the more prolonged the turning maneuver becomes. Also, it is most noticeable where the sudden appearance of something large and "threatening" produces an apparent "panic situation." Instead of what seems to be the beginning of a tight turn, as previously discussed, the action is most often seen as an attempt to retreat over their forward path. Here there develops a "logjam" and confusion. The immediate response is for the clump of fishes to spread out into a more or less circular area, out of which the school is seen to beat a hasty retreat. Figure 18 shows such a performance which theoretically, at least, could move off in any direction but, so far as our observations go, has usually been close to the opposite direction of the abandoned advance. The conventions of Figure 17 have been used and the same number of frames cover this sequence. The seeming difference of speed is simply that badly frightened fish move faster than relatively placid ones and therefore make up much of the time lost in the greater length of their confusion-imposed travel. This area sometimes develops a central clear spot devoid of fishes, and a true "fish mill"[11] is transiently developed.

The angular measurements between the track of a school before the turn and after it can only be precise in photographs taken with the camera pointed straight down. This is nearly impossible with feral fishes because such schools simply move away from anything directly overhead. The photographs on which Table 2 are based are those which approach that position as nearly as possible. This departure from the vertical naturally tends to slightly blur the accuracy of the angles and thus serves to produce a greater spread in the apparent angles. This effect has less influence on the mean values of each clustered group. To help counter this source of error, a transparent dial was prepared with the sectors shown in Figure 16. Hand held, it can be tipped at an angle appropriate to the angular amount of departure from the vertical with which the eye or camera viewed the scene. A

FIGURE 18.—A slower turn of the school shown in Figure 17, with confusion at the turning point. The directions of the two paths, into and away from the melee, are indicated by arrowheads.

variety of items shown in such a film helped establish the needed correction with sufficient accuracy for present purposes. Although little use could be made of it in the direct observations because of the rapidity of the action, it was invaluable in studying strips of motion picture film. Small cues that helped establish the proper angle of tilt of the viewing dial included principally the amount of the sides of the fishes that could be seen plus other objects incidentally included in the photographs.

Absolute turns enforced on schools of *Mugil cephalus* Linnaeus and *Pollachius virens* (Linnaeus) by the end of an aquarium were studied by Radakov (1972). These are in contrast to the preceding studies of turning in open water where the actual cause of the turn was often obscure, but irrelevant to the mechanics of turning. The aquarium studies show nothing like the "sharp turns" but are close to, if not identical with, the present "slower turns" where the school breaks down and reforms on the retreat path. Here and in Radakov's (1972) work, there is considerable mixing and the place of individual fishes in the school after these turns may be grossly altered. In the confines of an aquarium there is practically no choice of turning angle and the complex situation in turning in open water does not exist.

General Traffic Problems

Road traffic of automobiles may seem to be very remote from a school of fishes. Close examination, however, reveals that the two have common roots and that, despite their apparent differences, they are isomorphic. Both cars on a road and fishes in a school can be treated as embodiments of mathematical expressions concerned with mass movements of redundant units. The mathematics of the behavior of automobiles developed along with their proliferation, following the need for

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[11]A term used by Parr (1927) to cover the case of a fish school swimming in a more or less circular path, where every fish is following those ahead of it. The clear center that these mills sometimes develop has been discussed by Breder (1951).

increasing specific and detailed control of their movements. Thus, from a purely empirical beginning these studies have gradually developed into the present traffic theory, most of which has developed in the last 10 yr. Introductions to its considerable literature are given by Ashton (1966) and Gazis (1967).

Some of the similarities and differences between cars and fishes in the attainment of an organization of free-flowing traffic is indicated by the following comparative listing of the two types of redundant units.

Fish	*Automobiles*
1. Fishes, schooling or not, operate freely in three dimensions, but most free-swimming fishes, especially those that form schools, operate mostly parallel (although not necessarily close) to a usually horizontal surface, either the surface of the water or the bottom. These two mark the vertical limits within which the fishes must stay. Horizontal boundaries may vary from too close for schools to exist to practically limitless expanse, in the strictly physical sense. Schooling fishes can go in any direction but only with their school.	1. Cars, in traffic or not, are confined to a surface, which is not necessarily a plane and is often a warped surface, where the extent of warping eventually limits the possibility of use by cars. Cars must stay on their roads but do not necessarily stay with their fellows. They may strike out alone wherever there are connections with other roads, except where accompanied by restrictive road signs forbidding a given maneuver or by the general rules of behavior.
2. Other strictures are those with which only schooling fishes are constrained. Here fishes all swim in a common direction, mostly in parallel paths, and in single files. Collisions are rare or absent, their avoidance evidently being rooted in their highly developed sensory mechanisms: vision, lateral line and cupulae[12] senses, and hearing. There is no provision for "night driving" except in species carrying their own illumination. Others loosen their	2. Other strictures are those with which only cars, especially in traffic are constrained. These controls are maintained by laws to run in an indicated direction in single files or in parallel paths, depending on the width of the road and its indicated number of lanes. Collisions occur with monotonous frequency. The protections are only the sense organs of vision and hearing. Night driving illumination is normally present.
ranks or break up on nights sufficiently dark to eliminate vision.	
3. Fishes form well-defined patterns; for hydrodynamic reasons they are quadrilaterals.	3. Cars form "diamonds," or if the road has less than three one-way lanes, parts thereof.

In both cases there are valid reasons for not following closely behind the unit directly ahead and for not traveling in tandem positions. The resulting staggered deployment permits passing and lane shifting with a minimum of confusion. It is this arrangement of units and their possible movements that is largely responsible for the irregularities in any instantaneous structure of the swimming patterns.

In the case of a traffic jam of cars or the equivalent conditions of pods[13] of fishes, the pattern formed by units is nearly obliterated.

The shape of the diamond formed by four cars is related to the speed of travel and is determined by the rules of the road covering the increase in distance to be given the car ahead with an increase in speed. Also the rules require the passing car to speed as fast as practicable in passing the slower car. Thus, the faster the traffic, the farther the hexagon or diamond departs from the regular, attenuating along the axis of travel.

That the fish and a car with its human driver are closely comparable should be clear from the preceding and the following outline indicating that the relations between the two dynamic systems do in fact constitute an isomorphism. Two central nervous systems, one of a fish whose body is vehicle, power plant, and pilot, and the other, that of a human who is the pilot, enveloped in a capsule comprising the vehicle and power plant, operationally calls for the same kinematic pattern and trajectories of behavior. As these are both systems with feedback in which all essential variables are evident, the canonical representation and the ordinary algebraic forms of equations can be calculated. This will not be done here as it would

In fishes, the same results are obtained by those ahead leaving both advantageous and disadvantageous water movements in which the followers, by taking the path of least resistance, fall automatically into positions that mark out the diamond. The lengthening of the figures as the fishes' speed increases is very slight as compared with that of the distance increase with cars.

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[12]See Cahn (1967) for a survey of the function of these systems.

[13]This term has been defined by Breder (1959).

not be relevant to present purposes and would carry away from the intent of this communication, although the equation of Breder (1954) should be useful to such a study.

The main thrusts of the students of traffic flow have been concerned with such things as problems of delays, queueing, road junction, traffic signals, analogies to fluid movements, and follow-the-leader sequences.

The study of fish schools has not yet reached into these matters, although they all bear a one-to-one resemblance to similar items in schools. This undeveloped area is difficult to enter into deeply partly because there is no facile way to keep track of each individual. The analysis of the behavior of individuals in a school based on the data of Hunter (1966) could be considered as a start in this direction.

Influence of Body Forms

There is a marked positive relationship between schooling and the extent of streamlining of the general contours and of the drag-reducing surface details of fishes that, in the most advanced obligates, can be considered exquisite. Parallel to this is an equally marked negative relationship between schooling and special surface features of the eruptive sort. At this end of the series, the fishes are not schoolers at all, nor even aggregators, but are usually solitary, neutral, or agonistic toward their fellows. All of this can be shown to be related to mechanistic details covering the manner of life of the individuals involved.

For example, we know of no obligate schoolers such as clupeids or scombroids that have any drag-producing extensions, while the vast majority show beautiful fairing even in the manner that the maxillary fits into a matching recess when the mouth is closed and in the slot that the depressed dorsal fin fits into as shown in *Scomberomorus.* Such niceties are not to be found in the facultative schoolers such as most of the Salmonidae, Cyprinidae, and Serranidae. In the essentially nonschooling fishes, the streamlining often becomes less effective and outgrowths from the integument and eruptive structures become more and more extreme as in *Hippocampus*, the Scorpaenidae, Cyclopteridae, and Diodontidae. With this comes slower swimming speeds and an increasing tendency to reduce swimming to a minor roll, as in some of the Scorpaenidae and all of the Antennariidae.

The remainder of fishes to be considered here are those that show a depth[14] equal to or greater than their lengths. These are often facultative schoolers. Families in which this is a usual or frequent condition include the Stromateidae, Ephippidae (including the extreme platacids), Chaetodontidae, and Acanthuridae. Many others show an approach to the condition, as in the Pomacentridae. In addition to these, there are a considerable number of families in which one or a few species have the necessary characteristics, as the Carangidae and Cichlidae.

The schools that are formed by fishes of great body depth are superficially very similar to those formed by fishes with fusiform outlines. A school of deep-bodied fishes is, however, automatically tighter because the greater depth of body intrudes into the swimming areas of the layer of fishes above as well as the layer below.

There is both mechanical and hydrodynamic interference and an optical occlusion that is much more severe because of the greater area of the sides of these fishes. This leads to greater difficulty in making sharp turns. These conditions can only be relieved by loosening the school in the vertical direction. How much mutual swimming facilitation is lost by this loosening is not known. Figure 19 illustrates these conditions with a head-on photograph of an extremely loose school of *Chaetodipterus faber* (Broussonet).

The only other fishes known to form schools are those in which the longitudinal axes do not lie parallel to their line of travel. They include various characins, the "head standers" of aquarists, and some aulostomoids, the best known of which are *Aeoliscus* and *Macrorhamphosus*. These evidently swim with the head up or down (Atz 1962, Klausewitz 1963). There is no data on any aspect of their hydrodynamics nor on their mucus. These forms, therefore, are not discussed here.

Sizes of Fishes in a School.

The variation in the lengths of individuals in a school usually reaches no more than 30%. The difference between the length of the largest fish minus that of the smallest fish in a given school is expressed as a percentage in this notation. Data from Breder (1954), recalculated for present pur-

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[14]This is not the body depth of taxonomists, but the vertical depth of the entire profile, including the extent of the dorsal and anal fin in that dimension.
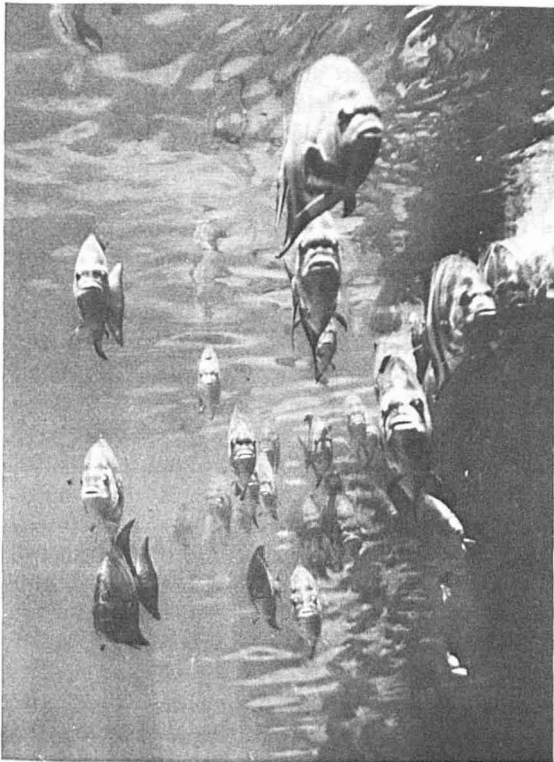
FIGURE 19.–A head on view of a loose school of *Chaetodipterus. faber.* From Herald (1961). Photo by Fritz Goro.

poses, yielded the following comparative values: *Harengula humeralis* (Cuvier) 12.5, *Jenkinsia* sp. 24.2, and *Atherinomorus stipes* (Müller and Troschel) 25.0. Additional data on *Jenkinsia stolifera* (Jordan and Gilbert) taken from Breder and Bird (1975), based on Grand Cayman fishes, gave 31.7. All are below the 30% level of variation except the last. A school of *Ictalurus nebulosus* (LeSueur) still being herded about by their parents, however, had 42.9. It is known that when several family groups are present, the young fish often become mixed. This may well be the cause of this greater variation, a similar feature being found in extra large schools of adult clupeids, as discussed by Breder (1967).

The fate of injured and parasitized schooling fish has not been given much attention and it has generally been assumed that such unfortunates do not long survive. This view has been nurtured by the fact that a captured school of fish most often contains no individuals that show either wounds or evidence of gross parasitism. That there are striking exceptions to this has been shown by

Guthrie and Kroger (1974). They reported that individuals of both *Brevoortia tyrannus* (Latrobe) and *B. patronus* Goode, with vitality reduced because of depletion caused by injury or parasitism, are to be found in estuaries schooling with smaller, younger, but healthy individuals normally present in these relatively protected areas. Outside waters yielded no such composed schools.

The relative sizes of the healthy young fishes and the handicapped older ones and the ratios between the largest and smallest individuals are given below as percentages.

Estuarine	Young	Old
B. tyrannus	52.7	10.4
B. patronus	73.6	44.2
Oceanic		
Both spp.	–	63.4

Only one group has an index of low variation in lengths, 10.4. The others all have indices of high variation reaching to the extreme of 73.6. If the schools of both young and old are each taken as a whole then all groups would show very high variation, i.e., 63.6 for *B. tyrannus* and 80.0 for *B. patronus.*

There is only one way these figures can be interpreted. The schools of both species are a mixed lot of lesser schools, as would be expected of fishes that persist in forming enormous schools that mix broods from different spawning areas and that are hatched at various times in waters of different temperatures. This genus would seem to be the most prodigious gatherer of huge aggregates of a single species on the American Atlantic coast.

In the usual, more uniform schools, where the variation is less than about 30%, the geometric structure is observably more uniform. Theoretically, at least, the smaller the variation in the size of the fishes the nearer the lattice could approach geometrical perfection. Schools of fishes where there is larger variation in size tend to break in direct proportion to the magnitude of the variation. In enormous schools with great size variations breaking up is not always possible but does lead to considerable churning as individuals of similar sizes gravitate together.

Effects of Mirrors

The confronting of animals with mirrors has been practiced for many years, for both trivial and serious purposes. The vast majority of such presentations has been made to one subject at a time,

489

e.g., Svendsen and Armitage (1973). There have been few cases of mirrors being introduced to groups, such as fish schools. Pitcher (1973), using mirrors for certain photographic purposes, noted some of the reactions of his fish subjects. In both cases above and almost all others, the studies have been made on captive animals.

Information on the reactions of individual fishes within a tightly organized school is not readily obtained. Experiments on captive schools yield results that are naturally suspect, primarily because of the usually gross changes in the behavior of schools confined to small quarters and the length of time in days or weeks, even in a relatively enormous container, that it takes to reach apparent stability. Analysis of motion pictures taken of feral schools cannot be expected to supply much more than occasionally fortunate sequences. One difficulty is the interference of other members of the school or of other species exterior to it. Mirrors introduce something to which fishes generally respond and thus the possibility of reasonably interpreting their responses exists. The experiments and their results follow.

A submerged mirror, 39 × 57 cm, was hung near an observation dock or other suitable location which yielded data on fishes in schools in their native habitats. The school's presence was in no way forced, nor were they present because of any attractiveness mirrors may have, since the sites selected were normally visited daily by these schools.

Four species, three of the Clupeoidei and one of the Mugiloidei, reacted to this mirror, each in a different manner, as follows.

Anchoa hepsetus (Linnaeus) showed the most striking reactions. All the schools of this species were large, at least containing 1,000 fishes and usually far above that number. The schools appeared at this place only during the daylight hours and moved off to deeper water for the night. These movements were independent of the tidal stages. The horizontal component of the tidal flow clearly regimented these fishes because at slack tide they became somewhat disorganized.

If the mirror was submerged while this species was absent, the fishes schooled on arrival would regard it simply as any other solid object, such as a pile, that had to be avoided by changing their course. In doing this, schooling fishes normally leave a clear space between them and the object. In this case it averaged close to 20 fish lengths. If the fishes were present before the mirror could be

lowered, it was allowed to slide directly into the school, which produced little disturbance, other than a few transient "shock waves" as the normal space was formed around the mirror. It was noticed early that the distance kept by the fishes from the back of the mirror, painted black, was a little greater than that kept from the face of the mirror.

After the elapse of about 1 h after the introduction of the mirror, the portion of the school opposite the mirror's face made slight "bulges" toward it, which were promptly resorbed. Nothing like this appeared on the part of the school opposite the black backing of the mirror.

After another hour, the school had moved closer to the face of the mirror, approximately 10 fish lengths away. When this was once established, individual fishes would sally forth from the perimeter of the school opposite the mirror and swim to within four fish lengths of the mirror and momentarily run parallel with their reflection. This would be followed by a hasty retreat to the school. The action, repeated frequently by various individuals, would seem to be explicable as follows. A peripheral member of the school could see the school's reflection twice as far as the mirror surface. To join that "other" school required that the adventuresome individual had to negotiate that apparent distance. The fish traveled about nine fish lengths before it turned back. Here the fish found that one fish in the reflection is coming at him and running side-by-side with him, at an apparent distance of two fish lengths. This kind of behavior is not the "normal" in the situation of a few or one fish attempting to join a much larger group, at least in any of the species under study. The usual manner in which one or a few fishes join a large school is to quietly approach the larger body and pick up its rate of speed and slowly merge into the main body. There is never any evident specific act on the part of the affected fishes of the school. They seem to react to the "intruders" as they do to the other members of the school, constantly adjusting their positions by small amounts.

The above is not true of two schools of more nearly equal size when in the process of merging. The smaller will approach the larger at a rate of speed apparently inversely proportional to the volume of the smaller school. The larger school will approach the smaller at a much slower speed also inversely proportional to its volume. When the two schools come within a distance equivalent to about

four fish lengths, both schools show a bulge on the side closest to the other school and in so doing automatically loosen their ranks slightly, but sufficiently to allow the two bulges to merge, forming a single school where there had been two. This type of merging can usually be found between schools that do not differ in size by a factor as large as four.

The above describes what are evidently the normal sequences to expect when two schools of various size relationships have an encounter that may lead to merging. This leads to the idea that the "behavior" of a mirror image is sufficiently unusual to prevent the further development of a process leading to merging, the fishes evidently recognizing a difference between another fish and their own reflection.

Sardinella anchovia Valenciennes and *Brevoortia patronus* Goode avoided coming close enough to the mirror for the development of any further reaction. The first was present frequently in large schools which tended to stay away from the dock area in deeper water, but frequently came into the shallower areas at which time they revealed no indication of "nervousness." The second was seen only as young fish in very small schools of not more than 30 fast-moving individuals, that gave any solid structure a wide berth, which is characteristic of this species, at this place at least. *Brevoortia* in a 10-foot circular concrete tank formed a school of about 30 individuals that averaged about 10 cm in length. They had lived there for about 10 mo. These fish were exposed to the mirror for 1 day in August and 4 continuous days in November. Prior to the introduction of the mirror, the school circled the tank close to its wall. The introduction of the mirror disrupted this path of the school which then formed a tight mill as far away from the mirror as possible. At no time were the fish observed to approach the mirror. Only dropping food close to its reflective surface would cause individuals to move toward the mirror, and then only to snap at the food and retreat rapidly. The fish fed less during the presence of the mirror. After the mirror was removed 6 days passed before the mill broke up and the former swimming pattern was resumed. *Harengula pensacolae* Goode and Bean, not seen around the dock when the mirror was used, behaved not unlike the *Brevoortia* in the concrete pool.

Mugil curema Valenciennes, in its very young surface swarming stage of not over 2 cm, forms very loose schools not at all like those of the adults. These young, on encountering the mirror, would try persistently to swim into the mirror, seemingly disregarding their mirror image that just as persistently "opposed" them. Occasionally when such a group left the mirror for reasons unknown, a single fish would remain and continue to try to swim through the mirror for a long period, evidently almost to exhaustion.

These observations were carried on from 8 June to 10 September 1973, weather permitting, and represent many repetitions of the facts and interpretations. It is impossible to present these notes in a more formal manner at this time. They clearly have bearing on the present study and suggest the desirability of going into this matter further as another project which would in any case lead away from present purposes.

The observations indicate that there is a much wider range of difference in response to the mirror image than had been expected and therefore that the bonds that hold a school together are not identical for each species, even if the total result appears as a very similar geometric structure. It would seem that the response of a fish to a fellow (here its mirror image) that approaches on a true and unswerving collision course from which it will not (cannot) budge is a truly frightening experience. The difference in response between *Anchoa* and *Mugil* in this case is especially striking. *Anchoa* acts in a manner that one might anticipate, while the action of *Mugil* in placing their mouths together has never been seen at any age or size.

LOCOMOTOR PROBLEMS

With large numbers of fishes of one kind swimming closely together in a common direction, the locomotor needs of the participants would obviously have influence on the structural nature of the school, which in turn would also affect some details of the locomotor efforts. Both classical and contemporary hydrodynamics have to be invoked in any attempt to understand this mechanical aspect of school formation and operation.

Flow Patterns

To answer the question of whether water flow induced by the propulsive activity of the fishes themselves can help or hinder other fishes following them depends on the direction and strength of the flow and the angle of entry of a fish encoun-

491

tering the flow. The solution of such problems lie in the realm of classical hydrodynamics. See Lindgren (1967) for a brief, but explicit statement of the hydrodynamics involved. Fishes leave no wake in the usual sense of the word, but do leave a series of dying vortices, alternately on either side of the swimming axis of their producer. The rotational direction of the flow within the vortices on one side is always the same and is opposite to the rotation of those on the other side. The flow within the vortices is such that, on the side nearest the axis of the fish producing them, the flow is opposite to the direction of travel of that fish, while on the side away from the axis the flow is in the same direction of travel as the fish. These rotational directions are opposite to those of vortices formed in a typical Karman trail produced by a rigid solid. A following fish thus has the choice of swimming through the side that would help it on its way or the other that would retard it. Swimming through a vortex center would push the head of the fish to one side before the center was reached and to the other side after the center had been passed. The fish that follows is normally found in the water flow that is in its direction of swimming, see Rosen (1959), Breder (1965), and Weihs (1973a). This arrangement evidently helps the locomotor efforts of all but the lead fishes. As the energy in the vortices dissipates rapidly it is doubtful if more than the immediately following fishes benefit significantly. As each fish produces a similar short-lived set of vortices there is no appreciable additive effect of successive rows of fish ahead. Thus all the fishes after the first transverse row receive approximately the same energy input from the vortices, so long as they remain in the specified positions. The value of this has not been measured as yet or even estimated.

These friction reducing effects evidently influence small fishes to sometimes closely associate with much larger, usually solitary, fishes of other affinities. The small attendant fishes evidently gain locomotor advantages that are otherwise only obtained by schooling with their own kind. Many authors, including Breder (1959, 1965, 1967) and Aleev (1963), have noted a variety of such fishes. These fishes station themselves close to and in definite positions relative to the larger fish, often a shark. The behavior is habitual, as in *Seriola*, but may be occasional, as in *Caranx*. Shuleikin (1958) discussed the hydrodynamics of *Naucrates ductor* (Linnaeus) in its persistent association with large sharks.

Weihs (1973a) indicated additional energy saving advantages consequent on fish swimming his diamond pattern; the channeling effect of rows of similar fishes, the effects of the phase of the tail-wagging of one fish with respect to the tail phases of its near neighbors, and the extent of length variations in the participating fishes. He calculated this variation as up to 50%. Actually over 60% variation has been found in unquestionable schools (Breder 1954), although it is impossible from this data to determine the permanency of such groups or the efficiency loss at this greater range of variation.

Active fishes, especially schooling types, lack the protuberances and hollows often present on the bodies of sluggish fishes. Aleev (1963) enumerated many instances of the latter. He indicated that this lack of streamline integrity leads to the production of minor vortices and that these disturbances, depending on their size and point of origin, could lower the locomotor efficiency of a fish. The utility of the larger terminal vortices, here under discussion, could be reduced or destroyed, thus eliminating one of the advantages of school formation.

Turbulent Friction Reduction

Until recently, students of fish locomotion were not in agreement concerning what function in relation to swimming, if any, was served by the presence of the mucus that covers the bodies of living fishes. Aleev (1963), in a well-documented review, indicated that he agreed with Richardson (1936) and Gero (1952) that whatever part it may play, the effect must be very small. That this could not be so was mentioned by Rosen (1959) and Walters and Liu (1967). Recent advances in hydrodynamics now indicate clearly that it has a very considerable role.

Polysaccharides are known to be released by a variety of aquatic organisms, both plant and animal. One of the effects of the presence of those forming long-chain molecules is friction reduction in turbulent water flow. Some of the history of the development of this information was recorded by Newton (1960), Barnaby and Dorey (1965), and Hoyt (1966, 1968, 1972, 1975). These papers discussed naturally occurring polysaccharides from algae as well as synthetic high polymers, some of the latter being used for very practical purposes as very efficient reducers of turbulent friction. The application of extremely small amounts of such materials can reduce drag by over 60%.

Rosen and Cornford (1970, 1971) had shown by means of a special type of rheometer that there are great differences in the friction reducing abilities of the slime of various species of fishes. See Jakowska (1963) for a discussion on the extent of the wide variety of other kinds of utility ascribed to the mucus of various fishes. It would seem to be certain that these effects are dependent on the polysaccharides inherent in fish mucus, although for present purposes it is not necessary to know just what components of fish mucus account for friction reduction.

Successive dilutions of fish slime with the water of the individual's habitat have been plotted against reduction of friction in terms of percent by Rosen and Cornford (1970, 1971). In some cases the curve rises extremely rapidly, reaching a reduction of turbulent friction of over 60% with water dilution to only 5% mucus. Others, with evidently less potent slime, show a much smaller rise in friction reduction, reaching 50% or less with a water dilution to 50% or more of slime. The most extreme case reaches only 8% reduction in friction with full strength slime.

It is notable that the two species with the fastest rise in friction reduction are rapacious and strike at relatively large prey. These fish can move from a resting position to their highest speed in a remarkably short time. The three species at the other end of the friction reduction series feed on much smaller organisms in proportion to their own size, for which violent pursuit is completely unnecessary. The two species with the most efficient drag reduction do not form obligate schools and are often solitary, while the three with the least effective mucus are schoolers and only one drops to the facultative status.

The preceding data on the reduction of turbulent friction by means of long-chain polymers, and the demonstration of the great effectiveness of the mucus exuded by some fishes, as well as the geometrical patterns in which schooling fishes arrange themselves, leaves little room for doubt that the fishes so organized may attain a locomotor advantage from the mucus trail trapped in the vortices left by the fishes that preceded them.

The fishes with sharp rise in friction reduction in Table 3 and Figure 20 are all nonschoolers or at most facultative: *Paralichthys californicus* (Ayers), *Sphyraena argentea* Girard,[15] and *Micropterus dolomieui* Lacépède. Those with a slow rise in friction reduction are all schoolers and are primarily obligate[16] schoolers: *Scomber japonicus* Houttuyn, *Sarda chiliensis* (Cuvier), with *Salmo trutta* Linnaeus and *S. gairdneri* Richardson as facultatives. The nonschoolers are capable of showing a sudden acceleration from a resting position and apparently attain their highest possible speed in a matter of seconds or less. The hydrodynamic aspects of extreme acceleration from a position of rest, shown by slender fishes such as barracuda, are treated by Weihs (1973b). This can be critical in overtaking relatively large prey. Schooling fishes that normally swim at a continued steady pace evidently cannot perform in such a manner and even the marginal members seldom try.

Uskova and Chaikovskaya (1975) noted, in a paper on the chemical nature of the protein com-

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[15]It is recognized that the Pacific *Sphyraena argentea* tends to form schools more readily than the larger Atlantic *S. barracuda* which is usually solitary. The smaller Atlantic congeners approach *S. argentea* in this respect.

[16]A term defined by Breder (1967).

TABLE 3.—Drag reduction by fish mucus, based on data from Rosen and Cornford (1970, 1971).

| Species	Drag reduction (%)	Mucus concentration (%)	Length (cm)
1 *Salmo gairdneri* Richardson (Rush Creek)	61.8	50	28
2 *S. gairdneri* (Grant Lake)	62.0	50	33
3 *S. gairdneri* (Lundy Lake)	20.5	50	23
4 *S. trutta* Linneaus	63.2	25	33
5 *Sphyraena argentea* Girard	65.9	5	76-79
6 *Scomber japonicus* Houttuyn	56.9	50	38-41
7 *Sarda chiliensis* (Culvier)	6.4	100	73
8 *Micropterus dolomieui* Lacépède	62.0	50	33-42
9 *Pomoxis annularis* Rafinesque	61.7	20	—
10 *Lepomis machrochirus* Rafinesque	60.1	20	15.3-20.4
11 *Paralabrax clathratus* (Girard)	58.7	25	43
12 *P. nebulifer* (Girard)	17.4	20	33±
13 *Paralichthys californicus* (Ayres)	60.9	5	53
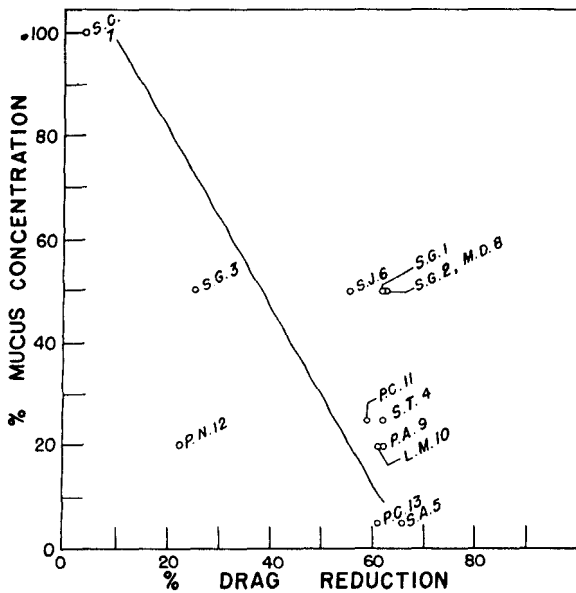
FIGURE 20.—Graph of the effectiveness of fish mucus on drag reduction. Based on the data of Rosen and Cornford (1970, 1971). The numbers and letters at each point are explained in Table 3, giving the name and number of each fish in the left hand column. See text for full explanation.

ponents of fish mucus, that the hydrodynamic efficiency of the fishes they studied varied directly with the extent of the basicity of their surface mucus. The fishes measured were Atlantic bonito, *Sarda sarda* (Bloch), sea bass, *Serranus scriba* (Linnaeus), and stargazer, *Uranoscopus scaber* (Linnaeus), given here in the order of descending basicity. This is consistent with the present studies based on the lubricity of certain polymers.

The mucus of a fish in a school does more than reduce the drag on its producer since it washes over those that follow. This means that the "leaders" have only their own mucus to ease their passages while the "laggards" receive all the benefits bestowed by those ahead of them. The net effect is to produce a lubricity gradient from zero to the maximum which is dependent on the size of the school. To maintain a steady pace, fishes in the forepart of the school must use more muscular power than the others while the last members require the least effort to hold their positions. As fatigue sets in, the "front runners" would have a choice of accelerating their efforts or holding a steady pace and thus permit those following to pass ahead of them until they find a place requiring an effort compatible with the magnitude of their tiring, which could carry them to the trailing

end positions of the school, if necessary. Zuev and Belyaev (1970) indicated that in a school of *Trachurus*, the individuals in the front part beat their tails faster than those in the rear. This condition would naturally follow the lattice-vortex-mucus thesis as developed here.

Thus, this condition of graded positions in respect to ease of swimming and the matter of muscular fatigue may be a large factor in the maintenance of the integrity of a school and explain the internal churning so often seen in fish schools. The very general changes in positions of individuals within the structure of a school could thus be impelled to a large extent by the individual urge to attain a position demanding the least swimming effort. Also this urge would insure the usual prompt reassembly of a school after being violently dispersed and suggests that the closed figure "mills" of schooling fishes, that would otherwise seem to be trivial and pointless, form a relatively quiescent rest period in a favored place. Fish mills have been noted by many students, beginning with Parr (1927). They can be developed from many other sources than the one noted above. Often they are derived directly from extrinsic events, as discussed by Breder (1965). The development of an evidently intrinsic mill is shown there by three photographs that may truly represent the formation of a true "resting mill" as suggested above.

There is too little known about the complexities of fish mucus to permit much further progress into the details of its relation to school formation and maintenance or its importance to other matters. For instance, how constant are its characteristics and are there rhythmic variations in them related to season, reproductive periods, or type of food ingested? Are there changes in the mucus with age or condition of the fish? Is the mucus of marine fishes more stable than that of freshwater fishes? Since ocean water is chemically more uniform than fresh water it might be expected that these features were reflected in the mucus.

Experiments with Drag-Reducing Polymers

Fish mucus, in the amounts necessary for these experiments, is difficult, if not impossible, to obtain and handle without some decomposition and reduction of the long-chain molecules. Additives of some bacteriostatic chemical or refrigeration merely introduces other difficulties that could make interpretations uncertain.

Furthermore, the drag reduction of a fish slime diluted with water that produced a 25% reduction just after its removal from the fish, was inert 3 h later, according to Hoyt (1975). He also gave a hydrodynamic explanation on why it is possible for very small fishes to gain an advantage from their mucus although the operational mechanics are different than those available to larger fishes. This concerns differences in the boundary-layer transition from laminar to turbulent flow in relation to the Reynolds numbers. Fish mucus does not dilute easily with water by mere contact, but does so easily with agitation. Rosen (1959) used the term "reluctance" to designate this condition. Polymers, especially those manufactured to have high drag-reducing characteristics as measured on a rheometer, have drag reduction features that are comparable to or exceed those of fishes' surface mucus in the small quantities required to obtain maximum effects.

The material used was a water soluble resin, a high polymer of ethylene oxide, from the Union Carbide Corporation, and generally known by its trade name Polyox[17]. The significant characteristics, as given by Hoyt (1971) follow

Polyox F.R.A. (Lot 1163)

Molecular weight	Max drag reduction (%)	Concentration (%)	
		Max D.R.	½ max D.R.
6,000,000 (ca.)	67.8	15	1

This particular grade of Polyox was used because of its unusually high molecular weight as the purpose here was merely to establish whether such products would induce a change in the swimming efficiency of the fishes. Hoyt (1975) considered a minimum molecular weight of 50,000 of the drag-reducing element to be necessary for friction reduction to be expected.

Polyox is reported to have very low, if any, toxicity, (Smyth, et al. 1970, Wade 1970). For the purposes of this study, toxicity tests were also run on a variety of fishes. Nothing whatever occurred that would suggest any physiological disturbance on any of the test fishes. Both *Poecilia reticulata* Peters (fresh water) and *Hippocampus erectus* Perry (salt water) produced young when subjected to concentrations far higher than any required here. The only item showing obvious adjustments

to the change in lubricity of the water was that mature examples of *Hippocampus erectus* were unable to use their prehensile tails effectively on the smaller supports provided in their aquaria. That is, they simply slipped off plastic rods, of circular cross section, if the rod diameters were below a certain magnitude relative to the grasp of their tails. With larger rods they had no trouble and were readily able to "grasp" the supports and hold on in normal fashion. Those that could not find a suitably sized "perch" coiled their tails so that about three-quarters of a circle was formed at right angles to the body axis and then "sat" with the partial circle laid on the bottom of their aquarium. Apart from being somewhat restless, they apparently were just as well off as the others. The *Poecilia* moved about in what appeared to be their normal random manner, but whether they moved a little faster or not could have only been determined with great difficulty and would not have contributed to the problems under study. None of the fishes tested after the preceding preliminaries showed any distress from the addition of Polyox.

The Gulf menhaden, *Brevoortia patronus* Goode, was used for tests on drag reduction. This species is an obligate schooler and, as with many such schoolers, the ability to spread its caudal fin is severely limited. There is a strong possibility that none of them exercised this slight ability at all. Also, these fish accommodate well to aquarium life if provided adequate swimming room and a few companion fishes, a feature not common in many members of this family. The fishes selected for testing were first established in a circular concrete tank 4+ m diameter, with a water depth of 1 m.

Specially made aquaria were used for these experiments. They measured 25 × 25 × 90 cm and were filled with synthetic seawater[18] to a depth of 20 cm providing a total water volume of 45,000 cm³. These were established in a perfectly light-tight room, actually a Navy Sea Van without windows, remote from vibrations and sounds. Lights were controlled by a time switch for day and night effects and a thermostat controlled the temperature. The test aquarium was placed on the floor and the others on rocks at a convenient height. Precautions were taken to protect the fishes from being startled by motions, vibrations, or other

disturbances outside their container. There is no reason to suppose that the results were so influenced.

Two grams of the dry granular Polyox were dissolved in a small portion of the synthetic seawater. This was then returned to the test aquarium by allowing it to drip back by means of a siphon tube nearly closed by a screw clamp. The final concentration of Polyox in the aquarium became approximately 42 ppm.

A motion picture camera facing down was erected so that its optical axis was over the geometric center of the tank. Photo floodlights were set up as required. The view included most of the aquarium, omitting only the ends of the tank where the fishes were forced to turn back, as these tests must be made with the fishes moving in a nearly straight line. Also included in the camera's coverage were tapes marked in centimeters. One ran along the top edge of the tank and the other along its bottom, thus providing an index to the lengths of the fishes and their distances of travel. The aquarium had its sides blocked with bluish cardboards, except on the sides toward the lights. These were higher than the aquarium and off to one side sufficiently to eliminate reflections into the camera's lens. The test fish were added and allowed to adjust to the new situation for about 1 h. The tank in which they had lived for at least 1 wk was identical with the test tank, except that it had all four sides covered with similar cardboard guards.

Photographs were taken after the lights had been turned on gradually to full voltage. It was found by experience that normal film speed was fully adequate for our analysis. Sufficient footage was exposed to insure an adequate number of straight runs of single fish.

When the above procedures were completed, the Polyox was allowed to drip into the tank, which took about 10 min. After 1 h had elapsed, its mixing was considered completed, for in addition to the aerating devices, the four very active fishes provided continuous mixing. After this time interval the photographic procedures were repeated and the experiment was terminated.

The results of these experiments are given in Table 4 and their analysis is illustrated by graphs in Figure 21. Graphs A and C clearly show the difference between fishes swimming in synthetic seawater, initially devoid of any long-chain polymers, and in the same water to which the polymer has been added. The speed of the fishes is approximately double in the latter, as are the tail beats. In this experiment, after the first run (S1) was made in synthetic seawater, the tank with its contained fishes was left as it was until 2 days later when another run (S2) was made. The new speed readings were a little higher, but the proportional corrections were not. If more refined measurements show that a small difference is measurable, it should be due to the additions of organic substance in the interim, consisting of the body wastes of the fish as well as their own surface slime produced in this period. Added to this must be the dissolved matter from the food given to the fishes. To minimize all this, all particles not consumed directly were meticulously removed. The manner of handling data was that of Bainbridge (1958). The greater refinements of the methods of Hunter and Zweifel (1971) were not deemed necessary for the present simple purposes. Because of the large differences between the speeds of fishes in the same water, with and without long-chain polymers, the slight possible spreading of the caudal fin in this species could not increase the area of the tail by more than a negligible amount in these experiments. Later another set of four

TABLE 4.—Calculations based on experiments on drag reduction in *Brevoortia* by polymers. TL = total length. TB = tail beats.

| Date 1973	Water state	Fish TL (cm)	Run length (cm)	Run time (s)	No. of tail beats	Speed (cm/s)	TB/s	cm/s TL
13 Sept.	Synthetic	6.30	19.50	1.33	6	14.58	4.51	2.31
		6.60	25.00	1.67	7	14.90	4.19	2.26
		7.10	23.30	1.95	6	11.99	3.08	1.69
11 Oct.		9.00	23.00	1.44	4	15.10	2.78	1.68
		7.50	15.00	0.89	4	16.85	4.49	2.25
	+ Polyox	7.90	29.00	0.89	7	32.58	7.87	4.12
		7.50	35.00	1.11	8	31.53	7.21	4.20
		8.00	32.00	1.11	6	28.83	5.41	4.80
		7.00	34.00	1.11	9	30.63	8.11	4.37
6 Nov.	Bay	6.60	10.00	0.78	3	12.82	3.85	1.94
		10.00	36.00	2.00	4	18.00	2.00	1.80
	+ Polyox	6.60	47.00	1.11	5	42.34	4.50	6.42
		10.00	44.00	1.06	8	41.51	4.55	4.15
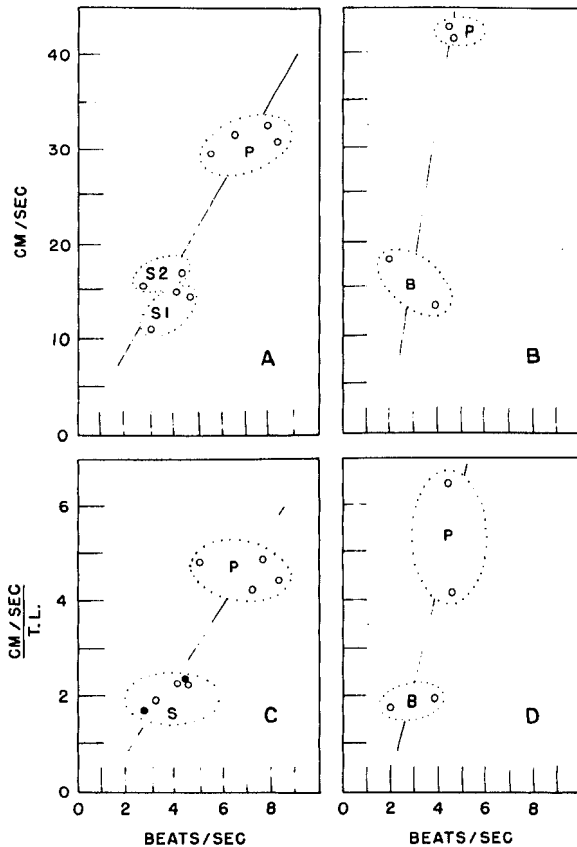
FIGURE 21.—Graph of experimental analysis of the relationship of tail beats to speed in waters of various degrees of lubricity. S = synthetic sea water. B = bay water. P = Polyox added. S2 in graph A is shown in graph C by black spots. See text for explanation.

fishes were similarly tested. These were somewhat larger than the first. Grossly polluted but sand-filtered bay water was used. The results were in good accord with the first set, the readings running a little higher and the slope of proportionality being a little steeper.

Measures of the varying amplitudes reached by swings of the tails were not made as they vary with the tempo of the cycles, as noted by Bainbridge (1958), and contribute no additional information germane to this study.

A direct result of these experiments is very clear. The fishes had a choice of two possible extreme responses to an increase in the water's lubricity. They could maintain their former speed by appropriately reducing the frequency of the tail cycles, or they could so increase their tail beat rate and thus their rate of translation. Obviously they

could respond by some intermediate response by partially using each of the above two responses. Present data cannot be used to determine these finer distinctions. However, the amounts of the speed increase in both cases strongly suggests that most, if not all, of the gain was by increase of speed.

It might be thought that the fishes were swimming at their accustomed rate in the situation of these experiments and so would not change their rate of swimming even when the changed drag effects reduced the effort required. The phrase "accustomed rate" may or may not be the same as their "optimum speed" as defined by Weihs (1973a). As they did change their pace it seems most probable that the fish were swimming close to their maximum, possibly induced by the increased illumination.

The differences in speed of the fishes between the nontreated water and that with Polyox added, expressed in percentages, is impressive. Experiments 1 to 5 and 6 to 9 (synthetic seawater) show a mean increase of 66+%. Experiments 10 to 11 and 12 to 13 (bay water) show a mean increase of 63+%. The crude percentage figures show no significant differences between the two cases. The equivalent figures, using the correction values for size of the individual, follow: Synthetic seawater, experiments 1 to 9, mean increase 58+%. Bay water, experiments 10 to 13, mean increase 35+%. Further analysis may show this to be a real difference.

Cahn's (1972) studies tend to confirm the importance of both the hydrodynamic and mucus elements in the formation and maintenance of schools of *Euthynnus affinis* (Cantor). The fish used by her were about 40 cm in total length and the project was concerned with lateral line studies. She found that placing a transparent plastic partition between two fish that had been swimming in parallel courses with the partition, with one somewhat ahead of the other as the first point and one of the side points of Weihs' (1973a) diamond, resulted in the fishes changing to a side to side position. Without questioning the value of the lateral line organs, there is also the value of the mucus and vortices and the "cues" from them which may be handled by the lateral line system. How much these sense organs are directly involved with the maintenance of fish schools is not yet clear. Williams (1967)[19] did not, " . . . believe

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[19]Williams (1964), followed by Hamilton (1971), believes that schooling is primarily a matter of cover seeking.

497

that the lateral line is important in schooling behavior." In the same publication Walters and Liu (1967) ". . . postulate that the boundary layer acts as a hydrodynamic amplifier . . ." that is involved in transferring precise information on changes in water movement that the fish encounters as it swims ahead, reaching the fishes brain via the lateral line system. In a school, much of such information concerns the water movements produced by the swimming activities of the fishes ahead, probably by the bending of the cupulae that indicate the direction of flow of the currents and its strength. Other experiments carried out by different investigators point the same way as, for instance, the work of Pitcher (1973) with mirrors. This is not in discord with the related work reported here and both can be accounted for by the effects of the lattice pattern and the hydrodynamic and the mucus cues. Also the work of Shaw and Tucker (1965) and the interpretation of their results by van Olst and Hunter (1970), based on an optomotor device, indicated that the test fish reacted more to the fishes ahead of it than to the moving target spot.

Another source of possible information has been pointed out by Smith (1930) in some little-noticed studies. These have shown that *Carassius auratus* (Linnaeus) can draw samples of the surrounding water into its lateral line canals and expel them as new samples are drawn in. This behavior certainly suggests the possibility of a chemical or other sensory device that could distinguish the concentration of the mucus of preceding fishes. Present understanding of the relation of the sensory possibilities related to schooling organization clearly suggests that such activity of the lateral line could be a part, or even an important element, in a following fish's ability to locate the most favorable position to be stationed in respect to the mucus of the preceding individual.

Fish at the front of a school receive locomotor benefits from only their own production of mucus. All the rest receive benefits from the mucus of those ahead; those at the very end of a school thus receive the most benefit. This is sufficient to account for the "churning" sometimes seen in schools, the leaders falling back while others press ahead, all of which helps maintain the integrity of the school as previously noted.

The peripheral individuals in a school often keep trying and usually do eventually attain a more central position, evidently for reasons similar to those given above. The rapid reorganization of a school after violent disruption is apparently similarly motivated.

The existence of fish mills, as noted in the prior section, may not be the trivial phenomenon it is generally thought to be. Instead, in the present view, it may be a resting device with an important purpose. If the fishes reach a point of fatigue that would slow the school down to an extent inimical to the schools integrity, the mill formation would supply that necessary respite.

All three of the preceding observable items of activity, as noted, have a consolidating effect on a school and none show any tendency toward school dispersion.

The works of Belyaev and Zuev (1969), Zuev and Belyaev (1970) and Weihs (1973a) discussed the hydrodynamic effects of one fish on another in a school, considering only the water movements induced by the swimming efforts of each member of the school. This is all in basic agreement with the present theoretical treatment of the school organization. Adding to this, the effects of the drag reducing abilities of the mucus released by the fishes involved can only result in much higher efficiency.

Furthermore, there is no evidence that more mucus cannot be released by fishes to ease their muscular efforts when necessary. There are, however, strong probabilities that such abilities are indeed present. Species that use their mucus for other purposes have this faculty developed to a high degree, as in *Rypticus* (Maretzki and del Castillo 1967), that exudes a toxic mucus in great quantities when attacked or handled or many of the parrotfishes that envelope themselves in a "cocoon" of congealed mucus on nightfall (Winn 1955). Quality control is also possible with many fishes under appropriate stimulation. All calculations at this time involving mucus production are somewhat uncertain and must remain so until it is known whether the mucus is exuded at a rather steady rate or is subject to wide fluctuations, somewhat after the manner of perspiration in various mammals.

It is possible that the closing up of ranks, when a school is in flight from some danger, may destroy the assistance of both vortices and mucus. Under this kind of emergency, involving maximum energy expenditures, this loss may have to be accepted. Possibly such a situation could call for an extra outpouring of mucus.

498

DISCUSSION

The two basic purposes of this paper are the establishment of the primary space lattice formed by schooling fishes and the role that their surface mucus plays. Both features are supported by theory and empirical data and both expedite the swimming efforts of the fishes. This alone gives sufficient reasons for the formation and the maintenance of schools.

The question of how much of the schooling phenomenon is a simple following of the paths of least resistance, with automatic avoidance of other fishes, how much is social imitation, and how much is mediated by communication between individuals is not answered here. The phrase "social imitation" is discussed at length by Radakov (1972) as is the status of the term "communication" discussed by Tavolga (1974). The latter indicated that the mechanisms involved can begin as the optomotor orientations of Shaw (1960, 1961). He added that possibly the responses of the fishes ". . . even as adults may be primarily taxic." The rheotactic response to vortices and to fish mucus, reported here, may be equal to or of greater influence than the optical response, since they are fully operable in the dark, but not nearly as precise as the visual response. This could account for the fact that schooling fishes do not fully lose contact with each other in darkness even in species not given to sound production (Breder 1967).

It is recognized, of course, that there is more to the activity of any fish than efforts to avoid possible physical exhaustion. An evaluation of the importance of other activities or even an enumeration of those that are more evident will not be attempted here. However, another approach to the overall problem is noted as follows. The "following reaction" of Crook (1961), based on bird flocks, has been discussed in connection with fish schools by Shaw (1960, 1962), Hemmings (1966), and van Olst and Hunter (1970). The expression is evidently very nearly, if not completely, identical with the "social imitation" of Radakov (1972).

These data suggest a hypothesis that could go as follows. A group of fossil fishes, not living in schools, but within swimming distances of each other, may form the background. One fish crossing in back of another and encountering its vortex trail would find that self-propulsion required less effort. It is not unreasonable to suppose that after a few such encounters, a tendency to follow would develop. This might be without any instinct to follow or imitate but not without prior experience with the vagaries of water currents, which each fish encounters on its first feeble swimming attempts as a hatchling; nor is there any reason to dismiss the alternative, that the order is opposite. In Recent fishes the latter is most probably the case. However in the early fishes, which are considered above, the first move to follow could have been solely on a hydrodynamic basis. From here on, with the establishment of a primitive school, its continued existence and development or extinction would be regulated by selective processes, depending basically on whether schooling hindered or enhanced the species' ability to survive. It is visualized that this process could have taken place many times in various groups, especially among fishes with relatively scanty mucus production. Also, this process would probably be easily reversible so that fish schools could appear and disappear according to environmental or physiological changes that made schooling or a solitary life favor a species' survival.

Detailed conparisons between schools of various taxa, or between schools formed by a single species at various times, or under varied conditions have not been made. It would seem however, that all schools are not necessarily isomorphic but are probably at least homomorphic, in the sense of Ashby (1956).

In a fully theoretical paper, Hamilton (1971) supported the view of Williams (1964, 1967), that most types of animal aggregations owe their existence basically to each animal (vertebrate or invertebrate) trying to hide behind another. With this we have no argument (Breder 1967) and our presentation here, on the locomotor utility of fish schools, exists comfortably with or without it. The question of which came first, hiding or benefiting from an enhancement of swimming efforts, involves no interference. They could have developed together or independently, each little advancement of one helping the development of the other.

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