The Structure and Function of Fish Schools

Schooling serves to reduce the risk of being eaten. Each fish employs its eyes and lateral lines, which are sensitive to the displacement of water, to match the speed and the direction of all the other fish in the school

by Brian L. Partridge

How do they do it? The question occurs naturally to anyone watching a school of silversides moving slowly over a reef in clear tropical waters. Hundreds of small silver fish glide in unison, more like a single organism than a collection of individuals. The school idles along on a straight course, then wheels suddenly; not a single fish is lost from the group. A barracuda darts from behind an outcropping of coral, and the members of the school flash outward in an expanding sphere. The flash expansion dissolves the school in a fraction of a second, yet none of the fish collide. Moments later the scattered individuals collect in small groups; ultimately the school re-forms and continues to feed, lacking perhaps a member or two.

Although the schooling of fish is one of the most familiar forms of animal social behavior, until recently it was little understood, partly because of the difficulty of observing minute changes of position and velocity in a school under natural conditions. The fact that a great many species of fish congregate in schools suggests that the behavior offers a considerable evolutionary advantage. How the school is formed and maintained, however, is only beginning to be understood in detail. My colleagues and I have approached this question by recording on videotape schools swimming in a large circular tank. It had been thought that each fish maintains its position in the school chiefly by means of vision. Our work has shown that the lateral line, an organ sensitive to transitory changes in water displacement, is as important as vision.

Our work has also shown that the fish school is not a regular geometric structure like a crystal lattice. In each species a fish has a "preferred" distance and angle from its nearest neighbor. The ideal separation and bearing, however, are not maintained rigidly. The actual distance and direction vary greatly, approximating the ideal only over a long period. The result is a probabilistic arrangement that appears more like a random aggregation than a lattice. The tendency of the fish to remain at the preferred distance and angle, however, serves to maintain the structure. Each fish, having established its position, uses its eyes and its lateral lines simultaneously to measure the speed of all the other fish in the school. It then adjusts its own speed to match a weighted average that emphasizes the contribution of nearby fish. The combination and comparison of information from the two sensory systems provides the basis of all the intricate maneuvers of the school.

Although most people have an intuitive sense of what a fish school is, students of animal behavior have spent much time trying to define the notion precisely. Do two fish constitute a school? Do three? Is a school that has a million members made up of half a million pairs? Does a school have a leader?

There seems to be an important qualitative difference between a pair of fish and a larger group. My analysis of videotapes of European minnows swimming in a tank shows that when there are two fish, one leads and the other follows. The follower adjusts its speed and direction to match those of the leader; the speed and direction of the leader, however, are not influenced by the movements of the follower. When a third minnow is added to the tank, the pattern changes: in a group of three or more fish there is no leader. Each minnow adjusts its speed and heading to agree with those of all the other fish, with the neighbors nearest to a given fish having the greatest influence on it. Thus in a sense the entire school is the leader and each individual is a follower.

One of the most striking qualities of a school of fish is its polarization: the parallel arrangement of the members. Polarization has been cited repeatedly in efforts to define the concept of a school. When fish feed, they often form a loose group, with the members facing in many directions. When the school is in motion, however, the polarized arrangement tends to prevail. Moreover, when the school is threatened, its members often move closer to one another and align themselves more uniformly with their neighbors. That the polarization of the school is more pronounced under a threat suggests it may be connected in some way with the adaptive advantage conferred by schooling behavior.

The role the school plays in the life of the individual fish varies greatly from one species to another. In some species fish spend all or almost all of their time in a school. In other species fish join schools only occasionally, spending most of their time as isolated individuals. Fish that spend all or most of their time in schools are often called obligate schoolers; those that form schools part of the time are called facultative schoolers. In much of the work done on fish schools it has been assumed that there is an important difference between obligate and facultative schools. My work with minnows and cod, which are facultative schoolers, and with herring, which are obligate schoolers, suggests on the contrary that in all three species the school is formed and maintained on the same principles. The only difference

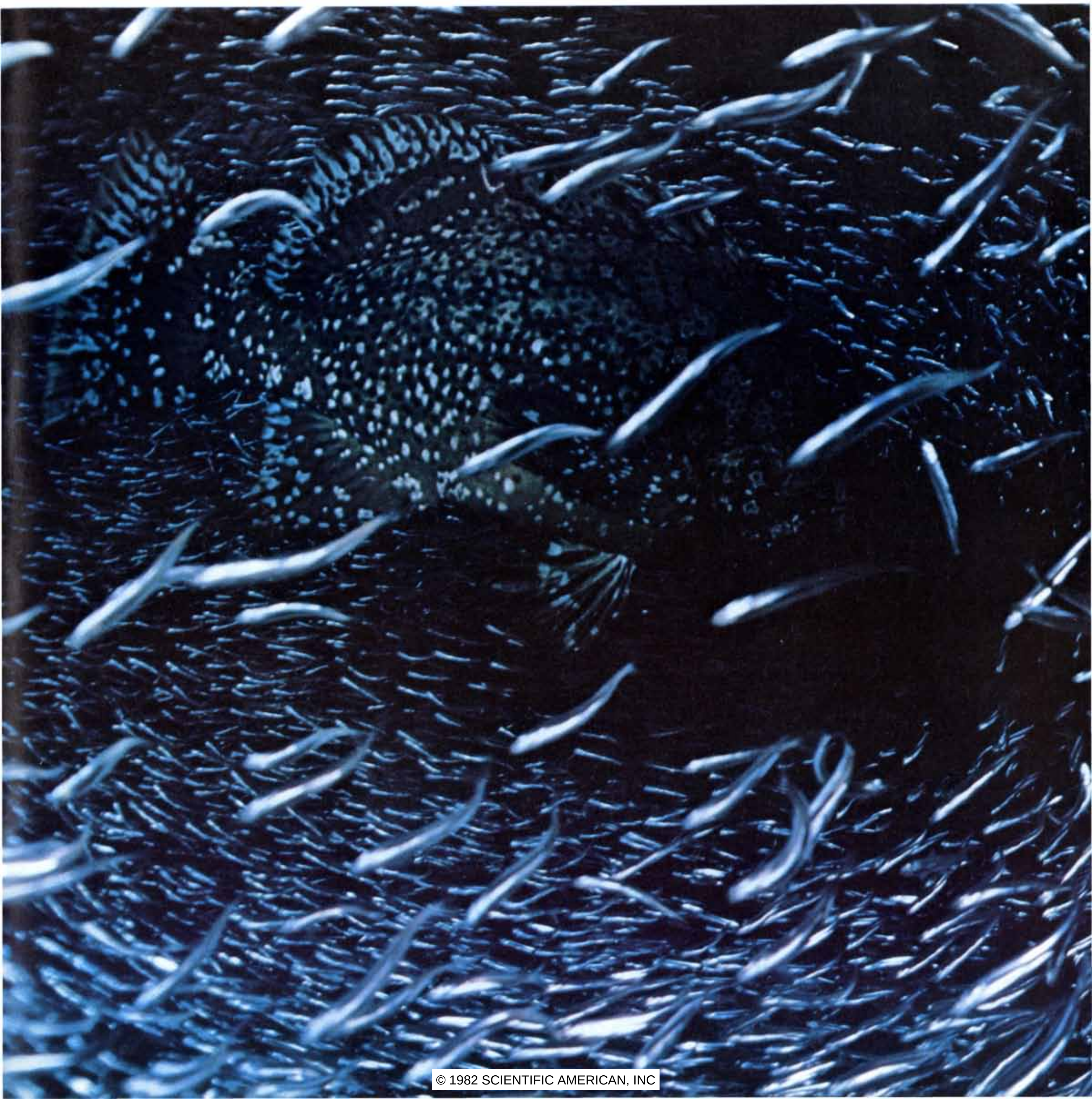
ATTACK ON A SCHOOL OF SILVERSIDES is shown in a photograph made in a cave in the Florida Keys; the attacking fish is a grouper. More than 10,000 species of fish form schools. Most of them are small fish that are prey rather than predators. For prey the adaptive value of schooling lies in reducing the probability of detection by a predator and in reducing the risk of being eaten once the school has been detected. As the photograph suggests, one way the school reduces the risk of being eaten is by confusing the predatory fish as it makes its strike.

seems to lie in the amount of time the fish spend in a school. From these observations it is possible to formulate a useful working definition of a school: It is a group of three or more fish in which each member constantly adjusts its speed and direction to match those of the other members of the school.

Evelyn Shaw of Stanford University has estimated that out of about 20,000 species of fish more than 10,000 species collect in schools during some part of their lives. The species that school, however, are not a representative sample. Most of the fish that form schools are small; it has generally been thought that the main evolutionary advantage of schooling lies in protecting such small fish from predators.

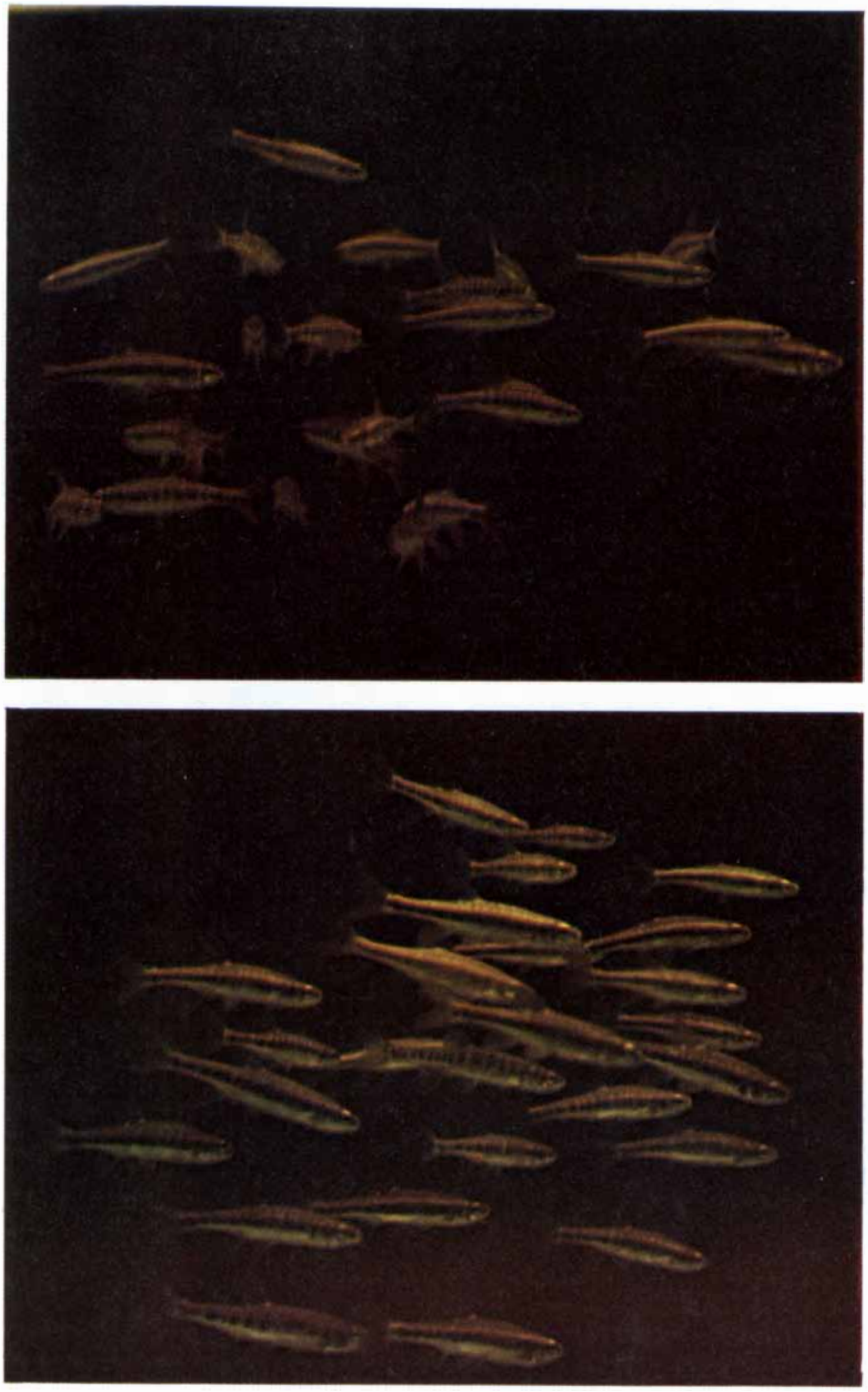
It might seem that a school made up of thousands or even millions of fish, however small the individuals are, would be highly visible; actually a school is not much more likely to be found by an ocean predator than an isolated fish is. The reason has to do with the optical character of the medium in which both the prey and the predator live. Contrast is extremely important for distinguishing an object from its background. In a large body of water the scattering of light by suspended particles and the absorption of light by the water itself greatly reduce the contrast. As a result, even in water of exceptional clarity the greatest distance at which an object can be seen is about 200 meters, and the distance does not depend on the size of the object. In practice the maximum is usually much less. (Scuba divers consider a visibility of from 30 to 50 meters to be exceptionally good.)

Consider three fish swimming close together in a simple school. The area within which each fish can be seen is defined by a sphere whose radius is the maximum distance of visibility. Since the fish are in a compact group, the spheres overlap to a great extent. The chance of a predator's finding the school



is therefore only very slightly greater than the chance of its finding a single fish. Indeed, the chance of a predator's finding the school is about one-third the chance of its finding at least one of the three fish if they were separated.

The example of a school with three members may appear trivial. It turns out, however, that in the open ocean a predator's chance of finding a school of 1,000 fish is only slightly greater than its chance of finding one fish. If the predator, on discovering the school, eats exactly one fish, then an individual fish's risk of being eaten is about a thousandth of what it would have been if the prey had been discovered on its own. The advantage afforded by being in a school is thus substantial, and it appears to increase with the size of the school.



POLARIZATION, or parallel arrangement, is one of the most conspicuous features of a fish school. When the school is threatened, it becomes more highly polarized and more densely packed. The effect is shown in photographs of European minnows in a tank. In the top photograph the minnows are undisturbed. The bottom photograph shows them soon after a pike, which is a predatory fish, was put in the tank. Schools of some species are ordinarily more polarized than those of other species, a fact that was once thought to constitute an essential difference. It now appears that all schools are organized according to the same principles.

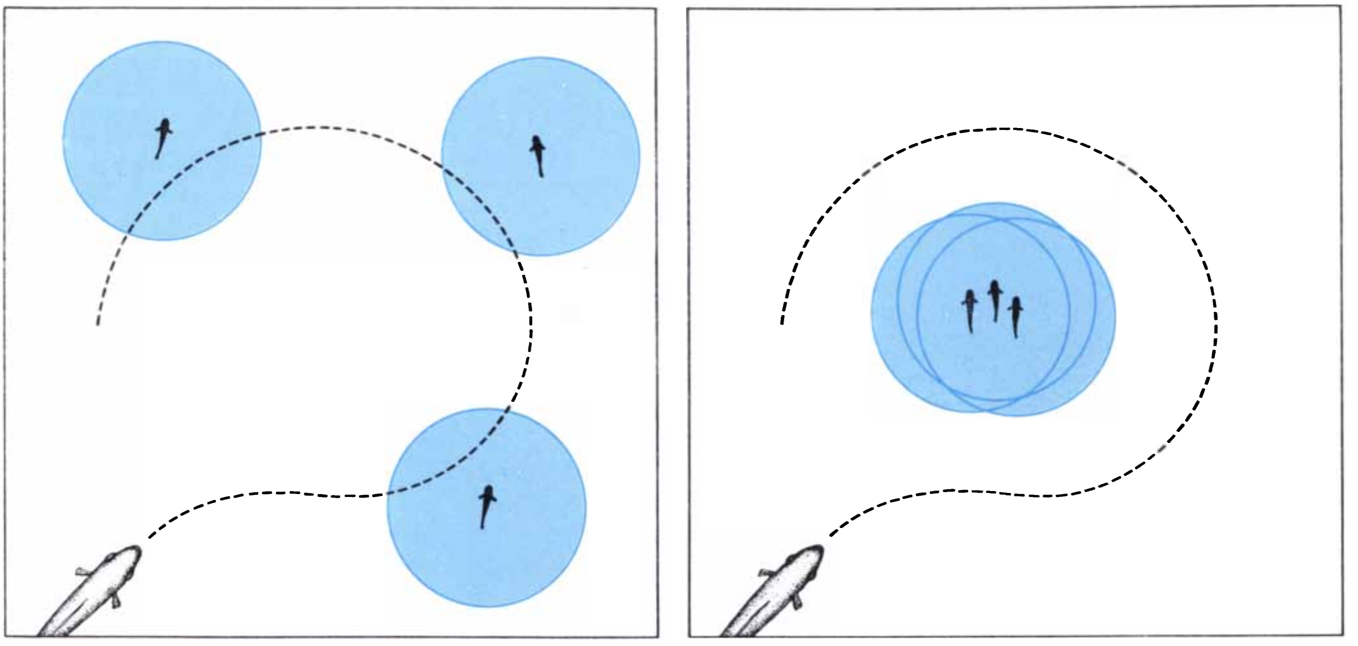
Several considerations suggest, however, that for the school to have flourished as a social form over a long evolutionary history it must provide some benefit beyond reducing the probability of detection. One confounding observation is that some fish form schools even in the presence of predators, where there can be no possibility of escaping detection. Benoni H. Seghers of the University of Western Ontario has shown that there are so many predators in the streams of Trinidad that guppies are constantly within sight of predators. The guppies continue to school. Moreover, their daily routes to and from feeding grounds take them past many predators. Many species of fish living on the coral reefs off the coast of Florida spend their entire lives within a few feet of predatory barracuda and groupers; nevertheless, schooling is common among the prey species. The notion of predators searching a limitless ocean for scarce prey clearly cannot explain such schools.

Furthermore, the school must be at least slightly more conspicuous than a single fish. It follows that an individual might reduce its chance of detection by leaving the school. The persistence of the school suggests that it continues to be of value to its members even after detection.

Another deficiency of the "detection" theory can be illustrated by again considering the three-fish school. Although the school is not much easier to find than a single fish, the survival of the individual fish is not necessarily enhanced. Suppose that when the school is found, the predator eats all three of its members; then none of the prey will have gained an advantage by being in the school. On the other hand, if the school were so large that a predator could not possibly consume all the fish, an advantage might remain.

Even if it can be established that more fish survive on the average when they swim in a school, it does not follow that schooling is advantageous for any particular fish. Natural selection acts on the individual, and in general there is no benefit to the individual in improving the welfare of other members of the group. There are exceptional circumstances, however, in which behavior that benefits the group might be favored by selection, namely when the members of the school are closely related. If an individual has many genes in common with the other fish in a school, the survival of those fish tends to perpetuate the individual's own genes.

By analyzing the structure of enzymes that exist in several chemical forms, Moira Ferguson and David L. G. Noakes of the University of Guelph in Ontario have shown that golden shiners (a freshwater species) in any one school are more closely related to one



PROBABILITY OF DETECTION is reduced by forming a school. Because of the scattering and absorption of light in the ocean the greatest distance from which an object of any size can be seen is roughly 200 meters; the maximum is usually much less. In the diagram the circles represent the greatest distance from which a single fish can be seen. The illustration shows the view from above; in the ocean the radii would, of course, form spheres. If three fish are isolated from one another, the chance of a predator's finding at least one of them is fairly great (*left*). If the three fish form a school, the circles representing the maximum distance of visibility overlap to a large extent (*right*). The probability of a predator's finding the school is therefore only about one-third the probability of its finding at least one of the isolated fish. If on finding the school the predator ate all three of its members, schooling would have been of no benefit. For this reason schooling must somehow also reduce the likelihood of a fish's being eaten after the school has been discovered by a predator.

another than they are to members of other schools. Hence the "kin selection" mechanism may be operating in this species. On the other hand, there is probably little genetic similarity among the ocean fish in a school because larvae from different parents are intermixed as they float freely in the water.

It seems that in many species schooling can offer a substantial evolutionary advantage only if it reduces the chance that an individual will be eaten once the school has been found. There are several ways it might do so. Albert Eide Parr, one of the first workers to study schools in a quantitative way, observed that a school is more densely packed and more highly polarized when it is under attack. Parr hypothesized that open-water fish respond to the lack of cover in the ocean by hiding behind one another; the school is the result. It has also been suggested that a predator might perceive a dense group of small prey as a large, frightening object, but one would expect natural selection to favor predators that are not fooled in this way.

A more plausible explanation of the adaptive value of the tightly packed school is that it reduces the predator's chance of making a successful kill. A predator facing a large number of prey often has difficulty choosing a single fish to attack. The phenomenon has been designated the confusion effect, but it may result from two quite different processes. One process takes place in the central nervous system: the predator simply cannot make a choice among the members of the school. Many predators prefer to strike prey that are distinct from the rest of the school in appearance or behavior. Even very small differences are enough to overcome the predator's inability to make a decision, but in many schools the fish are almost identical in appearance, and the predator may have difficulty selecting one.

The second process may have its origin in the peripheral nervous system. It is the sensory confusion caused by a large number of prey moving around the predator. Even if the predator makes the decision to attack a particular fish, the movement of other prey in the vicinity can be distracting. The predator's difficulty can be compared to that of a tennis player trying to hit two tennis balls at once.

The mechanism of sensory confusion seems to me more likely than that of indecision to be responsible for the predator's dilemma. If there really were no reliable criteria for selecting a fish to attack, natural selection should favor predators that choose randomly and quickly. Sensory confusion, on the other hand, is an indirect consequence of perceptual sensitivity to movement. There should be strong selective pressure against a predator's evolving less sensitive movement detectors because they are needed to find prey.

Whatever the mechanism, there is substantial evidence that schools confuse predators. Sean Neill and Michael Cullen of the University of Oxford have studied attacks by pike and perch on schools of bleak and dace, which are European freshwater fish. Increasing the number of prey from one to six and then to 20 reduced the frequency of the attacker's strikes and the probability of success.

By diminishing the predator's chance of finding prey and confusing the predator once the prey is found the school is of benefit to each of its members. The advantages discussed so far can be attributed primarily to the form of the school itself rather than to the active cooperation of its members. By cooperating, the members of the school can reduce still further their chance of being eaten.

Schools of fish engage in several dramatic evasive maneuvers. The tactic adopted depends in part on how rapidly the predator is approaching. The tactics can be illustrated by the responses of various prey species to barracuda, a common predator on schools of small fish in tropical waters. The barracuda has evolved a shape well suited to a quick strike, which is its characteristic attack. It has a long, torpedo-shaped body with a pair of vertical fins near the tail. In a strike the fins act like a second tail, providing a powerful forward impetus. Such a body plan is not efficient for sustained high-speed swimming. The barracuda tends to sidle up to its prey and then strike in a single motion.

When the barracuda moves slowly up to a school, the prey may back away, creating a cavity around it. More of-

SCHOOL OF PREDATORY FISH swims in a parabolic formation with the concave side of the parabola forward. The fish are giant bluefin tuna. The photograph was made by the U.S. National Marine Fisheries Service in a census of the tuna population. It has long been known that some predators, including tuna and barracuda, congregate in schools. It was thought, however, that schooling merely increased the predators' visual range: if one fish found prey, the others could join in the kill. The author's analysis of the tuna school suggests that they hunt in a more truly cooperative manner. The tuna apparently work together to drive schools of prey between the outstretched ends of the parabola, then surround and destroy the prey.

EVASIVE TACTICS employed by schools of prey are shown here and in the two illustrations on the opposite page. The photograph shows a school of dwarf herring forming a vacuole, or cavity, around a barracuda. The tactic adopted depends partly on how fast the predator is approaching. The torpedo-shaped barracuda with its pair of vertical fins near the tail is well adapted to a quick strike but not to sustained high-speed swimming. It often sidles up to its intended victims before striking. As the barracuda moves slowly toward the school the dwarf herring form the vacuole, maintaining sufficient distance to escape if the predator attacks.

ten, however, the school splits into two parts in front of the predator. The halves of the school turn outward, swim around the barracuda and rejoin behind it. The tactic has been named the fountain effect by Geoffry Potts of the Laboratory of the Marine Biological Association at Plymouth, England. The result is that the predator is left with the school behind it. If the barracuda turns, the maneuver is repeated. By a succession of such movements the school can evade a predator it cannot outrun.

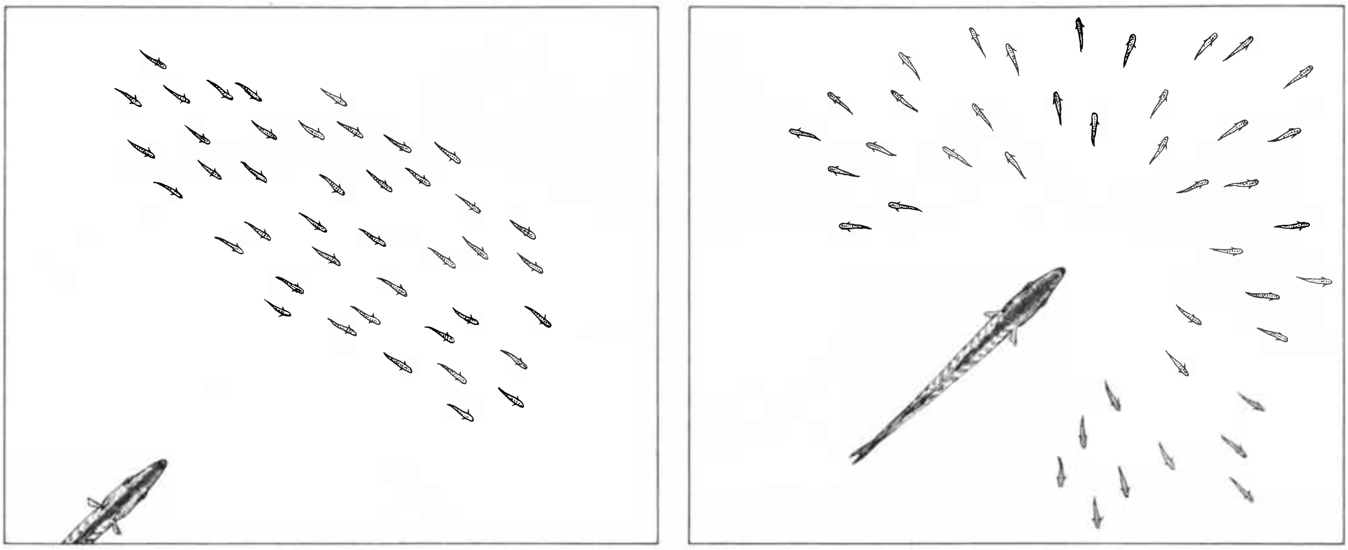
When the barracuda strikes, maneuvers as stately as the fountain effect are of little use. In response to a quick strike each fish darts from the center of the school. In such a flash expansion each fish moves radially outward, propelled by a single flick of the tail. The movement resembles a bomb burst. In as little as a fiftieth of a second each fish accelerates from a standing start to a velocity of between 10 and 20 body lengths per second. The entire expansion can take place in half a second.

Because the expansion is created by roughly simultaneous tail flicks throughout the school it seems it cannot be coordinated by any means that would require each fish to register the movements of its neighbors. In all probability each member of the school "knows" where the other members will go in the event of an attack. The hypothesis is given some support by the fact that collisions have never been observed in fish with all their sense organs intact.

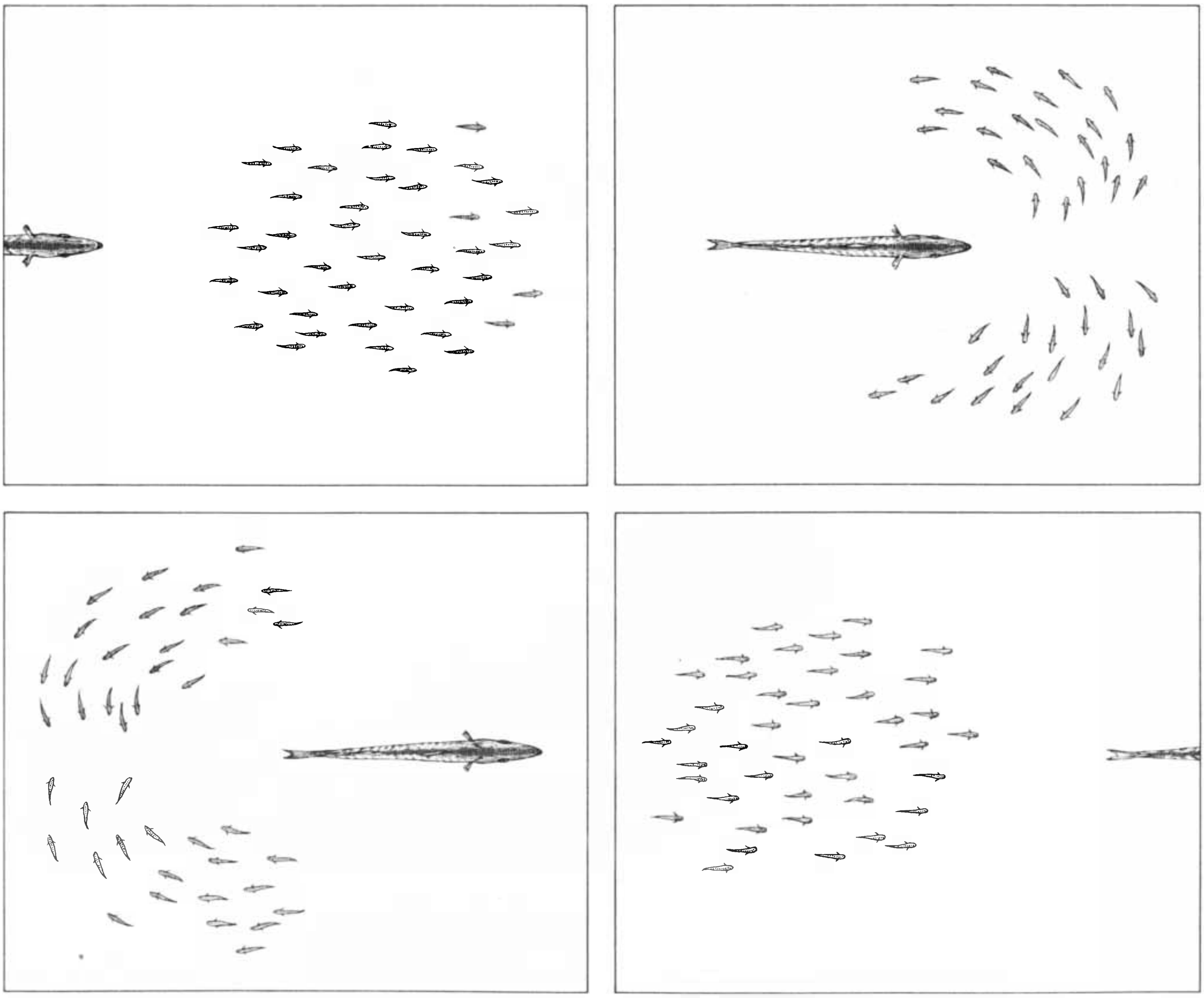
Although most work done on schools has concerned species of fish that are consumed rather than consumers, some predators also form schools; among them are the barracuda and the tuna. It has long been assumed that when predators school, they act more or less as a group of individual hunters. Forming a school could nonetheless have an adaptive value by increasing the search area of the hunter. If one member of the school finds food, the other members can take advantage of the find. If the members of the school remain barely in sight of one another, the search area is at a maximum. This is a much looser and more individualistic form of hunting than that seen among lions or wolves, where the pack can bring down the prey together, or among dolphins, which herd their prey into shallow water.

Recently I have begun to suspect that some predatory fish also coordinate their hunting in a cooperative way. I have analyzed the structure of schools of giant bluefin tuna (a fish that can reach three meters in length and more than 400 kilograms in weight). Aerial photographs of tuna schools made by the U.S. National Marine Fisheries Service for counting the tuna population show that the arrangement of the tuna in the schools is remarkably regular.

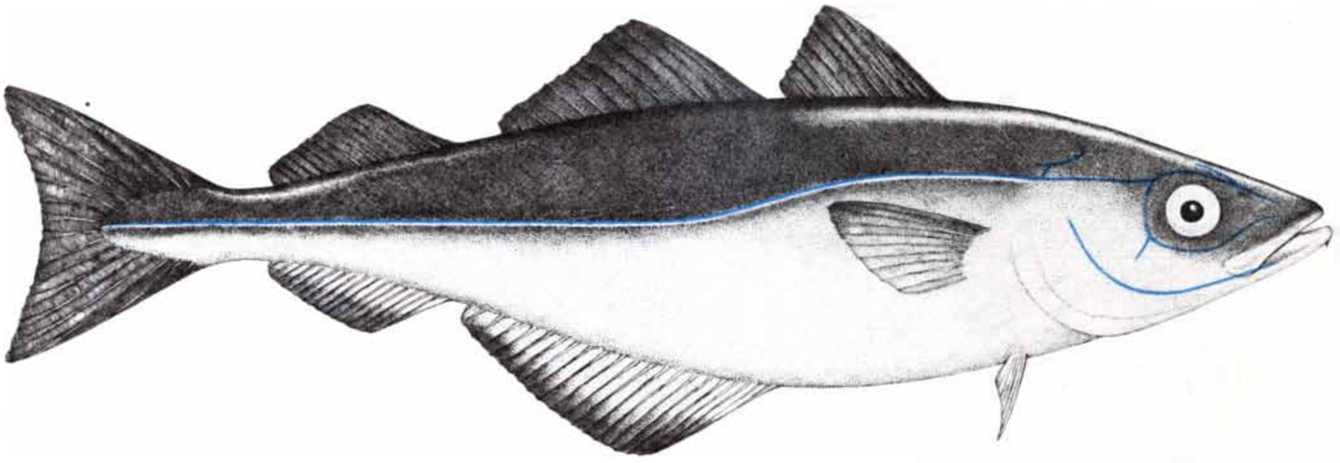
Tuna schools of 50 or more members



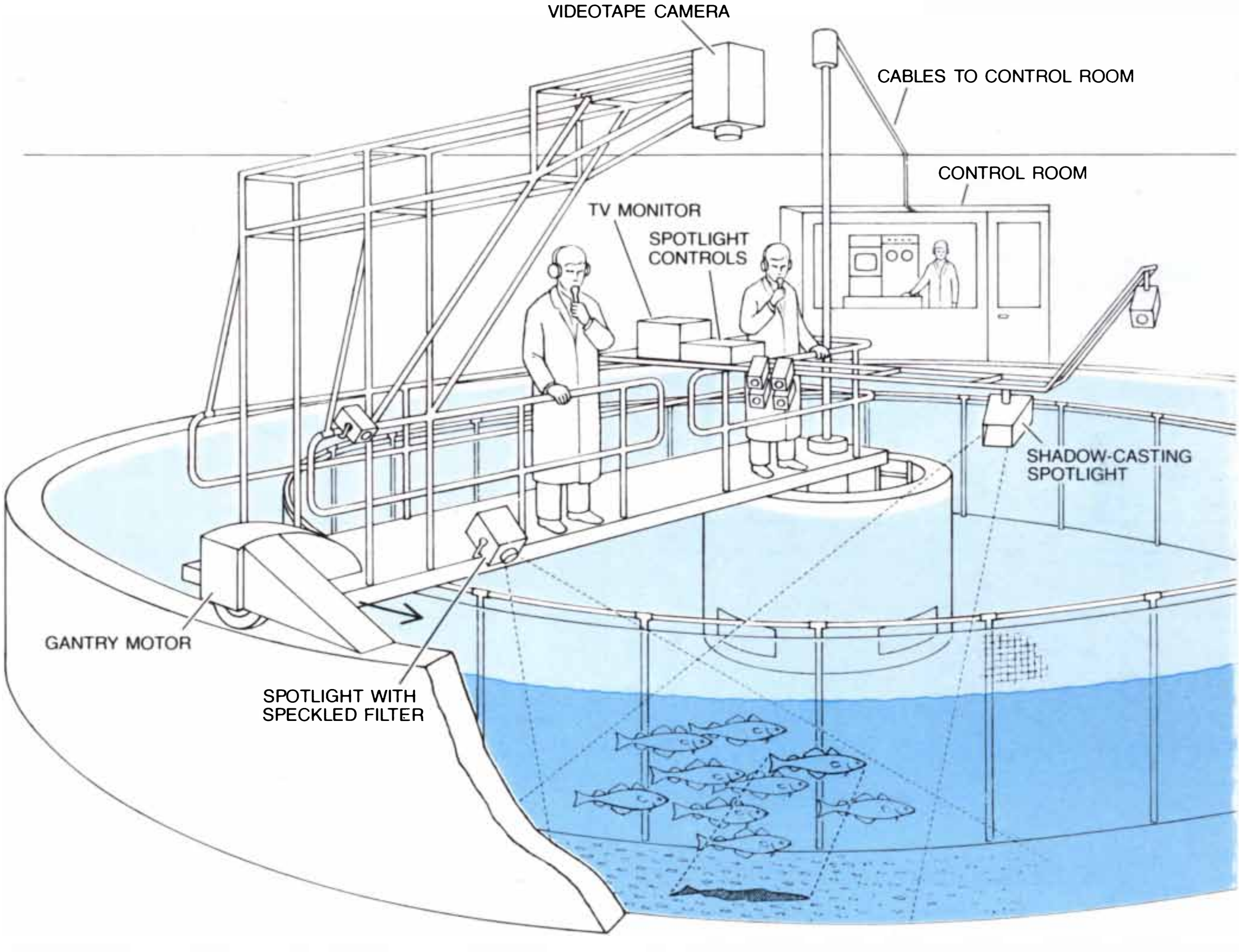
FLASH EXPANSION is the most dramatic of the evasive tactics of the dwarf-herring school. As the barracuda strikes, the school expands in the form of a sphere. The entire expansion can take place in as little as half a second. It is accomplished by a single movement of the tail on the part of each member of the school. Collisions in the course of the expansion have never been observed in fish that have all their sensory organs intact, and so it appears that each fish must "know" where its neighbors will go in the event of an attack.



FOUNTAIN EFFECT is a tactic that enables a school of small, slow-moving prey to outmaneuver a predator it cannot outrun. As a barracuda moves toward a school of dwarf herring the school splits and flows in two groups behind the larger fish, which is carried forward by its own momentum. The school re-forms behind the barracuda. If the predator turns to face the school again, the maneuver is repeated.



LATERAL LINE, an organ sensitive to transitory displacements of the water, provides information that helps a fish to maintain its position in a school. The lateral-line canal is shown in color on a drawing of a pollock (*Pollachius virens*), a saltwater fish closely related to the cod. The pollock has been utilized in much of the author's work. The lateral line is made up of gelatinous canals connected by pores to the external environment. Inside the canal are thousands of hair cells, which are much like the sound receptors in the ear of a terrestrial vertebrate. The response of the hair cells to the displacement of water gives the pollock information about the speed and direction of neighboring fish. The author's work has shown that schooling fish compare information from the eyes with information from the lateral lines.



FISH SCHOOLS IN THE LABORATORY were studied by the author with apparatus at the Department for Agriculture and Fisheries for Scotland in Aberdeen. The circular tank is 10 meters in diameter. A plastic fence created a circular channel 1.5 meters wide. The gantry projecting from the central stanchion held a videotape camera, other equipment and observers. Schools of from 20 to 30 fish with numbers branded on their side were trained to stay over a speckled spot projected from a light on the gantry. As the gantry rotated at a constant speed the school moved to keep pace with the speckled spot. A beam of red light was projected diagonally through the school from the stanchion. From above, the distance between a fish and its shadow in the red spot indicated the depth of the fish. Videotapes were made, and an observer gave a description of the positions of the fish. A plot of the coordinates of each fish in successive frames of the videotape was made with the aid of a computer. It yielded information about the adjustment of position that takes place in the school.

may divide into smaller groups when hunting. The smaller schools consist of between 10 and 20 fish spread out along a curve closely resembling a parabola, with the concave side forward. Achieving a regular spacing of individuals along a parabola is a difficult feat because the distance and the angle between each pair of tuna are different. That the form of the school is maintained in spite of this difficulty suggests it must provide a considerable advantage in hunting.

The possible nature of the advantage can be considered by means of an analogy with the functioning of a parabolic mirror in a telescope. Any light ray parallel to the axis of the parabola is reflected from the concave surface toward the focus. It is possible that a similar effect operates when a parabolic school of tuna swims parallel to its own axis. If the prey react to the curved school as if it were a solid wall, they will be driven into the focus of the parabola, which is the most convenient place for the tuna to surround and consume them.

For both predators and prey the value of the school thus depends on the ability of its members to coordinate their movements quite closely. Some of the advantage is derived from the geometric form of the school, but much of it comes from the tactics employed by the school. In addition the adaptive value of the school increases with its size. As a result of such evolutionary factors schools with a million members are not uncommon.

How is such a large group organized? Finding the answer required a means of recording very small changes in the position of each fish in the school over a long period. The record was made possible by a unique apparatus at the Department for Agriculture and Fisheries for Scotland in Aberdeen. The department's fish laboratory has a circular tank 10 meters in diameter and one meter deep. Putting a plastic fence in the tank yielded a channel one meter or 1.5 meters across, depending on the experiment.

Projecting from a stanchion in the center of the circular tank is a rotating gantry. The five-ton gantry is large enough to support two observers and many pieces of equipment. From the gantry we projected a speckled spot of light onto the floor of the tank. It is possible to train a school of fish to stay over such a spot. When a school was put in the tank, the first few days were spent training the school to stay over the spot as the gantry moved around the tank.

Because the school is a three-dimensional structure it is necessary to examine the vertical relations within it as well as the horizontal relations. This was done by mounting a second spotlight on the gantry. The light was projected downward at an angle through the school. When the school was observed from above, the distance between each fish and its shadow indicated the height of the fish above the bottom.

A videotape camera was mounted on the gantry. As the gantry followed the school the camera recorded the horizontal positions of the fish; measuring the distance to a fish's shadow yielded its depth. In each frame of the tape the position of each fish in three dimensions was recorded with the aid of a computer. More than 35,000 frames were analyzed, providing more detailed information on schools than had ever been gathered. Most earlier work was based on visual observation or on no more than a few hundred frames of film.

In addition an observer riding on the gantry as it followed the school gave a continuous commentary on the positions of the fish. The commentary was recorded and later coordinated with the video tape. To make the analysis of the tape easier the fish were branded with numbers. A cold metal brand was applied to the side of the fish, where it left a temporary mark. Utilizing this setup, my colleague Tony J. Pitcher and I observed schools of cod, herring and a third fish much like the cod, which is known as the saithe in England and the pollock in the U.S. In most cases the schools consisted of about 20 fish.

One of the most persistent misconceptions about fish schools is that they have a regular geometric form, such as the cubic lattice characteristic of some crystals. Such a regular form has not been observed in the schools of any fish species. Our work shows that the structure is a rather loose or probabilistic one, and that it results from each fish's applying a few simple behavioral rules. The first rule is that each individual maintains an empty space around itself. For each species there is a characteristic minimum-approach distance within which neighbors do not come. The absolute distance depends on the size of the fish; it is usually about three-tenths of a body length.

The minimum-approach distance is not, however, the distance that is generally maintained between the fish in a school. In each species there is a typical preferred distance to the nearest neighbor, which is usually about one body length. In general only one neighbor at a time is at the preferred distance from a particular fish. (In a cubic lattice several neighboring fish would all be at the same distance.)

The spatial relations among the fish in a school change constantly as the fish adjust their speed and direction. For this reason the distance to the nearest neighbor is not uniform, even for a single fish. The preferred distance is a statistical abstraction, found by averaging the actual distances over a long period.

Fish of any one species also tend to keep their nearest neighbor at a particular angle with respect to their body axis. Like the preferred distance, the preferred angle is a statistical quantity. At any given moment only a few fish may have their nearest neighbors at the preferred angle, but over a long period the preferred angle predominates.

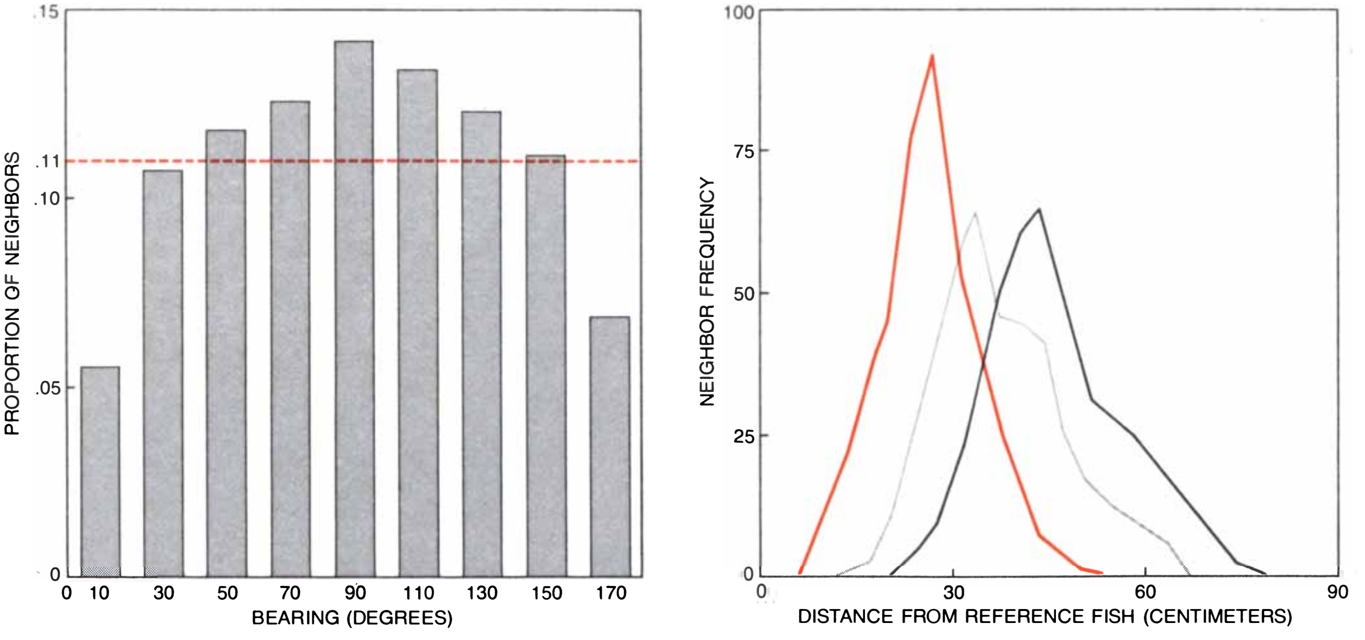
One useful measure of the degree of structure of a school is the average ratio between the distance to the second-nearest neighbor and the distance to the nearest neighbor. The closer the ratio is to 1, the more uniform the structure is. In a cubic lattice the ratio is exactly 1. The ratio varies considerably among species. For herring it is about 1.1, for pollock 1.3 and for cod 1.5. A ratio of 1.5 is only slightly less than the ratio of 1.6 that would be observed if the fish in the school took up positions at random.

Several other measures suggest that schools of herring are organized in a more regular way than those of pollock or cod. Even when such differences are taken into account, however, it appears that most schools are organized on the same lines: by the maintenance of a preferred distance and angle. Attempts to distinguish species on the basis of whether they are facultative or obligate schoolers or of how highly polarized the school is now seem misguided; such categorical distinctions probably do not exist. Fish schools seem to vary along a continuum in their degree of organization. Other workers have shown that schools of squid, frog tadpoles and even flocks of certain birds are organized on the same principles.

In our work we were particularly interested in the function of the lateral line in determining the structure of the school. Most species of fish have a prominent lateral line on each side of the body. The displacement-sensitive receptors that make up the line are known as hair cells and are much like the receptors in the ear of a terrestrial vertebrate. The hair cells are placed in canals laid out in a complicated way on the head of the fish and in a roughly linear arrangement between the head and the tail.

Although it had been suggested that the lateral line plays a role in the formation of the school, most workers thought vision was much more important. In the 1920's Parr hypothesized that schooling was accomplished by vision alone. According to Parr's scheme, a fish is attracted by the sight of a member of its species but repelled if it comes too close. The cohesion of the school is thus the result of balanced attractive and repulsive forces, both originating in vision.

To test whether the lateral line might not also have some influence we observed schools of pollock that included fish that had been temporarily blinded or had had their lateral lines cut behind the operculum, the bony flap covering the gills. The pollock were blinded by placing opaque contact lenses over their eyes. When the blinded fish were placed in a school of unimpaired fish, they re-

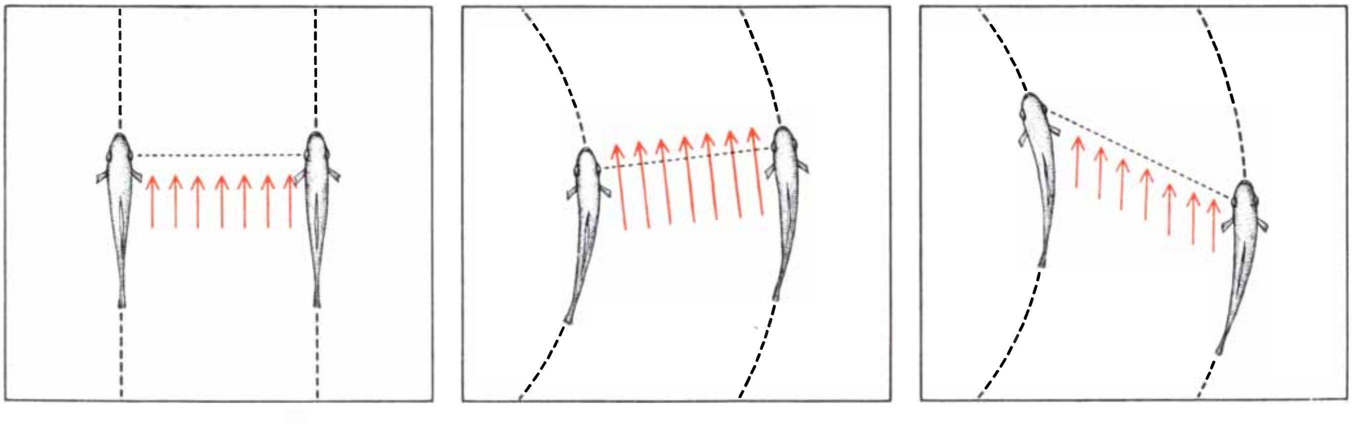


STRUCTURE OF A SCHOOL is loose and probabilistic, unlike the regular arrangement of atoms in a crystal lattice. The structure is the result of the tendency of each fish to keep its nearest neighbor at a particular distance and angle. The graph at the left shows where the nearest neighbor is likely to be found in the area around a given pollock. Zero degrees is directly ahead of the fish; 180 degrees is directly behind. A pollock's nearest neighbor tends to be roughly alongside it, as the tallest bar at 90 degrees indicates. The broken line indicates where the neighbors would be found if the fish took up positions at random. The graph at the right shows how often the nearest neighbor (*color*), the second-nearest neighbor (*gray*) and the third-nearest neighbor (*black*) are to be found at various distances. The nearest neighbor is most commonly at a distance of from 25 to 30 centimeters, or about one body length. The horizontal spread of the curves shows that the preferred distance and angle are statistical abstractions: at any moment numerous fish are at other distances and angles.

sponded to changes in speed and direction by the school and maintained their position among the other fish. Behavioral changes were observed, however: the blinded fish tended to swim somewhat farther from their nearest neighbor than pollock ordinarily do.

Fish whose lateral lines had been cut were also able to school. In contrast to the blinded fish, however, those whose lateral lines had been cut swam closer to their nearest neighbor than pollock generally do. Only if the fish were both blinded and had had their lateral lines cut did they fail to maintain position. The results suggest that information from both the eye and the lateral line is utilized when fish school. The distance maintained by the eyes alone is smaller than the distance maintained by the lateral lines alone; the preferred distance in the unimpaired fish lies between these values. Vision does seem to provide the attractive force between members of the school (the pollock swim farther apart without it); the repulsive force, however, appears to be provided by the lateral line (without it the fish swim closer to one another).

Other results suggest that vision is the more important sense for maintaining distance from and angle to the nearest neighbor. The lateral line appears to be most important for determining the neighbor's speed and direction. Strong evidence that both senses are being utilized at once comes from measurements of the correlation between the speed and direction of a particular fish and those of other fish in the school a short time before; such correlations can indicate what standard of reference each fish employs in adjusting its velocity. For neither speed nor heading is the correlation between a fish and its nearest neighbor very strong. Moreover, the results show that the school has no leader:



CONTRADICTORY INFORMATION can be given by the eyes and the lateral lines. When the school swims in a straight line, the senses are in agreement. The eyes tell the fish on the left that its neighbor is keeping up; the lateral lines tell it that its neighbor is swimming at the same speed (*left*). When the school turns in an arc and the neighboring fish remain side by side on parallel courses, the eyes of the inner fish tell it that its neighbor is keeping pace. Because the outside fish must swim a greater distance, however, the lateral lines tell the inner fish that its neighbor is swimming faster (*middle*). If the inner fish accelerated to match its neighbor's speed as measured by the lateral lines, the school would disintegrate (*right*). When information from the senses is contradictory, vision apparently takes precedence.

speed and direction are not closely related to those of any other single fish.

The strongest correlations are observed between the speed and direction of the individual and the average speed and direction of the entire school. The average that is most strongly correlated is not the simple arithmetic mean of the speeds and headings of the members of the school. A fish is much more strongly influenced by its near neighbors than it is by the distant members of the school. The contribution of each fish to the average is inversely proportional to either the square or the cube of the distance.

A correlation based on the square of the distance and one based on the cube are about equally accurate in accounting for our observations. If the school were maintained by vision, one would expect the correlation to depend on the square of the distance. Discriminations made by vision depend in part on the area of the perceived figure. The area decreases with the square of the distance.

If the school were maintained solely by the lateral line's sensitivity to water displacement, on the other hand, one would expect the correlation to depend on the cube of the distance. The volume of water displaced varies inversely with the cube of the distance. The fact that the correlation based on the square and the one based on the cube are about equally strong suggests that both senses are employed.

Although both the eyes and the lateral lines appear to be in use when fish school, there are times when the information from them is contradictory. Such a conflict arises when the school turns in an arc (as it does continuously in a circular tank). If two fish make the turn side by side, the fish receive conflicting information. For example, the eyes of the fish on the inner course tell it that its outer neighbor is just maintaining position. Because the fish on the outer course must cover a greater distance to keep up, however, the information from the lateral lines tells the inner fish that the outer neighbor is swimming faster. Our work shows that when the information from the two sensory systems is in conflict, the information from the eyes takes precedence.

In investigating particular forms of animal behavior biologists have tended to look for a single sensory explanation. It is now known that schooling is accomplished by comparing information from more than one sensory source. Certain other phenomena, such as the navigation of homing pigeons, also seem to require multiple sensory systems. This might have been expected for evolutionary reasons alone: selection would tend to favor the animal capable of exploiting the most information. When the intricate maneuvers of the fish school are completely understood, it may be found that still other senses participate.