

STUDIES ON SOCIAL GROUPINGS  
IN FISHES

C. M. BREDER, JR.

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## INTRODUCTION

SINCE THE LATE 1920's there has developed an increasing interest in the manner in which, and the reasons why, certain fishes group themselves into masses, generally referred to as schools. This interest has found expression in the publication of a very considerable number of papers, which, while varied as to intent and purpose, have all sought to elucidate the phenomenon, or at least certain aspects of it. This activity followed on the pioneer paper (Parr, 1927), which provided some theoretical considerations which gave a basis for the work that followed. It is not surprising that different workers so engaged have used almost as many definitions for the term "school" as there have been students. Recent reviews that have attempted to clarify terminology include Morrow (1948), Atz (1953), and Keenleyside (1955). While they all make interesting interpretations and present various semantic attitudes, the necessity still remains for any writer in the field to explain his own particular usage.

The present contribution attempts to further such studies. To do this adequately it was found necessary to include studies on, and discussions of, all other forms of social organization known to occur in fishes, a fact that explains the reason for the above title. These studies and considerations have been integrated under four principal headings, the reasons for which are explained in detail below. While there is a summary covering the salient points, there is no separate section for discussion, because it was found more satisfactory and convenient to handle the discussions of the separate matters at the places where they occur.

**1. DEFINITIONS AND EXPLANATIONS:** This part explains the terminology employed and defends its use, for the purposes of this paper at least. It includes a comparative discussion of all the other recognizable and definable types of social organization.

**2. SPECIAL FORMS OF SOCIAL GROUPINGS:** This part presents discussions on items involving primarily new data concerned with special forms of social groupings.

**3. SPECIAL ENVIRONMENTAL INFLUENCES ON FISH GROUPINGS:** This part considers primarily new data that involve direct environmental influence on individuals in refer-

ence to their social attitudes.

**4. STRUCTURAL NATURE OF FISH GROUPS:** Here, under various subheadings, an attempt is made to analyze further the organization and structure of fish social groupings. It has been found useful to invoke elementary cybernetic principles, which are explained where they occur.

The field work involved has covered a variety of places, including both fresh-water and marine environments. The species mentioned and the context will be sufficient to make clear where the various items were studied. These localities are as follows:

**FRESH WATER:** Various sites in northern New Jersey, including the State Hatchery at Hackettstown, a variety of small streams and ponds, and the author's property at Mahwah. Various places in Florida, including Mountain Lake Sanctuary, Myakka River State Park, Silver Springs, and a variety of roadside ditches and small lakes.

**MARINE:** The Lerner Marine Laboratory at Bimini, Bahamas, and many places on the Florida west coast from Tarpon Springs to Naples, including principally the Cape Haze Laboratory at Placida on Gasparilla Sound and the author's property on Lemon Bay.

Although a great many people assisted in carrying out these activities, the following individuals must be especially thanked for their hospitality: Dr. Eugenie Clark, Director of the Cape Haze Laboratory, and Mr. R. A. Hayford, Superintendent of the Hackettstown Hatcheries.

The author was in charge of the Lerner Marine Laboratory at the time the pertinent work was done there.

The laboratory work was carried out mostly at the Lerner Marine Laboratory, the laboratories of the Department of Fishes and Aquatic Biology at the American Museum, the Cape Haze Laboratory, and the author's quarters at his New Jersey home.

This study was supported in part by a grant from the National Science Foundation.

Appreciation for aid is extended to Dr. Vladimir Walters for his constructive criticism of the manuscript and his many valuable suggestions. Mr. Logan O. Smith, who made the under-water photographs shown as plate 76, has generously permitted their publication herein because of their obvious bearing on these studies.

## DEFINITIONS AND EXPLANATIONS

THE TERMINOLOGY AS CURRENTLY USED by authors discussing schooling and related matters is neither consistent nor satisfactory, and it will probably take a considerable semantic evolution to produce a satisfactory and generally acceptable nomenclature of the subject. This situation makes it essential, so far as the purposes and needs of this paper are concerned, to preface any discussion with as precise definitions as possible. The need of such definitions applies especially to the context of the present paper, partly because of the wide variety of matters and ideas which are brought together, in an attempt to correlate them, but more particularly because of the necessity to refer herein to conditions in all the known or conceivable conditions of social groupings in which real or hypothetical fishes could be expected to be found.

The above situation, moreover, makes it imperative first to give some of the conceptual background that has led to the present attempt at analysis. As all the published definitions are clearly derived from considerations of real fish schools, it was thought useful to pose an abstraction consisting of an area in which motile bodies, such as fish, could be physically deployed. Neglecting, at the start, the fact that they are motile and can move in a three-dimensional space, a physical model may be made of a set of dominoes (face down, so as to be identical). These are then given the restriction that they can move (be moved) on a surface (two-dimensional) but not piled one upon the other. Clearly there is a limited number of ways in which they can be deployed on, say, a table top. A very large surface is conceived of as comparable to a lake or ocean, not a small pond or aquarium, in order to remove the restriction of a boundary.

A study of the distribution of the dominoes might start with the individuals very far apart, so that each domino would satisfy anyone's definition of "solitary." These could be brought together from these sites to any degree of nearness, say, a complete set of dominoes within the area of a circle with a 3-foot radius. Compared with the rest of the surface, they might be considered as "clumped," "crowded," or some other word indicating

some kind of approach to one another. At this point the effect of relative magnitude must be taken into consideration. Dominoes of ordinary size evenly distributed within a circle 6 feet wide would hardly be "crowded," or fish as small as dominoes in a similar condition could be considered only as localized or, at most, loosely grouped. Thus the spacing between objects is most conveniently expressed in terms of the size of the objects. This feature of absolute size need not be considered in this discussion of terminology but appears below in more important connections.

To return to the dominoes in the circle with a 3-foot radius, it is obvious that they could be moved closer and closer and finally brought into contact. Clearly the "school" and the "aggregation," which are synonymous to some authors but not to others, are both located somewhere between the extremes here noted, for a static model of dominoes, as "solitary" and "in contact." It should be clear that if the widely spaced dominoes, randomly orientated, are moved closer and closer and finally are brought in contact, without disturbing their original orientation, their being moved into contact would leave spaces, mostly triangular, and they would not be packed very tightly. If now they were all swung so as to point in a common direction, further packing would be possible, and they would cover the reduced area very much as a brick pavement, and no vacant areas would remain. The conditions that obtain in both cases are indicated in figure 1. Herein lies the basis of the geometrical differences between the various types of fish groups and their terminology which has given rise to so much confusion in the usages of different authors. Obviously, as we show above, the coverage of a surface of identical static objects is modified by their distances apart, their shapes, and their orientations. The limiting cases at each end of a continuous series are, respectively, infinite distances between units at one end to complete contact between units at the other end. Bearing on this but aside from the present line of thought is the geometry of surface coverage which has been discussed in other connections

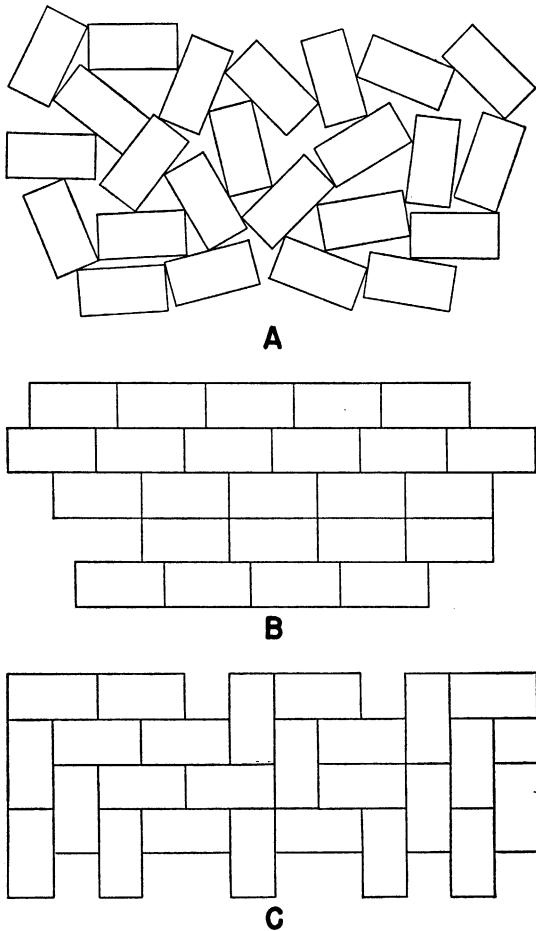


FIG. 1. Deployment of dominoes. A. Randomly distributed dominoes pushed to contact, showing typical interspaces. B. Systematically distributed dominoes, all in full contact. This type of distribution permits of two types of array, that shown being with the long sides forming continuous lines. The other possibility arrays the dominoes with the short sides in continuous lines. The case in which both short and long sides are in continuous lines is the limiting case of either of the above conditions. The sides not forming such lines may be at random or with any possible repetitious arrangement. Still other systematic systems of all-over coverage can be arranged but none seems pertinent to present considerations. They include those frequently seen in ornamental brick work, such as herringbone and many others. C. Unsystematically distributed dominoes, all in full contact, with no interspaces remaining. This type is without polarization and may be irregular, as here shown, or may follow any of a great variety of patterns.

most recently by Breder (1947a), Steinhaus (1950), Weyl (1952), and Bonner (1952).

Obviously, orientation can, in a purely geometrical sense, vary from complete randomness to complete restriction of orientation, whether the dominoes are infinitely remote or approach actual contact. Only when they approach one another to distances comparable to the greatest dimension of a domino does their independence of orientation figure in the geometry of the situation. If the dominoes are permitted to swing freely around their mid-points, they can then approach one another to only a little more than one domino length without mutual collision or interference. This situation is a close approximation to a grouping of fishes that are not all orientated substantially in one direction and is what the author in earlier publications has called an "aggregation" as opposed to a "school." A grouping that permits a domino to turn around on its axis is just about the spacing ordinarily found in fish groups, with individuals showing independent orientations. This provides a minimum of what the author has called "swimming clearance" and is evidently necessary for such swimming without collision. If, however, the dominoes are all pointed "one way" and permitted only a slight oscillation on either side of their mutually parallel axes, it is clearly possible for them to be packed much more closely, as is shown in figure 2. The now restricted swimming space is reduced as though a "bite" proportional to the restriction on oscillation, and on each side, had been taken out of the circle of gyration of "swimming clearance" on the unorientated group. This type of grouping is very close to what various authors, including the present one, have called "schools" and is the type of association on which Parr (1927) based his theories and arguments. If, next, the dominoes are brought to contact, as is discussed above and shown in figure 1B, we have a situation homologous to that of a mass of fish in physical contact and pointed in a common direction. Such assemblages of fishes do occur naturally and are discussed in a later section. Groups of *Mugil* so arrayed are referred to as "pods" by commercial fishermen where they occur, and that term is adopted herewith to distinguish contact groups from assemblages in which there is

space between each fish in the group. In fact, there are also pods of fish the individuals of which are without a common orientation. In the case of rigid dominoes this would require irregular packing as shown in figure 1C. However, with the flexibility characteristic of fishes showing such habits, the fitting to contact is more elaborate.

Definitions follow that have been framed with the above concepts as their bases. In their framing, recognition of the dynamics of motile fishes has been made, and adherence to past usage has been continued so far as the

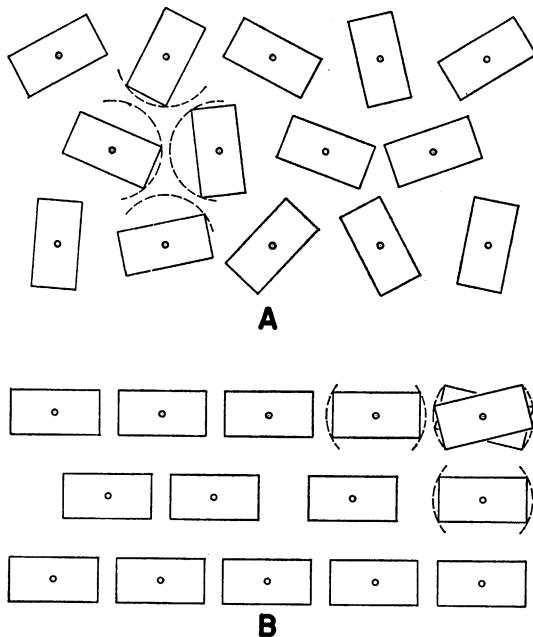


FIG. 2. Deployment of dominoes. This figure differs from figure 1 in that the dominoes are permitted a certain amount of rotation about their centers. A. Here the dominoes are permitted full rotational clearance and are packed as closely as possible with the small clearance. Dashed lines indicate amount of clearance. B. Here the dominoes are given a small permissible oscillation, with the amplitude indicated on the upper right-hand domino. Packing is as close as this arrangement permits with the same clearance as in A. The two outer rows are equally spaced and in the middle row, the first two are advanced one-half, as in common brick laying, the third is advanced another one-fourth, and the fourth is even with its companions above and below. Dashed lines indicate amount of clearance and of oscillation. See text for full explanation.

present considerations permit. For clarity and to avoid ambiguity, in so far as possible, each definition is followed by explanatory notes indicating how other workers have used terms to cover the phenomenon defined. Whether or not these definitions find little or much acceptance is unimportant. They suffice to give precision to the contents of this paper and it is hoped will help to clear the way for the eventual establishment of a fully rigorous set of definitive and thoroughly objective terms.

**SOLITARY:** The solitary, individual, or lone fish in the frame of reference above discussed is the limiting form in one direction. It shows zero or less attraction for and towards others of its kind. In mathematical terms it thus may represent either a type of fish that is neutral towards its fellows or one that is hostile or repellent, that is, shows negative attraction. Although no experiments or observations have been made that could discriminate between the neutral and the negative, it is to be presumed that the active repulsion shown by the latter would tend to separate such types by greater distances than those of the merely neutral. It would seem that indifference would separate individuals by a smaller mean difference than would hostility. The more vigorously hostile fishes might well be normally separated by distances that insured that the minimum would be the distance at which they could not see their fellows. The neutral, contrariwise, might approach one another to a point close to that of swimming clearance for randomly orientated forms. They thus might conceptually be confused with some forms showing a very slight attraction towards each other. Because the occurrence of such a situation would depend on some influence other than sociability, it is expected that it would be transient and show no persistence on disturbance, such as would be present if the fishes were attracted towards one another. There appears to be no discussion of this limiting case in the literature.

The possibility is not excluded that in this class of solitary fishes may be unintentionally included a social group, held together by sounds emitted or by some other means of recognition, but with the individuals separated by large distances and perhaps not in visual contact at all. One possible situation

could conceivably exist in which the visual stimuli were negative but the sounds emitted produced positive stimuli. Such a case would yield a widespread group seemingly solitary. No such case is known to exist, but if any actually does it would not be grossly evident and probably could be recognized only by elaborate instrumentation and analysis.

**AGGREGATING:** The aggregating species are attracted to their kind, *per se*, independently of the accidental circumstances that might have brought them together in the first place, such as favorable temperature, local abundance of food, or other environmental detail. They display no particular polarity as a group, nor is the group capable of any specific directional movement. These types of fishes are ordinarily orientated without reference to the orientation of other individuals. This usually results in "random" orientation, which simply means that each fish is reacting to other elements in its environment to this extent and not especially to the other fishes. Under certain conditions it is possible to confuse this situation with the case in which orientation is principally a social phenomenon. In a strong flow, for instance, it is essential for neutrally buoyant fishes to face into the stream and swim upstream as fast as the current carries them down, if they are to hold a steady position. Holding such a position is optically mediated, and if several take an optical "fix" on a single rock it could easily appear that this was a social phenomenon. Furthermore, if one fish took such a "fix" on another, it would not, under such conditions, necessarily imply a social reaction. While it is true that many forms that so act in flowing water also show social response in standing water, and probably most such fishes show both kinds of response under conditions of flow, such is not necessarily so in all cases. It would probably take considerable experimentation to establish a separation in the motivation of such behavior. This form of grouping is often called "schooling" and cannot be distinguished from "schooling" as defined for the purposes of this paper. Such usage was employed, for example, by Allee (1931), Morrow (1948), and Keenleyside (1955). The views of these students are discussed under the next heading.

**SCHOOLING:** The schooling species are at-

tracted to their kind to a degree of unanimity of behavior that impels them to swim in substantially similar paths, pack themselves more closely than is possible if not all orientated in one principal direction, and perform as a troupe of like-acting individuals in which independence of action is reduced to near the vanishing point. This is to say that the group is polarized and capable of forward movement as a unit. While it is impossible to determine just what Parr (1927) had in mind in terms of the present concept, the species he worked with are typical schooling ones, and his whole development of viewpoint was centered about fishes swimming in parallel courses; therefore it is to be presumed that he used the term "school" in the sense here employed. Breder and Halpern (1946) defined a fish school as that type of aggregation "... in which all individuals are orientated in a common direction, regularly spaced, and moving at a uniform speed."

It would still be possible to consider "aggregations" as a larger class containing both "unorientated individuals" and "schools." The author feels that there is little choice at this time. Atz (1953), however, argued for keeping the two cases as separate and parallel entities, a course that has been followed here. Keenleyside (1955) objected to separating the two on the basis that all fish in a school need not swim at the same speed, that fishes in a stationary school may be quite still and the spacing may vary, and they need not all be orientated the same way, as when feeding. His paper should be consulted for the full details. There is really very little difference in point of view, and it reduces nearly entirely to the meaning assigned to the words by the writer. The objection that the fish need not all move at the same speed is, of course, literally true if the fine structure of the school is studied. Such a study had not been undertaken at the time the attempted definition was written. Since then these details of school structure have been discussed by Breder (1951). The point is that, because the school moves forward as a unit, the shifting positions of various members must provide a mean speed for each member; otherwise in time some would drop out or run ahead of the group. This may be in fact adjusted by the supposition that more energetic individuals travel

longer courses than those that swim a simple straight course.

The next three points, which state that fishes in a stationary school may be quite still, that the spacing may vary, and that they may not all be orientated the same way, indicate that the student is not talking about a school in the present sense. The point about the stationary school and variation in spacing may actually be a reference to a "standing" school in a flow, which is discussed above under "aggregating."

In a very compact school, fishes have two choices of movement in relation to their fellows. They may line up, nose by nose, with their nearby companions and synchronize their swimming strokes, a feature that is conspicuously different from less precise schooling and obvious at a glance. The other way is not to line up, nose by nose, but to hang back alternately and let the yaw of their heads come opposite the mid-part of the body, the

place of least lateral movement, in a quincunx pattern. In this second way, synchronization is not of any importance, and the difference in the appearance of the group, compared to that of the first, is marked.

When one fish passes another, in the second case, synchronization may be established, which allows the follower to come abreast of the advance member and then to lead him by an equal distance. When the follower reaches the forward position, synchronization again may drop out. Obviously the following fish must avoid the sweep of the tail of the fish ahead, either by such means as described or by a general loosening of the school. Such loosening is often to be seen when there is some momentary disruption of the smooth flow of an advancing school.

**PODDING:** The podding species resemble the aggregating and schooling species, except that they do not leave swimming clearance, and as a consequence they come into contact.

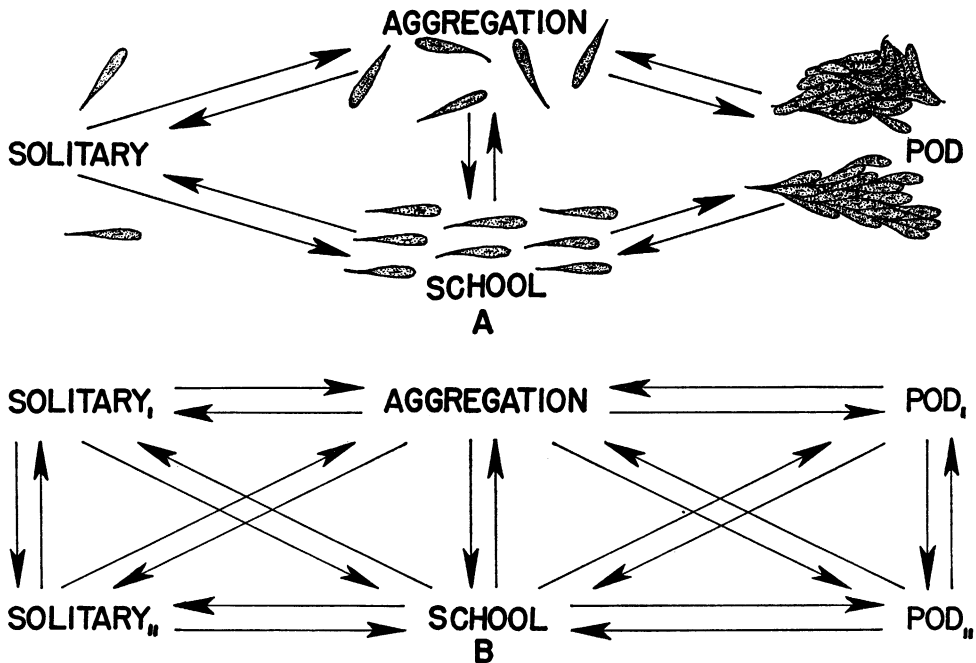


FIG. 3. Diagram of relationships between various forms of fish grouping. A. The usage in which the solitary and pod formations are each considered as a single type, while the intermediate ones are considered different, depending on the form of the orientation. B. The usage that considers each type of grouping as of two forms depending on orientation. The two terminal types are each considered under one name, with subscripts. Obviously the intermediate type could be treated the same way, using either "aggregation" or "school," with similar subscripts. See text for full explanation.

In this kind of contact they may make considerable forward movement if they are substantially pointed one way, but if randomly organized the pod may form an amorphous or ball-shaped mass with no forward translation. These pods then are of two kinds, related to aggregations and schools, respectively. This form of fish association is obviously the other limiting case, in which there is no inhibition to intimate approach and the individuals move together until stopped by the physical limits of their bodies. This type of grouping has not been considered in the literature in connection with such studies, and consequently there are no references or points of view to discuss.

These definitions and explanations thus appear as nodes along a line reaching from one limiting case to the other. That these four cases are not mere arbitrary points in the passing from one end to the other is developed in the course of the study. It is shown below that there are both physical and mathematical reasons why fish groups appear at these four nodal points and that, while they may pass from one node to another, groups of fishes are seldom found at midway points between them, except as rather rapid transitional forms, as a movement from one type of association to another is being made. A diagram of the relationships of these forms of fish grouping is given in figure 3, in which two possible arrangements of the transition

possibilities are given. This should clearly establish the relationships indicated for the various types of association.

Obviously the diagrams as given (fig. 3A, B) represent two alternative manners in which the relationships might be shown. The two terminal forms, "solitary" and "pod," might be given two names, each depending on whether the fishes were orientated in agreement with one another or not, as has been done with the two central nodes. In the case of the solitary distribution, whether neutral fishes faced the same way or not would probably in all cases be meaningless. In the pod distribution it would not be meaningless, as it would appear that the random pod would not be polarized, whereas the other would and consequently be capable of distinct forward motion as a unit. Either case would be as clear as the other for purposes of this discussion. The diagrammatic figures of fishes in their relative positions indicate unequivocally what is meant by each of the six associational types represented. The arrows indicating transition probabilities are discussed in detail in connection with the cybernetic approach to the problem. The only theoretically possible transition omitted is between "solitary" and "pod," which is not known and probably does not occur. The others, as is discussed below, all have actual representation in real fish groups.

## SPECIAL FORMS OF SOCIAL GROUPINGS

BEFORE THE GROUPINGS of fishes are further analyzed, a variety of special cases that have not been reported or have been little noted in connection with present interests is presented and discussed separately, in order to permit a more satisfactory continuity in the later portions of the discourse. This section is followed by another in which special environmental influences are similarly treated. While this treatment may appear to be a purely arbitrary arrangement, it was found to be the only one practicable. Because of the vast

amount of interdependence of the various items of behavior and environment brought into this study of fish groupings, these two sections are intimately interconnected in many ways, and their separation, for purely practical reasons, should not obscure this fact.

The last section, which follows the two above noted and which considers the structural nature of fish groups, develops the essential unity of the system composed of these groups and their environment.

### PODS AND SPAWNING

*Mugil cephalus* Linnaeus, on the Gulf coast of Florida at least, is ordinarily found in schools of greater or less size. The mature fish change their habits from simple schooling to one of pod formation in September or October and show this condition until at least late February. This behavior continues with interruptions through and after the spawning period, so that spent fish may be found in pods well after the peak of the spawning season has passed. That is to say, during the period of the three to four coldest months these extremely tight groups of fishes in physical contact may be found. The peak of the spawning appears in late November or early December, varying with the latitude and the particular year. This information is based on personal observations and commercial fishermen's activities, records, and statements. It agrees fully with the published data of Broadhead and Medford (1954). These groups of mullet are for the most part in close physical contact, as is shown in plates 70 and 71 of pods under different conditions. The photographs clearly indicate that they are advancing groups of fishes which, unlike what is here called a school, have disregarded the maintenance of "swimming clearance." These fishes are feeding on dense plankton which has accumulated just under the surface of the water. Usually this species browses on the bottom. See Hiatt (1947) and Ebeling (1957) for data on the feeding methods involved. The single fish ahead of the pod and facing it in figure 1 of plate 71 has been literally squeezed out by

the press of its fellows and is returning to the group. Often single individuals will be seen to leap ahead when the pack becomes unusually dense. Looser and smaller schools are more common in April and May, as shown in plate 72.

The young of both *Mugil cephalus* and *M. trichodon* form aggregations at the sea surface as shown in figure 1 of plate 75. These aggregations will school briefly if sufficiently disturbed, but placed in an aquarium they persist in forming a rather tight school, as is shown in figure 2 of plate 75, whether other species of fishes are present or not. Evidently the restricted surface area of the aquarium is responsible for the persistence of the school.

Under special conditions various siluroids will group in such a manner as to be in equally close physical contact. During conditions of cold water in a state of approaching quasi-hibernation, ameirids are not infrequently found in pods, usually all heading one way and into whatever slight flow may be present in their chosen site of wintering. *Plotosus* under quite different conditions group in massive clusters which seem to be nearly or completely randomly orientated. These groups are likely to be formed in coral cavities but not necessarily so. Knipper (1953), for instance, reports young *Plotosus anguillar* (Lacépède) of about 28 mm. in length as grouped in more or less globular clusters in open places on the bottom, so formed as to be thought by him to resemble sea urchins, as a matter of protective resemblance. These fish



were apparently in contact, although at no place does the author specifically so state. Sato (1938) in discussing *Plotosus anguillaris* (Lacépède), like Knipper, also nowhere states definitely that the young groups of fishes are in contact. He does indicate that the groups are primarily visual assemblages and that the behavior is not unlike that of young *Ameiurus*. The fishes he studied were between 7 and 8 cm. in total length, and lost their aggregating activity when the water reached as low as 11° C.

Schiche (1921) and Bowen (1931 and 1932) were well aware of the contacts made between young and old *Ameiurus nebulosus* (LeSueur) and *Ameiurus melas* (Rafinesque) and discuss the senses involved. As the siluroids are notably thigmotactic and cryptic, it is not in the least surprising that among them there is more of a tendency to form pods than in fishes that are generally not thigmotactic. That such forms as *Mugil* would form pods evi-

dently calls for some further explanation and may be connected with some unknown peculiarity of their reaction to cold or of their reproductive act, or both. Evidently, what Breder (1940) thought to be courtship in *Mugil cephalus* may have been some elementary stage in pod formation in a rather confined place and may or may not have had reproductive significance.

None of these cases of "pod" formation has been studied in any detail and not at all from the present standpoints. It should be instructive in many ways to attempt a clear analysis of such behavior. It is more than likely that many more cases in other species and for different reasons would be found to form such groups. Unfortunately most of the casual mention in the literature to what may be such "pods" are much too vague as to detail to be of sufficient significance to quote in present connections.

#### THE PROBLEM OF LEADERSHIP AND HIERARCHY

Groups of fishes, including what are here called aggregations, schools, and pods, are, in general, leaderless. That is clear from the most casual observations and need not be labored at this time. Parr (1927) in his analysis discussed the matter fully. Conceptually, however, it does not follow that all groups of fishes must necessarily be composed of individuals so much alike that the associations are invariably between equipotential individuals. In fact it is easy to establish that in a variety of situations the individuals are not equipotential and that in groups in which such equality is absent there may be other types of relationship.

Instances of such extreme forms as a small carangid's "schooling" with the dorsal fin of a large shark have already been commented on by Breder (1954), in which the large member is probably not even aware of the presence of the smaller. Less extreme is the situation described by Medcof (1957) for the behavior of *Alosa sapidissima* (Wilson) on its spawning grounds. Whether or not the behavior described by this author was part of the reproductive act or in some secondary way connected with it was not determined. However, it was clear that a single fish was

the leader of a more or less single-file procession. The fishes, sometimes in contact, would form a tight circle, in which the same one fish was at the head of the group as much as when the tight circle gave way to an open figure. This fish may, of course, have been a female and the rest males in some prenuptial performance, as suggested by the observer. Such a situation is, nonetheless, from the standpoint of fish associations a leadership in which one individual has an influence much greater than any of the rest, all of which are evidently equipotential at their level of influence.

The behavior of *Pomolobus pseudoharengus* (Wilson) described by Graham (1957) is quite unlike anything seen or heard of by the present author. It is noted here only because it may be associated with spawning in a manner somewhat analogous to that discussed above for *Alosa*. In the behavior described, ". . . each school undulated from the surface of the water to the bottom (6 feet) over a zig-zag course. The school frequently broke the surface of the water, but the surfacing was not accomplished simultaneously by every member of the school. The leaders broke the surface first and the rest of the school surfaced in follow-the-leader fashion. The splash

produced is characteristic; in fact the alewife schools may actually be identified by the sound of the splash." This took place on the afternoon of June 25, 1950, on a sunny placid day, with the temperature of the air 22.5° C. and that of the water about 17.6° C. near the bottom.

Gudger (1944) lists and comments on various cases of fishes swimming in single file or even grasping the tail of the fish ahead to form a chain. *Amphioxus* is similarly discussed by Gudger (1945). These are all old, uncertain, vague, or questionable references to the literature, insufficiently detailed to be analyzed for present purposes. They are, however, of considerable historic interest. If any one of these cases could be properly established as a feature in the behavior of any fish, it probably could be derived from a school or polarized pod and not have necessarily any particular reference to leadership or hierarchy.

Less striking performances, but of the same basic nature as the above, may be seen on the spawning grounds of many kinds of fishes. This behavior is especially marked in the Cyprinidae and Catostomidae in which many males may attend one female, generally much larger than her consorts. Figures of such behavior in a variety of catostomids are given by Reighard (1920). In these cases the dominance of one fish because of the sex drive and the sex ratio is the basis of the behavior and could if desired be conceptually eliminated from consideration with associations of a "social" nature. However, it is obvious that any such precise stricture would be purely arbitrary.

Cases in which the "leadership" is of a non-sexual order are to be found in goldfishes, in and out of their reproductive periods. In instances in which goldfishes are kept in pools of sufficient size so that they may form bands and wander about together through otherwise "empty" water, partial leadership is evidently based on color or markings. Thus, in a group of plain yellow goldfish in which a few pure white individuals are included, the latter may usually be found at or near the head of such an aggregation when it moves forward more as a school. This feature disappears when the group stops and fans out randomly. This was first noted in goldfishes

in Mountain Lake Sanctuary, Florida (pl. 73, fig. 1). While it was not possible to make statistical measurements, it was obvious that the white fishes were in the van of these processions almost all the time. This detail of school structure was checked in a pool on the author's property, with similar results. It would appear that this is probably nothing more than a difference in visibility of the white compared with the yellow fishes and that there is a stronger reaction on the part of the other fishes to move towards the most conspicuous members, which in this situation are presumed to be the white ones. The converse was also noted, in that dark gray goldfish kept disappearing against the background of the bottom and were most often not to be found in small groups of which every individual could be counted. Such an interpretation would check well with the data of Breder and Halpern (1946) and Breder and Roemhild (1947), who demonstrated that the social behavior of goldfishes differed in a locomotor sense with differences in the pigmentation of the individuals that were involved. This tendency of white fish to be followed more than yellow ones in a group predominantly of the latter color would thus be a gross appearance of the results of the behavior that was statistically measured by the above workers in a more refined manner.

The well-known case of the gray snapper, *Lutianus griseus* (Linnaeus), and the schoolmaster, *L. apodus* (Walbaum), appears to be one of this order of relationship. In the West Indies the former is usually much more abundant than the latter. They live in essentially similar places, and separate schools of each can generally be found. Occasionally a single *L. apodus* is seen in a school of *L. griseus*, but there is evidently no record of the reverse relationship. As its common name implies, the gray snapper is basically a grayish fish, while the schoolmaster is basically yellowish. When one of the latter fish is present in a school of gray snappers, it stands out distinctly, and when the school is moving along it is, as is the white goldfish above discussed, usually in or near the forefront of the moving body of fishes. Natives say that the name "schoolmaster" was derived from this fact. This would seem to be associated with its more striking and brighter colors. These

two species resemble each other notably, except for coloration, but there are other rather intangible differences. In most places anglers report that the gray snapper is a much more "wary" fish and consequently harder to catch. A limited personal experience would tend to bear this out. At night these two species evidently separate considerably, each moving towards different areas for feeding, a matter discussed at length by Longley and Hildebrand (1941).

Closely related to the above considerations is the problem of hierarchy. The approach of one fish to another may be considered positive or negative if it results, respectively, in a pacific swimming along together or in aggression on the part of the approaching fish. The latter, if the activity is general and violent enough, leads inevitably to a status of isolation and solitary behavior or to the establishment of a peck order within an aggregation. A school, as here used, is automatically reduced to an aggregation on a very slight appearance of aggressiveness by relatively few individuals. From this it follows that when both an aggressiveness and a tendency to form groups are present, a hierarchy may be established. Basically when these are just balanced, they may persist for some time, but unless there is some special extrinsic influence that is responsible for the balance, which is usually temporary at best, one falls below the other in value, and the fish move either to a properly aggregating condition or to one of solitary existence. Such extrinsic influences may be limited feeding areas, or restricted breeding sites, involving conflict brought on primarily by territoriality or crowding caused by overpopulation or other matters. In the first case, limited feeding areas, there is often a cessation of hostilities among solitary fishes, such as barracuda, when they strike individually into a school of food fishes, and the schooling habits of the prey itself make a "restricted feeding area." The predators usually simply avoid one another. Bottom-feeding fishes, such as many kinds of gobies, will often drive another off before striking a quiescent food object. This would seem to be little more than an extension of their territoriality which notoriously weakens when the individuals are off their home territory. The peck order, with crowd-

ing, has been extensively studied in laboratory aquaria, for here such crowding may be produced quite incidentally or unavoidably, and not infrequently leads to destruction of the lower members of the hierarchy. In a state of nature this type of relationship is not often seen, because usually there are other effects that depress the activity of the fishes. For example, mild suffocation, as happens in a drying pond, will reduce the aggressive activity, as was demonstrated on *Aequidens latifrons* (Steindachner) by Breder (1934). Eddy (1925) indicated that the young *Ameiurus melas* and adult *Schilbeodes insignis* intensified their aggregating on stimulation, by caffeine and strychnine sulphate, and reduced it on suppression, by chloretone and potassium cyanide, all in very small concentrations. Both excessive heat and cold produced similar results. These data, taken with the many casual references in a host of experimental papers, as well as personal observation in the field and in aquaria, seem to indicate the simple physiological condition that organisms sickened or otherwise subdued by unusual environmental conditions fail to respond in their typical fashion. Their social responses, hostile or social, evidently are among the first to drop out under these conditions.

The case in which reproductive activities interfere with group formation in fishes is much more complex and varies widely with the species involved. The case of *Gasterosteus aculeatus* has been discussed by Otterstrøm (1912) and Parr (1931). Since then many details have been developed by a large group of European workers. The gist of this work is that out of the breeding season both sexes form aggregations or schools, but when the males develop their red breeding colors, they become aggressive and disperse, but the females continue to school until the actual egg laying is about to begin. After the reproductive period is over the groups reform. Much of this has been summarized by Tinbergen (1942 and 1953) and commented upon by Keenleyside (1955). Basically similar data have been given for various cichlids by Breder (1934) and Baerends and Baerends-van Roon (1950) and for centrarchids by Breder (1936). The comparable items in the behavior of *Bathygobius soporator*, which is territorial at

all times, are discussed by Tavalga (1954).

Perhaps the best example of a fish that is found in aggregations and schools while at the same time displaying usually a mild form of peck order is to be found in certain of the cyprinids. *Danio malabaricus* Jerdon and *Brachydanio rerio* Buchanan show schooling, as a fright school, aggregating as a general situation, and some hierarchical behavior as a casual event. The first is discussed by A. Haas (1956), and the other two are discussed by Breder and Halpern (1946). These second two attitudes may represent the closest approach to a mixture of aggregation and hierarchy. The schooling is definitely induced by extrinsic effects while the hierarchical tendencies appear to be chiefly intrinsic and presumably of sexual origin. *Phoxinus* in schools actively drive off smaller or larger individuals or groups, according to Berwein (1941), which could be conceived of as peck-order behavior, as above mentioned, but elevated to a group level.

The only other data that seem to bear on the matter of schooling and hierarchy are

given by Hoar (1954) whose classic studies of the behavior of young salmon brought out a point otherwise unobserved in such studies. Of young *Oncorhynchus kisutch* (Walbaum), which he found to be more aggressive than any of the others of the genus studied by him, he wrote, "It may be noted here that the aggressive behavior displayed by coho does not produce an orderly arrangement of pecking with respect to particular individuals and has, therefore, been termed nipping" (Hoar, 1951). Nonetheless, he considers this effect dispersive and notes in other connections that coho smolts ". . . show marked territorial behavior, rest near solid objects, and are not markedly stimulated to movement by current. These observations seem to explain the relatively slower downstream movement of coho smolts."

The wide-ranging aggregations of *Mustelus canis* (Mitchill) show a certain degree of hierarchy in that the smaller avoid the larger to the extent that a difference in length of as little as 6.7 per cent will elicit the reaction, according to Allee and Dickinson (1954).

#### FISHES IN ORDERLY FILES

A very interesting photograph, which has been published in various popular magazines and finally commented on by Gudger (1949), Bonner (1952), and Thorpe (1956), would seem to have a much simpler explanation than has been given it. The picture, here reproduced as plate 74, figure 1, shows a group of trout arrayed in extremely regular ranks in what is evidently a "standing school" in rather swift water over a series of riffles. These transverse ridges are common enough in trout waters where there is a sand bottom, but usually they are not places where trout customarily station themselves. While no details are available and the photographer is unknown, after extended inquiry by both Gudger and myself, it appears that the situation was one in which only less preferable areas were available to the fishes.

On the downstream side of these sand ridges a slight eddy is formed, which presents a line of comparatively still water in which such fishes usually come to rest. Fish in other situations downstream of a small rock or fallen log rest similarly and can be seen regularly in suitable locations. This fact alone can

easily account for the transverse parallel rows of fishes which follow the riffle marks closely. Grant (1951), commenting on the situation, was well aware of the mechanics involved.

The apparent "pairing" of fishes in groups of two along the transverse rows is to be explained by a peculiarity of the social reactions of these fishes. In nearly any group or near-school of trout it can be noted that, unlike herring or mackerel, such uniform spaces are left by the fishes between one another. Differences in the distances usually can be seen through such an assemblage. The minimum distance is about as well marked as in those other forms, but it is apt to be expressed mainly between two fishes. It is as though it was not possible for the individuals to "keep track" of a fish on each side of it. In a moving group of such fishes this is not a static matter, for usually any two fish retain their close positions for only a short time, as it were, changing "partners" all the while. This does not show well in still photographs, but figure 2 of plate 74 indicates the condition.

In connection with all such cases of the

form of standing "schools" in flowing water, it must be remembered that it is possible to arrange the distribution and form of the schools into almost any outline desired by suitable adjustment of the amount of flow and its direction, together with whatever other influences happen to be involved in the forming of a specific group. Such an arrangement is seen in perhaps its simplest and

purest form in winter groups of fishes under such conditions, as, for example, has been discussed by Breder and Nigrelli (1935). Anyone with access to a trout-hatchery trough of fingerlings can cause the fish to line up in a manner similar to that shown in plate 74, figure 1, by wedging strips of wood of suitable size and cross section across the troughs at the bottom.

### FISHES IN BALLS

There are various reports on fishes found in aggregations or schools that more or less resemble globular masses or balls. Allen (1920) reported the occurrence of *Sardinella coeruleus* (Girard) in a compact symmetrical ball approximately 6 feet in diameter. It was under attack by loons. The ball indented at the point of attack, but apparently no fish were caught. Springer (1957) reports such assemblages in *Jenkinsia* and *Lagodon*, both in the open ocean. A theoretical assemblage in a uniform environment aggregating with a minimum of exposure would take on a spherical form. Certainly these same species in shallow shore waters show other forms of schools, resembling more a thin sheet of varied outline than a thick, compact mass as described. This may conceivably indicate purely an adaptive reaction to the "thin" sheet of water between surface and bottom as seen in such environments. The influence of light and the effects of one fish's casting its shadow on another in reference to the shape of the group are discussed below under the heading Reactions to Light Intensity.

*Sebastes paucispinis* (Ayres) also forms such balls of massed fishes in open water, as is indicated by plate 76. Because it is physically impossible for a pattern to be placed with complete regularity on a sphere, whorls or other interruptions must make their appearance. The ball in figure 1 of plate 76 shows this geometrical necessity clearly, in an instance in which the fishes line up in a pattern of mostly concentric circles. The physical counterpart of such school formations is, of course, a drop of non-miscible fluid in water of equal specific gravity which forms a sphere, subject to such deformations as currents or other similar influences dictate but which permit it to remain as a "massive" drop. When such a drop is allowed to drift

into a vertically restricted space between the bottom and the surface of the water, it spreads out, involving influences of surface tension, capillarity, and so on.

*Plotosus* of various species form tight groups which are not schools in the sense here used, but are pods in which the fishes are in close contact and sliding over one another. Further details are covered in the section on Pods and Spawning above.

Bolster (1958) showed by means of an echorecorder that the long axis of herring schools was parallel to the direction of the current. This effect was most marked over a smooth sea floor where flat or trough-shaped. When the significance of the form of the outline of a fish group is considered, it should be noted that Tokarev (1955) attempted to define the activity of various fish schools by the outline that the schools showed. Thus he wrote that, when plankton is sparse, a school of young *Mugil* moves rapidly, the formation is tight, the school is teardrop-shaped, and feeding occurs as individuals at the rear of the school move up and replace those at the front which, after having left the school to snap at plankton, drop back to the rear, all members of the school thus feeding in rotation. As the concentration of plankton increases, the forward movement of the school diminishes, its anterior end fans out, the school takes on an oval shape, and the fishes feed simultaneously. With still greater concentration of plankton, the forward movement of the schools ceases altogether, and the fish feed at random. *Atherina* and *Trachurus* are described as showing similar feeding habits. While there are evidences of a very slight tendency in schools of *Mugil* to feed somewhat in this fashion, it is extremely doubtful if any American species are so systematic in their behavior. The description of *Mugil* feed-

ing on surface plankton in another part in the present paper sets forth the reasons for our thinking that the above is a considerable oversimplification.

The chance of finding one of these globular masses of fishes in a situation in which analytical examination would be possible is remote, but it is possible at least to obtain hints as to their structural nature by various oblique methods. The young of *Mugil cephalus*, when in the "Querimana" stage, spend much of their time in small groups in a single layer at the surface of the sea. They may be in a well-formed school or in a simple aggregation. Fright is evidently one of the principal school-forming influences. If netted and transferred to an aquarium, they immediately form a very tight school at the surface of the water, which is usually elliptical in outline and several fishes deep. This they maintain for long periods and return to promptly on any unusual disturbance.

The fishes in the sea vary the forms of their schools according to their activity and external influences, although these schools are not infrequently roughly elliptical. When in this form, the long axis is commonly little more than twice the short diameter. Because of the elongated shape of these fishes and their spacing, in such a school there are usually about as many fishes along the long axis as along the short. This condition is even more marked when a group is transferred to an aquarium and forms its fright school which has a much greater constancy of shape. One such school of 32 individuals, which was photographed 10 times over a period of a few days, showed the fishes to be deployed in the following manner:

Axis	No. of Fishes		
	Mean	Maximum	Minimum
Length of school	5.3	6	5
Width of school	4.8	6	3
Depth of school	4.3	5	3

It is evident from the above that the number of fishes on each of the three diameters does not differ greatly, so that, if the dimensions of the fishes were equal on each axis, the form of the school would not be very far from a sphere. Actually it differs considerably from a sphere, and the form may be approximated by the multiplication of the number of fishes along the three dimensions, as follows:

Length	$5.3 \times 1 = 5.3$
Width	$4.8 \times \frac{1}{2} = 2.4$
Depth	$4.3 \times \frac{1}{3} = 1.4$

This is very near the proportions of the three dimensions as found in these schools. It gives a relative measurement of how close these fishes pack themselves. They may pack themselves twice as many in a given distance in the width of this close school and still maintain swimming room and three times as many in the depth of the school, as all the swimming motions are in the horizontal plane. There is, of course, a flattening at the water surface of what otherwise would likely have been an approximation of a prolate ellipsoid. Plate 75 shows the fish both in the sea and in an aquarium.

If it is granted that these fright schools are formed by each fish's trying to reach the middle of the group or "hide behind" its fellows, such a formation would be expected on purely physical grounds. It becomes a matter of presenting a minimal surface, which would normally form a sphere, but is here distorted by the comparatively large size of the units that comprise the group, their elongate shape, and polarization. The tremendous schools that were referred to earlier, if they have the same or some comparable genesis, should be able to attain a much closer approximation to a sphere, because the vastly greater number produces a much larger body in which the individuals are relatively much smaller. According to the few published accounts, this form does obtain.

### COLLECTIVE PROTECTIVE BEHAVIOR

Fritz Haas (1945) postulated "collective mimicry" for insects (grasshoppers) that in small tight groups resembled nearby whole caterpillars. This concept was evidently new in the area of protective resemblance, involv-

ing not an individual effect but a large, multi-individual component. Cases that various students have thought to be more or less similar to it in fishes have been described by Breder (1948) for small groups of *Eucinosto-*

*mus*, Knipper (1953) for juvenile *Plotosus*, and Springer (1957) for very large groups of *Jenkinsia*. As in all such questions, it is not easy to separate the size of the subjective component from that of the purely objective one. That a compact group of fishes, such as a pod or school, might resemble some other object and thereby gain a measure of protection is, of course, a perfectly defensible *a priori* idea. How perfectly any such case might work out or to what extremes it might be developed, however, would be determined by the totality of the environmental factors and the past history of the situation. Cases such as the above, however imperfect they may be and how much investigators subjectively may read into such behavior items, must almost surely protect at least at times, and to that extent be useful to, the species. In other words, a selective "lever" would certainly seem to be present at least. Young *Ameiurus* congregate in a manner not entirely unlike that described for young plotosids, but in fresh-water ponds where there are no echinoids. Here the bottoms are likely to be dark colored or blackish, and the young fish are simply inconspicuous. It is noteworthy that Knipper's *Plotosus* were heavily pigmented, practically black against a light sand background, and seem to belong to that group of fishes that reverses the pigmentary situation and thereby attains an inconspicuous status, such as described for other light sand dwelling marine fishes by Breder (1946, 1948, 1949a, 1955) and Breder and Rasquin (1955b). This condition in itself would help make for protection amid a group of dark sea urchins.

With the above considerations comes the question of what relationship to grouping the individual fish bears which is found solitary but in close association with and resembling some other object, such as a leaf. A list of the known cases of this sort was given by Breder (1946), with a discussion of their biological implications. An especially interesting case is that of young *Lobotes surinamensis* (Bloch), which have been shown by Breder (1949b) to aggregate with a swirl of mangrove leaves and so much resemble them, both as to form and color and manner of floating, as completely to disappear before one's eyes. Such questions occur as, whether this behavior arose directly and the species was always solitary, or

whether this is a further extension of the aggregating habit, or whether at one time the ancestors of the present-day form once schooled with one another instead of leaves. In such cases one could imagine that on a simple selection basis it became more "profitable" for a fish to school with leaves and so widely scatter the individuals. Without the invoking of a predator to account for this behavior, it could conceptually be derived by assuming that these fishes had aggressive tendencies, and in the establishment of a hierarchy it became more useful to individuals to aggregate with inert "individuals," i.e., leaves, than with the active individuals, i.e., other fishes. The question would then become, Is the present-day behavior a result of protective response against a predator only or is it that only in part and primarily against fellow fishes? There are no data on the subject for this species, but in the case of *Chaetodipterus faber* (Broussonet), which when small operates in a similar way with mangrove seed pods, it is known that it is destructively aggressive if placed with its fellows. At a little larger size these fish school together and are entirely passive. Bearing on this is the report by Yabe and Mori (1950) of finding the normally schooling *Katsuwonus* and *Neothunnus* accompanying drifting timber.

Welty (1934) showed that goldfish ate more when with companions than when alone, a matter of social facilitation, and one long known in a general way to aquarists. He also showed that goldfishes ate less daphnia if the abundance of the latter became very great. This he attributed to a "confusion effect," and Allee (1938) drew the inference that groups of fishes ate more and presumably were better off for it than if solitary, but reduced their food intake if too many food objects were present, and that therefore the food objects, which could just as well have been small fishes, attained a certain amount of protection by aggregating because of this alleged confusion effect. While there is doubtless some element of validity in both these experimentally demonstrated propositions, much more experimental work and analysis must be done in this area before it would even begin to be useful to attempt extrapolation to the possible survival value of such matters in a state of nature. Questions that are not

answered include: Is feeding to satiation beneficial to goldfish? What effect does fullness of stomach have on hesitancy to strike at a daphnia, if non-active food was used instead of daphnia, such as the bottom organisms which ordinarily form the basic diet of goldfish? What would the results have been like, and so on? All of these could be the subject of direct experimentation. Also, is the whole matter one that might be reduced to the reactions of the fish to moving objects—catch a particle before the other fellow on the one hand, too many moving particles give visual saturation and fatigue on the other? The first represents behavior that can frequently be seen when one fish evidently ignores a food object until another moves for it and then rushes in ahead to strike at it just ahead of the other. The second is, of course, the "confusion effect," and while this may be one way of expressing the action, it is certainly anthropopathic and might have more to do to with some such matter as speed of digestion.

That there is such a thing as a confusion effect in hawks when they strike at large flocks of starlings, as discussed by Horstmann (1950 and 1952), seems to be much more likely. Actually it would seem reasonable to suppose that cessation from feeding is not necessarily a measure of any particular inhibition but is caused by a whole series of details, varying with each species and the conditions under which the action takes place. Thus it is entirely conceivable that a very hungry hawk might well be trying very hard to catch a starling but failed because of the milling complex and an inability to get an effective optical fixation on any one bird, while the above-mentioned goldfish might not have been trying to catch daphnia, for more or less obscure reasons related to its internal economy. The formation of globular groups, when under attack as noted in the previous section, may represent such behavior in schooling fishes.

To return to the more central parts of this section, it may fairly be inferred that groups of animals being preyed on obtain a certain amount of security from predation by the totality of all conceivable items of behavior of the individuals involved which interact with the limitations of the predators. Then it

should follow that the more important this type of behavior became to a species the greater the likelihood is that there would evolve, on a straight basis of selection, special forms of schooling or pod formation, such as are described above.

Various persons have suggested that the grouping of fishes or other organisms exposed them to greater dangers of predation, in which cases, contrary to the preceding, the behavior of the predators exceeded the ability of the prey to protect themselves by these means. Certainly the striking of a young *Sphyraena* in a school of *Jenkinsia*, or the striking of a *Caranx* in a school of *Sardinella* (pl. 77, fig. 2), seems to represent such cases. There is clearly no hesitancy on the part of either predator, and the motions of the strike are precise, rapid, and of great economy of locomotion. The milling mass of prey seems not in the least to suggest any indecision on the part of the feeder. Illustrative of this behavior is the following, which was undertaken incident to the studies of Breder (1951). The introduction of a young *Tylosurus acus* (Lacépède) of the size that would readily prey on *Jenkinsia* (about 10 inches) caused very minor activity. The school tended to avoid the rather quiescent hound fish, but then they tended to avoid practically any object. When the fish struck into the school and took a member, a minor tremor ran through the group, but no great rushing about. One of the most notable things incident to this was that, no matter how vigorously the fish fed, the *Jenkinsia* refused to pass over whatever thermal barriers may have been present. This agrees perfectly with Breder's (1951) inability to "chase" them into a thermal state lower by no more than 0.1° C. The *Tylosurus*, however, suffered no such inhibitions and ranged widely throughout the pool, seemingly entirely indifferent to or unaware of such a minute temperature difference.

Avoidances are a little more pronounced in the case of *Selar crumenophthalmus*, which usually makes a small swirl on the approach of any larger object. Such a short-lived swirl is shown in figure 1 of plate 77. It is likely that such considerations led both Breder and Nigrelli (1935) and Baerends and Baerends-van Roon (1950) to inconclusive comments on the supposed utility of fish schools in gen-



eral. The alleged use of the long upper caudal lobe of *Alopias* in herding together schools of fishes is discussed by Bridge (1904) and later by Nichols and Murphy (1918) and Bigelow and Schroeder (1948). There is, of course, no reason to suppose that any of these effects is mutually exclusive, and it seems most likely that all, as well as many more that have not been observed or imagined, exist. Thus these interrelations between feeder and food that occur in compact groups probably show almost a complete range of possible transitions from the absence of some factor to its full dominance, or any intermediate position, which might or might not be related to one or more of the host of other factors involved. Thus, while Sette (1950) thought that copepods might escape a feeding mackerel by darting a short distance to one side and so avoiding the feeder if it was alone, he doubted that this method would suffice for escape from a school of mackerel. Others found that in other schooling fishes, the act of feeding on such organisms was always in the nature of a direct strike at individual organisms. Such observations were reported by Breder and Krumholz (1943) for young *Anchoa mitchilli* (Cuvier and Valenciennes) and *Harengula pensacolae* Goode and Bean, by Verheijen (1953) for *Clupea harengus* Linnaeus, by J. J. Graham (1957) for *Pomolobus pseudoharengus* (Wilson). *Jenkensia lamprotaenia* (Gosse), *Sardinella macrophthalmia* (Ranzani), and *Brevoortia tyrannus* (Latrobe) have all been observed to perform in a similar manner.

An approach to this problem might start with a survey of the details of the feeding habits of these fishes and the manner in which those that feed upon them actually do take their food. J. J. Graham (1957) notes that there is a difference in the feeding behavior with different foods as is indicated by his following statement: "Mills formed in laboratory tanks offered opportunities to observe the feeding movements of the alewife school. These observations and those taken in the field showed that the alewife does not take its food by random straining of water. When *Daphnia* were introduced into the laboratory tank along the course of the mill, the milling ceased and each alewife pursued its prey. Strained liver, which formed a cloud when introduced into the tanks, also had the same

effect excepting that it was consumed by swimming through the cloud and the breakdown of the mill was not into individuals but into numerous small groups. A possibly similar relationship between the compactness of a school and the size of the food upon which it feeds has also been shown for the mackerel (Sette, 1950)." While it is tempting to suppose that the feeding mode of such creatures is a function of the ratio of size of food to feeder, it is nonetheless possible that on survey the relationship will be found to be much more complex. Tending to bear this relationship out is the fact that the even relatively small *Polyodon* strains daphnia by dropping its lower jaw and using its mouth very much in the manner of a "pushed" tow-net (personal observation) or the manner of feeding of large oceanic forms, such as plankton-feeding whales and *Manta*. The descriptions of the feeding of *Rhineodon typus* Smith on both small and large fish by Gudger (1941) and Springer (1957) are also in agreement with this view.

A feature that has evidently not been considered in connection with the effects of and the influences on fish groups of various kinds is that, as has been demonstrated by Welty (1934), goldfishes under experimental conditions show quicker learning when in the company of previously trained individuals than when solitary. Whether this is by imitative behavior, which seems improbable, or by the mere fact that these fishes (goldfishes) are evidently under a condition of "distress" when solitary, is yet to be determined. Ochiai and Asano (1955) show that *Orizias* will swim through the meshes of a net less reluctantly if companions are present. Unlike the goldfish experiments, these companions had no prior experience with the experimental situation. Both these experiments would seem to indicate merely that aggregating fishes tend to follow the leader, the leader being any fish momentarily with a little more "enterprise" or greater visibility than most of its fellows. Probably without this condition the establishment of persistent schools would be impossible. In this connection it should be borne in mind that it has also been demonstrated, as is discussed in other connections, that these same fishes eat more and are less "restless" when in the company of a few compan-

ions than when alone. Eddy (1925) showed that the metabolic rate was reduced in grouped *Ameiurus*, and Schuett (1934) reported similar facts for *Carassius*. Stefan (1958), working with *Phoxinus* and *Gasterosteus*, by oxygen analysis has been able to show that species that normally schooled consumed greater quantities of oxygen when solitary than when in a group of their own kind. When blinded they again consumed more, which bears out the importance of vision to the schooling habit. These findings are, of course, in keeping with the results of other authors that are based on some measure of locomotor activity. The larger oxygen consumption under conditions of isolation or blinding was found to be more comparable to the oxygen consumption of fish of a normally solitary nature. It was further possible for her to show that olfaction played an important part in the grouping of *Phoxinus* and little, if any, in that of *Gasterosteus*, on a basis of oxygen consumption in water in which fishes of their own kind had been swimming. It should be noted in this connection that various adverse influences have been shown to produce aggregations or schools, as, for instance, in *Micropterus dolomieu* Lacépède by Townsend (1916) for cold, in *Aequidens latifrons* (Steindachner) by Breder (1934) for carbon dioxide, in *Lepomis auritus* (Linnaeus) by Breder and Nigrelli (1935) for cold and carbon dioxide, and in *Micropterus pseudoplites* Hubbs by Langlois (1935) for chlorine. These reactions to adverse conditions may have survival value. The reactions to cold particularly seem to bear more than a passing resem-

blance to the pods of *Mugil* which are seen in the winter time only.

Many of the marked schooling fishes are extremely silvery, including most of the Clupeidae and many of the Scombridae, Carangidae, and Atherinidae. Burnette and his co-authors (1952) were aware of this circumstance, especially in reference to *Sardinia caerulea* (Girard). Evidently the flashing of the sides of such mirror-sided fishes makes their presence visible at a much greater distance than would be possible without it, which may have significance in the reestablishment of schools after a dark night. Also many of the Mugilidae are silvery, while *Mugil cephalus*, which is herein discussed at length, is much less so than are most of its congeners. To prevent the preceding remarks from being misunderstood, it is necessary to make note of the fact that silvery fishes in their ordinary quiet swimming blend into the background because of the mirroring of the background in both quality and color by their sloping reflective sides. However, when they make turning movements, so that their sides reflect the light coming from above, they give forth a silvery flash that is distinct from both above and below the surface of the water. Under these conditions such fishes become conspicuous. The other two species of *Mugil* on the Florida Gulf coast, *M. curaema* and *M. trichodon*, are decidedly silvery and are much more oceanic in habit than slightly silvered *Mugil cephalus* (the black mullet of the region) which spends much time in the very turbid shallow bays.

#### HETEROTYPIC AND HOMOTYPIC GROUPS

In the studies on the social behavior of *Jenkinsia* undertaken in the 12-foot circular pool at the Lerner Marine Laboratory, most of the attention was given to homotypic groups, as reported by Breder (1951). Another series of experiments considered the effects of the presence of different species, including both predators, reported in the preceding section, and fishes so similar in size and general appearance as not to be readily distinguishable.

At one time in January, 1952, a group of *Anchoa hepsetus* (Linnaeus) became available

which when established in the pool formed a large school. These fishes so nearly resembled the *Jenkinsia* in size, shape, and general deportment, that it was sometimes difficult to be certain which species was under observation. Neither species of fish was confused in the slightest. Each maintained a separate group as soon as the schools formed. Frequently when the two schools were halfway across the pool from each other they would swim towards each other, but when the distance had been reduced to about 1½ feet, they would turn away and refuse to approach

more closely. Whatever recognition mark was operating, it evidently disappears at a distance of greater than 18 inches. When temperatures were low and the schools tended to break down, this specific separation also tended to disappear. It would seem that at these lower temperatures their physiological and psychological integrity was more or less generally impaired. There is a brief prepublication reference to this situation in Atz (1953).

The strong "antipathy" that these two isospondyles showed for each other is the more remarkable, for strikingly different-appearing fishes of one species will usually be accepted in a homotypic school. While the above studies were being made, a large school of *Sardinella macrophthalmia* (Ranzani) stationed itself off the laboratory dock. In it was a decolored individual much lighter than the rest which was seen off and on for a period of seven weeks. Careful observations were made to try to detect any evidence of differential behavior on the part of the whitish fish or on the part of other members of the school near it. At no time was any evidence seen of behavior that would indicate that any of the fishes involved behaved other than "normally" when the whitish individual was close by. A photograph taken from the dock (pl. 73, fig. 2) shows this light-colored specimen and gives some indication of its conspicuous appearance. Actually in full-life colors it was much more conspicuous than the photographic rendering in monochrome suggests. The above is not to imply that there was no differential response, but only that none could be detected by simple observation, for it has been shown by Breder and Halpern (1946) that by suitably detailed analysis a mixed group of yellow and gray goldfish behaves differently from a group of either color alone, but it does imply, however, that fishes will always necessarily group with distinctly different-looking individuals of the same species.

Also placed in the pool was a school of small *Harengula* nearly twice the size of the other two species. These also maintained a monotypic group except at low temperature. Actually it was obvious, moreover, that there was less repulsion between the *Harengula* and the anchovy than between the other two combinations. The above observations all re-

fer to situations in very clear water, with the fishes fully visible to one another at all the inter-fish distances involved. Considerations invoking other sensory modalities are discussed elsewhere.

Related to these thoughts is the work of Keenleyside (1955) who found that, if he removed the dorsal fin of a group of *Pristella riddlei* (Meek), a test fish would show preference for an unoperated group if given a choice. The black target mark shown by the intact dorsal fin would seem to be the determining factor, although there may have been added cues in a slight difference in swimming associated with fin mutilation.

To be compared with such matters are small groups of a variety of local fishes that were held in a large pen at the Lerner Marine Laboratory year after year. Many of them formed aggregations or schools. *Seriola dumerili* (Risso), *Caranx sexfasciatus* (Quoy and Gaimard), *Caranx ruber* (Bloch), *Tarpon atlanticus* (Cuvier and Valenciennes), and *Albula vulpes* (Linnaeus) regularly maintained separate monospecific schools. Ordinarily a newly introduced individual would wander aimlessly until sighting or being sighted by the resident group of its own species, whereupon recognition was obviously instantaneous and merging immediate. In the nearby open water young *Caranx sexfasciatus* from 3 to 6 inches long are generally to be found in groups of three to a dozen or more showing typical schooling behavior. Others, in this same size class, and often in view of the schoolers, behave otherwise. Rarely are these individuals found swimming along as solitary fish, but more usually are to be seen schooling with some other fish. For example, a group of six large *Mulloidichthys martinicus* (Cuvier and Valenciennes) was seen to be attended by two *Caranx*, each independently and persistently "schooling" with two different individual goatfish and not paying the slightest attention to each other. The small *Caranx* were obviously hard pressed to keep up with the larger goatfish which were swimming along easily. They were not feeding, and it is possible that this association resembles the feeding association between goatfishes and various gerrids, in which the latter follow along and catch such food objects as the goatfish miss when they root in the bottom

with their barbels. Such a condition may be primary to most of these unusual associations.

Most fish schools are monotypic, but there are occasions when various more or less superficially similar forms may school or aggregate together. Such mixed schools are comparatively frequent in the young stages of various *Eventognathi*.

A very common case in the New York region is that of common schools of the post-larval cyprinid *Notemigonus crysoleucas* (Mitchill) and the post-larval catostomid *Erimyzon sucetta* (Lacépède). In ponds these two tend to stay in common schools, or at least in aggregations, throughout the first winter. Superficially they are remarkably similar in appearance in the early stages, but they are strikingly different in detail. The head of the first is well covered with integument and pigment, while that of the latter has a depigmented clear stripe from near the snout to the origin of the dorsal fin.

A cloth dip net full of fry from a large school was permitted to grow up in a lily pond and was transferred to an aquarium with the coming of fall. At the end of November, they were still aggregating together. There is on careful examination a slight difference in their behavior during the daytime. More *Erimyzon* are closer to the bottom of the aggregation on the average, and at feeding more *Erimyzon* pick off the bottom and more *Notemigonus* feed at the surface or high in the water, although all partake of each item of behavior noted.

At night, however, a distinct difference

appears. *Notemigonus* merely rest quietly and lighten their lateral stripe somewhat. *Erimyzon* on the other hand sink to the bottom, resting lightly on the caudal and pelvic fins, and change their pattern from a simple lateral stripe to one of blotches so that the striped effect largely or completely disappears. With the coming of light the fish rise from the bottom and return to the striped phase and re-join the group of *Notemigonus*. Plate 79 shows these changes. The daylight picture (pl. 79, fig. 1) shows all the fish up from the bottom. Three *Erimyzon* are seen one over the other to the left of the picture, their somewhat wider lateral stripe serving to identify them. Another is viewed head on near the bottom at about the center line of the picture. The clear stripe on the head can be seen. All the other fish well in focus are *Notemigonus*. The nighttime picture (pl. 79, fig. 2) was taken by flashlight, the photographic equipment having been left in place since the other picture was taken. Four *Erimyzon* rest on the bottom, the one in the left foreground showing the blotched phase clearly. The fishes off the bottom are all *Notemigonus*. It is noteworthy in this connection that immediately after the flash bulb was used, one of the *Erimyzon* died, and all were evidently distressed, while the *Notemigonus* only showed slight fright. As would be expected, these fish with the exposed brains are evidently much more sensitive to rapid and large light intensity changes than are the others, a matter more fully discussed in the next section (see especially under *Cypselurus*).

## SPECIAL ENVIRONMENTAL INFLUENCES ON FISH GROUPINGS

FOLLOWING THE NEED to discuss in some detail certain of the more special aspects of fish groupings comes the need to examine certain of the special influences that the environment exerts on them. Similarly these are discussed as separate items, in order to permit more satisfactory continuity in the latter portions of the discourse. The reasons for treating the material in this manner are given at the beginning of the preceding section.

### THE INFLUENCE OF LIGHT AND TEMPERATURE

It is desirable to consider the effects of light and temperature together, partly because physically they are derived from a common source and differ only in wave lengths. Because such features of the environment involve several aspects of the reactions of fishes, it is necessary to digress into these matters sufficiently to establish a proper basis for the purposes of this paper. Fishes may react in a complex pattern to light and temperature by modifying their pigmentary pattern, their locomotor behavior, and their social responses. Commonly all three types of response are involved, and each may have a direct effect on the others. For this reason the following treatment is divided into two parts, Pigmentary Reactions and Locomotor Reactions, while the corresponding "social responses" are discussed within these two parts where they are pertinent, without any heading as they are expressed mostly through the mediation of the other two.

#### PIGMENTARY REACTIONS

Pigmentary response to environmental stimuli in teleost fishes, accomplished primarily by means of an adjustment of the positions of the granules in the various chromatophores, has been the subject of study by many researchers. The most obvious and widespread reaction of this kind is that in which fishes tend to match the tone, and often the color, of the background against which they are seen. Until recently this kind of reaction has received almost the entire attention of researchers in the field and has been summarized by Parker (1948). That this reaction to background is not inevitably pres-

The relationship of this section to the next one has likewise been indicated at the beginning of the preceding section. As these three sections handle rather complexly interlocked concepts, it was thought advisable to preface each of them with these explanatory comments, which taken together should constitute adequate guidance to a clear understanding of the viewpoint under development.

ent, varying only in extent from a condition of nearly no ability to that of the most marked and rapid background matching, has been shown by Breder (1946, 1958, 1949a, and 1955) and by Breder and Rasquin (1950 and 1955b). They have indicated that various fishes from the most diverse groups showed responses to both environmental stimuli and hormonal treatment precisely contrary to the background matching of others.

Before the materials in the present contribution are considered, it is necessary to understand a point of view expressed in some of the earlier papers. In discussing various general behavioral matters, Breder (1949a) gave a list of six kinds of behavior response to various stimuli, of which only the fourth, "possible pigmentary reactions," need concern us directly at this place. As a point of departure it may be useful to consider this list and extend it to include newer data. The list follows, with various annotations and comments. The italicized words represent new definitive terms intended to clarify the relationships of the various pigmentary responses.

#### "POSSIBLE PIGMENTARY REACTIONS"

"A. In reference to the background"

"i. Matching background"

*Direct responses*

"1. In general tone"

*General direct response*

"2. In pattern detail"

*Detailed direct response*

The above list obviously covers the classical cases, as summarized by Parker (1948), and may be most conveniently called by the italicized terms.

“ii. Opposing background”

*Inverse response*

This covers the various cases of fishes that always or at some time in their ontogeny arrange the granules in their chromatophores to contrast with their background. Cases that have been studied follow, with the references:

- Haemulon melanurum* (Linnaeus); Breder and Rasquin (1950)  
*Chaetodipterus faber* (Broussonet); Breder (1946, 1948), Breder and Rasquin (1950, 1955b)  
*Stathmonotus hempillii* Bean; Breder (1949a)  
*Nodogymnus* sp.; Breder (1955)  
*Antennarius multiocellatus* (Cuvier and Valenciennes); Breder (1949a)  
*Ogocephalus radiatus* (Mitchill); Breder (1949a)

All the fishes in the above list are acanthopterygians and have light-protected pineal areas, and the two tested, *Haemulon* and *Chaetodipterus*, were found by Breder and Rasquin (1950) to react to adrenalin by blanching their normally dark irises only. Rasquin (1958) greatly extended these studies on a number of species and included both the morphology and the histology of the pineal organ and the pigmentary reactions to a variety of hormones. She demonstrated that the blanching of the iris is caused by the reaction of the perineural system of the melanophores to adrenalin, the iral melanophores belonging to that system. The fishes tested were arranged in three groups: forms in which all the melanophores reacted, forms in which only the perineural system reacted, and forms in which none of the melanophores reacted. The last group is represented by two species of Chaetodontidae, and one each of the Acanthuridae and Monacanthidae. Some relationship, not completely clear as yet, exists between this circumstance and the degree of exposure of the pineal organ. No fish listed after the Sphyraenidae, in classifications arranged with the Persoces first in the acanthopterygians, has been found with other than a permanently covered pineal area. No member studied in this assemblage reacts wholly to adrenalin. All have been found to show either no reactions whatever or, at most, a blanching of the iris. The peculiar details found in the scombriform fishes are surely secondary specializations. Various aspects of these features are discussed by Rivas

(1953) and by Rasquin (1958) for *Gymnosarda* and *Thunnus*.

Parallel with the above experiments, a series of tests were carried out on the light responses of certain fishes when under the influence of intermedin and of adrenalin. These are not reported here in detail, as for present purposes it is sufficient that fishes that had no melanophores over the pineal area, *Anoptichthys* and xanthic *Carassius*, showed scarcely any change in their response to light. They averaged a little less light negative, which was nearly neutral in these fishes before injection. The readings were just at the edge of statistical significance. *Asty-anax* with their well-covered pineal showed a definite change from a negative reaction to light to a strong positive reaction. The possible significance of this fact to schooling behavior is taken up below in its proper place.

It is to be noted that all the cases so far studied concern fishes that contrast dark pigments against a light background. None showing light pigments against a dark background have so far been discovered.

“iii. Indifference to background”

*No response*

This classification covers forms that show no grossly evident response to background, such as *Carassius* or *Pomacanthus*. It is to be understood that this is relative rather than absolute and that probably no teleost exists that does not move chromatophore granules to some extent in response to such stimuli, but the cases mentioned certainly do not move the granules enough to induce optically notable matching of background.

“B. In reference to emotional state”

“i. Unvarying with state”

*No intrinsic response*

“ii. Varying with state”

*Intrinsic response*

This classification covers the remainder of the tabulation on pigmentary reactions and does not immediately concern present considerations. It should be noted, however, that in the complex of activity that is “behavior,” the item “B” acts more or less independently of and may interfere with the full expression of “A” or in some cases may fully suppress the latter.

The relationship of the other items of be-

havior, such as hiding, freezing, and so on, which may be carried on simultaneously with the pigmentary response, makes the totality of behavior seem probably more kaleidoscopic than it is in fact. The number of qualitative and quantitative variables, however, under a given set of circumstances makes it often very difficult to analyze the complex fully. In the present studies the locomotor responses to light and its various qualities and to background are considered separately from the pigmentary responses. It is evident, however, that the movements of the whole fish (locomotion) and the movements of the pigment granules (color and pattern change) are both hormonally and nervously controlled and are generally the first things teleosts do in response to a given stimulus.

#### LOCOMOTOR REACTIONS

As in the case of the preceding section on pigmentary response to various stimuli, this section is largely explanatory and classificatory. While the influence of light and temperature on fishes is usually considered as an individual matter between a fish and these features of its inanimate environment, it can be shown that these influences have a direct bearing on the reactions of a fish towards its fellows. In addition to the gross aspects of the fish's being able to see adequately or not and of being cooled or heated to a point where normal reactions are no longer possible, a host of more subtle influences bears on the social behavior of the species involved. With these reactions the present treatment is especially concerned.

#### VISUAL REACTIONS

In addition to adjusting the state of their chromatophores to match or contrast with background many fishes will swim only over a matching (or contrasting) background. This may be frequently observed in the field, where schools of clupeids swimming over light sand refuse to pass over a dark weed bed unless there is absolutely no way to avoid it and vice versa. Various studies have been made on the special features of such behavior by Brown and Thompson (1937), Breder and Halpern (1946), Breder (1947b, 1951, 1955), and Breder and Rasquin (1955a). The significance of these studies in present connec-

tions is that they can be invoked to explain, in many instances, why schools, on approaching one another, will at times merge and at other times refuse to merge. The difference in pigmentation, especially of clupeids that have been living over dark and light backgrounds, respectively, is rather difficult to detect under usual field conditions. However, in the few cases in which the author was clearly able to distinguish a difference between the fishes, the behavior was found to be in accordance with the above view. Jones (1956) found that *Phoxinus* would not cross a dark background band when illuminated by from 0.17 to 0.08 meter-candles. Related to this is the work of Kanda and Koike (1958a, 1958b) and of Kanda, Koike, and Ogura (1958a, 1958b) who demonstrated that a variety of fresh- and salt-water fishes were more repelled by vertical nets that reflected long wave lengths than by those that reflected short ones. That is, the fishes would pass through the meshes in the following order: the fewest through red, more through yellow and orange, and the most through green and blue. This apparently has to do with visibility and contrast with the background. Color (wave length) was found to be more important than intensity (brightness), which is in good general agreement with the foregoing data based on other considerations and experiments.

#### EFFECTS OF LIGHT QUANTITY AND QUALITY

Most fishes, in addition to showing pigmentary and locomotor responses to backgrounds, show marked locomotor reactions to the presence and absence of light and to its various characteristics such as intensity and wave length. That the pineal organ and associated structures are light sensitive has been known since the work of von Frisch (1911a, 1911b) and Scharrer (1927). Because it developed that the morphology of the pineal organ and associated structures, as well as various hormones, had a considerable influence on the reactions to light, included in this section are the records of a variety of pertinent experiments on which a preliminary report was made by Breder and Rasquin (1950). The morphological, histological, and endocrinological portions have been covered by Rasquin (1958) and should be consulted

TABLE 1  
REACTIONS OF SPECIES NOT ESPECIALLY  
TREATED IN SUBSEQUENT TABLES  
(In each experiment the choice was between a  
dark and a lighted chamber. Explanatory de-  
tails of each case are given in text. The  
means are those for the lighter cham-  
ber in each case. In each case 4 fish  
were used and  $N=500$ .)

Means	Standard Error	Means Expressed as Percentage
<i>Sardinella macrophthalmia</i> (Ranzani)		
3.988	0.029	99.8
<i>Leptocephalus</i> sp.		
2.52	0.035	26.0
2.86	0.055	43.0
<i>Anoptichthys</i> (Arroya)		
2.122	0.014	6.1
<i>Carassius auratus</i> (Linnaeus)		
0.884	0.060	-55.8
<i>Strongylura notata</i> (Poey)		
2.024	0.049	1.2
2.000	0.044	0.0
<i>Lebistes reticulatus</i> (Peters)		
4.000	0.000	100.0
3.440	0.050	72.0
<i>Mollienesia sphenops</i> (Cuvier and Valenciennes)		
2.416	0.083	20.8
<i>Mugil trichodon</i> (Poey)		
0.93	0.067	-53.5
<i>Synodus synodus</i> (Linnaeus)		
1.04	0.085	-30.7
3.000	0.000	100.0
2.74	0.019	82.7
<i>Betta splendens</i> (Regan)		
1.074	0.039	-46.3
<i>Haemulon melanurum</i> (Linnaeus)		
1.862	0.046	-6.9
1.52	0.040	-24.0
0.13	0.016	-93.5
0.028	0.009	-98.6
<i>Eucinostomus gula</i> (Cuvier and Valenciennes)		
0.032	0.009	-98.4
0.418	0.038	-79.1
0.97	0.025	-3.0
2.638	0.021	31.9
1.646	0.039	-17.7
3.978	0.006	98.9
3.15	0.037	57.5
2.87	0.052	43.5
0.934	0.028	-53.3
3.228	0.032	61.4
2.578	0.038	28.9

TABLE 1 (Continued)

Means	Standard Error	Means Expressed as Percentage
<i>Tilapia macrocephala</i> (Bleeker)		
1.204	0.032	-39.8
<i>Apogonichthys stellatus</i> (Cope)		
3.478	0.082	73.9
2.61	0.039	30.5
<i>Pseudupeneus maculatus</i> (Bloch)		
4.000	0.000	100.0
<i>Abudefduf saxatilis</i> (Linnaeus)		
1.552	0.066	-22.4
2.670	0.074	33.5
<i>Abudefduf analogus</i> (Gill)		
2.706	0.058	35.3
2.342	0.062	17.6
<i>Thalassoma bifasciatum</i> (Bloch)		
0.744	0.039	-62.8
1.325	0.044	-33.75
1.34	0.024	-33.0
0.228	0.027	-88.6
<i>Scarus croicensis</i> (Bloch)		
0.000	0.000	-100.0
2.200	0.055	10.0
<i>Sparisoma radians</i> (Cuvier and Valenciennes)		
4.000	0.000	100.0
0.904	0.052	-54.8
<i>Carapus bermudensis</i> (Jones)		
1.000	0.000	100.0
<i>Monacanthus ciliatus</i> (Mitchill)		
4.000	0.000	100.0
3.916	0.039	95.8
0.906	0.042	-54.7
2.492	0.030	24.6
<i>Histrion histrio</i> (Linnaeus)		
2.042	0.029	36.1

in reference to the photokinetic experiments reported herein, as they were carried out simultaneously as part of a common study. The basic data in this study were obtained by placing the fishes to be studied in a shallow aquarium, twice as long as wide, divided across the middle so that the fish had a choice of two equal areas, which could be differentially illuminated. The method and procedure were described in detail by Breder and Rasquin (1947). They wrote, in part, "The fish to be tested were placed in this container and allowed to accustom themselves to the surroundings for 10 minutes. The number in



the lighted half of the tank were then noted every five seconds for 100 times. Each such experiment was repeated five times. Thus 500 observations form the basis of each full test. The justification of such a procedure is indicated in Breder and Halpern (1946) and Breder and Roemhild (1947).” Privolnev (1956) has independently developed an essentially similar method.

The basic data resulting from these experiments are given in table 1 by species. The column headed “means” is in each case the mean of 500 observations as above described. The important details of each experiment are explained in the text where they are pertinent. The statistical treatment of the comparisons are standard and identical with the earlier work noted above.

In the present studies, concerned with binomial distribution of four fishes, 4 represents full light positiveness, 0 full light negativeness, and 2 represents light indifference, actually the mean of binomial distribution. In the preliminary note (Breder and Rasquin, 1950) it was thought more understandable to the general reader to reduce these values to +100 per cent, -100 per cent, and 0, respectively, values that are related to the direct notation used here by the following equation:

$$Y = (X - 2) 50,$$

in which  $X$  = the values as used here and  $Y$  = expressions in positive and negative percentages. This practice has been retained here. Only in table 1 do the actual means and their standard errors appear. Elsewhere they have been transformed to the expressions in percentage of light positiveness. The standard errors are all proportionally as small as those of table 1.

**REACTIONS TO LIGHT INTENSITY:** The origin of these studies was merely an attempt to determine if certain blind cave fishes were light sensitive (Breder and Gresser, 1941a, 1941b). Later, Breder and Halpern (1946) extended the method to other species. The present part of this paper is to be considered a still further extension of those studies. Table 1 lists experiments that are concerned purely with a choice between a bright and a dark chamber, for which there is no further breakdown. The remainder of the tables pertinent

to this work cover fishes that were studied in greater detail. Various refinements were added to these studies which appear in later tables. Tables 2 and 3 list later experiments with cave fish, in which in addition to the light-dark choice, the fishes were tested against light ratios in the two chambers of intensity of 1 to 2 and of 1 to 4.

In the experiments with a choice between two different light intensities, both light sources were overhead, and a large, light, cardboard separator was suspended vertically over the line separating the two chambers. The light values were read with a direct reading photometer. It is clear from table 2 and figure 4 that, while it is able to distinguish light and react accordingly, *Anoptichthys jordani* is light negative, while *A. hubbsi* is light positive. Only the pair of values between light and darkness has statistical significance. The reactions to different light intensities do not differ significantly from each other nor from random distribution.

The individuals of the above experiments were also tested as solitary cases. The data of these tests are given in table 3. The fact that here again there is no evidence of a correlation between phototaxis and light intensity is perhaps most easily demonstrated by the scatter diagrams of figures 5 and 6. The first shows the means both for the fish tested individually and in groups of four. The social

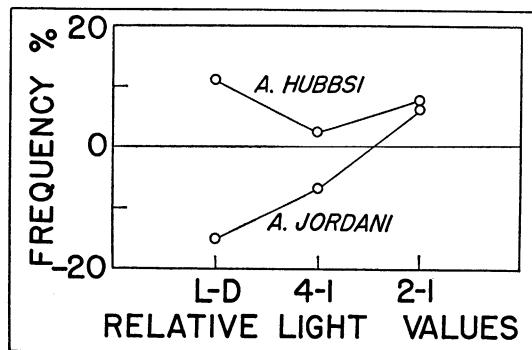


FIG. 4. Reactions to various differences in light intensity. In horizontal index, “L-D” indicates light and darkness, and the numerals “4-1” indicate the difference if the greater was four times the lesser, and so on. Readings were always made in the brighter chamber. Two forms of *Anoptichthys*. Data from table 3.

TABLE 2

## REACTIONS OF BLIND CAVE FISHES TO VARIOUS COMPARATIVE LIGHT VALUES

(All readings refer to fishes in brighter end. Foot-candles are mean values of brighter end.)

Light Ratio	Foot-Candles	Fishes and Their Individual Nos.	Per Cent Positive	
<i>Anoptichthys jordani</i>				
2-1	495	Nos. 1, 4, 6, 11	2.2	
2-1	270	Nos. 1, 4, 6, 11	10.1	
		Mean of all	6.1	
<i>Anoptichthys hubbsi</i>				
2-1	405	Nos. 2, 3, 4, 5	18.7	
2-1	420	Nos. 2, 3, 4, 5	- 3.4	
2-1	245	Nos. 11, 12, 13, 14	3.3	
2-1	217	Nos. 3, 5, 8, 10	13.0	
		Mean of all	7.8	
<i>Anoptichthys jordani</i>				
4-1	457	Nos. 1, 4, 6, 11	- 6.2	
4-1	259	Nos. 1, 4, 6, 11	- 2.7	
4-1	280	Nos. 1, 4, 6, 11	-18.6	
4-1	285	Nos. 1, 4, 6, 11	0.6	
		Mean of all	- 6.7	
<i>Anoptichthys hubbsi</i>				
4-1	360	Nos. 2, 3, 4, 5	- 9.0	
4-1	482	Nos. 2, 3, 4, 5	1.0	
4-1	280	Nos. 2, 3, 4, 5	0.9	
4-1	285	Nos. 2, 3, 4, 5	5.2	
4-1	243	Nos. 3, 4, 8, 10	14.9	
		Mean of all	2.6	
<i>Anoptichthys jordani</i>				
L-D	372	Nos. 1, 2, 3, 4	-15.8	
L-D	380	Nos. 5, 6, 7, 8	-39.6	
L-D	252	Nos. 1, 4, 6, 11	3.9	
L-D	250	Nos. 1, 4, 6, 11	-18.3	
L-D	460	Nos. 1, 4, 6, 11	-10.4	
L-D	392	Nos. 9, 10, 11, 12	- 8.6	
Mean	351	Mean of all	-14.8	
<i>Anoptichthys hubbsi</i>				
L-D	453	Nos. 2, 3, 4, 5	20.5	
L-D	362	Nos. 2, 3, 4, 5	25.7	
L-D	307	Nos. 7, 8, 9, 10	9.3	
L-D	320	Nos. 11, 12, 13, 14	- 5.5	
L-D	320	Nos. 3, 5, 8, 10	14.5	
L-D	302	Nos. 11, 12, 13, 14	2.2	
Mean	344	Mean of all	11.1	
Comparison of the two forms				
Fish		L-D	4-1	2-1
<i>Anoptichthys jordani</i>		-14.8	-6.7	6.1
<i>Anoptichthys hubbsi</i>		11.1	2.6	7.8
Statistical comparison				
		$d/\sigma_a$		
<i>A. hubbsi</i> L-D —				
<i>A. jordani</i> L-D		20.0	Significant	
<i>A. hubbsi</i> 4-1 —				
<i>A. jordani</i> 4-1		1.3	Not significant	
<i>A. hubbsi</i> 2-1 —				
<i>A. jordani</i> 2-1		0.6	Not significant	

TABLE 3

## INDIVIDUAL READINGS OF FISHES USED IN GROUPS OF FOUR IN TABLE 2

(All readings made with only one end lighted.)

Foot-Candles	Fish No.	Per Cent Positive
<i>Anoptichthys jordani</i>		
377	1	9.6
361	2	12.0
362	3	9.6
372	4	16.8
365	5	- 1.2
367	6	10.0
363	7	0.4
357	8	- 3.6
385	9	-12.0
387	10	-17.2
352	11	13.2
345	12	- 6.8
Mean	366	
<i>Anoptichthys hubbsi</i>		
—	1	4.4
345	2	12.8
363	3	36.8
384	4	14.4
361	5	41.6
295	6	11.6
290	7	12.0
302	8	46.0
302	9	6.8
290	10	16.8
322	11	13.6
312	12	8.4
320	13	11.6
318	14	8.0
Mean	323	
Means of groups of four compared with sum of same individuals as isolates		
Group of Four Fish	Sum of Four Isolates	Difference
<i>Anoptichthys jordani</i>		
-15.8	12.0	27.8
-39.6	1.4	41.0
- 8.6	-5.7	2.9
3.9	4.8	0.9
-18.3	4.8	23.1
-10.4	4.8	15.2
Mean of all	-14.8	
<i>Anoptichthys hubbsi</i>		
94		
89-92	20.5	26.4
96		
89-92	25.7	26.4
109		
105-108	9.3	20.4
114		
110-113	- 5.5	20.4

TABLE 3 (Continued)

	Group of Four Fish	Sum of Four Isolates	Difference
117			
90, 92, 106, 108	14.5	35.3	20.8
119			
110-113	2.2	20.4	18.2
Mean of all	11.1	21.5	
Statistical comparison			
$d/\sigma_d$			
<i>A. jordani</i> in groups —			
Random		6.11	Significant
<i>A. hubbsi</i> in groups —			
Random		4.61	Significant
<i>A. jordani</i> as isolates —			
Random		0.58	Not significant
<i>A. hubbsi</i> as isolates —			
Random		3.43	Significant
<i>A. jordani</i> isolates —			
<i>A. hubbsi</i> isolates		3.53	Significant
<i>A. jordani</i> groups —			
<i>A. hubbsi</i> group		20.06	Significant

implications of these data are discussed in another place.

By various modifications of the eyes and

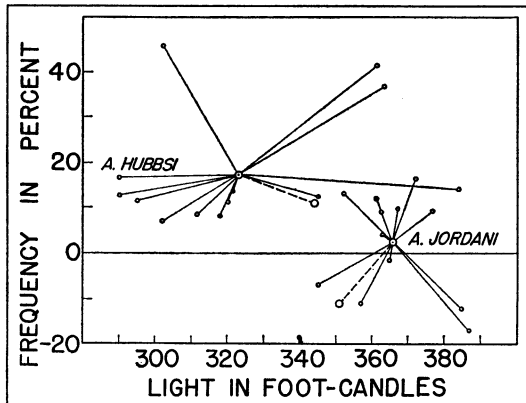


FIG. 5. Comparisons of behavior of *Anoptichthys hubbsi* and *A. jordani* to various light intensities when alone and in groups of four. The small circles indicate individual values of solitary fishes. The larger circle with which they are connected by a fine solid line represents the mean of these values. The large circle connected with it by a dotted line shows the means of the same individuals when read in groups of four. The scatter of the individuals gives a good representation of the extent of individual differences which these fish show. The data are from tables 3 and 4.

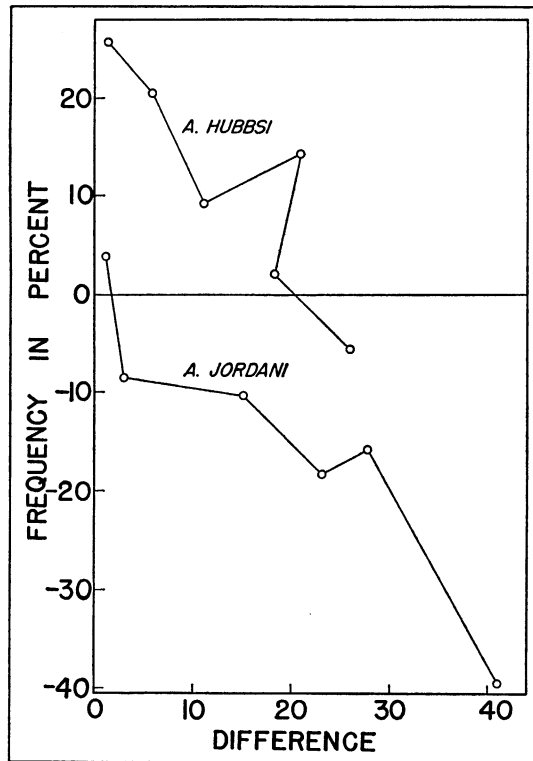


FIG. 6. Measurement of the group effect in the attitude of two forms of *Anoptichthys* towards light. The horizontal index represents the difference between the same individuals read separately and then averaged from the readings of them measured in groups of four. In each case the fish proved to be more light positive in groups than when isolated. The vertical index refers to the positive frequency of the fish in groups of four. It thus appears that the less positive to light the fish were the greater the difference between them in groups and when alone. Data from table 3.

pineal region, certain of these behavioral reactions may be further illuminated. Table 6 gives the data on such experiments carried out with *Astyanax mexicanus*, and the data are diagrammed in figure 7. They show clearly that pinealectomy of these fishes makes them much more light negative than they normally are, which is the reverse of what blinding does to their phototaxis. As has been pointed out by Breder and Rasquin (1947), these fish normally tend to hide in cavities. Hence under conditions of the choice box they retreat to the dark end on any frightening stimulus. When they are blinded,

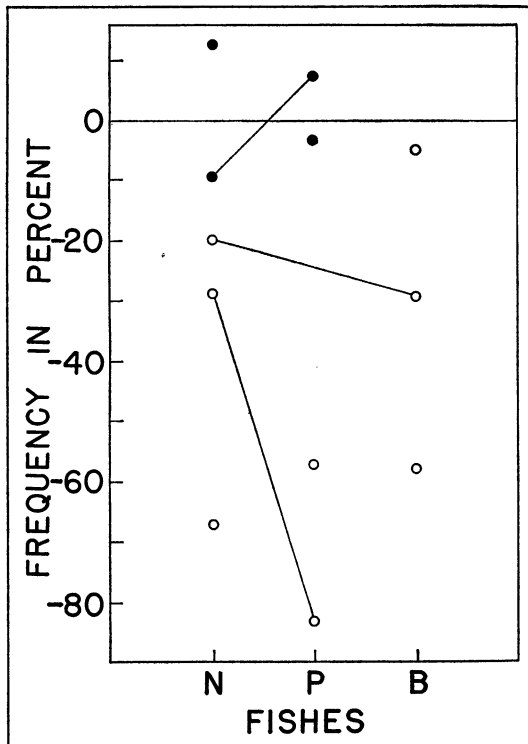


FIG. 7. The effects of pinealectomy on *Anoptichthys* and of pinealectomy as well as blinding on *Astyanax*. Dark circles indicate *Anoptichthys*, and light circles indicate *Astyanax*. Values from fish measured before and after operation are connected by a thin line from normal (N) to pinealectomized (P) or to blinded (B). The unconnected circles are measurements of other fishes for checking purposes. The data are from table 8.

this reaction largely disappears. Naturally, unwanted visual stimuli are easily eliminated during these experiments by screens, but others, principally jars to the building which are unavoidable, induce retreat to the dark chamber. Blinding eliminates the retreating reaction, and such blinded fish show no response to a jar other than a slight twitch. These fish are nevertheless light negative when blinded, just about as much so as the cave fish *Anoptichthys jordani*. Both normally have the pineal area protected from direct light. The fish here listed in table 6 were blinded by optic nerve section, unlike those reported by Breder and Rasquin (1947) which had only the lenses removed and consequently remained strongly light negative. Here again no correlation could be estab-

lished between the intensity of illumination and the degree of light positiveness in either the normal or the operated animals. The comparatively light-positive blind fish from Sótano de la Tinaja evidently become slightly more so on removal of the pineal. The differences are slight, but significant. The case of *Phoxinus laevis*, the fish on which von Frisch did early work concerned with the influence of the pineal on pigmentation, is interesting in present connections. This fish is normally optically controlled to a considerable extent. The intact animal is slightly light negative and behaves not greatly unlike *Astyanax* in regard to hiding under things such as leaves or overhanging rocks. On being blinded, it becomes strongly light positive, as it has a well-exposed pineal. Capping this area in either a blind or intact animal makes it even more light negative than blinding alone makes it light positive. The figures are given in table 8 and in figure 8.

Optically intact *Brachydanio rerio* is notably reluctant to enter a dark chamber. In fact many individuals will not do so at all. Experimentation with a less reluctant group of individuals supplied the data for table 4. Unlike the blind cave fish these fishes are optically active, and it is evident that their sense of discrimination between light values is acute. Although these fishes were not so reluctant to enter a dark chamber as most individuals of these species, nevertheless they showed a sharp preference for a light four times as bright as another. When the difference was only twice as great, they either

TABLE 4

BEHAVIOR OF FOUR *Brachydanio rerio* IN REFERENCE TO VARIOUS LIGHT VALUES

(All readings refer to fishes in the brighter end. Foot-candles mentioned are mean values of the brighter end.)

Light Ratio	Foot-Candles	Per Cent Positive
L-D	322	39.8
2-1	464	-36.1
2-1	430	0.3
4-1	485	32.6
L-D	Fry of pre-school age	96.7

TABLE 5  
 REACTIONS OF *Gambusia* SP. TO LIGHT OF VARIOUS INTENSITIES IN REFERENCE  
 TO SEX, TIME OF DAY, AND SEASON

(All readings refer to fishes in the brighter end. Foot-candles mentioned  
 are mean values of the brighter end.)

Time of Day	Sex	Per Cent Positive	Condition of Fish	
March, 1950				
Day	Female	-41.4	Normal	
Day	Female	- 3.6	Normal	
Night	Female	-25.6	Normal	
Day	Male	-38.2	Normal	
Night	Male	-18.2	Normal	
Day	Male	-74.6	Pineal uncovered	
Day	Female	-43.6	Pineal uncovered	
Night	Male	-92.6	Pineal uncovered	
Night	Female	-95.8	Pineal uncovered	
Day	Male	-43.3	Head blackened	
Day	Female	90.0	Head blackened	
July, 1951				
Light Ratio	Foot-Candles	Sex	Experiment Number	Per Cent Positive
L-D	120	Female	190	-93.6
2-1	120	Female	192	12.9
L-D	80	Male	193	91.2
2-1	100	Male	194	18.2
L-D	80	2 f, 2 m	195	34.5
2-1	80	2 f, 2 m	196	0.0
Statistical comparison				
			$d/\sigma_a$	
Night, pineal exposed, male and female			2.2	Probably not significant
Night, normal, male and female			1.9	Not significant
Female 2-1			0.9	Not significant
Female 2-1 — Random			2.7	Probably significant
Male 2-1 — Random			4.8	Significant
May, 1952				
Time of Day	Sex	Per Cent Positive	Condition of Fish	Set No.
Night	Female	- 71.4	Normal	1
Night	Female	- 5.8	Head blackened	1
Night	Male	- 71.3	Normal	2
Night	Male	- 49.8	Head blackened	2
Day	Female	- 62.6	Normal	3
Day	Female	65.8	Adrenalin injected	3
Day	Female	- 95.3	Normal	4
Day	Female	5.4	Blinded	4
Day	Female	- 0.4	Black head + adrenalin	4
Day	Female	-100.0	Normal	5
Day	Female	- 22.4	Blinded	5
Day	Female	- 2.0	Black head + adrenalin	5
Day	Female	- 99.5	Normal	6
Day	Female	14.3	Adrenalin injected	6
Day	Female	-100.0	Normal	7
Day	Female	98.0	Black head + adrenalin	7

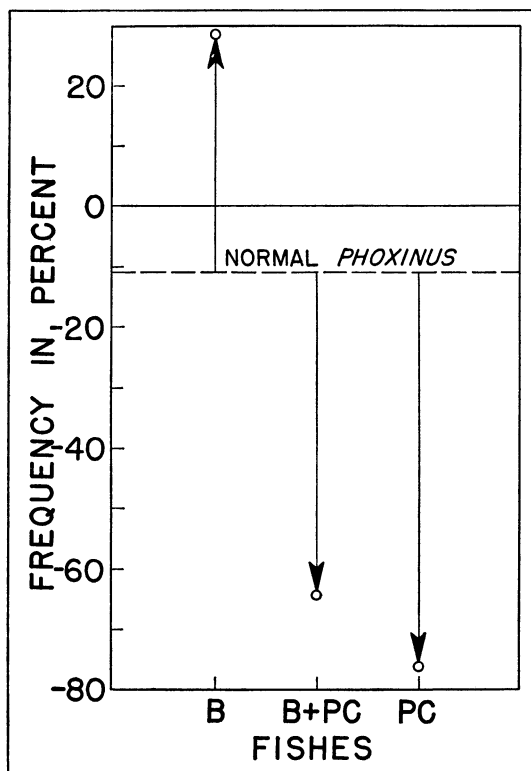


FIG. 8. The effects of blinding and covering pineal on *Phoxinus*. The reaction of the normal fish is indicated by the dashed horizontal line, and the departures therefrom, following experimental procedures, are indicated by the light circles to which arrows point, to blinded (B) and covered (C). Data from table 9.

showed no preference or actually, in one case, showed preference for the dimmer light. Young preschooling fish showed a strong avoidance of the dark, as do most of the adults. Actually most of the low readings were caused by the activity of one fish which was much less light positive than most. Figure 9 shows these reactions graphically. The value nearest the line of indifference is not significantly different from randomness. The other values are all fully significant.

*Strongylura notata*, on the other hand, shows no departure from randomness in either a choice between light or dark or one between two light values, one twice the other (table 1).

*Gambusia* sp. shows a marked sexual dimorphism in respect to its light reactions and also towards its strongly diurnal reactions.

In other words, it is apparent that both sex and time of day influence the readings obtained on these fishes, which shows up clearly, however, only after the pineal areas have been modified. The overlying chromatophores may be removed on these fishes, which allows better light exposure, or they may be covered more fully by the placing of a drop of India ink on the top of the head. The pertinent data are given in table 5. In these tests normal *Gambusia* are found to be slightly light negative, ranging from -41.4 per cent to -3.6 per cent in females and from -38.2 per cent to -18.2 per cent in males. Because the extreme values are both daytime readings of females, evidently the intact pineal is inhibiting the changes here under scrutiny. Covering the pineal of the males in the daytime does not cause them to move out of this range reaching -43.3 per cent, whereas a female so treated becomes nearly fully light positive, i.e., 90.0 per cent.

Exposing the pineals in the daytime causes both sexes to be more light negative than when normal, the females only slightly so, the

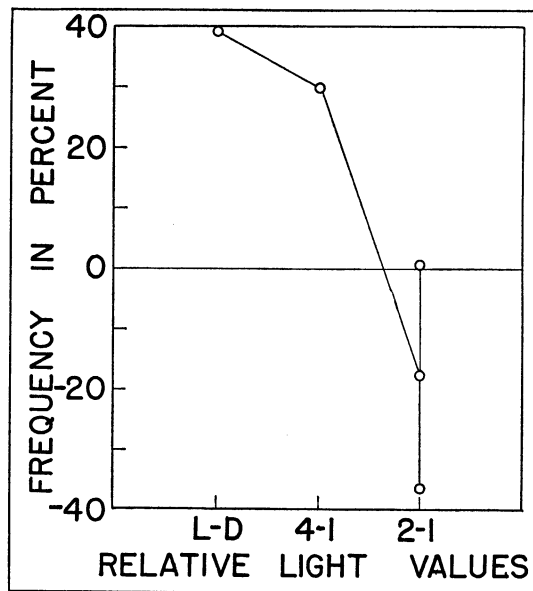


FIG. 9. Reactions to various differences in light intensity. In horizontal index, "L-D" indicates light and darkness, and the numerals "4-1" indicate the difference if the greater was four times the lesser, and so on. Readings were always made in the brighter chamber. Normal *Brachydanio rerio*. Data from table 5.

TABLE 6  
BEHAVIOR OF BLIND AND PINEALECTOMIZED *Astyanax* AND *Anoptichthys*

Light Ratio	Foot-Candles	Per Cent Positive	Fish and Condition
<i>Astyanax mexicanus</i>			
L-D	—	-12.3	4 normal fish
L-D	—	-35.1	Same
L-D	—	-38	Same
L-D	—	-26.7	Same
		<i>Mean</i> -28.4	
L-D	—	-68.9	Pinealectomized
L-D	—	-65.2	Same
L-D	—	-87.3	Same
L-D	—	-99.7	Same
		<i>Mean</i> 82.8	
L-D	—	- 4.7	4 blind fish
L-D	—	-56.9	3 pinealectomized fish
L-D	356	5.6	No. 1, normal
L-D	362	-64.0	No. 2, normal
L-D	370	-37.2	No. 3, normal
L-D	405	16.0	No. 4, normal
		<i>Mean</i> -19.9	
L-D	390	-67.0	Nos. 1, 2, 3, 4, normal
L-D	433	- 4.8	No. 1, blinded
L-D	433	-60.0	No. 3, blinded
L-D	430	-22.0	No. 4, blinded
		<i>Mean</i> 28.9	
L-D	345	-57.7	Nos. 1, 3, 4, blinded
<i>Anoptichthys</i> (Tinaja)			
L-D	—	-16.5	4 normal fish
L-D	—	-22.4	Same
L-D	—	4.5	Same
L-D	—	- 1.9	Same
		<i>Mean</i> 9.0	
L-D	—	3.9	Same, pinealectomized
L-D	—	- 1.1	Same, pinealectomized
L-D	—	- 3.9	Same, pinealectomized
L-D	—	33.1	Same, pinealectomized
		<i>Mean</i> 7.7	
L-D	—	- 3.1	3 pinealectomized fish
L-D	—	13.2	4 normal fish for check

males, on the other hand, showing a prominent difference, well below that of the normal males. Both sexes with exposed pineals when read at night become nearly completely light negative, and the reactions of one sex in this regard are indistinguishable from those of the other.

The work described above was done in March, when the light values are less, the days are shorter, and the water is cooler than in the summer time. It was found that during July and August the males are extremely

light positive, while the females are light negative. At this season the fish are most active, both sexually and otherwise. This situation was taken advantage of in the checking of their response to light of various values. The data are given in the lower part of table 5. Males tested in groups of four were nearly fully light positive, while females similarly tested were just as light negative. Under conditions of light in the ratio of two to one, the behavior of each became completely indifferant and could not be distinguished from

TABLE 7

BEHAVIOR OF FOUR *Atherina stipes* IN REFERENCE TO VARIOUS LIGHT VALUES

(All readings refer to fishes in the brighter end. Foot-candles mentioned are mean values of the brighter end.)

Light Ratio	Foot-Candles	Per Cent Positive
L-D	209	94.2
L-D	175	73.1
L-D	180	85.6
	<i>Mean</i>	<i>83.7</i>
2-1	175	99.7
2-1	105	62.8
2-1	105	38.6
2-1	179	65.9
	<i>Mean</i>	<i>66.1</i>
Earlier work without foot-candle measurements		
Normal fish reported in table 10		
	Maximum	100.0
	<i>Mean</i>	<i>44.2</i>
	Minimum	-77.9

randomness. The clue to this kind of behavior is evidently rooted in the aggressive sexual behavior of the males at this season. Casual observation of an aquarium or pool full of these fishes discloses that the males are actively pursuing females most of the time, while the latter spend much time hiding and dodging under such objects as floating leaves. As the pursuit has an optical basis, it is not surprising that in such a choice box the males frequent the lighted end and the females the dark end. This view of the basis of the behavior can be further supported when a mixed group of two females and two males is placed in the choice box. The group then becomes light positive, as, under the somewhat frightening conditions, there is not much sexual activity, and the fishes tend to form a fright aggregation, the less reactive females now seeking the association of the more active and responsive males. As with unisexual groups, there is no selection between different light intensities where one is twice the value of the other. The work shown in the last part of table 5 is further confirmation of the general remarks above, all experiments involving blinding and adrenalin tending to reduce the light sensitivity to zero. Adrenalin alone, or in

combination with a covered pineal, makes the fish clearly and definitively light positive. The calculations for the statistical significance or its lack in these readings may also be found in table 5.

*Cyprinodon baconi*, which is a markedly diurnal species, actually "roosts" among plant stems when night falls (pl. 80). It is also sexually dimorphic. The data of table 9 are the results of an attempt to determine what influence sex and the fishes' marked periodic behavior had on their light reactions. These tests were made during March just as the male shows the first faint tendency to put on spring colors. Unlike *Gambusia*, there is no evidence of a difference in reaction in the sexes of any great moment. Both show a slight departure from indifference in the daytime and a marked light positiveness at night which is considerably greater in the females. Breder and Rasquin (1950) considered this species "practically light indifferent" on the basis of many fewer experiments. This case is so close to indifference that only extended experiments could differentiate their reactions from randomness. Barlow (1958) showed that *Cyprinodon macularius* Baird and Girard moved in cold water at night and into warmer in the daytime. The experiments on *C. baconi* were carried out at uniform temperatures.

Young immature *Abudefduf analogus*, always light positive, also showed an increase in positiveness after dark (see table 1), with means of 35.3 per cent at night against 17.6 per cent in the daytime. *Scarus croicensis*, fully light negative by day, showed a slight amount of positiveness by night, -100 per cent to 10 per cent in the two experiments in table 1. *Sparisoma radians*, only generically

TABLE 8

BEHAVIOR OF *Phoxinus laevis* IN REFERENCE TO LIGHT AND DARKNESS UNDER VARIOUS RESTRICTIONS

(All readings were made in the light chamber.)

Per Cent Positive	Condition of Fishes
-10.5	Normal
28.5	Blind
64.1	Blind and pineal covered
-76.1	Visually intact, but pineal covered



TABLE 9

THE REACTIONS OF *Cyprinodon baconi* TO LIGHT BY DAY AND BY NIGHT

(All readings were made in the light chamber.)

Day, Per Cent Positive		Night, Per Cent Positive
	Males	
-18.0		24.4
17.1		37.8
-20.5		46.8
-0.8		30.5
-3.2		6.4
22.3		64.8
32.0		41.3
1.0		45.7
Mean -9.8	Mean	37.2
	Females	
-53.2		100.0
32.1		81.8
-2.0		-1.1
12.3		41.9
12.5		56.5
27.0		69.4
17.9		23.5
13.0		66.5
Mean 4.3	Mean	54.8

different from the preceding species, showed reverse behavior, being fully light positive by day and light negative by night, 100 per cent as against -54.8 per cent. As these fish are found together in the same weed beds, a further ecological study of their inverse behavior should be worth while.

*Monacanthus ciliatus* males are more positive towards light in the daytime, as is indicated in the first two experiments, 100 per cent to 95.8 per cent in the daytime as against -54.7 per cent to 24.6 per cent at night, a mean difference of 97.9 per cent and -5.0 per cent.

The observations on the other species listed in table 1 are in close agreement with those of Breder and Rasquin (1950). *Sardinella*, *Leptocephalus* sp., *Anoptichthys* (Arroya form), *Lebistes*, *Mollienesia*, *Apogonichthys*, and *Carapus* are all distinctly light positive, *Histrio* is practically neutral, while *Synodus* and *Eucinostomus* show variations falling on either side of the line of neutrality. The remainder (*Carassius*, *Betta*, *Haemulon*, and *Tilapia*) are all distinctly light negative.

None of them suggested sufficient difference from expectation to warrant the carrying of this type of analysis further in their cases.

Unlike the fishes above discussed, tests on *Atherina stipes*, summarized in table 7, showed almost as much preference for the more brightly lit end of the choice box, although the difference was only one of two times, as they did for a light and dark compartment. It is notable that these fish have a much more exposed pineal area than any of the others so far considered in this connection.

The type of choice box used in this work has always given surprisingly reliable and repeatable results, but *Atherina stipes*, which seems to be predominantly light positive, under certain conditions gives what appears to be a highly erratic performance. When this was traced to its causes, it was found that the groups did not change from time to time, but that there were strong individual differences between the fishes. That is to say, one fish would be nearly or entirely light positive and another nearly or entirely light negative (see table 10). The means given in table 10 were all made in a short time during November. Later, in the spring, this difference between individuals tended to disappear. It is not completely clear why this one species, of the many so studied, presents this peculiarity, but it is evidently associated with the season

TABLE 10

BEHAVIOR OF CERTAIN INDIVIDUALS OF *Atherina stipes*

(All readings were made in the light chamber.)

Per Cent Positive	Condition of Fishes
-77.9	4 normal
32.6	4 blind
31.0	4 pineal covered
81.5	4 normal
68.0	4 normal
	Single fish showing variety in reaction
98.0	1 normal
-100.0	1 normal
-42.0	1 normal
100.0	1 normal
100.0	1 normal
100.0	1 normal
32.8	1 blind
100.0	1 pineal covered

of the year, the sex cycle, and, more particularly, the immediate past history of the individual. Because of this peculiarity, work involving blinding and capping was dropped. All such procedures with *Atherina* immediately stopped any light-negative tendencies, and all readings on other than fully intact fish were well above the line of neutrality, some clustering about at 50 per cent and others at 100 per cent.

In the attempts to understand the behavior of *Atherina* it became evident that often, if not always, the placing of a drop of ink on the pineal area of an individual caused much disturbance to the fish; erratic swimming and general disorganization frequently followed. The impression was obtained that these results were caused by a confusion in sensory cues. As these fish concentrate the granules in the melanophores over the brain in light, they must be accustomed to have light fall on whatever sensory cells are so exposed simultaneously with the formation of retinal images. Conversely they disperse the melanin granules on the coming of night when retinal images are faint or absent. The drop of India ink places the pineal area in a nighttime condition while the eyes are giving daytime cues, which in itself may well be sufficient to elicit the observed "confusion."

A related matter was observed on some aquarium-kept *Cypselurus heterurus*, of from about 15 to 50 mm. in length. These are notoriously difficult to keep in aquaria and are extremely sensitive to handling and incident shock. The fishes in question, however, had thrived for three weeks and were showing a good growth rate, being fed continuously with *Artemia*, which they took avidly. In mid-January, 1951, because of some completely unrelated experimental work, the lights normally on in the aquarium room in which the *Cypselurus* were located had been left off until well after dark. When the lights were turned on, raising the illumination on the tanks instantly from 0 to 26 foot-candles, the fish showed strong shock reactions. Several spiraled around and down and lay upside down on the bottom. One died, but the others recovered. The aquarium had been blackened on four sides except for a narrow band around the top, so that as the fish fell they passed into a region of much dimmer light. If this had

not been so, it is probable that more would have died. The fact that some of them lay upside down on the bottom also contributed to their protection, but it is doubtful if this reaction was deliberate on the part of the fish.

Previously it had been repeatedly noted in the daytime and in the evening with the lights on that the brain was well exposed when the granules of melanin are concentrated. It was observed that the dead fish and the others immediately after the light was flashed on had their brains well covered, more so than had ever been noted before. Such individuals taken about an overboard light evidently come to its influence slowly and concentrate their granules to some extent during that period. As the fish returned to normal under the influence of the light, their granules concentrate to the usual daytime conditions. See also the note on *Erimyzon* under Heterotypic and Homotypic Groups above.

Other fishes in these aquaria, such as *Jenkinsia* and *Sardinella*, notably "jump" when a strong light is turned on or off, but no others have been noted to show such violent reactions as these extremely delicate flying fishes.

The erratic nocturnal behavior of *Strongylura* in the sea, when a strong flashlight beam is directed at it, may be similar in origin.

Under natural conditions the coming and passing of daylight are evidently slow enough for such fishes to make proper pigmentary adjustments without any shock. It would seem that only under such experimental conditions could this shock effect be elicited. The passage of a shadow, as from a bird, certainly makes such fish react, and such reaction is probably a protective measure, but that kind of passing shadow is far too transient to produce a damaging shock.

One fish that is well able to expose or cover its pineal area is *Haplochilus panchax* (Hamilton Buchanan). While this species may "start" when there is a sudden light change, it certainly is not subject to any disorganization under such conditions. Miede (1911) was aware that a "spot" on the top of the head was bright and shining in bright light and became a deep black in the dark, and found that the melanophores involved were reactive to as little as the passage of a hand above the fish.

A rather unexpected bit of behavior was displayed by young *Mugil trichodon* (Poey). In the sea these are found in small schools, generally in very shallow water over sandy bottoms and in full sunlight. Usually they hesitate or even refuse to go under the shadow of a dock or similar object when the light is bright. They have a very well-developed pineal "window" in the skull. Nevertheless in the choice box they were distinctly light negative, with a mean value of  $-56.9$  per cent. Blinding caused them to become light positive to the extent of 19.6 per cent, an effective change of 76.5 per cent. At the present writing the reason for this unanticipated behavior is not clear and needs further study.

When fishes are watched in a school, it is usually impossible to note any reaction at all when one fish passes over another. Generally there is a diffusion of light, so that no very sharp shadow is formed. However, in very bright sunlight and sufficiently clear water a sharp shadow may be formed, and then usually the reaction is as it would be to any other shadow. That is to say, any effect that is at all discernible is of a fish avoiding a shadow on its head. This was seen very markedly in a rather quiescent school of 5-inch *Mugil cephalus* near the Cape Haze Laboratory dock, where it could be clearly seen that the under-riding fishes all had their heads out of the shadows of their fellows above them. The movements of these fishes are sufficiently deliberate to make it possible to see that the lower tiers of fishes moved appropriately as a shadow encroached on their heads.

All these features involving the pineal tend to change with age, for no matter how the organ is constituted the overlying tissues become thicker and less transparent as size increases.

Normal young of *Pseudupeneus maculatus* (Bloch) are nearly fully light positive. A reading of 100.0 per cent was obtained from those taken directly from the sea, but that of some that had been kept in the laboratory with a roof over them was 98.1 per cent.

In one experiment *Abudefduf saxatilis* (Linnaeus) entered the dark compartment, stayed a while, and then swam freely in and out, with a score of  $-22.4$  per cent. Subsequent tests on this species showed that these fish

gave either positive or negative scores, evidently depending on some subtle influence we have not yet been able to designate. The related *A. analogus* (Gill) gave only positive scores.

The above-described test runs on a variety of different fishes give rather clear indications of the variations and complications in the reactions of fishes to light, involving as they evidently do nearly all the reactive capabilities directly or indirectly involved in their social behavior. They are obviously sufficiently complex to prevent any statements beyond those that already have been given in individual comments about each.

A related feature which cannot be treated by the methods described above is the effect of a sudden change in the intensity of light in either direction, which in many cases results in the fishes' seeking a lower level. This reaction is the one usually made to a passing shadow and presumably has considerable survival and directional value. The latter value includes the determination of a diurnal or nocturnal habit and seasonal movements, as the following studies indicate. Johnson (1939) reported, for instance, that the distance from the surface at which herring were found was proportional to the height of the sun, and that there was a pre-dawn eastward movement and a post-sunset westward one. Such a report gives a measure of the low light values that these fish, as adults, seek. Low moons are also said to have an attractive influence on these fishes. It seems likely that many oceanic fishes are similarly influenced into a daily movement that is the result of the vertical and horizontal components so imposed. Dannevig (1932) found that young codfish reacted by sinking in cloudy weather and that four-day old cod and spawning adults showed positive phototaxis. Breder (1934) found that young cichlids descend to the bottom in response to any sudden change in illumination, but are otherwise photo-positive, a condition that, with their guarding parents, makes them seek shelter when a parent shadows them, which it does on any disturbance. Davidson (1949) reported that salmon descend to the bottom on a sudden change in illumination, while steady illumination caused them to rise in the water. Woodhead (1956) found that the movements of *Phoxi-*

*mus laevis* Linnaeus were restricted above certain light values, in that they would not enter an area brighter than 0.2 meter-candles, unless hunger overcame this avoidance.

Jones (1956) showed that this species has no inherent daily rhythm of locomotor activity and that it is active by day and quiet by night in an aquarium with no fittings. If, however, some kind of shelter is provided, such as a hollow brick, the fishes become active at sunrise and sunset. Blinded individuals respond to daily variations in light intensity and are more active at night than in the daytime. Sullivan and Fisher (1947) found that trout reacted more sharply in dim light than in bright light towards a less illuminated area. Hoar (1955a) showed that the young of *Oncorhynchus nerka* could apparently control the amount of light reaching the pineal area by appropriate pigmentary movements, and thought that differences in the degree of development of this complex might be responsible for differences in the degree of negative phototaxis that these fishes show.

The dispersion of schools in darkness has been so often reported that it is to be expected unless otherwise shown. Recent papers include one by Imamura (1953) on *Trachurus japonicus* (Temminck and Schlegel) and one by Ellis (1956) on *Gadus callarias* Linnaeus, even in depths of 100 fathoms. The work of the Japanese students especially (Tauti and Hayasi, 1926; Kawamoto and Nagata, 1952; Kawamoto and Kobayashi, 1952; Kawamoto and Niki, 1952; Owatari, Furuya, and Furuya, 1953; and Maeda, 1955), which goes into details of the manner in which fishes gather about lights, submerged or over the surface, is all in basic agreement that the fishes involved are establishing a position relative to a certain light intensity, and that this shows a basic agreement with their general behavior.

**REACTIONS TO WAVE LENGTH:** A considerable amount of work has been done on the influence of wave length on the movement of fishes since Walls (1942) summarized earlier controversy: Mookerjee (1934), Kawamoto and Takeda (1950 and 1951), Kawamoto and Konish (1952), Maeda (1955), and Ozaki (1951 and 1952). Their conclusions all point to the blue-green region of the spectrum as being most attractive and red and violet the

least. This is clearly on a basis of wave length as apart from intensity. Kawamoto and Takeda (1951) thought they could establish that certain species were attracted to red. This is almost certainly not the case, at least for the fish they used (*Anguilla*), which is thoroughly light negative, and, by the nature of the physical characteristics of their choice box, light-negative animals would most surely gather under the red or violet, as no dark compartment was provided.

A few checks with colored lights were undertaken with the preference chambers previously described. They were confirmatory of the above, and a few additional items not brought out in the references mentioned were uncovered. The basic data are given in table 11. With certain exceptions, which are discussed below, all the values showed a preference for blue light over red and a preference for green light over red and a preference for green over blue.

In one case *Sardinella* showed a strong preference for red over blue. In this case the fishes used had been kept in total darkness for one hour before the experiment was begun, which shows the effect of past experience, the tendency for many fishes to be reluctant to move from one light condition to another, and is indicative of the point of our objection to the interpretation of Kawamoto and Takeda (1951) in considering that they had established that the eel was "attracted" to red light.

*Jenkinsia* showed a strong preference for blue over green, differing sharply from the other fish so tested. As with *Sardinella*, one case showed a strong preference for red over blue. Here, too, the fish had been in darkness for a period prior to the test.

The explanation of these somewhat complex data can be shown best in a quasi-graph, as in figure 10. It is clear from this that, under the conditions of the experiments, *Sardinella* are repelled by colored lights, although it has been previously shown that they are, within the limits of their past history, strongly photo-positive. These data seem to indicate that the shorter the wave length the greater the repulsion. However, when given the choice of two wave lengths the fish chose the shorter in each case. *Jenkinsia* and *Atherina*, on the other hand, were strongly positive to

TABLE 11  
RESPONSES OF FISHES TO A CHOICE OF COLORED LIGHTS

(All readings refer to values of the first-mentioned color. The bulbs used were Mazda lamps of 25 watts commonly used for advertising signs. Their distance was adjusted so as to give a reading of about 2 foot-candles at the water's surface. All readings were made just after nightfall, between 8.00 and 9.00 P.M. The values represent the means of the number of tests listed, in terms of per cent.)

No. of Tests	Blue-Red	Green-Red	Green-Blue	Red-Blue	Green-Dark	Blue-Dark
<i>Sardinella macrophthalmia</i>						
5	50.0	51.0	56.0	-40.8	-89.8	-98.2
5	28.3				-97.7	
	39.5					
<i>Jenkinsia lamprotaenia</i>						
6	96.2	100.0	-45.6	100.0	100.0	100.0
1			-99.7			
			-72.6			
<i>Cyprinodon baconii</i> (male)						
5	21.2	40.9	94.0	47.0	14.6	7.0
2		36.8	65.2			
1		14.6				
		34.1	78.1			
<i>Cyprinodon baconii</i> (female)						
5	99.1	88.8		11.5	19.9	7
<i>Atherina stipes</i>						
6	92.9	98.7	-86.3	99.8	100.0	100.0
2		70.6	89.6			
1		98.9				
		82.7	1.6			
1	-91.8		<i>Sardinella</i> from darkness			
1	-89.0		<i>Jenkinsia</i> from darkness			

all wave lengths. These two notably photo-positive forms performed similarly when given a choice, and different from *Sardinella*. Here they were strongly repelled, relatively, to red, and *Atherina* became practically indifferent in the blue-green combination, possibly not possessing a close discrimination of the shorter wave lengths. *Jenkinsia*, on the other hand, showed high selectivity, with a marked preference for blue and a distinct avoidance of red.

The slightly light-positive *Cyprinodon*, both males and females, showed a slight preference for the colored lights as against darkness, the males being significantly more red-positive than the females. Strangely, the choice of blue over red was strong in the females and not nearly so marked in the males which on the other hand showed a marked preference of green over blue.

A general tendency is evident for fishes to respond more definitely towards the shorter wave lengths (the blues and greens) and much less towards the longer wave lengths (reds). The definite reddening of solar light near sunrise and sunset is thought to have some significance in the economy of fishes. At least on the approach of sunset, it might be associated with initiating preparations for the night by diurnal fishes. In fact it might be imagined that the reactions to red light in experimental devices by diurnal fishes might be caused by such a condition.

Little work has been done on the possible perception of wave lengths shorter than those of the visible spectrum. Two approaches may be made to this, one using natural sunlight and the other some artificial source of ultraviolet. Both methods have been tried, and their results are reported in table 12. The

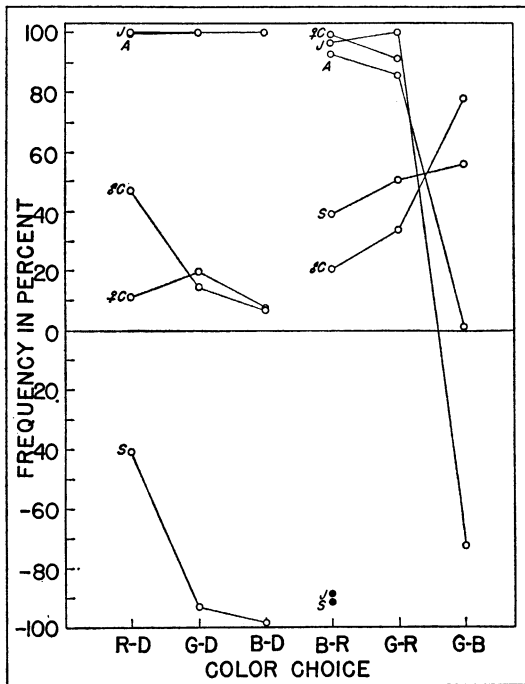


FIG. 10. Reactions to lights of various colors and to darkness of various species of marine teleosts. The letters on the horizontal index represent the choice with which the fishes were confronted, as follows: R, red; G, green; B, blue; D, darkness. The chamber in which the reading was made is mentioned first. The light circles represent experiments in which the fishes had previously been in daylight; the dark ones, those in darkness. The initials on the various curves indicate the fishes as follows: A, *Atherina*; C, *Cyprinodon*; J, *Jenkinsia*; S, *Sardinella*. Data from table 14.

first method is readily accomplished by placing the choice box in a quiet sunny place when the sun is high and covering one-half with clear polished glass. It is then possible to determine if the movements of the fishes are other than random on a basis of the difference between the wave lengths that will be stopped by the glass. It is clear from this table that *Jenkinsia* are ultra-violet positive to a very marked extent. *Atherina* treated similarly show characteristically individualistic behavior, as has been discussed at length earlier. This reaction to light, whatever its real genesis, evidently carries over into the ultra-violet. In agreement with their sexual differences in respect to phototropism, male *Gambusia* are ultra-violet positive and

the females are negative, roughly in accord with their reactions to visible light.

The experiments involving the use of artificial sources, while not so clear as the sunlight experiments, tell essentially the same kind of story. *Anoptichthys hubbsi* showed a positive reaction and *A. jordani* a negative one when one-half of the choice box was covered with glass and equal amounts of visible and ultra-violet radiations were sprayed on each. When tested with illumination balanced so that the foot-candles of visible light on one side were equal to the foot-candles of visible light from both the ultra-violet and the other source, the fishes were slightly light negative. Why this should be so is not clear, but possibly the fish were reacting to different spectral qualities within the visible range of the mixed and unmixed radiation. Under similar conditions *Brachydanio* showed a strong positive reaction to the ultra-violet. The erraticness of *Atherina* is in keeping with its known responses to visible light, some individuals being light positive and others negative.

Although little work has been done on fishes with respect to their ability to recognize the ultra-violet, as long ago as 1935 Beebe reported experiments in the sea in which he was able to concentrate fishes gathered in a beam of visible light into the small compass of an ultra-violet spotlight. The responsiveness of various aquatic invertebrates to ultra-violet wave lengths has long been known to be of importance in their economy. Reactions to infra-red, so far as known, seem to be similar to any other thermal reactions. So far as experiments have gone, these reactions are indistinguishable from those to ambient temperature or visible light. Because of the rapid extinction of both ultra-violet and infra-red in water, they can only be of importance very close to the surface.

**REACTIONS TO POLARIZED LIGHT:** Although there has been a recent increase in the understanding of the position of light polarization in natural waters, e.g., Waterman (1950, 1951, 1954, and 1955), Waterman and Westoll (1956), and Bainbridge and Waterman (1957), and indication of its significance to invertebrates, there is no evidence as yet to show whether differential polarization of light has any direct or indirect influence on the orientation or social structures of any fishes. If there

TABLE 12  
 RESPONSES OF FISHES TO ULTRA-VIOLET RADIATION  
 (All readings made in the ultra-violet chamber except as noted.)

Per Cent Positive	Conditions	
	Chamber Read	Chamber not Read
	<i>Jenkinsia lamprotaenia</i>	
56.0	Outdoor sunlight, 6200 f.c.	Same, covered with glass, 6200 f.c.
	<i>Atherina stipes</i>	
-68.9	Same, 5400 f.c.	Same, 5400 f.c.
2.5	Same, 6000 f.c.	Same, 6000 f.c.
59.1	Same, 5200 f.c.	Same, 5200 f.c.
	<i>Gambusia</i> sp.	
	Females	
-63.5	Same, 5400 f.c.	Same, 5400 f.c.
	Males	
10.6	Same, 5400 f.c.	Same, 5400 f.c.
	<i>Anoptichthys hubbsi</i>	
6.9	Direct sun lamp, 160 f.c.	Protected with glass, 160 f.c.
10.3	Sun lamp with glass, 160 f.c.	Mazda only, 160 f.c.
15.1	Sun lamp, 160 f.c.	Mazda only, 160 f.c.
-10.3	Same, 230 f.c.	Same, 230 f.c.
-15.9	Same, 200 f.c.	Same, 200 f.c.
7.5	Same, 180 f.c.	Same, 180 f.c.
-15.5	Same, 175 f.c.	Same, 175 f.c.
Mean	-12.7	
	<i>Anoptichthys jordani</i>	
-3.1	Direct sun lamp, 165 f.c.	Protected with glass, 165 f.c.
-20.3	Sun lamp, 230 f.c.	Mazda only, 230 f.c.
-16.4	Same, 170 f.c.	Same, 170 f.c.
8.3	Same, 170 f.c.	Same, 170 f.c.
-3.8	Same, 185 f.c.	Same, 185 f.c.
-4.4	Same, 150 f.c.	Same, 150 f.c.
Mean	-5.8	
	<i>Brachydanio rerio</i>	
36.1	Same, 180 f.c.	Same, 180 f.c.
	<i>Atherina stipes</i>	
-69.2	Same	Same
-100.0	Same	Same
-100.0	Same, 100-watt Mazda	Same
-91.0	100-watt Mazda	Sun lamp
-52.9	Same	Same
- 2.3	Sun lamp	100-watt Mazda
88.8	Same, 175 f.c.	Same, 87 f.c.

is actually no direct effect in the case of fishes, it would be surprising if there is not some indirect effect, as the crustaceans for which such a response has been demonstrated are normally fed upon by a variety of fishes.

#### PHOTOPERIODISM

Obviously the effects of photoperiodism would be expected to have an effect on the

responses to light in terms of a cyclic variable, and in fact some of the experiments reported showed evidences of what may be its influence, although most of these have been on too coarse a scale to be much modified by influences of the magnitude of a photoperiodic effect. The most pertinent paper to present considerations appears to be that of Kawamoto and Konish (1955); these authors

showed that there is a definite diurnal rhythm in the responses to an artificial light in a darkroom by *Girella punctata* Gray and *Rudarius ercodes* Jordan and Fowler. Other workers concerned with the thermal resistance of fishes showed that goldfish were more resistant to cold in winter and to heat in summer. As shown by Hoar (1955b, 1956b), such resistance is not merely a matter of acclimatization to lower and higher temperatures but is associated with the hours of daylight, as was demonstrated by keeping the fishes in a standard thermostatically controlled temperature where only the light varied. Hoar (1958c) showed, in addition, that fingerling *Salmo gairdneri* showed differential rheotropic responses under differing conditions of light and temperature, tending to run with the current with decreased temperature and long hours of light (16) and to run counter to the current with decreased temperature but shorter hours of light (eight).

#### INTERRELATIONS OF LIGHT AND HEAT

It has been shown experimentally that the ambient temperature has an important bearing on the sign of the reaction of the response to light when varied beyond certain limits. Andrews (1946) showed that *Catostomus commersonii* (Lacépède) at the age of two years was light negative in shallow water but positive in deep water. This situation he referred to the lower light values found in deeper water. Sullivan and Fisher (1947) showed that trout selected temperature more sharply in dim light than in bright light. Andrews (1952), working with young, but mature, goldfish, found that they became insensitive to light if the temperature was raised to a certain value, which varied with the temperature of the water to which they had become accommodated. Thus, if conditioned to 12° C., they became insensitive to light at a little less than 22° C., but, if conditioned to 24° C., they became insensitive at a little over 30° C. These figures were found to vary with the age of the fish, as well as with the temperature to which they had been accustomed, with the general conditions that the insensitivity appeared higher in ratio to the temperature of the conditioning water. He showed that the heat receptors involved were distributed along the lateral line system.

Barlow (1958) in a study of the behavior of *Cyprinodon macularius* in the Salton Sea showed that these fishes moved into cool shallow water with the coming of darkness and into the warmer and deeper places with the coming of daylight.

Studies related to this relationship of reactions to light and water temperature were carried out in the following manner. On April 17, 1952, five mature *Carassius auratus* were placed in an outdoor lily pool, having wintered over in a cool aquarium in a cellar. The pool was the larger of two, last mentioned by Breder (1946). The fishes immediately buried themselves under the dead leaves that floored the pool. Here they remained until warming temperatures caused them to come out of their "hibernation." The observations on this behavior, which began on April 29, are given in table 13. The record was considered terminated for present purposes on May 30. After May 24 the fishes showed no tendency to bury themselves.

These data were grouped in periods of five days and are clearly indicated in figure 11, which shows nicely how with increasing tem-

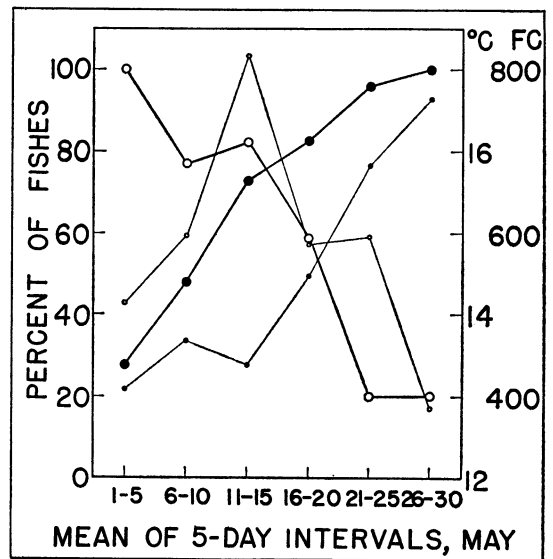


FIG. 11. Behavior of five goldfish during May in terms of five-day means. Large dark circles: mean number of fishes not buried, in per cent. Large light circles: per cent of fishes resting on bottom, but not buried. Small dark circles: mean water temperatures. Small light circles: mean foot-candles.



perature more fish came out and stayed out and how those that were out swam more and more in mid-water or near the surface as the season advanced. After the water had reached a mean of a little over 16° C., there was no returning to burial.

During this period incident light was read directly in foot-candles with a photometer. As the season advanced, the light became more intense but was later subdued by the growth of the tree leaves that shade the pool. This is also indicated in figure 11. A curious relationship appeared which, although obvious to the observer, is not clear from the data until the number of foot-candles per fish not hiding is plotted against the mean temperature. Then it is apparent, as in figure 12, that, with higher light values and colder water, the fish returned to hiding, although they were active in even colder water if the light values were less. This strongly suggests that the change of sign of phototaxis, as discussed by Andrews (1946), is not a simple threshold-passing but an interaction of the two vectors. It is easy to assume a utilitarian value for such a relationship, but not so easy to assay the physiological mechanism involved. Further but less detailed records indicated that the water temperature increased slightly into the middle of July but then began to fall off, although of course air temperatures were still higher in that month. Meanwhile a lush growth of shrubs and shade trees had a marked cooling effect and lowered the amount of light incident on the water. This falling-off of the light was already apparent in June. From that time on, very few fish hid in or on the bottom, fright from any cause driving them to hiding under some pachysandra which by this time had grown over and hung into the water in some places.

Obviously these "field observations" check nicely with the experimental work reviewed above.

To extend this line of study, experiments were carried out in aquaria on young fish as follows. Four goldfish of a single brood at about an inch in length, two slate gray and two yellow (transparent-scaled type), were distributed two each to two aquaria, each 2 feet by 1 foot by 1 foot. Temperature differences were maintained by a thermostat-heater in one and an ice bag in the outside filter of

the other. These two tanks were connected by pipes and a pump, as described by Breder (1957), so that there was chemical identity, which was maintained except during the course of the experiments. Even when the pump was not operating, there was some interchange because of the thermal difference between the two tanks. One-half of each tank was shaded with a cover and side shades of dark paper.

From table 14 and figure 13 it is obvious that the fish shunned the light in proportion to its intensity. Also it is evident that the

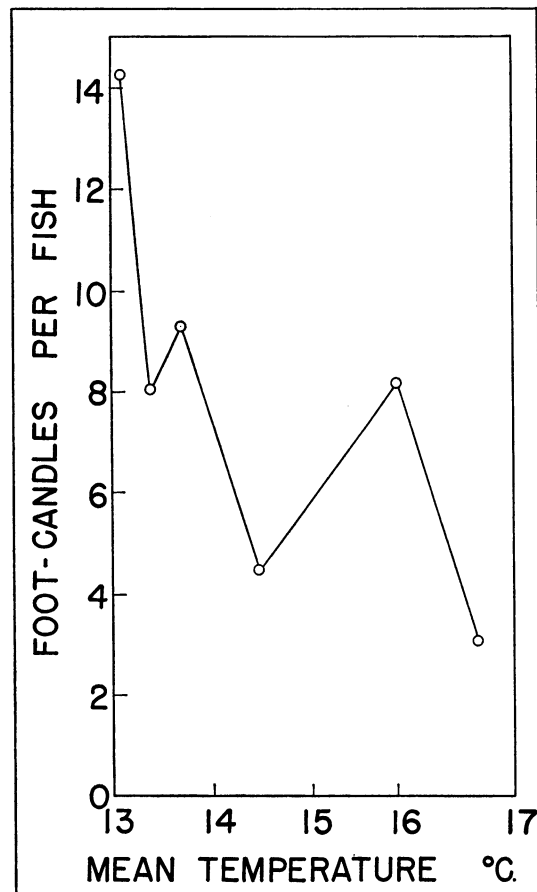


FIG. 12. Relationship of light reactions of five goldfish in reference to mean temperatures. The vertical index, foot-candles divided by number of fish not buried, gives a measure of light reaction. This indicates that the fishes were less light positive at low water temperature than at high, within the range included. Above this range of temperature the effect, if present at all, is too small to be measured by such means.

TABLE 13

RESPONSES OF GOLDFISH TO LIGHT AND TEMPERATURE IN A POOL IN SPRINGTIME  
(Data taken in 1952 on five fish under conditions of rising temperature and expressed in means of five-day periods.)

Days in May	Mean Degrees Centigrade	Mean Foot-Candles	Per Cent of Fish Out	Per Cent of Fish on Bottom	Foot-Candles/Fish Out	Number of Observations
1-5	13.1	513	28	100	14.3	26
6-10	13.7	595	47	77	9.3	27
11-15	13.4	819	73	82	8.0	28
16-20	14.5	587	82	59	4.4	32
21-25	15.8	588	96	20	8.2	15
26-30	16.6	385	100	20	3.1	25

yellow did so considerably more than the gray. The semi-translucent condition of the yellow fish may affect their reactions by admitting more light to their pineals. Note that there is a pronounced drop in the case of the yellow fish between 15 and 100 foot-candles, but in the case of the gray this occurs between 100 and 200 foot-candles.

When the fish are compared in greater detail, as is done in figure 14, it is again evident that the yellow are more light negative than

the gray. No case is shown for the former in which the mean values reach higher than 0.88, whereas in the case of the gray fish there are three instances in which the mean values exceed 1.00, which indicates these to be light-positive values. In the case of the yellow fish, there is a general trend for the fish to become more light negative the higher the water temperature. The values for the gray fish are more erratic, which indicates again a greater independence from the temperature-light relationship, at least in this range.

It is perhaps not surprising to find that the cruising speed of goldfish is proportional to the temperatures of the water in which they are kept, within their normal range of temperatures (Fry and Hart, 1947). Also, it has been shown by Shaw, Escobar, and Baldwin (1938) that goldfish has its activity greatly reduced at very low light values (less than 0.05 foot-candles), but at higher values (3 to 55 foot-candles) little difference in activity can be found.

Keenleyside and Hoar (1954) reported that the rheotactic responses of young *Oncorhynchus keta*, *kisutch*, and *nerka* were positive at lower temperatures and negative at higher ones. These are further influenced by the light, for they found that the presence or absence of a shelter modified the responses. If exposed to light, the young salmon showed negative rheotaxis, but if a shade was present, positive.

Hoar (1956a) showed that fry of *Oncorhynchus gorbusha* (Walbaum) are negatively phototactic before they have formed their

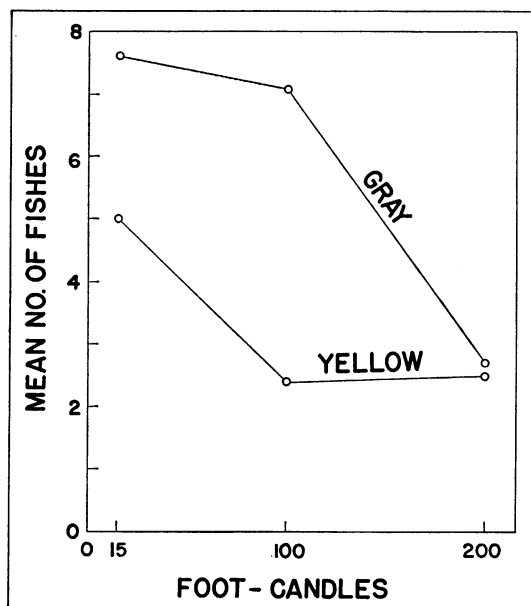


FIG. 13. Behavior of gray and yellow goldfish in reference to light intensity and use of shelter from direct light. Light in foot-candles is compared with mean number of fish out of shelter.

TABLE 14

CALCULATIONS OF REACTIONS OF GRAY AND YELLOW GOLDFISH TO LIGHT AND TEMPERATURE

(The first numbers in parentheses are the numbers of fish out, i.e., in the lighted chamber, and the second in parentheses are the number of observations. The mean number of fish out is the first divided by the second. Two aquaria were employed; one contained two gray fish and the other two yellow fish, scaleless type.)

Temperature in Degrees Centigrade	Mean Fish Out at Various Light Intensities					
	200 Foot-Candles		100 Foot-Candles		15 Foot-Candles	
	Gray	Yellow	Gray	Yellow	Gray	Yellow
19-20	0.07+ (1)(14)	0.14+ (13)(92)	0.74- (28)(38)	0.88- (36)(41)	1.19 (68)(57)	0.73+ (38)(52)
21-22	0.12- (2)(17)	0.37+ (3)(8)	0.59+ (108)(182)	0.12+ (18)(146)	0.50 (3)(6)	0.55+ (5)(9)
23-24	0.33+ (4)(12)	0.50 (3)(6)	1.10+ (64)(58)	0.06- (4)(72)	0.43- (3)(7)	0.28 (7)(25)
25-26	0.25 (10)(40)	0.14+ (1)(7)	0.75 (922)(28)	0.27+ (9)(33)	1.18 (46)(39)	0.24 (6)(25)
27-28	0.40 (17)(43)	0.07+ (1)(13)	0.39- (7)(18)	0.31 (19)(32)	2.00 (4)(2)	0- —
	(34)(126)	(31)(126)	(229)(324)	(77)(324)	(84)(111)	(56)(111)

Light Intensity	Number of Observations	Mean No. of Fish Out	
		Gray	Yellow
15 f.c.	111	0.76-	0.50+
100 f.c.	324	0.71	0.24-
200 f.c.	146	0.27-	0.25-
	All 581		

first school, but immediately thereafter become positive, retreating to cover on any sudden change in light intensity. *Oncorhynchus keta*, on the other hand, establishes schools which are not easily disrupted by light changes but seem to be determined more by the water currents present when they were formed. Hoar, Keenleyside, and Goodall (1957) extended such studies to other species of *Oncorhynchus* and found that the reactions of the fry to light varied markedly from one form to another. That is, the advanced fry of *O. keta* and *O. gorbuscha* were found to be strongly light positive, while *O. nerka* was negative, and *O. kisutch* was light indifferent but became inactive at very low intensities. Recently emerged fry of *O. gorbuscha* rose to the surface as light intensity fell, but those of *O. keta* did not. Fry of *O. nerka* were light negative at this stage and were never so light positive as those of *O. keta* and *O. gorbuscha*. These details are given

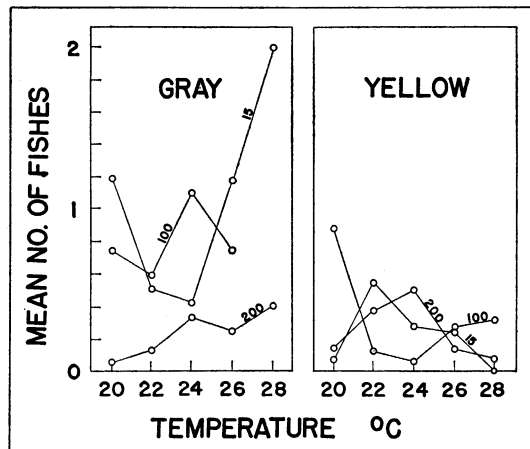


FIG. 14. Behavior of gray and yellow goldfish in reference to light and heat. Water temperature is compared with mean number of fish out of shelter with reference to the light intensity. The numbers indicate the higher limit of two-degree intervals. Lines connect points with a common light intensity, which is indicated in foot-candles.

here to emphasize the range of variation in light reactions that may be found in congeneric forms living in essentially the same habitats. No doubt shifts in the attitude of fishes towards both light and heat have played a considerable part as isolating mechanisms. The above-discussed work was based on experiments in which the fishes were presented with a choice of light or dark chambers in aquaria similar in principle to experiments reported herein. Hoar (1958b) ascribes the differences of responses that he found in the young of various species of *Oncorhynchus* to basic differences in the endocrine system.

In order to attain a clearer understanding of the reasons involved in the changes in attitude of schooling fishes towards aggregation with differences in light and temperature, the preliminary studies of Breder (1951) on *Jenkinsia* were extended by the utilization of more refined instrumentation. A Leeds and Northrop "Micromax" recording unit provided with two pens was so arranged as to plot a graph of temperature in degrees Centigrade direct by use of that company's "Thermohm" and to plot the incident light by means of a Weston photocell in milliamps directly convertible to foot-candles. This was calibrated and checked at intervals by concurrent readings taken with a photovolt foot-candle meter. Incidental notes were made directly on the paper roll of the recording device. This was in continuous operation for considerable periods of time, interrupted only by such servicing as was occasionally necessary. The thermocouple was immersed in a test tube containing water and sealed in. This was built into a small stand which was placed at a given point in a pool 12 feet in diameter. The test tube was immersed nearly to its lip. Thus there was ready transfer of heat, but no metal came in contact with the water in which the fishes swam. A small shade was provided so that direct sunlight could not reach the thermometric element. The photo-cell mounted on a board was placed at the edge of the pool near the thermometer. It was protected from rain by a clear glass cover. No difference in reading could be detected by the presence of this cover. Readings taken from the machine-drawn graph, every hour on the hour, for two sample periods in November and January

are given in figure 15. This shows at a glance, for instance, that during November the water temperature dropped rather sharply and that during January it was rising rather uniformly while the incident light did not vary greatly. The daily behavior of these two variables is in clear relief. Still further analysis is given in figures 16 and 17 which show the maximum, mean, and minimum of temperature and light by days and also the time of day of the occurrence of maximum temperature and light. The tides taken at this time from a Bendix water level recorder appeared to bear no relation to the behavior of the fishes.

The primary and basic results which this analysis of physical data brings to bear on the observed behavior of the fishes under its influence may be sketched as follows. During the November period the fishes started out as of November 13 with a well-formed school which gradually broke up and became variously diffuse as the temperature fell while the light remained virtually constant (see espe-

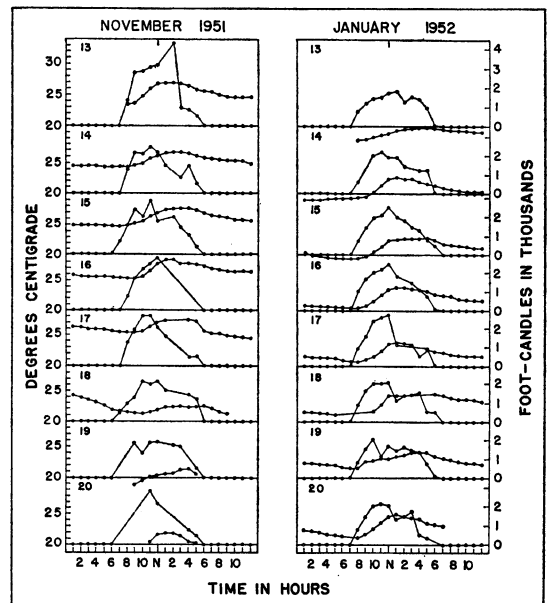


FIG. 15. Temperature and light conditions in a circular pool during comparable periods of November and January. Data picked from continuous temperature and light records made by a Leeds and Northrop "Speedomax" recorder. Each point represents recording as each hour passed. Black circles refer to temperature in degrees Centigrade; light circles, to light in foot-candles.

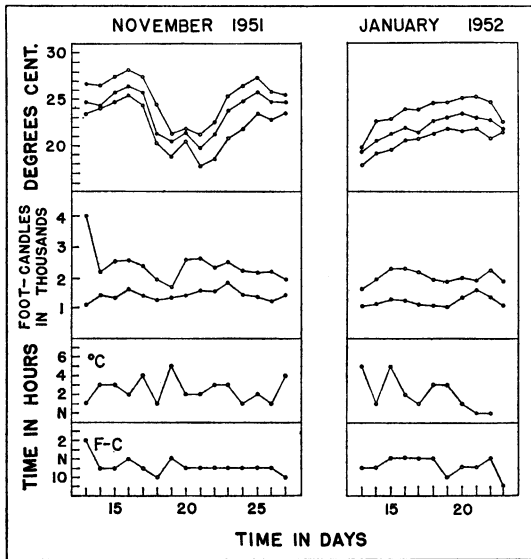


FIG. 16. Time and magnitude of maxima and minima of temperature (top graph) and light (second graph) from the same source as in figure 15. There is no minimum indicated for the light readings, as each night it fell below the instrument's threshold. The dark circles indicate mean values. These were obtained by taking the average of the hourly readings for each day. The third and bottom graphs give, respectively, the hour at which the maximum temperature and that at which the light readings occurred.

cially fig. 16). In figure 16 also is shown the return of the temperature to the levels of November 13 to 15. During this period the school reconstituted itself. Contrariwise, with the very low temperature of January 13, the fishes were in loose groups or merely diffuse. By the twentieth of January the school had reformed, although the temperature was no higher than the November temperature on which the school broke up, which seems to indicate that there is a considerable amount of accommodation to the general level of temperature of the period immediately past. Comparable reactions appear in behavior influenced by light and concerned with the immediate past history of the individuals. Furthermore, it seems that fishes in many cases are generally reluctant to change from a physiological or a psychological condition to a new one, even if the change is "for the better." General homeostasis and the avoidance of shock and stress in both the physiological and psychological sense may be at-

tained by such reluctance. Such behavior could easily be thought of as having a very high survival value. The heat-regulating mechanism of birds and mammals should give a very considerable relief from at least the physiological importance of avoidance of shock and stress. The above considerations, based on fishes that live in a school continuously and are not subjected to extreme temperature variations, are perhaps not so clearly expressive of these changes in attitude as are those of more northern forms which evidently have more strongly marked differences relative to light and temperature differentials. It was partly for this reason that the preceding studies on goldfish under the influence of springtime increase in light and temperature in the latitude of New York were undertaken.

Balls (1951) and Dragesund (1958) found correlations between the depth at which schools of herring swam in the open sea and light intensity. The behavior of these herring is in good agreement with the results discussed above in reference to behavior and the correlation between light and temperature. Studies on the feeding habits of goldfish under differing conditions reported by Hirata (1957) show similar relations to light and temperature.

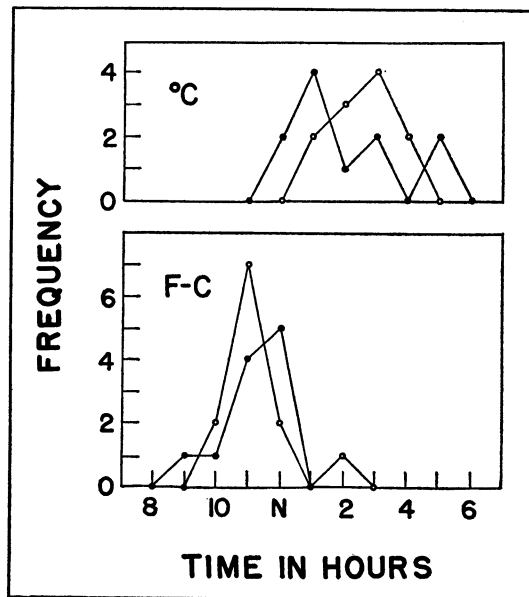


FIG. 17. Distribution of hours of maximum light and heat. Light circles represent November 13 to 23; dark circles, January 13 to 23.

## THE INFLUENCE OF PAST HISTORY OF INDIVIDUALS

It is reasonable to suppose that an animal usually tends to seek a light intensity similar to that to which it has been exposed. That is to say, a certain hesitancy to go from a brightly lighted place to a dark one or vice versa is to be expected. In the case of teleosts, this is intensified because of their great use of chromatophore adjustment in reference to background and albedo. It has been shown by Brown and Thompson (1937), Breder (1947b), and Breder and Rasquin (1955a) that many fishes when given a choice will swim over a background most nearly matching themselves. (See text above under the headings Collective Protective Behavior and Pigmentary Reactions.)

In the case of *Jenkinsia*, for example, the reluctance to change their light exposure may be easily demonstrated. The data of table 15 and figure 18 need little additional comment. Fishes were brought from various degrees of light intensity directly to the choice box. These were: outdoors in bright sunshine, outdoors in the shadow of a building, outdoors on dull days, in lighted laboratory room 24 hours, from outdoors two hours after dusk and in dark room 24 hours. In the order mentioned the fishes passed from fully light positive to very light negative.

If *Atherina stipes* is treated in a similar manner, as is shown in table 16 and figure 19, certain prominent differences appear. The general trend is similar, but the regularity of *Jenkinsia* is not present. The cause of this is discussed above in other connections and is clear from the list of "daylight" fishes in table 16 which are arranged in decreasing photopositiveness. This reinforces the data of table 11, further underlining the presence of two kinds of individuals, those that are light positive and those that are light negative.

It has been shown in several cases that the social attitude of fishes may be modified by their past experience with other fishes. This should be expected in any case, as it has been shown herein earlier that fishes' past experience with physical conditions modifies their attitude towards such conditions. All the experiments so far seem to indicate a "preference" for a *status quo* or a resistance to a

change of situation, i.e., a homeostasis. This may be in regard to the amount of incident light, the nature of the background, or the presence or absence of companions. Illustrative of this is the hesitancy of certain normally aggregating fishes, which have been held in solitary confinement, to join a group of their own kind when such are presented, as discussed by Breder and Halpern (1946) and Breder (1951). (See text under the heading Heterotypic and Homotypic Groups.)

Related to these matters are habituation and learning. Hoar (1958a) was able to show with juvenile salmon that, when permitted to run in a channel, there was not immediate obliteration of their course of swimming when the restrictions forming the channel were removed. This is in good agreement with the remarks of Breder and Atz (1952) on the restriction of movements.

Breder and Halpern (1946) showed that the eggs of *Brachydanio rerio* if hatched in isolation produce fish which at the age of six months promptly join a school when such was first presented. On the other hand, fish that were isolated at the age of six months and were returned to the group after six months of isolation hesitated to join a school for a period that ranged from one day to a week. The fry of this species do not aggregate or school for the first two months of life and scatter on fright instead of schooling on fright as they do after that time. Shaw (1957) found that the pre-schooling period lasts for nine days in *Menidia menidia* (Linnaeus) and that it could be retarded but not eliminated by isolation for the first 17 days of life. Shaw (1958a, 1958b, 1958c) gives further details indicating that the first approaches of one fish to another are without parallel orientation when the fish are 5 to 7 mm. long, and that parallel swimming appears when they are 8 to 10 mm. long, but persists only after a length of 12 mm. has been attained, usually by 17 days from hatching. In the early phases the distance between fish and fish and their relative speeds are irregular as compared with their later behavior. Fish reared in still water showed no significant differences in these reactions from those reared in flowing water. Schooling reactions involv-

TABLE 15  
EFFECTS OF PAST HISTORY ON THE PHOTO-  
SENSITIVITY OF *Jenkinsia lamprotaenia*  
(All readings were made in the light chamber.)

Date	Per Cent Positive	Groups of 4 Fishes		
	Sunlight			
1/28/50	100.0	Set 1		
1/28/50	100.0	Set 1		
1/29/50	100.0	Set 2		
1/30/50	100.0	Set 3		
1/30/50	100.0	Set 3		
1/31/50	100.0	Set 4		
1/31/50	100.0	Set 4		
2/ 2/50	100.0	Set 5		
2/ 2/50	100.0	Set 5		
2/ 7/50	100.0	Set 6		
6/ 7/50	100.0	Set 7		
1/31/50	95.5	Set 4		
	Shadow outdoors			
1/30/50	99.6	Set 4		
7/11/49	99.0	Set 4		
2/16/50	2.0	Set 8		
1/29/50	-100.0	Set 2		
	Dull day outdoors			
7/14/49	99.7	Set 8		
2/ 5/50	-100.0	Set 7		
	In laboratory room			
1/30/50	99.1	Set 3		
1/29/50	- 50.0	Set 2		
1/30/50	-100.0	Set 2		
	At night			
1/31/50	100.0	Set 4		
2/ 7/50	93.4	Set 10		
2/ 7/50	50.8	Set 8		
2/ 5/50	35.0	Set 9		
2/ 5/50	- 99.3	Set 6		
1/30/50	- 99.7	Set 2		
6/ 7/50	-100.0	Set 9		
1/29/50	-100.0	Set 2		
1/30/50	-100.0	Set 3		
	From darkroom			
2/ 7/50	- 26.8	Set 10		
2/12/50	-100.0	Set 11		
	Synopsis			
Environment	No. of Tests	Maximum	Mean	Minimum
Sunlight	12	100.0	99.6	95.5
Shadow	4	99.6	23.6	-100.0
Dull light	2	99.7	- 0.2	-100.0
Laboratory room	3	99.2	-16.9	-100.0
At night	9	100.0	-24.7	-100.0
Darkroom	2	-46.9	-73.4	-100.0
	<i>Mean of all outdoor values: 91.6</i>			
	<i>Mean of all indoor values: -30.0</i>			

ing the presentation of a fish in a glass tube showed some inhibition, which is referred to the restrictions placed on the fish in the tube.

Berwein (1941) reported that schools of *Phoxinus* drove away individuals or small schools of smaller individuals or solitary larger ones, a matter that did not enter into the studies mentioned above as the work was confined to fish of the same size class. He also noted that the smaller sizes tended to keep nearer the surface. This, of course, might be based on the pineal influence, as discussed above, as the larger fish tend to have more fully covered pineal areas, or on mechanical sorting resulting in more uniform allocation of light through the school.

The influence of the group effect in respect to locomotor behavior is brought out clearly in the data reported in tables 2 and 3 and figures 5 and 6. If the difference of the means of four fish tested together is compared with the sum of the means of the same fish tested singly it is found that there is a consistent measurable difference, which is analyzed in table 3 under the column headed Difference. The means of four fish tested together are in all cases less than the corresponding sum of the same individuals tested one at a time. Also it will be noticed that there is a strong tendency towards an inverse ratio, in that the larger the mean of four tested together the smaller the difference between it and the sum of the same fish tested singly, which may be most concisely demonstrated by a graph plotting these two values against each other as in figure 6. It will be noted that the two forms show different slopes and, of course, occupy different areas in the graph, because one is photo-positive and the other photo-negative.

The only reasonable interpretation that can be given of these differences is rooted in the known locomotor behavior of other fishes in reference to groups of various sizes as has been studied by Schuett (1934), Escobar, Minahan, and Shaw (1936), and Breder and Nigrelli (1938). This work has shown that goldfishes swim faster when alone or in crowded conditions than when in some intermediate-sized group, and also that their pattern of swimming differs in a similar manner. This has been interpreted to mean that in nature a fish lost from its group has more

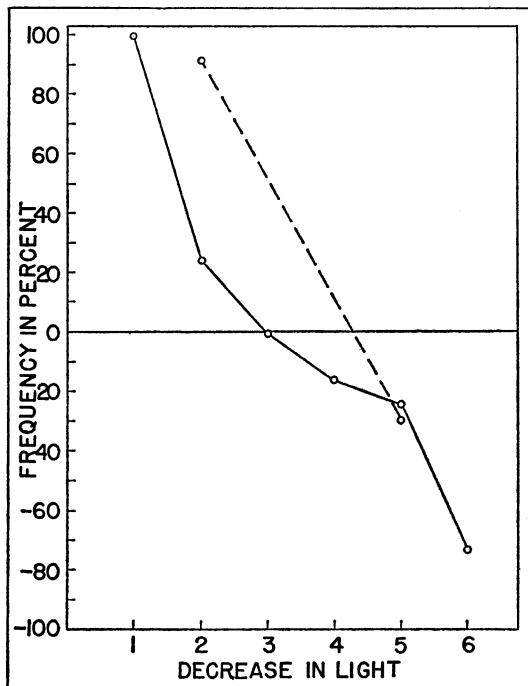


FIG. 18. The effect of the immediate past on *Jenkinsia*. The numbers on the horizontal index indicate the following light conditions previous to the tests: 1. Fish from outdoors in open sunshine. 2. Same as 1 but fish in shade. 3. Same as 1 but on dull overcast day. 4. Fish in laboratory for 24 hours. 5. Same as 4 but after night had fallen. 6. Same as 4 but fish had been kept in dark room for 24 hours. The dashed line indicates the mean of all outdoor and all indoor values. Data from table 15.

chance of regaining it by wide ranging and fast swimming. Overcrowding may, of course, be overcome by the same kind of activity, initially at least. Observations in the field, with such considerations in mind, clearly indicate that when such a "lost" fish speeds up its activity it also is less susceptible to other stimuli that at other times it would react to, such as food or quick movements on the part of the observer. All that need be assumed in interpreting figure 6 is, therefore, that the solitary fish is reacting to that state as do many other species, i.e., "paying less attention" to general external stimuli of a non-violent sort than it would when in a group of companions. Expressed another way, the more cohesive the group the more it tends to be controlled by the reactions of the

individual most sensitive to external stimuli. Thus the light-negative *Anoptichthys jordani* might be expected to be more so in a group than when alone. However, the light-positive *Anoptichthys hubbsi* also becomes more so when in a group. This matter is not too easily explained away. Actually both forms become more light positive when alone, for reasons which are not fully explainable at this time.

The actual performance of the individual fish, the sum of their means, and the mean of groups of four fish are spread out in figure 5. Here it is clearly seen that in a group, *A. jordani* is light negative, as all earlier work has indicated when it is in a group of four. The present value of  $-14.8$  per cent compares well with  $-24.5$  per cent obtained earlier by Breder and Rasquin (1947) on other but comparable material, as does that of *A. hubbsi*, 11.1 per cent in the present material as against 9.3 per cent of the earlier work. It is clear here, too, that enough of the first have become light "positive" when alone to pull

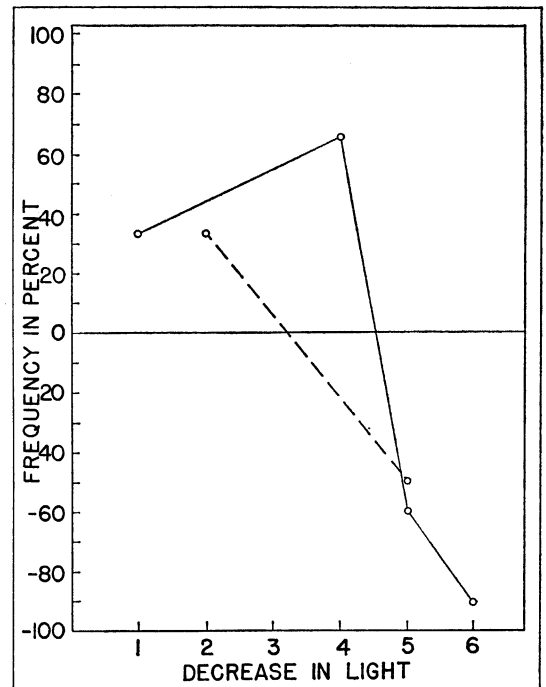


FIG. 19. The effect of the immediate past on *Atherina*. Horizontal index same as in figure 18, with which this is to be compared. The dashed line compares the outdoor values with the mean of the indoor values. Data from table 16.



TABLE 16  
EFFECT OF PAST HISTORY ON THE PHOTO-  
SENSITIVITY OF *Atherina stipes*  
(All readings were made in the light chamber.)

Date	Per Cent Positive	Groups of 4 Fishes		
	Daylight			
1/25/50	100.0	Set 1		
2/27/50	100.0	Set 2		
2/27/50	100.0	Set 3		
6/ 4/50	99.5	Set 4		
1/25/50	99.3	Set 1		
3/26/50	97.9	Set 5		
3/26/50	92.1	Set 5		
2/ 8/50	89.8	Set 6		
6/ 5/50	88.6	Set 7		
2/ 2/50	85.0	Set 8		
3/27/50	87.5	Set 9		
2/12/50	80.0	Set 10		
2/18/50	92.9	Set 7		
2/12/50	42.6	Set 10		
1/26/50	- 50.2	Set 11		
1/25/50	8.0	Set 12		
1/26/50	- 70.9	Set 11		
2/ 2/50	- 72.9	Set 8		
1/27/50	- 87.5	Set 13		
2/ 8/50	- 91.2	Set 7		
1/26/50	- 97.6	Set 11		
1/26/50	- 99.0	Set 11		
1/27/50	-100.0	Set 13		
1/27/50	-100.0	Set 13		
	In laboratory room			
6/ 4/50	65.6	Set 4		
	At night			
1/25/40	0.4	Set 1		
1/25/50	- 8.0	Set 12		
1/27/50	- 33.8	Set 13		
6/ 3/50	- 57.3	Set 7		
1/26/50	- 74.6	Set 11		
1/25/50	- 82.6	Set 1		
1/27/50	- 82.9	Set 13		
6/ 3/50	- 94.0	Set 4		
1/26/50	- 96.9	Set 11		
	From darkroom			
2/12/50	- 91.0	Set 14		
	Synopsis			
Environment	No. of Tests	Maximum	Mean	Minimum
Daylight	24	100.0	33.1	-100.0
Laboratory room	1		65.6	
At night	9	0.4	-58.9	- 96.9
Darkroom	1		-91.0	
	Mean of all outdoor values: 33.1			
	Mean of all indoor values: -50.4			

the value close to the line of light indifference. It is noteworthy, however, that only two of the 12 fish actually are individually close to that line. Only one of those that were light negative exceeded the mean of the group of four fish.

The least light positive of *A. hubbsi* form a large, compact group, only three being more positive than their mean, which indicates that three individuals had very high values as compared with the high ones of the other form which comprise exactly half of the total. One way of expressing this is to say that these fish agree in becoming less repelled by a lightless chamber when not alone.

Calculations of significance are given in table 3. It will be noted that all the calculations pertinent to figures 5 and 6 are significant except that the sum of the isolates of *A. jordani* cannot be distinguished from random distribution, although all but two fish clearly show values highly significant, either positive or negative.

Associated with the past history of the individuals and their social and other attitudes is naturally the state of their endocrine organs. Rasquin (1958) has shown that the pigmentary reactions of fishes may be altered in various manners, according to species and evolutionary level, by the injection of adrenalin and intermedin. While the basic facts were known, no previous attempt had been made to survey any great variety of fishes in this regard. Much of this survey was carried out simultaneously with the experiments discussed in this part of the present paper, and they relate directly to the survey in many places. Also the association of these studies on pigmentary behavior with morphological and histological descriptions of the pineal area has a bearing on the matters herewith under consideration.

That these same fishes show modification of locomotor behavior in reference to light should not be surprising. The following notes should be sufficiently illustrative for present purposes.

A marked change in preference to light conditions and to choice of background may be demonstrated with the injection of adrenalin. Fishes that show the classic blanching reaction on such injection become more light positive, while those that do not show other

TABLE 17

## THE INFLUENCE OF ADRENALIN ON THE ATTITUDES OF FISHES TOWARDS LIGHT AND DARKNESS

(Each experiment records the behavior of the same fishes before and after injection with adrenalin. In each case a choice of a light compartment and a dark-covered one was available. Each figure represents the mean of two tests.)

Species	Per Cent Positive		Difference
	Before Injection	After Injection	
<i>Cyprinodon baconi</i> (female)	-96.5	15.8	112.3
<i>Cyprinodon baconi</i> (male)	-69.5	-23.5	46.0
<i>Gambusia</i> sp. (female)	-62.6	65.8	128.4
<i>Gambusia</i> sp. (female)	-100.0	98.0	198.0
<i>Mugil trichodon</i>	-34.3	-95.4	-61.1
<i>Haemulon flavolineatum</i>	-100.0	-90.4	9.6
<i>Abudefduf saxitalis</i>	-99.4	-99.8	-0.4
<i>Sparisoma radians</i>	96.4	49.7	-46.7
<i>Scarus croicensis</i>	-67.3	-94.9	-27.6
<i>Scarus croicensis</i>	85.9	18.0	-67.9
<i>Monacanthus ciliatus</i>	100.0	80.8	-19.2
Arranged in order of mean increase			
163.2	<i>Gambusia</i>		
79.1	<i>Cyprinodon</i>		
9.6	<i>Haemulon</i>		
-0.4	<i>Abudefduf</i>		
-19.2	<i>Monacanthus</i>		
-46.7	<i>Sparisoma</i>		
-47.7	<i>Scarus</i>		
-61.1	<i>Mugil</i>		
Experiment with blind <i>Gambusia</i>			
Normal	Blind	After Injection	
-95.3	5.4	-4.0	
Experiment with <i>Gambusia</i> on black and white backgrounds			
% on white background			
Normal	Injected		
-99.5	14.3		

reactions. This is brought out in table 17. The difference in response to adrenalin between normally melanophore-free fish and those that have melanophores present is mentioned above under the heading Locomotor Reactions in more general connections.

All cases of the classic type showed increases in the percentage of light positiveness, the maximum being 128.4 for one set of *Gambusia* females, the minimum being for male *Cyprinodon* at night when they should have been sleeping, but even they showed a 46.0 per-cent increase, the mean of all being 95.5.

The case of the non-classic type of fish showed a decrease of 27.6 per cent.

As should be expected, adding adrenalin to

a blinded *Gambusia* does not change its light neutrality.

Dark fish picked a black background in preference to a white, but after injection picked the white, showing a change of 113.8 per cent. This, too, is in keeping with all work on selection of background in such fishes.

Table 17 shows these changes in detail. In the lower part of that table the fishes used are arranged in decreasing order of change towards light positiveness after the injection of adrenalin. The order approximates that of their accepted position in phylogeny, except for *Mugil*. It should be recalled that this is one form with an exposed pineal that showed light-negative reactions in the choice box.

## STRUCTURAL NATURE OF FISH GROUPS

THE PRECEDING FOUR SECTIONS (Introduction, Definitions and Explanations, Special Forms of Social Groupings, and Special Influences on Fish Groupings) cover mostly new data necessary to a more general consideration of fish assemblages. The present section, under its various subheadings, considers the more theoretical aspects of this study, and because, taken together, they present the views and conclusions arrived at, it has been unnecessary to present a separate Discus-

sion. Throughout this section reference is made to various aspects of fish groups in terms of cybernetics. The cybernetic point of view so far as it concerns the present studies is taken up in detail below under the subheading Cybernetics and Fish Groups. The terminology of Ashby (1954 and 1956) has been followed throughout, and it is recommended that readers not familiar with the subject consult these two works in the case of any seeming lack of clarity or ambiguity.

### CIRCULAR MOVEMENTS IN ANIMATE AND INANIMATE OBJECTS

There is a basic similarity among all rotational movements, reaching from those of natural phenomena to man-made wheels. They are all, in the cyberneticist's view, either homomorphic or isomorphic. These would include hurricanes, tornadoes, and any cyclonic movement of fluids in the broad sense, fish mills and similar organic activities, and by extension the influences that are responsible for whorls of hair and of leaves, and so on. They are all in some manner the result of rotational and not translatory influences. Certain comparisons of them have already been indicated by Breder and Halpern (1946).

Translatory influences often serve to disrupt rotational manifestations, as in wind movements and where hair whorls give way to smooth pelage. Where such destruction of rotational movement does not follow, the combination of the two may appear as harmonics, or, viewed the other way, harmonics

are present except where either translatory or rotational influences are reduced to zero. These changes may be produced by either intrinsic or extrinsic influences. The studies on *Jenkinsia*, *Brevoortia*, and *Ameiurus* strongly suggest the former; the latter are obvious.

There is considerable difference in the mechanics of the mills formed by various species. Kimiura (1934) found that mills of *Sardina melanosticta* (Temminck and Schlegel) rotated as a whole, when not disturbed, so that the fishes retained their relative spacing, and the mill rotated at a constant angular velocity of from 8 to 10 degrees per second, while Breder (1951) found that mills of *Jenkinsia lamproatenia* did not rotate in such a uniform fashion, but that there was considerable slippage between the inner and outer ranks of individuals. This would appear to be a specific matter, and it is possible a single school might change its milling behavior in this respect.

### INTERNAL STRUCTURE OF SCHOOLS

The movement of the school as a whole is the "composition of velocities" of each individual in it, or is the "geometrical sum" of their individual trajectories and speeds in which each fish represents a vector. The individuals in such a group influence their neighbors, to equalize the speed of each fish. In a well-knit school there is little change of position of fishes, but in a looser one there is a constant shifting as individuals accelerate or decelerate. This condition could be thought of

as similar to turbulent flow, where the fishes are continually changing the arrangements of the individuals, as is commonly found. Laminar flow could be similarly compared to fishes that hold fixed positions in their group and, in its full form, is probably just about as rare an occurrence in nature as is the true laminar flow of fluids.

Not only do the acceleration and deceleration influence the compactness of a group, but so does the manner of swimming influence

this feature and perhaps more importantly. Some species show so much yaw in their swimming movements that their trajectory appears to be almost random darts. This is especially marked in rather stiff-bodied fishes such as *Jenkinsia*. Fishes with more flexible bodies, in which there is a larger proportion of backward-moving muscular waves, usually show less yawing. This is especially marked in fishes in which there is more than one-half of a wave length, or better, existing on the fish at any one time, as their opposed effects more effectively damp the yawing tendency. In fishes with paddling pectorals or other fully balanced locomotor devices the yawing may be reduced to zero. There is thus considerable variation among different kinds of fishes in the extent of the angular excursions they may show from the axis of their travel.

These angular differences are of a much smaller order than those that serve to separate "schools" from "aggregations." They are small enough to insure that the group is moving forward in a common direction, but large enough to require swimming room that can accommodate the extent of the angular displacement. They are, nevertheless, primarily similar to the larger displacements, which in aggregating forms prevent uniform forward translation. The differences in the compactness of schools of different species measured by Breder (1954) could, of course, have been calculated alternatively from measurements of the angles of displacement between the fishes instead of the distances.

Fishes in a tight school are automatically constrained to face in the same general direction, for otherwise the school would break up, with individuals moving in all directions as in a simple aggregation. Certain structural features of the locomotor equipment of the individuals are of considerable basic importance in this connection. Most, if not all, of the fishes that normally live in "permanent" schools display no, or very limited, abilities to back up. This is especially notable in the mackerels and herrings with strong schooling habits. The forms with more mobile pectorals, such as goldfish and many other Ostariophysi, while forming schools at times do not retain the formation for long, merging freely into mere disorientated aggregations or breaking up into isolated smaller groups or individuals.

It would seem that this marked ability and tendency to back up freely may be instrumental in disrupting the schooling tendency. On the other hand, there is no compulsion on fishes with rather rigid pectorals to form schools from such reasons. The notable inability of sharks to back up does not prevent them, in many cases, from being solitary or traveling in very loose packs. Here their rather poorly developed optical equipment may well be a schooling inhibitor. In other words, mobile and flexible pectoral fins may tend to discourage permanent school formation in many fishes, while stiff pectorals with no backing ability present no such impediment towards the maintenance of such formations.

Various students have noticed the extent of variation in size of individuals that will make an acceptable school, i.e., one that will have sufficient coherence to persist as a social structure for more than a passing phase (see Kimiura, 1934; M. B. Schaefer, 1948; Breder, 1951, 1954; and Nakamura, 1952). Varying with the species involved, this difference in size is not so much as 50 per cent in any of the cases examined. It has also been noted by various students; Kimiura (1934), M. B. Schaefer (1948), Breder (1951), and W. Schäfer (1955) have shown that the smaller individuals in schools normally tend to swim above the larger individuals in *Engraulis*, *Neothunnus*, *Jenkinsia*, and *Clupea*, respectively. *Atherina stipes* Müller and Troschel and *Menidia menidia* (Linnaeus) have also been seen to organize their schools in this manner. Present studies shed no clear light on why these particular size restrictions on the acceptability of school mates should be held, nor why the smaller individuals tend to swim above the larger. It is possible that the latter item is influenced by the fact that, in general, the smaller the fish, the more shallow will be the water acceptable to them. Also, as previously noted, by the placing of the smaller individuals in the upper layers more light reaches the lower layers of the school. This type of segregation may be the beginning of the separation of a school into two groups of individuals of more nearly comparable size. In fact this mode of adjustment may be a normal part of the behavior of regularly schooling forms invoked as variations in the

growth rate of individuals tend to spread the sizes in such a group beyond its cohesive limit. Berwein (1941) found hostility on the part of schools of *Phoxinus* towards schools of smaller individuals and larger solitary ones. This is apparently the only case reported of such aggressiveness in strongly aggregating species that often form schools.

The transmission of cues or information through an assemblage of fishes has received very scant attention. The modalities involved would seem to be limited to the following receptors, perhaps in the following order of importance: visual, auditory, olfactory, gustatory, and tactile. All but the first should be able to function in the absence of light just as well as with it present. The behavior of schooling or aggregating fishes in darkness has indicated, in all experiments and observations, the large importance of vision in positioning the fishes in their social unit.

Because sound travels in water at a rate somewhat over four times its speed in air, a sound would be expected to disturb fishes in a school with such unanimity that it would be practically impossible to detect which fish heard and responded first to such a disturbance. Observations and field experiments do not yield this effect except under very special and exceptional conditions. Usually there is a well-marked "wave" of movement which passes over such a school at a much slower rate than the speed of sound even in air. The movement noted is usually in the form of a small "start" of each fish which appears as a "flurry" of activity that passes from one end of the school to the other, in a short but measurable time, which varies widely from a large fraction of a second to a few seconds, depending on the size of the school, the direction of the sound in reference to the shape of the school, and cross interference from other stimuli. If no other factors are at work within an average, more or less elongated school, and the sound source lies on the projected axis of the group, at least two phenomena prevent an almost instantaneous response of each fish in the group. The presence of the mass of fishes between the sound source would seem clearly to interfere with the hearing of those individuals that are on the far side of the school. This would be proportional to the mass of intervening fish, the

nature of its disposition in the space occupied, and the nature of the sound itself. The sound-absorptive effect of fish muscle and other structures would be reinforced by the fact that the fishes are separated by small distances, and their arrangement in a school with its many reflecting surfaces should make the group act as a very effective silencer, somewhat after the principle of a Maxim silencer on a gun. The reality of such an effect is attested to by the reflected sound from a school of fishes which registers so clearly on an echo sounder. It is, of course, the remainder, not reflected back, that penetrates, or is absorbed by, the fishes, only the attenuated residue reaching the far side of the school. It appears, then, that the speed of transmission of the disturbance under such conditions is near the rate at which each agitated fish transmits its agitation to its nearby neighbors and therefore much slower than the speed of sound. In a few cases in which a sound was produced on the broadside of a school, the "flurry" was so fast as to be nearly beyond detection. Response to sound is thus based on direct perception of sound and on the perception of the response of neighbors. The relative amounts of these two cues may vary from 100 per cent to zero, the second increasing while the first decreases as the stimuli pass from one side of a school to the other. Another feature that increases the difficulty in studying this subject is the rapid conditioning that fishes show and the short time it takes for them to pass to a refractory condition in which they simply fail to react at all to a sound which has become familiar and is therefore one to be disregarded. Precise and formalized experiments are difficult to establish for the reasons discussed above, and the data on which these views were based consist of an accumulation of observations from docks and similar places in which fishes could be made to show the "start" reaction by sharp sounds made on the dock itself or the hull of a small boat.

Because at least some of the species of schooling fishes are capable of producing sounds, hearing may come into play on dark nights or in very opaque water, not to maintain a school, but to keep the individuals from losing one another completely. Westenberg (1953), who considered sound produc-

tion in this connection, ascribed sound production to *Decapterus russeli* Rüppel as being faintly audible to the human ear. It is significant in this connection that students of fish-produced sounds, such as Fish (1954) and Moulton (1958), in their lists of fishes that make sounds, included many typically schooling species in the Carangidae, Clupeidae, Haemulidae, and Chaetodontidae. A number have been shown to have at least two sounds, one associated with reproduction and the other evidently of an alarm, recognition, or warning significance. The bibliographies of these two papers give the background of such studies but which need not be repeated here.

The reactivity of various small fishes to the body juices of their own kind or of other fishes is well known and need not be discussed here. However, one experiment concerned with that type of behavior, which was undertaken by Verheijen (1956), has special pertinence to the present study. By placing two aquaria close together but mechanically and otherwise separated, except for the possibility of clear vision from one to the other, he was able to cancel all but the optical stimuli between two equal groups of *Phoxinus laevis*. A drop of tissue juice from the same species caused the fishes in one aquarium to show the typical "fright" reactions, which in such small tanks take the form of the huddling together on the bottom of all the fish in a tight "fright" school. The fish in the other tank showed essentially the same behavior but were about 10 seconds slower in forming their "fright" group. This delay was taken to represent the loss of the effectiveness of transmission of information when only the sight of a reacting companion was permitted and there was no possibility of the fishes' receiving any direct chemical stimulus. There is thus evidently a large element of "following the behavior of the other fish" in these reactions within a school or aggregation. The data of this experiment would seem to be analogous to the reactions to sound as previously described, i.e., disturbance, and reaction to it by those that could receive it, but otherwise reaction to the behavior of companions. In this connection it should be emphasized that the sense of smell is evidently very acute, as is witnessed by the

studies of Walker and Hasler (1949) who showed that *Hyborhynchus notatus* (Rafinesque) was able to distinguish very delicate differences in the odors of various aquatic plants.

The tactile influences would come into only direct fish-to-fish effect in the case of pods, on which we have no experimental data, and as a tactile response to water movement caused by other nearby companions. This action is sufficiently analogous to sound to need no special treatment here, as is that of the influence of light sensitivity of the pineal region in reference to vision.

More violent disturbances may either disperse a school or drive it closer together; Parr (1927; for *Gobius*), Breder and Nigrelli (1935; for *Lepomis*), Graham (1931; for *Scomber*), Spooner (1931; for *Morone*, *Scomber*, *Spratella*, and *Sardina*), Bowen (1931; for *Ameiurus*), Shlaifer (1942; for *Pneumatophorus*), Breder (1951; for *Jenkinsia*), and Burnette and others (1952; for *Sardinops*) all make mention of closer packing under disturbance. Dispersal is mentioned by Bowen (1931) for *Ameiurus melas* and by Pearson and Miller (1935) for *A. natalis*. The seeming antagonism between these two lists is evidently rooted mainly in the violence of the disturbance and the state of the school as a group as well as the individual conditions of the fishes comprising it.

The various shapes that schools may take are referred to wherever necessary in all the preceding matter. It may be useful, at this point, to consider the conceptual limits to the deployment of the individuals in a school. To start with the minimum of two fishes, they might arrange themselves abreast or in single file or with one fish somewhat in advance of the other. This last case, as it is not symmetrical, could be of two kinds: advanced fish to the right or advanced fish to the left. Obviously any intermediate positions could appear between these four points of reference. For the present, if we limit the considerations to those four, for simplicity, the rest will become quite understandable.

If a large school is to be formed in which each individual behaves *in detail* as the others, we can have the fishes building a single file of indefinite length or all of them abreast for an indefinite advancing front. As

is shown above in the section Special Forms of Social Grouping, these two types are rare to the point of being a curiosity. If, similarly, a larger school is built along either a right or a left advanced position, a diagonal advancing front is formed, right or left end ahead. Actually no such case appears to have been recorded. Nonetheless, these are the positions most often found in real fish schools, but so randomized as to destroy any long-line effect. In many schools it is as though several files of both right and left types were jumbled. The single-file and the all-abreast types of formation may be considered limiting forms, with all the other possible positions finding greater representation in real fishes. This could be anticipated on probability considerations alone.

The general outline of such a school has also been referred to earlier in many connections. On a basis of what was learned from the study of small *Mugil* schools in the section Fishes in Balls, it would seem that the shape of a large school of small fishes should approach the spherical, if it is away from the surface and the bottom in open water, modified only to the extent that the shape and polarization of the fishes are able to distort it. This effect increases with the reduction in numbers of fishes in the school which relatively increases the size of the fishes with respect to the group as a whole. Schools flatten out considerably against the water surface and not infrequently to the extent of being only one fish deep. The essentially "plane figure" then performs in a way similar to the three-dimensional school, in the absence of interference, approaching the circular as modified by the form and polarization of the fishes. The distortions from this basic pattern would then be referable to the totality of operating influences, both those that are ordinarily considered extrinsic and those that are intrinsic.

Thus far schools have been studied more or less as mass effects, with but little regard to the movements of individuals that make up the aggregation. By a simple means of cinematographic analysis, the movements of one fish in reference to the movements of its companions may be conveniently traced. Motion pictures taken from directly above may be used as follows. Projected a frame at

a time on a drawing board, the motion pictures may be used to trace the path and speed of any or all individuals in a school. The technique simply calls for placing a dot on the "nose" of the chosen fish or fishes, a frame at a time, and then connecting these dots with a line which becomes the trajectory of the fish. Taken at silent speed, each sixteenth dot marks the passage of one second. By this means the following data were collected for analysis.

Figure 20 shows the change in locomotor

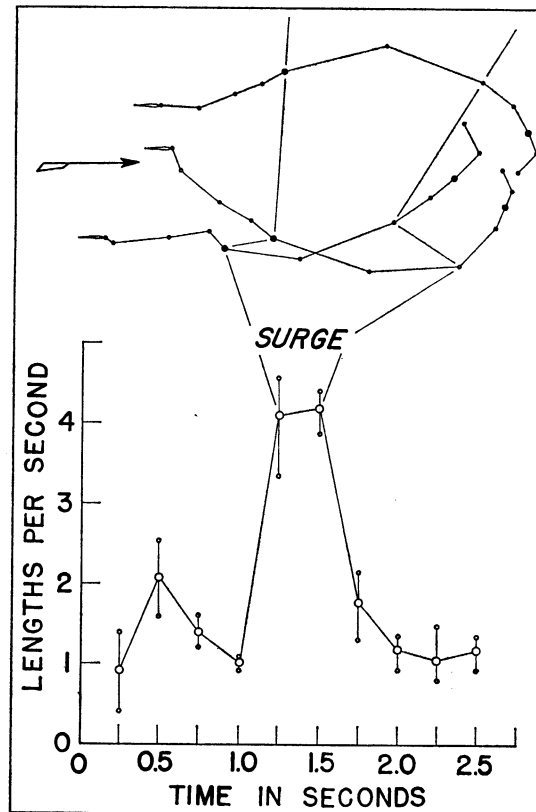


FIG. 20. Change of speed and paths of three fish in a school of *Jenkinsia* over which a shadow has passed. The arrow in the upper left indicates the direction from which the shadow, of a hand, approached. Each point on the paths of the three fishes represents 0.25 second and the larger dark ones represent 1.00 second. The shadow reached the fish just before the first full second and passed on before the next quarter second was reached. The increased speed of the fish lasted for a little over 0.5 second as is indicated, as well as the tendency to return to the source of the disturbance, in the diagram and its accompanying graph.

speed and direction of three typical fish in a school of *Jenkinsia* following the passage of a shadow, in this case a hand moving over the fish from behind in the direction of the arrow in the figure. Expressed in fish lengths per second, the graph incorporated in this figure indicates the extent of acceleration in response to this incident and its duration in time before the fish lapsed back to their former speed. The diagram also shows the tendency to return to the source of the disturbance as the paths of the fish turn back on themselves, after the surge forward, a matter that has been discussed in detail by Breder and Halpern (1946) and Breder (1957). The small light circles on the path of the fishes indicate intervals of one-quarter of a second, and the larger dark spots indicate the passage of one second. The three circles at each quarter-second interval on the graph indicate the maximum, mean, and minimum values for the three fish. As this school was closely knit, the three are typical of the group as a whole.

The individual reactions to a thermal wall, which have been studied by Breder (1951) in terms of the whole school, as shown in figure 21, based on the paths of three advance members of a school meeting a mass of water of slightly lower temperature, are typical of the group as a whole. The time marks on the paths of the fish are as in figure 20, and the numerals note elapsed simultaneous seconds. Figure 22 is a graphic representation of the above paths. The index "distance from

start" refers to the curve that runs from the lower left to the upper right, while the index "lengths per second" refers to the other curve running from the upper left to the lower right. The elapsed time is numbered the same as the diagram on the abscissa. The mean distance from the starting point measured in a straight line is indicated, together with the maximum and minimum of the three fish, connected by vertical lines to smaller circles. It will be noted that the fish up to and including the sixth second are progressing at a steady pace. This has been calculated to show a mean rate of 1.26 lengths per second. The angle with X to  $51^{\circ} 40'$  and the deviations from it are small in spite of the irregular path of one of the fishes. Inasmuch as the lines represent the tracks of the three lead fishes, they give a fair approximation of the behavior of the school as a whole, as it was moving along smoothly in the usual manner of fish schools. This smooth flow of the school changes rapidly after the sixth second, as the influence of the cold water causes the fishes to turn back. Actually the termination of the fifth second is the final one in which no influence of the cold wall is indicated. In figure 22 the turning is quite apparent. In this graph are also indicated the distances per second traveled in the succeeding seconds. The extremes which were very small are not indicated. It may be noted that there is a marked decline in the rate of speed from the first second on. The fifth second shows a sharp

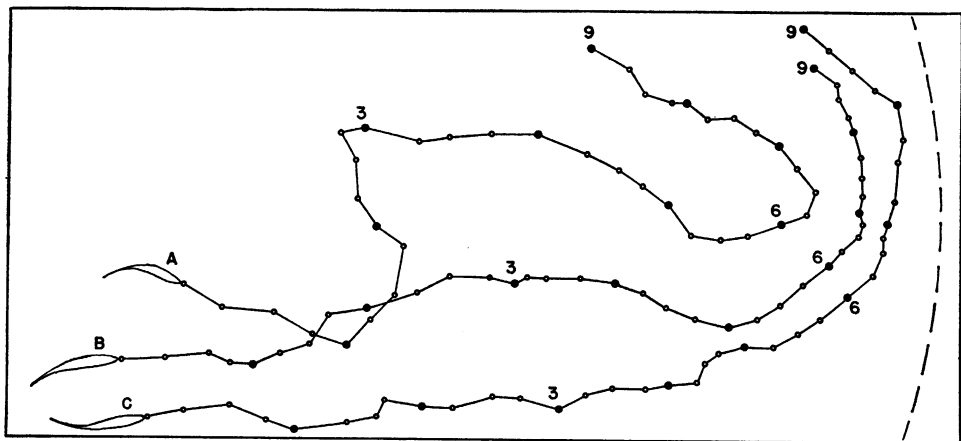


FIG. 21. The paths of three individuals in a school of *Jenkinsia* as it approaches a mass of water a fraction of a degree below that within which the fishes are swimming. The points are as in figure 20. The dashed line at the right represents the extreme advance of any of the school members into the cooler water.



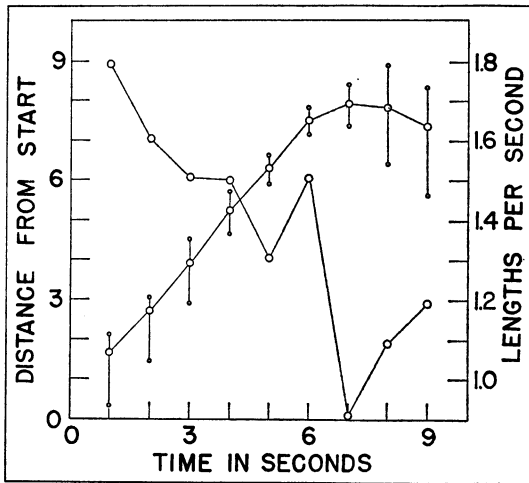


FIG. 22. A graphic analysis of the data in figure 21. The horizontal index employs the same numerals on the paths as in that figure. The vertical index, distance from start, refers to the curve, which rises from the lower left to the upper right, where it starts to descend as the fish turn back on themselves. The vertical index, lengths per second, shows clearly how the fish slow down as they encounter the temperature fall and then speed up again as they turn away from it. Both vertical indices are the mean of the three fishes in terms of their mean length.

drop after the earlier periods had been sloping off to the horizontal. This is believed to indicate the first effect of the sensing of a lowering temperature, while the apparently asymptotic form of the earlier part of the curve is believed to be a return to normal swimming speed after some unknown "fright," such as the end of the surge period in the shadow-influence experiments. While the fish were still going forward at their "normal" pace, as measured in a straight line from the origin, their actual speed decelerates only to pick up again in the sixth second which is the first period in which turning is apparent in the diagram. From here on there is a marked deceleration which shows recovery towards "normal" speed in the least two periods, when, as indicated by both the diagram and curve of distance from origin, the fish are passing out of the influence of the cold wall.

These three fish had the following ratios of standard lengths, if the smallest is taken as unity: 1.00, 1.14+, 1.10-. In all cases except the values for the first second, the largest shows the maximum values and the smallest the minimum values on the graph, with the intermediate in between. In this first period the largest shows the minimum and the intermediate the maximum. This is

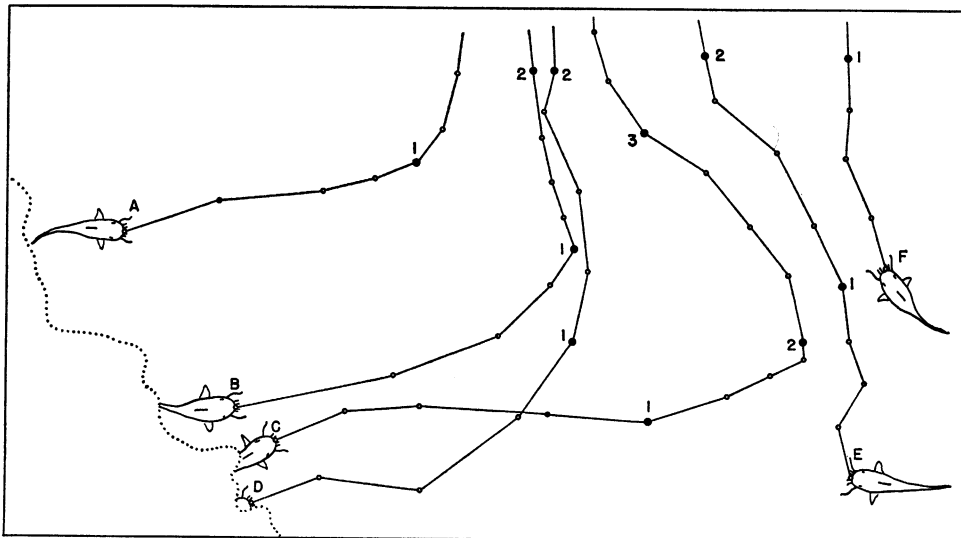


FIG. 23. Behavior of six individuals in a school of young *Ameiurus*. The four entering from the left are emerging from a mud cloud the school had stirred up, indicated by a dotted line, and the two from the right are part of a portion of the school that had become separated and is here rejoining the larger group. Points represent 0.25-second intervals. The full seconds are numbered, like numbers being simultaneous.

thought to be caused by some earlier experience, as the fish were decelerating, as noted.

If the values are taken in which no evident influence can be detected, i.e., intervals 2 to 5 inclusive, the influence of absolute size may be more clearly seen in fishes in an apparently uniform school. In these periods the smallest fish covered 1.8+ lengths per second, while the two larger fish, and more nearly of a size, covered 1.3+ lengths per second. Because, in the final analysis, the larger fish either have to retard themselves, or the smaller keep up as best they may, this situation must always be present to some extent unless the fish are of identical size. Probably, because of the strong attraction between fishes of this kind, both are in operation. Naturally, which one is going on, or if both are, cannot be distinguished by present methods.

The behavior of individuals of young *Ameiurus nebulosus* based on motion pictures taken of a wild juvenile family school is illustrated in figure 23. Fish A, B, C, and D, with innumerable others not shown, emerge from a thick cloud of silt stirred up by the school. Fish E and F are two advance members of another school, actually a separate part of one large group of juveniles. Fish A, B, and D turn, as do E and F, to form parallel moving ranks of the then-merged school. Fish C, however, races ahead to join the opposite school. As the schools join, this individual (C), and others of similar behavior not shown, become the central core of the new school. The path of fish C clearly shows how it speeds up to join the second school and then slows to turn and run at the speed of the new fellows. The relative locations of the positions (2), indicating the passage of two seconds, show how C lost his place and was displaced to the rear of the common school.

The school emerging from the cloud of silt was considerably faster than the other, while the one that changed sides and became retarded was slowest, as the following tabulation shows, in which mean speed is given in lengths passed per second:

These individual differences of members of a fish school combine to give mean and extreme values for the school as a whole and form the real basis of the considerations that led to the formulation of an equation descriptive of fish schools by Breder (1954). The above data also give added validity to the bearing that the size of a group has on the influence of the group on other groups.

The swirling behavior of this school caused it to break up in various fashions. The above-described behavior of individuals evidently gave rise to conditions illustrated by the diagrammatic school forms shown in figure 24. Here in A the school was found moving forward in a broadside manner. Simultaneously each end formed an oppositely rotating mill as the end members turned back on themselves as in B. When, in C, two independent mills were fully formed, the most central forward-advancing fishes were left, as indicated, like the ass that starved between two identical bundles of hay. In D the two mills remained as before, and the "lost" individuals formed a small semi-mill of their own. This happened to be slightly closer to the right-hand mill and quickly joined the latter, as in E. It was clear that the small group joined the large group, as the latter remained over the same place. These mills then retained their integrity, as in F, for as long as it was possible to continue the observation, a matter of some half hour or so. It is clear that these two mills had to take on these respective rotations, for, if they operated in reverse, they would have rolled in front of the advancing central fishes and would have been engulfed by them. This indeed may take place and very likely accounts for some of the otherwise inexplicable swirls found in these schools when they appear more like an amoeba with blunt pseudopodia than a group of fishes and in which the latter seem more as particles in protoplasmic flow. If one end turned forward and the other rearward, the result would be one large circu-

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	A, B, D	E, F	C	ALL FISH
Maximum	5.73+	3.28+	5.60	5.73+
Mean	2.72-	2.24-	2.79-	2.67+
Minimum	1.33+	1.72+	0.80	0.80

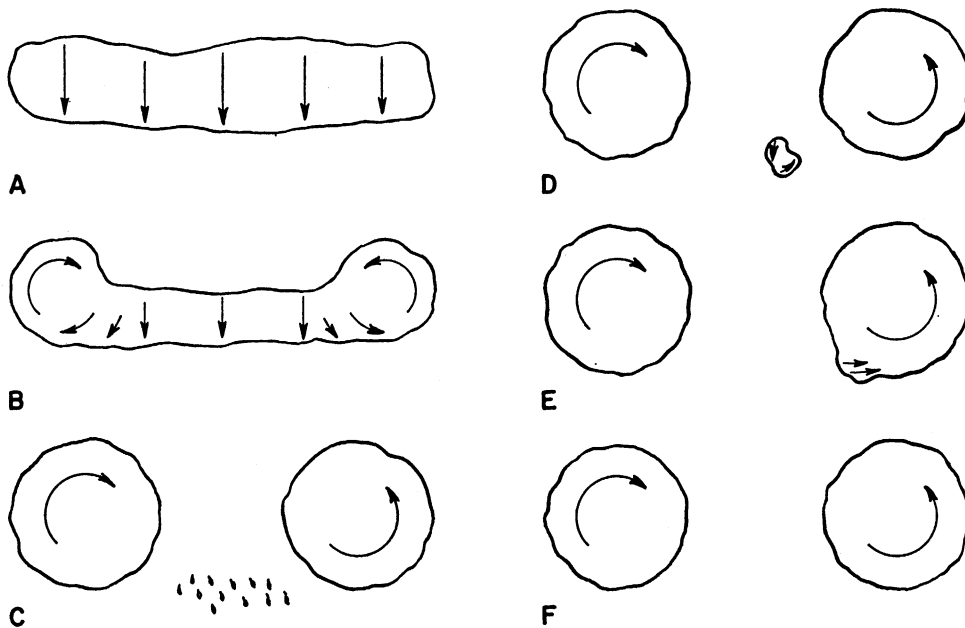


FIG. 24. Diagram of one way in which a school of young *Ameiurus* may break up. See text for explanation.

lar mill. This, too, can be seen from time to time in such a school.

The extrinsic influences that may turn a school under translation into a mill have been dwelt upon in detail by Parr (1927), and nothing of significance in present connections has been added to them, only various stimuli which will cause them to swerve so as to come into a position where the head of the school starts to follow the tail of the same body.

It has become apparent, however, that not all mills form in this fashion and some, for want of a better term, appear to be intrinsic, which they may indeed be in a very proper sense of the word. Such spontaneous mills have been described in *Jenkinsia* by Breder (1951), in young *Oncorhynchus keta* (Walbaum) by Hoar (1953), and are herein described for *Brevoortia tyrannus* (Latrobe) and *Ameiurus nebulosus* (LeSueur). Hoar wrote of his salmon that, "They will mill for a few minutes; they will then move off for some reason that I do not know, in a school." That statement also applies to the present author's observations, except for those described for some of the *Ameiurus* activity, which may be intrinsic only in the sense that the particular shape that the school happens to take

may trigger off the mill formation, while those mills that seem to form for no evident reason may well be caused by some transient chemical or temperature moiety not available to instrumental measure at the time of observation, or might be associated with some physiological change in sufficient numbers of the school members to set off the reaction. This behavior, which it would seem possible to place under experimental control, is still not reproducible at will, but attainment of such control would seem to be a first sound step in the direction of its analysis.

One possible source for the intrinsic development of a mill from an ordinary fish school would appear to be rooted in the question of exactly how equipotential the fishes in a school actually are. If they were completely equipotential, there would seem to be little likelihood of such "spontaneous" mill formation. If many in the school differed widely in their potential, the school would presumably be disrupted. It is conceivable that at some place between these extremes a condition could occur in which one or a few "individualists" could cause just enough internal disturbance to set up a flurry which would initiate a mill. It would seem possible that the type of analysis concerning the tra-

jectory of individual fishes might be a starting point for an objective testing of the above idea. A mill of *Jenkinsia*, evidently formed because of intrinsic influences, is shown in figure 2 of plate 78. Extrinsic influences in a school of *Sardinella* (in this case attacking *Caranx*) are shown as figure 1 of plate 77.

Related to the influences that may produce the formation of a mill are those that yield other usually less spectacular results. In fact the production of a mill is most likely the result of some more than usually strong influence which exerted in less degree would produce other movements with utilitarian uses which at this time no one has been able to ascribe to a mill.

Most of this behavior is too evident to need to be labored, such as the breaking up of a school during feeding periods when the food particles are of such a size that the fish strike at them individually, and a lesser disruption when they are feeding on much smaller particles by "straining."

The orientation of the school as a whole may, however, be conveniently and suitably discussed at this place, for this is clearly the summation of both intrinsic and extrinsic influences. A simple aggregation may be turned into a school by any influence that will make the individuals all face substantially the same way. Thus a flow of water in a pool otherwise still will force one of two actions on the fishes. Either they will seek quiet waters by active swimming away from the disturbance, or they will face into it and form a school, forced on them for purely mechanical reasons. It is for this reason that it is so difficult to distinguish a school primarily based on some obscure biological urge from one forced by simple extrinsic influence on a primarily

aggregating form. It is probably fair to say that a school that remains intact in still water is based on some psycho-biological factor. It may, however, not be so simple as that statement would imply, for such a school would be expected to move forward and therefore make its own relative flow of water past it. On the other hand, a simple disorientated aggregation cannot maintain its integrity in any considerable flow and is forced to form some sort of standing school in fast water. The two types of groups are so interconnected that it is difficult to make any purely objective separation, in spite of the fact that they are so readily distinguished on sight. Another way to consider the two is to consider an aggregation as a standing group, for, even if drifting along slowly, it makes relatively little progress because of the comparative independence of each member. When such a group finds itself in flowing water and points upstream it does so because it must, while most of the members take optical fixes on one another, which is essential to holding the position. A school, as here used, however, while appearing the same in a flow, is not swimming forward only because the water is flowing at the same rate in the opposite direction, but in still water is actually moving forward and maintaining the unanimity of orientation among the members. This might seem to be perilously close to a distinction without a difference. However, the matter is complicated by the fact that these differences cannot be separated on a specific, or even an ontogenetic, basis. It is impossible to make a dichotomy, if any in fact could exist, on less than the totality of the influences that have integrated the group in the first place.

### CENTRIFUGAL AND CENTRIPETAL FORCES

An equation descriptive of fish schools and other aggregations given by Breder in 1954 can be extended beyond the limits assumed at the time of its proposal because of the development of certain factual information not available at that time.

The equation was given as

$$c = a - (f_1 p_1) (f_2 p_2) / d^2 \quad (1)$$

in which  $d$  = distance between individuals or groups;  $f$  = numbers of individuals;  $p$  = poten-

tial of each individual;  $f p$  = repulsive force;  $a$  = attractive force; and  $c$  = a measure of the cohesiveness of the group.

This equation can be considered as a modification of the expression for centrifugal or centripetal force usually given as

$$F = mm/d^2 \quad (2)$$

in which  $F$  = force;  $m$  = mass; and  $d$  is as given above.

In equation 1,  $a$  may be considered as

standing for  $F$  as the centripetal force and the part after the minus sign as standing for  $F$  as the centrifugal force. The former has been reduced to a standard value by suitable manipulation, given in the earlier paper, and the second has been expanded to express the nature of the fish-to-fish influence more precisely. It is thus clear that the expressions are interchangeable as indicated. They have been so adjusted as to make the fishes come to rest at a specified distance apart, varying with the species, somewhat as a satellite finds its distance of stability, but in which the latter's velocity replaces the total influences of the fishes.

It was thought that there was probably no case in nature in which  $p$  equals zero except as a very transient phenomenon, as noted in the earlier paper. The behavior of *Mugil cephalus*, which had not been studied from this standpoint at that time, has been shown earlier to be clearly a case of this sort. In it  $p$  has a value of zero for extended periods in

the life of this species. It should be noted that the expression  $fp$  is an expansion of  $r$ , for repulsion, used in the primary equations of Breder (1954).

Fishes in a common school of one species were considered as equipotential in the earlier paper. The considerations of leadership in such a school, developed in a preceding section of the present paper, call for inequality between at least one fish and the rest. This is, to a degree, equivalent to the "schooling" of pilot fish with a shark and may be handled similarly, with the adjustment of the values of  $f$  and  $p$  accordingly. Extending the idea further, a case with a variety of degrees of "leadership" would call for a series of  $f$  and  $p$  values equal to the conditions in such a school. Actually this would represent not a school or simple aggregation of similar individuals but a hierarchy amounting to the equivalent of a peck-order or similar social structure of graded dominance.

#### CYBERNETICS AND FISH GROUPS

If each fish in a school be considered as a Markovian machine, which is isomorphic with every other unit, the school itself becomes a homeostatic device composed of absolute ultrastable subsystems. The regulation implied in such a situation would necessarily be Markovian, but, as regulation blocks the flow of variety, the uniformity of behavior of fishes in schools suggests that the whole system rapidly approaches, but, of course, never reaches, a determinate one. In this view a mere loose aggregation would be a system with a larger stochastic probability and more information. The seried and regular ranks approximated by a fish school, so strikingly different in an optical sense from an unpolarized aggregation, are evidently a consequence of close packing. This decay of variety, which so constrains the individuals in a fish school, may nonetheless have important consequences to the stability of the system, and the sharp transition from aggregation to school may well be controlled by some parameters, acting as step-functions. There is an obvious reason apparent that can account for the passing of individuals from random orientation to parallel swimming when the crowding reaches a certain condition of den-

sity. It is merely that no swimming could be possible without collisions in fishes so closely packed unless they all moved in an orderly fashion, as seen in schools where there is typically just about "swimming room" between individuals. The step-functions evidently operate at this point.

So that there can be no misunderstanding of the above, it is necessary to point out that it does not mean that, when fishes approach one another to form a school, they first converge to a non-polarized aggregation. They usually do not. Fishes that normally school swim directly towards one another and take up their positions at their appropriate distances from one another and face in the same direction. The preceding comments were concerned with the phylogenetic view, which points out that, whatever considerations brought about aggregating and schooling, the systems tended to become more nearly determinate in proportion to their density. It must be recalled, too, that only the most persistent schoolers spend more than certain parts of their lives in such close associations and that temporary schools form from loose aggregations for various reasons, often a disturbance such as the approach of a larger

fish, clearly the operation of a part-function.

Another step-function appears to operate when schooling fishes attain that position with respect to one another which represents a steady state between attraction and repulsion. While the first-mentioned is only an occasional matter, the second is in practically constant operation incident to the individual locomotor activity.

Because the fishes in a typical school are equipotential, it follows that information should be maximal in either a fish school or an aggregation, as compared with associations of unlike fishes such as pilot fish and shark combinations.

Another way to consider the fish school is to designate the school as a single Markovian machine in which each fish is an appropriately coupled transducer or "machine with input." Evidently the probabilities must be near 0 or 1 for each transducer and substantially equal in all in order for the system to show the great unanimity of activity characteristic of well-organized fish schools. In either case, as a single unit or as coupled machines, the concepts are merely different approaches to the same matter. The environment constitutes the parameters, of which many may be considered as null-functions for most of the time, such as temperature, light, and other slowly varying physical matters, while the predominant full-functions evidently involve mainly the fish-to-fish parameters. The part-functions and step-functions are noted above.

The variables in such a system involve all the above-named functions, as well as those of the internal milieu of the fishes, which are also parts of this ultrastable system.

Breder and Halpern (1946) compared vari-

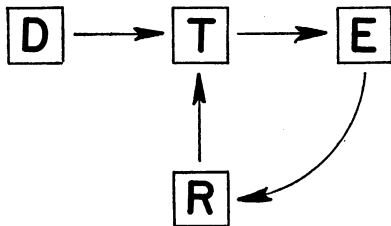


FIG. 25. Diagram of immediate effects in a closed loop regulator or error-controlled servo-mechanism.

ous inanimate systems, such as swirling leaves and iron filings in a magnetic field, with fish mills. These comparisons, if valid, would be considered isomorphic in the present usage, as noted above in the section Circular Movements in Animate and Inanimate Objects.

In order to make perfectly clear the basis for considering a fish school a physical representation of a Markovian machine, the following explanation is given. In the diagram of immediate effects (fig. 25) of a "closed loop regulator" or "error controlled servo-mechanism," *D* represents any disturbance tending to upset the stability of the machine, *T* represents the environment, *R*, the regulator, and *E*, the school. If operating successfully, the disturbances *D* do not drive *E* outside of set  $\eta$ , the "normal" form of the school. The control by the organisms is in the form of a dynamic system composed of *R*, the brain (or servo-mechanism), and *T*, the environment through which *D* operates. As shown in the figure this is a fully determinate machine, and a thermostat might just as well embody its representation as anything else. Because any such machine is but one kind of Markovian machine, the extreme in which all probabilities have become 1 or 0, the diagram may be shown as figure 26A, which indicates the arrangement of all probabilities. As we know from observation that fishes in a school do not behave so rigidly as a fully determinate machine such as a thermostat, and that some latitude is permitted the behavior of the individuals, but as we have no way of evaluating the exact probabilities of the actions within a school, a closer approach to the conditions that a real school represents may be approximated, as in figure 26B, in which the probability of homeostatic action is taken as 0.8 instead of 1.0 as in figure 26A. This value was taken because the fishes in a school are closely, but not completely, controlled. If lower values were taken, say 0.5 as is shown in figure 26C, a much more loosely constructed assemblage would embody it, perhaps not a school at all, but a mere aggregation. If the value were dropped low enough, a point of neutrality would be reached in which the fishes would be no longer grouped but would act indifferently to one another, and finally, if dropped still lower, would reach a condition of an asocial attitude, in which

the fishes would be solitary and widely separated. One point that this form of approach brings out nicely is that the social attitudes of fishes, from the extremely solitary to the extremely tight schooling types, can be arranged in a schematic system designated by the size of the probabilities displayed from 0 to 1. Natural groups certainly never fully attain either of these extreme values but exist at various points between them. The changing social attitudes of fishes in a specific ontogeny then can be expressed, theoretically at least, by changes in these probability values. For example, in the case of *Ameiurus*, the young exist in a very tight school until a certain age, of perhaps two months, has been passed, when they disperse to lead a more or less solitary existence. These then certainly embody a radical lowering of the probability figures at this time. Late in life, under various situations, they may return to more or less transient grouping which then represents an appropriate change to a higher probability value.

The above, of course, is the simple application of considerations derived from the characteristics of the Markov chain to a simple feed-back regulator. Small errors are permitted by the machine, indeed are necessary in order for it to function, which, by transmitting their information to *R*, enable the machine to operate in such a way as to prevent large errors which could cause the system to pass from set  $\eta$  and to its own destruction.

The matrix of transition probabilities of the diagrams of immediate effects shown in figure 26 is given as table 18, which perhaps shows more clearly how such systems, as they become less and less determinate, show less stereotyped behavior. It is notable in this connection that schooling fishes usually appear to be much more responsive to environmental stimuli than solitary fishes. Most solitary fishes either rest quietly or move along slowly, deflected from their activity, if at all, only by notably large disturbances. The fishes in a school, however, are mostly in a state of continual motion and respond constantly in an integrating activity which actually serves to hold the school together and gives it some continuity and permanence. It would seem that the regulator in a solitary

fish is blocking much of the information received, while in a school fish the information received (mostly from fellow school members) is acted upon promptly, with little blocking action at any point within the nervous system.

Bearing on this are the condition and kind of memory that would be expected to obtain in solitary and in schooling fishes. In the first

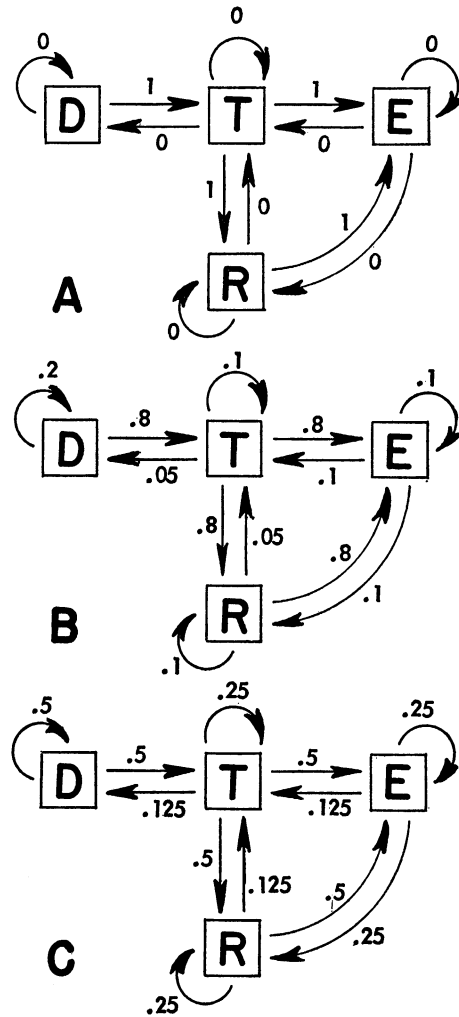


FIG. 26. Diagram of immediate effects in Markovian machine, with probabilities indicated. A. The limiting form, which is a determinate machine, identical with that shown in figure 1. B. A machine with very high probabilities and consequently nearly determinate. C. A machine with much lower probabilities, such as found in a looser assemblage. The matrixes of transition probabilities for these three machines are given in table 18.

TABLE 18  
 MATRICES OF TRANSITION PROBABILITIES OF  
 THE DIAGRAMS OF IMMEDIATE EFFECTS  
 SHOWN IN FIGURE 26

A. Fully determinate				
	D	T	R	E
D	0	0	0	0
T	1	0	1	0
R	0	0	0	1
E	0	1	0	0
B. Nearly determinate				
	D	T	R	E
D	.2	.05	0	0
T	.8	.1	.8	.1
R	0	.05	.1	.8
E	0	.8	.1	.1
C. Less determinate				
	D	T	R	E
D	.5	.125	0	0
T	.5	.25	.5	.25
R	0	.125	.25	.5
E	0	.5	.25	.25

case the contents of the stored information would be highly diversified, and little of it would be concerned with other similar individuals. Thus each fish would have a slightly different set of memories. One might mainly be concerned with waving water weeds, and another with large rocks incident to the particular micro-environment with which it was familiar. Even if the differences were not so gross as above noted, two individuals living a short distance apart on a similar rocky bottom would store a vastly different array of memories. These differences might in themselves help to maintain a solitary attitude, for the reactions to a "round rock" might well be quite opposite. The memories to be expected in schooling fishes would, contrariwise, be expected to deal principally with fishes closely resembling one another, and in which the details of inanimate environment would be definitely reduced. These fishes would then have much more common content in their memories than would solitary fishes. This in itself should tend to hold the group together. For this reason alone schooling fishes would always approach closer to a true Markovian machine than a number of

solitary fishes, in the sense that their memory content is so repetitive. It makes little difference whether a fish inside a school remembers only the preceding event or what happened one or two days earlier, for normally they would be the same for all practical purposes. Also, in this sense, the schooling fishes would have "less" memory content than those that lead a more diversified solitary life.

If we accept the idea that a fish school is a physical embodiment of Ashby's Markovian ultrastable machine, some curious questions can be raised. This form of machine was considered as "adaptative" or "intelligent" or "selective" by that writer. In this sense, can a group such as a fish school be described in these terms? That is, can it be so described as an entity in its own right and not merely the sum of the intelligences of the individuals composing it? This then would amount to a "super-organism," however primitive the intelligence was which it was able to display. The discussion on machines and the brain given by George (1958) in which the nature of complex logical nets is analyzed is most illuminating in this connection. Earlier studies such as those of Walter (1953) and Uttley (1953), together with others contained in the Transactions of the Institute of Radio Engineers for that year and in Shannon and McCarthy (1956), give interesting background material on these matters. Before the days of cybernetic analysis, ant colonies were sometimes discussed in such terms, but without any critical analysis. Would the present ideas indicate a return to those earlier and all but forgotten views?

Following such views then, a fish school that developed into a mill could probably be thought of as a derangement and a breakdown of the adaptive activity. Parr (1927) evidently had such an idea when he called the mill a "senseless activity." Because the extreme schooling fishes thrive poorly, if at all, when isolated does it mean in the above terms that they are so closely tied to their fellows that this separation is roughly equivalent to dismembering the machine rather than merely reducing its number of elements?

A variety of solitary fishes of few and scattered individuals often aggregate with leaves, twigs, and other objects which they more or less resemble. Would these school with their



own kind if given the opportunity? As one way of looking at the question, would they mistake a fellow fish for a leaf or other inert object with which they ordinarily associate, or would it be the other way? Would such behavior be a step towards or from schooling or at least aggregating? Certain fishes, such as young *Chaetodipterus*, will attack one another when placed together (Breder, 1946), while others, such as young *Oligoplites* (Breder, 1942), will aggregate together. Thus evidently the behavior in this respect can vary with the species in question. The adults of the above two genera often form schools and, if confined together in aquaria as adults, are usually peaceable in attitude towards their fellows. If there is such a transition from grouping with fellow fish to grouping with some other objects such as leaves, differences in attitude of the kind mentioned would be expected. This would follow because such shifts in behavior would be naturally modified by both the external environment and the heritage of the species involved, how far it had proceeded in the transition, and, indeed, in which direction it was evolving.

All the preceding considerations lead inevitably to thoughts on Ashby's "homeostat" with which he made such interesting comparison with the behavior of a brain. Its responses to disturbances in the maintenance of homeostasis and its adaptive behavior, which so clearly showed how "a system can be both mechanistic in nature and yet produce behavior that is adaptive," are most illuminating. The machine described by Ashby (1954) consisted of four identical elements, all equipotential and interconnected. In reference to this consideration of fish schools, it is perhaps natural to wonder if it is proper to consider the homeostat as a "school of four fishes." For purposes of discussion, accepting such a view is equivalent to saying that each fish is equivalent to a magnet and its associated circuits in the homeostat, and that the whole school is homomorphic, if not isomorphic, with the device. In such a view then, the magnets in their equilibrium central positions are equivalent to the fishes in their proper school spaces, all equally distant from one another.

Ashby carefully points out that each of the

four magnetic units of the homeostat are ultrastable in any combination of numbers including one unit. This suggests that there may be something different between the two systems, because a schooling fish alone is evidently in a critical state which may become quickly lethal. This difference is more apparent than real, for in the case of the single homeostat unit the circuits are arranged to feed back into itself, and one commutator, potentiometer, and its coil are eliminated. This may in fact, because of these differences, cause the single-unit device to resemble a normally solitary fish, which of course responds properly to disturbances with its particular internal arrangements. The schooling fish that has been made solitary should probably be looked upon rather as the equivalent of a homeostat unit which has had its three input circuits and three output circuits connecting it with its three fellows completely severed, with no compensating recircuity. Definitive experiments with truly schooling species are extremely difficult, for they are primarily fishes of open waters which do not take kindly to confinement in tanks. The constraint of such places, however practicably large, modifies their behavior and not infrequently hastens their demise by presenting obstacles towards their headlong flight of which they often take no heed. A single fish cut out from such a school "panics" to an even greater degree.

The extent to which fishes or other animals show ultrastability is also connected with the above. It would seem that animals with particularly astereotyped behavior, as seen in many insects, would have little more than simple stability as compared with that of the vertebrates generally. Also the persistence with which a given species continues to try an unsuccessful response to a situation would seem to be large in insects and the reverse, perhaps frequently too small, in many mammals. Both these matters are discussed more fully but in other relationships by Ashby (1954). Why fishes have stopped at schools and pods and have not gone on to more specialized organization, such as attained by the social insects, is not clear. Perhaps it is because they have never been able to establish an other than sexual differentiation of member. Might not the development be more

easily evolved by organisms with a stereotyped behavior than those with the behavioral flexibility of a vertebrate? It would seem to be a fair, tentative inference to suppose that these schooling fishes are at the extreme in fishes representing an approach towards simple stability. They also appear to continue an unsuccessful reaction too long, as compared with various more solitary fishes, especially those that build nests and show other elaborate behavior patterns and whose reactions suggest considerable behavioral differences in the opposite direction. The relationships of these considerations to learning, memory, and habituation in various fishes and the homeostat are too evident to need comment.

In connection with other matters Wiener (1948) discusses excessive oscillation or "hunting" in feed-back mechanisms in reference to both excessive and defective or insufficient feed-back and the appearance of apparently similar activity in various nervous disorders. It is interesting in present connections to note that Schuett (1934), Escobar, Minahan, and Shaw (1936), and Breder and Nigrelli (1938) carried out experiments which indicated that both crowded and isolated fishes (goldfish) swam faster, i.e., covered more territory, in a given time than when they were accompanied by some number of companions between these extremes (optimum number?). The random, zigzag wandering of an isolated goldfish would seem to be referable to a condition of defective feed-back, i.e., zero companions seen, irrespective of the subject's activity. That of the same fish under greatly crowded conditions would likewise seem to be referable to the case of excessive feed-back, in which, no matter what the activity of the subject, companions were numerous and too close.

In another way, the searching movements of small bands of fishes in very shallow water described by Breder (1951) would seem again to be referable to excessive feed-back but through a different part of the system which was involved not directly in the maintenance of the school itself but with the need for each individual and the whole group to avoid being stranded. In either case these "searching" or "hunting" movements appear to be closely analogous to similar movements commonly seen in recording potentiometers when

the tracing pen oscillates continually because of over-amplification in the feed-back circuit. Stark and Cornsweet (1958) considered such oscillations in both servo-mechanisms and organisms as the equivalent of malfunctioning or pathological manifestations.

Wiener (1948) wrote, "It is certainly true that the social system is an organization like the individual; that it is bound together by a system of communication; and that it has a dynamics, in which circular processes of a feed back nature play an important part." He was referring to human societies, but his statement is as true of other animal organizations and brings to mind the ideas of Wheeler (1928) who thought of ". . . the organismal character of the colony as a whole as an expression of the fact that it is not equivalent to the sum of its individuals but represents a different and at present inexplicable 'emergent level,'" when writing of the organization of colonies of social insects. The super-organism of Emerson (1939) and the *Überindividuelle* of Horstmann (1950) are all expressions of similar thoughts, as well as Ashby's (1956) use of "emergent" properties in connection with black-box theory in reference to both machines and organisms. This feature is noted above in other connections. Very likely a fish school with its comparative simplicity and usual equipotential status of each member would provide an excellent starting point for a further examination of such concepts. Wiener (1948) wrote in another place, "The degree of integration of the life of the community may very well approach the level shown in the conduct of a single individual, yet the individual will probably have a fixed nervous system, with permanent topographic relations between the elements and permanent connections, while the community consists of individuals with shifting relations in space and time, and no permanent, unbreakable physical connections." This was given in reference to social organizations in general. Another point he makes which is pertinent to present considerations is as follows: "A group may have more group information or less group information than its members. A group of non-social animals, temporarily assembled, contains very little group information, even though its members may possess much information as individuals." This certainly

would be in keeping with the behavior of many fishes, both solitary and social.

Ordinarily, in a school of two fishes, one finds the two fishes swimming in "tandem" or an "eye-to-eye" position. In larger schools, such a position seldom obtains except in special cases (as are discussed above under Fishes in Orderly Files). In other words, the interchanging positions of the individuals in a school of ordinary size are such that it is physically impossible for the individuals to maintain the "tandem" position of two fishes. In fact, a school so constituted would be a single file of fishes each side to side. If it is accepted that this basic tendency remains as an integrating influence, and departures from it are looked upon as deflections from it, these departures would then be the total result of such influences as varying sizes of the individuals, varying speeds of swimming, and all other small variates that contribute towards giving the school its particular shape as compared to a single row of side-to-side identical individuals in uniform forward motion. Bearing on this is the interesting discussion by Wiener (1954) of how it is possible to recognize a face at various angles or a circle of various sizes or positions or even as an ellipse when its plane is other than at a right angle to the line of sight. Because the fish eye, of schooling types at least, has a very wide angle of vision, a companion a little to one side or the other may be far to the rear or far ahead and still be completely in the field of vision of the subject.

The preceding considerations on the cybernetic point of view have an interesting bearing on the equation of Breder (1954) developed to describe fish schools and aggregations. The equation (1) is given and explained in the present paper under the heading Centrifugal and Centripetal Forces. This measures the spacing of the individuals, with stability reached when  $c=0$ , attraction when  $c<0$ , and repulsion when  $c>0$ . Various social attitudes of fishes are represented by the magnitude of  $a$  and  $p$  as follows:

Pods	$p = 0$	
Schools	$a > 0$	
	$c = a - (f_1 p_1) (f_2 p_2) / d^2$	(1)
Aggregations	$a > 0$	
Solitary	$a = 0$	

When  $p=0$ , the fishes move together to ac-

tual contact. When  $p>0$ , the fishes "rush together with limitations." The limiting case is represented by the solitary fishes when  $a=0$ . The fishes are either aggregating or schooling when  $a>0$ . All four descriptive terms (pods, schools, aggregations, and solitary) are represented by changes in the values of  $a$  or  $p$ .

Because the observed social behavior in fishes appears to show few cases of intermediates between the four named types, it would seem that these terms are not merely arbitrary convenient terms but represent four sites of central tendencies along a line running from the completely solitary to the pod type of social behavior. The fact that they sometimes pass from one type to another through rapid, almost instantaneous shifts seems to bear out this view. Thus, for instance, a school breaks up into a feeding aggregation with no evident transitional intermediate stages, most probably to be regarded as a step-function.

The equation above discussed says nothing about the orientation of individuals or their positions in reference to others. It confines itself to representing the nearness of the individuals' approach to one another and indicates the distance at which repulsion balances attraction, extending the series to where repulsion is zero on the one hand and attraction is zero on the other. Because such an embodiment of a machine as a fish school has already been considered as primarily Markovian, it follows that: (a) the position of individuals in a school or aggregation is a matter of probability; and (b) the orientation of individuals in such a group is also a matter of probability. Therefore the nearness of individuals, as determined by the preceding equations, as well as their orientation in reference to one another, is the mean of the mutual probabilities of each. Consequently, a loose group or aggregation has a matrix of lower probability values, while a tight aggregation, school, or pod has higher probability values. This tends, in extreme cases of great unanimity of activity, to reach near unity, the only value, except zero, found in the limiting form—the fully determinate machine. The positions (a) and the orientations (b) may or may not be independent, their degree of interlocking varying with the group of fishes under consideration. Thus, theoretically

at least, a series extending from the completely indeterminate to the fully determinate type of structure could have any values, fully independent of to fully dependent on one another, in terms of *a* and *b*. It should be apparent from the above why the simple equation concerned with attraction and repulsion, which deals in absolute values or in means, cannot enter into the kinds of probabilities of position and orientation for which it is necessary to invoke stochastic series and their sequelae.

Interaction between the two probabilities can be demonstrated when the individuals of an aggregation approach one another to "swimming clearance" while maintaining their random orientation. Usually schooling fishes maintain no more than "swimming clearance" between one another, as is noted above. It is obvious that "swimming clearance" between members of an aggregation must be considerably greater than "swimming clearance" between the members of a well-formed school, for in the latter the similar orientation of the members permits closer packing while maintaining the ability of individuals to swim without collision. This is made possible only by the fishes' relinquishing a considerable amount of their individual independence of action. Figures 1, 2, and 3 may serve as diagrams of the various relations between distances between fishes and orientation.

The above text discusses a series of homeostatic machines, with four easily recognized types and a smaller number of intermediate and generally transient situations. The question of why the four central types of social organization should be situated as they are,

along such a scale, presents an interesting problem. The evolutionist or ecologist probably would begin by speculating on the possible survival values of each type of behavior. We can take, however, the more detached attitude of the cyberneticist and consider the functional relationships of this series of machines, which in itself may be considered as a single Markovian machine, of which the observed fish groups are only physical embodiments of parts of the machine. Thus without invoking any biological notions, it is possible to explore more critically the fundamental nature of the operation of these homeostatic groups. Primarily the situation is approximated by the classification in table 19.

This simple classification of the groups helps to indicate reasons why intermediates between the named nodes in the series are scarce and transient. If *c* of the equation is zero or negative, there is no attraction. No group forms in either case. At all the other nodes, *c* is positive. In the aggregation there is attraction to the limit of swimming clearance between randomly or nearly randomly orientated individuals. It makes little difference, because the *probability* of irregular behavior is present and to prevent collisions a similar amount of clearance must be maintained. In the school there is a similar attraction between similarly orientated individuals, but closer because the regularity of behavior permits closer packing. The point of this is that the individuals must rely on low probability of departure from the standard behavior. In the pod there is no point at which repulsion equals attraction, and the fishes move to contact irrespective of their orientation or its lack. Viewed from this standpoint,

TABLE 19  
RELATIONSHIPS OF VARIOUS POSSIBLE FISH GROUPS

Groups	No. of Fishes	Distance Between Fishes in Terms of "Fish Lengths"	Positions in Reference to Other Fishes	Orientations to Other Fishes
Pods	>1	0	Fully positive	Near = to near random
Schools	>1	<1	Positive to ranked swimming clearance	Near =
Aggregations	>1	>, =, <1	Positive to random swimming clearance	Near random
Solitary	1	>1, to ∞	Neutral or negative	0

there is no need to labor the reasons why intermediate conditions are transient, for these four positions are stable, and the intermediates are merely faster or slower movements to one position of stability or another. A diagram of immediate effects is shown in figure 27. Its relation to figure 3 is evident. The change from any position of stability to any other three may be direct or through a chain of sequences. Models of many of these transformations can be found in fish groups on simple observation. Without any reference to such biological concepts as survival and adaptation, it appears that groups of fishes should be expected, on a basis of the equation and the above analysis, to show just about the "social attitudes" that they actually reveal.

Just what significance these types of behavior have to the survival and evolution of either the fishes or their behavior is not illuminated by the above analysis, and it itself should not be expected to provide such illumination. However, by an indication of the precise reasons why dynamic machines of this sort have points of stability of which fish groups form models, the road is cleared for a less subjective consideration of the place of these forms of social behavior in the economy of the groups that display them.

Because the preceding excursion into elementary cybernetics indicates clearly that the reasons for the existence of various groups are based on the stability of certain regions, it is possible to discuss abstractly the effects of such a condition on the units that comprise them.

As these machines are Markovian and homeostatic in four regions, it follows that the units that comprise such systems must find a way to exist under these restrictions. Other regions are unstable, and the system moves rapidly to one of four possible regions of stability. Whether, at any or all of these regions, the system becomes persistent or is destroyed is in no way indicated by the demonstration of this condition. Because real fishes, as corporeal representations of such a machine, show themselves, according to their kind, to be acting in a manner demanded of such a system, it follows that these regions of stability permit persistence varying with the phylogenetic and ontogenetic status of the species concerned. It must follow, therefore,

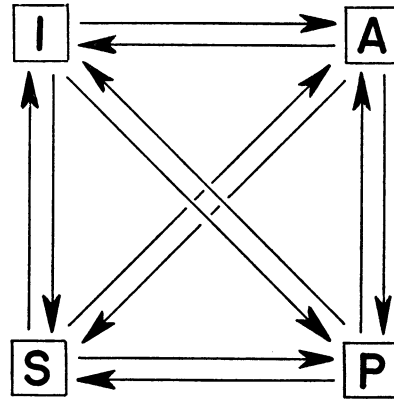


FIG. 27. Diagram of immediate effects in transitions between four nodal types of fish social structures. I, isolated (solitary); A, aggregation; S, school; P, pod.

that the fixing of the particular area of equilibrium must have operated through the genes in such a fashion as to produce the observed pattern. This behavior appears to be very largely innate, i.e., gene-fixed, and with comparatively little capability of being modified by learning, as has been indicated by Breder and Halpern (1946).

Thus the conclusion this leads to is rather the reverse of what is generally held by biologists, and such questions as "What good does it do fishes to form a school?" become pointless. That is to say, the social reactions of a species are bound to find areas of stability in both phylogeny and ontogeny. Those forms have succeeded that have been able to find, for their type of machine, a stability area sufficient for the machines to persist. Others must perish. This reduces such social organizations nearly to the level of a tropism such as phototropism, and very nearly similar statements may be made about any such phenomena.

If entropy is considered as measuring the degree of disorder in a system, it is attractive to consider the possibility of thinking of the various fish groups in terms of entropy. Thus the more disordered a group the greater its entropy, while in polarized pods and schools the entropy evidently approaches a minimum, i.e., the disorder is low. Naturally this disorder cannot be taken in merely static terms but must also be considered in terms of momentum, which is equally as im-

portant as position. Thus in any phase-space treatment of these ideas three coordinates of position and three coordinates of momentum would have to be invoked. Without attempting to push this thought beyond warrantable limits, it may be that such a system as an isolated, well-organized fish school could be treated from this standpoint. It would require considerably more information than is presently available before it would be worth while to carry this view further.

Rothstein (1958) discourses at length on a generalization of the entropy concept of statistical mechanics to cover the situation in communication theory.

A protocol can be developed that can compare these general considerations to the behavior of a real school by rather simple means. As discussed above, the equation of Breder (1954) considered only the nearness of approach of the fishes for its basis of calculation. This position is, of course, determined by the speed of a fish and its angle of trajectory. If the axis of movement of the whole school is taken as a base line, the angle of the trajectory may be read positive for counter-clockwise, and negative for clockwise, rotation in ordinary fashion. The precise direction of this base line is not important to the calculations, as any arbitrary line would serve for computation. It is, however, a little more readily understood if the direction of the group is taken, which is actually the mean of all the trajectories of the fishes involved. Such data may be obtained from a motion-picture film of a school of fishes taken vertically from above, as is shown in table 20. The actual trajectory of the three fishes is shown in figure 21. While the measurements were taken from the tip of the snout, if necessary a greater refinement could be introduced by taking the measurements from the anterior base of the dorsal fin, which is in the orthokinetic part, so that the yawing of the head and the sweep of the tail could be minimized. This cannot be so easily reduced in the angular measurements. The present angles were taken from a line through the base of the dorsal and the tip of the snout.

The above procedure merely gives a measure of the swimming trajectory of a single fish. If the amplitude of the swimming motions are small enough to be negligible, the

TABLE 20  
PROTOCOL FOR TRAJECTORIES OF  
THREE *Jenkinsia*

(These are shown in figure 21 for six simultaneous seconds. Time interval =  $\frac{1}{4}$  second, i.e., every fourth frame. S = distance = difference in position between tip of snout at every fourth frame in arbitrary units, i.e., mm. on original tracing. A = angle = degrees between course of fish and a line approximating the axis of the school to the nearest one-half degree.)

Fish A		Fish B		Fish C	
Mm.	Angle	Mm.	Angle	Mm.	Angle
11	-30.0	11	2.5	9	11.0
13	-4.0	11	6.0	12	9.0
11	-30.0	11	-23.0	10	-21.5
9	-18.0	6	-3.0	8	-25.5
9	48.0	7	25.0	13	7.5
9	48.0	8	20.0	8	10.0
13	80.0	9	59.0	5	67.0
8	143.0	10	8.5	10	-8.5
9	123.0	13	12.5	8	-7.0
10	93.0	9	25.0	10	15.5
8	120.0	10	2.0	7	-6.0
6	11.0	6	-5.0	10	-16.5
14	-14.0	3	29.5	8	27.0
8	9.0	5	-7.5	7	11.0
11	4.0	9	0.0	8	-2.5
12	0.0	9	-9.0	6	11.0
13	-21.0	7	-18.0	7	3.0
9	-28.0	7	-33.0	5	73.0
8	-35.0	8	-19.5	4	34.5
8	-35.0	9	-14.0	7	14.0

trajectory approaches a straight line. If not, it varies with both the angular divergences and acceleration. If the fishes involved are able to and exercise backing movements, *S* becomes negative at such times and the trajectory becomes fairly jagged. This undoubtedly has much to do with the fact that the tight schools are composed of fishes of no, or little, ability to back up, while the typical aggregating forms often have this ability well developed, a feature that is discussed above in other connections. It is evident from table 20 and figure 28 that there is a tendency towards regularity. That is, if the swimming were absolutely regular and measured at the same points on each cycle, the protocol would be completely regular and the phase-space diagram based on it would be symmetrical

and would be the path of a strictly determinate machine. Departures from it give a measure of its indeterminate nature and indicate its Markovian nature. Finally, the more "blurred" the figure becomes the less regular the movements become and the more difficult is the maintenance of any school or aggregation. Thus evidently a phase-space diagram must be cyclic to some extent in order to represent the activity of a school or aggregation. If the arrows passed out of the area of stability, either the fish would be represented as doing the physically impossible (as 20, 0, if 15 is assumed as the maximum speed possible), or the fish would show angular displacement large enough to represent disorganized movement. The transitions shown in figure 28 indicate that only small movements are possible during the time intervals chosen and that there is a large element of purely physical constraint in this machine, on which is overlain a psychological constraint on behavior which is the basis of school formation in the first place. The example chosen, *Jenkinsia*, while a regular schooling form, was the least regular in its ranks of any analyzed by Breder (1954), which is clearly reflected in the phase-space diagram.

It should be noted also in this phase-space diagram that (1), if  $S$  is uniform, all transitions are on a vertical line; (2), if  $A$  is uniform, say at  $O$ , the only place where it could occur for physical reasons, all transitions are on a horizontal line,  $O$ ; and (3), if both  $S$  and  $O$  are uniform, the diagram becomes a single point, which represents speed with no angular displacement. Actually a jet-propelled (respiratory) form, such as *Histrion*, a form employing an undulating membrane as a gymnotid, or a paddling fish, such as *Pheroides*, should be able to yield such a graph. Paddling, or rather rowing, forms, such as many labrids and scarids, surge forward on each stroke and would show a horizontal line on  $A = O$ .

Another way to consider these matters in reference to real schools is to consider the school as an error controlled regulator. Numerical data taken from Breder (1954) covering *Sardinella* may be used to express this view. The diagrams of figures 25 and 26 indicate the nature and physical relationship

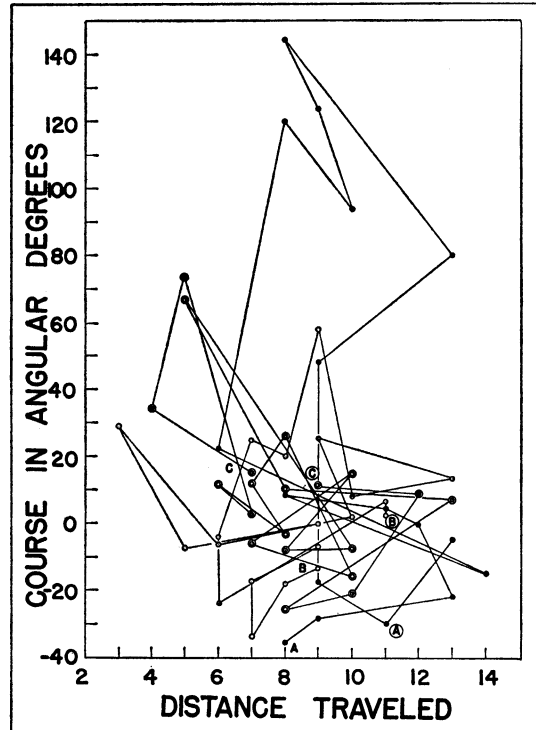


FIG. 28. Phase-space diagram of protocol of table 20. The start of each trajectory is marked by a circled letter, the end by the same letter. Repeated transfers between points are not indicated; for which, see table 20. See text for explanation.

symbols, which are described below for present purposes:

$E$  = Essential variables. Distance apart. 0.146 to 0.174 of a fish length apart, i.e., standard error of mean of 0.16.

$\eta$  = Range within which  $E$  must be kept.

$T$  = Environment (including parts of organisms involved). Locomotor mechanism.<sup>1</sup>

$D$  = Distances. Other fish increasing or decreasing distances.<sup>2</sup>

$R$  = Mechanism ( $R$  and  $T$  coupled keep  $E$  within  $\eta$ ). Decreases distance (Regulator) on increase and vice versa, light, eyes.

As  $E$  has been given as distance apart only,

<sup>1</sup> Environmental functions of null value, such as water temperature and so on, understood.

<sup>2</sup> These are strictly intrinsic disturbances caused by one fish's integrating with others. Such functions as predatory attack have been omitted from present considerations. Their relationships should be obvious. Such action will drive  $E$  out of  $\eta$  frequently with the reduction of the school by one or more members.

it should be obvious that this could also include "angle between" and would require similar treatment. In the case of a fish group,  $E$  could be a vector of any degree of complexity. The size of the angle, with the distance between the fishes, would be sufficient to distinguish a school of fishes as distinct from an aggregation, on a purely objective basis.

A group of fishes constituted of a number of equivalent units of which the speed, angular displacement, and distance apart are all mutually interacting is all that is required to produce the observed conditions. The variations described ranging from the solitary to the formation of "pods" and ranging from

groups of equipotential individuals to those in which some have greater influence, as well as the distances apart the individuals establish and the details of their orientation, are all readily accounted for in this view. Rigorous mathematical treatment would obviously be of very considerable difficulty and, for present purposes at least, would not in any case appear to justify an attempt. This difficulty is common to many approaches to biological problems, but nevertheless the consideration from the mathematical viewpoint often goes far towards clarifying difficult concepts, which otherwise tend to become involved in subjective controversy in which the wrong questions are debated.

### EFFECTS OF GROUPS ON POPULATION DENSITY

A consideration of the density of a theoretical population of sexual animals and its degree of sociability has been given by Philip (1957). He developed a series of formulas by which he was able to compare the reproductive potential of an asocial population with that of a social one and demonstrated, on a purely mathematical basis, that the latter had a distinct selective advantage over the former. He defined, for his purposes, an asocial population as one in which the individuals moved in a random manner as compared with his "social" population in which the members moved in such a way that, even at low population densities, no female remained unfertilized because of paucity of encounters with males.

It could be argued that the fish school represents an operation by such populations which might be considered the ultimate development of insurance of reproductive encounters. If a population of fishes moved purely at random, no school would form, and certainly most, if not all, of the individuals would be lost from the reproductive "pool." The maintenance of a schooling habit would insure against this eventuality, and it is conceivable that here is the real operational basis for the existence of such groups, either the so-called permanent or the temporary schoolers. In the first case would be the schooling isospondyles, such as herrings, and in the second those such as salmon and trout. Her-

ring and mackerel, primarily open-water fishes, usually keep in "permanent" schools, while salmon and trout usually form schools when migrating to a place which confines the fishes in small compass. That fishes range from the notably asocial to the extreme social would merely appear to be the long-time interplay of survival advantages. Thus the simple aggregations of many poeciliids evidently are adequate to insure the complete encounters of every female with a male under ordinary circumstances, while in such fishes as the abyssal ceratioids "random" encounters cannot be sufficient, the hazards of which have been guarded against not by schooling closely but by the permanent physical attachment of the males to the females, which in the present sense could be considered as the extreme of pod formation, or one might say as its "limiting form." At the opposite extreme the other "limiting form" could be the case in which purely random movements were sufficient to provide adequate reproductive encounters, a situation that would seem to have no representation in fishes. One effect of a migratory habit which has not been stressed is primarily that it provides an automatic assembly of fishes where sufficient encounters may take place. This would be useful only in the case of fishes in which such encounters would otherwise be too few to insure adequate reproduction. These features and many other similar ones are taken into account in the



Philip formulas by two terms:  $n$ , the density of population per unit area; and  $K$ , the saturation population density of the environment according to the Verhulst-Pearl population equation.

In developing a mathematical model for the study of encounters in randomly moving particles in two dimensions, Mosimann (1958) considered herding (or schooling), use of a special breeding habitat, and increased detection at the reproductive season as representing changes in certain of his parameters favorable to survival. His work refers mainly to the problems of sparse populations of terrestrial organisms, thus actually being concerned with solitary forms based on the mathematics of random encounters and its modifications. It serves to bring to focus, however, the various "choices" open to organisms in respect to reproduction and to reiterate the danger of assuming that, because a fish schools, it has been forced into such a pattern by selective pressures. It is equally possible to take the stand that its schooling habits have mitigated the need of other elaborate behavior directed towards reproduction, as the fishes were already in close proximity, for reasons that are as yet unclear.

That the relationships between populations and group form are complex has been nicely demonstrated by Langlois (1936). He established immature bass of similar size in fish-rearing ponds and studied the results of several identical arrangements, covering similarity of ponds, number and size of fish, and other pertinent matters. He found that even when two ponds started out seemingly the same in all respects the population structure in them often drifted in very different directions. From one he might obtain a uniform aggregation, differing only in showing a normal curve of variation. In another he might obtain a group of small fish and a group of large. The latter fed on the smaller and often refused any other food. Also their aggregating attitude was different from that of the group of small-sized fishes. In all he enumerated eight different types of social organization of this kind. There appeared to be no evident extrinsic influence that could be invoked to explain such differences, throwing the whole matter to the supposition that the causes are brought about partly by accident and partly by individual vicissitudes in early life which get one fish off to a much faster start than its fellows.

## EVOLUTION OF FISH GROUPS

FOSSIL REMAINS are such that no clear evidence can be obtained which indicates what type of social behavior the individuals may have expressed. The fact that many fish-bearing facies show large concentrations may indicate any of a number of conditions that have no direct bearing on social grouping. For instance, strictly asocial forms might have been trapped in the same drying basin and might be all concentrated in one place because of a uniformity of direct response to the prevailing conditions. This simple possibility makes futile any attempt to evaluate the sociality of crowded fossil slabs. Therefore the manner of evolution of schools or other societies can be interpreted only from the evidence to be found in living fishes and the structure of the individual fossils.

It has been indicated that the social attitudes of fishes must be such, in phylogeny, that they maintain the ability to find an area of stability sufficient for population persistence. If this is a valid view, it follows that no amount of interpretation based on the observable behavior of recent fishes could throw light on the manner in which the earlier fishes behaved. So far as evidence goes, the earliest fishes from the first may have stabilized around any one of the nodes, which they do today, or may have switched from one to another under the shifting pressures of a changing environment. The physical nature of these nodes would appear to make their changing with time very difficult to imagine.

This leaves us only with evidence that can be obtained from the physical structures of the fossils. That is to say, for instance, that a fossil, eel-like form would hardly be expected to school like a mackerel, but might form contact pods, or burrow in the bottom individually. Actually more can be gleaned from such considerations than may be at first apparent. As it has been shown that mobile pectorals, which permit backing, are associated with groups other than the proper schoolers, it seems safe to infer that this was so from the earliest times for the definite mechanical reasons already discussed. Because such mobile pectorals do not antedate the

subholosteans, it follows at least that the earlier types of body and fin design associated with open water, such as in the Haplolepidae, would not have the evident impediment to schooling that a mobile pectoral presents. Thus it is not unreasonable to suppose that many of the paleoniscoids, so herring-like in many ways, may well have formed dense schools and may have occupied an ecological niche very like that occupied by the present-day herrings. "Ecological niche" as used here is the equivalent of the cybernetic "area of stability."

These thoughts also seem to bear on the repeated appearances of parallelisms of body form in different phyletic lines. As the structures of an animal determine to a large extent its possible behavior, these, too, may be expected to show areas of stability. Conceivable forms that stood no chance of attaining an area of stability should not be expected to be represented. Because of this it should follow in a large sense that stability in form and stability in behavior must necessarily go hand in hand.

Because schooling fishes line up from intrinsic influences in still water, and others are forced to in flowing water, one cannot but wonder whether the first fish that schooled did so because of some influences causing them to take up life in a fast flow, and to hold their positions by swimming upstream as fast as it carried them down. This would call for optical fixation on some stationary object, often another fish doing the same thing. In any such group at least one fish must be able to see some stationary object, such as a rock, or the group as a whole cannot hold its position. The fact that such fishes do take optical fixes on one another might have a very real selection advantage, in keeping the fishes together, and more likely on adequate feeding grounds. The peripheral fishes would be the "anchor men." The transition from such a condition to forms that school continually and in still water would only call for this behavior to become transferred to the genetic system, a matter on which selection should be able to play a role.

## SUMMARY

### DEFINITIONS AND EXPLANATIONS

1. WHILE CONCEPTUALLY fishes could be any distance from their fellows, i.e., from contact to infinitely remote, they are mostly to be found at certain well-defined distances from one another.

2. These distances correspond to names, which have been used more or less loosely—"solitary," "aggregation," "school," and "pods." The last designates a group of fishes in physical contact. The first designates fishes at any distance apart greater than in an aggregation. An aggregation designates an unpolarized group of fishes more or less randomly orientated and with little more than swimming clearance between individuals. A school designates a polarized group of fishes with little more than swimming distance between individuals, a distance that is considerably less than that in an aggregation.

3. Because the form of these groups depends on both proximity and orientation of the individuals, satisfactory definitions are difficult. In another form of expression schools might be thought of as polarized groups and aggregations as unpolarized groups. Then there could be polarized and unpolarized pods, which exist, and polarized and unpolarized individuals, which is a meaningless expression.

### SPECIAL FORMS OF SOCIAL GROUPINGS

4. Such groups are usually composed of equipotential individuals, but differences may extend in one direction so that there is leadership, in that one or more individuals are more attractive than the others, or, oppositely, there is hostility when a hierarchy is established, which tends to destroy the group.

5. The more closely integrated groups may show "emergent" properties, belonging to the assemblage alone and not merely the sum of the attributes of each individual.

6. In certain extreme cases these close groups, schools or pods, may show deceptive resemblances to other objects, which may attain the status of a kind of mass mimicry.

7. Although most fish groups are composed of similar individuals of one species, there is a

vast variety of minor variations in their construction, including groups of more than one species and groups of peculiar form such as balls and regular parallel rows. Most of these are understandable on a basis of the effects of extrinsic influences or the limitations of discrimination of the sensory mechanism involved.

### SPECIAL ENVIRONMENTAL INFLUENCES ON FISH GROUPINGS

8. As both light and temperature influence locomotor and pigmentary social responses, the cues supplied through vision and through the phototactic mechanism lead to complications in the formation of groups and their dispersal, which find a variety of expressions in different species and in the same species at various stages in ontogeny.

9. The role of the pineal organ, while not especially complex in its phototactic influence in itself, evidently contributes importantly to a variety of the more puzzling things in the social life of fishes.

10. The reactions to various wave lengths are such that within the visible spectrum there is a general strong tendency for many fishes to respond more positively towards the shorter wave lengths (the blues and greens).

11. The general avoidance of the longer wave lengths by diurnal fishes may be responsible for their often hiding because of the reddening of daylight in the late afternoon, before the lowering of intensity has a distinct visual effect.

12. There is some evidence to support the view that some fishes show a positive reaction towards ultra-violet wave lengths, but this requires extended analysis beyond that suitable for inclusion in the present paper.

13. There is no evidence to suggest that fishes may be able, even at the surface, to distinguish radiant heat from ambient temperature or that they may be able to respond to the polarization of light.

14. Photoperiodism is evidently present in fishes to some degree, but the larger component in their behavior would seem to be the direct effect of the coming of darkness or other natural daily changes.

15. A marked relation exists between the

sign of the phototaxis of fishes and the temperature of the water, it being demonstrable that, in general, fishes tend to become light negative to bright light when the temperature is lowered beyond certain values, and of course, in the case of sufficiently high temperatures, also to avoid the light.

16. The recent past social history of an individual fish may exercise considerable influence on its social attitudes, even to the extent that social attitudes may be reversed.

17. Learning and feeding, at least, may be vastly facilitated in many fishes by social means.

#### STRUCTURAL NATURE OF FISH GROUPS

18. The details of structure of fish groups, especially schools, are examined with reference to the principles of cybernetics in order to facilitate comparisons with other systems showing what may be similar basic homomorphism or isomorphism.

19. The ability to back up is not possessed by all fishes, and it appears that the most pronounced and consistent schoolers are among those that lack this ability to a marked degree.

20. The ability to back up readily is looked upon as a deterrent to proper school formation, because fishes exercising this ability need more "swimming clearance," but many simply aggregating fishes customarily use backing movements extensively and the aggregation provides the necessary "swimming clearance."

21. The transmission of information through a school, even if the cue is a sound, is ordinarily transmitted at a slower rate, related to

the fish-to-fish optical or other transfer, evidently because of the silencing effect of the intervening fishes and their arrangement.

22. The individual trajectories of fishes in a school are considered from the standpoint of their mutual interference and the results on the structure of the school.

23. Because all fish "mills" are evidently not extrinsic in origin, it is thought that those that are not may have their genesis in unusual individual trajectories of less well-integrated individuals.

24. The establishment of hierarchies from schools is believed to be based on groups of individuals, all of which are not equipotential.

25. When a fish school is considered as a physical embodiment of a Markovian machine, it is possible to find purely mechanical reasons for various behavioral elements, such as the "searching" a school in very shallow water will undertake, and to see reasons why the "solitary," "aggregation," "school," and "pod" series represent points of stability.

26. With such a view it is possible to consider the fishes as parts of a system that imposes on them certain structures, such as aggregating or not, with which they have to reckon in an effort to survive, rather than to look on many of these features as the results and reasons why they have survived.

27. Within such a framework, then, the individuals would have to adjust their entire ontogeny to a population density and structure which are permitted by the system of which the individuals are redundant parts, while the equivalent adjustment of the phylogeny would be on a population level.

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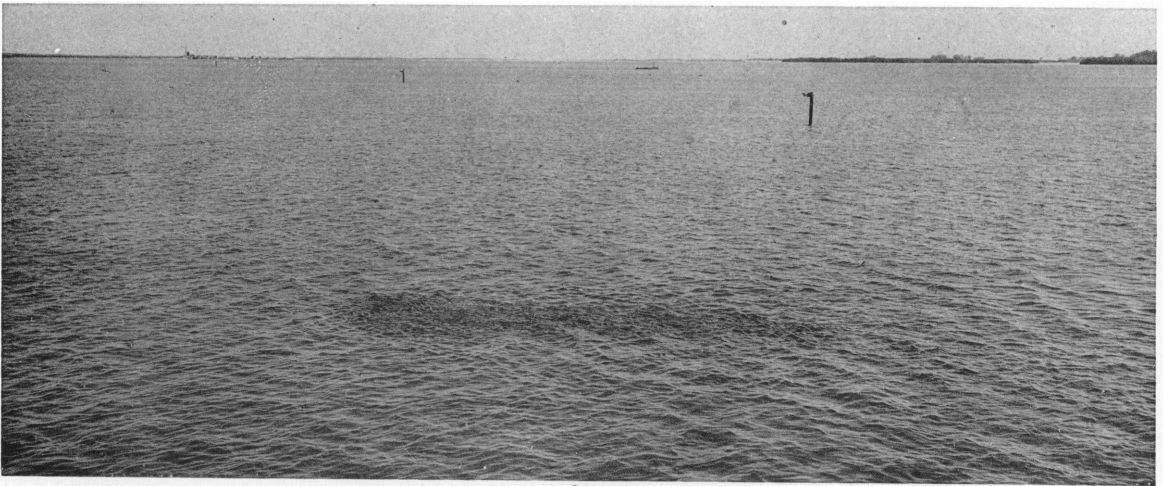








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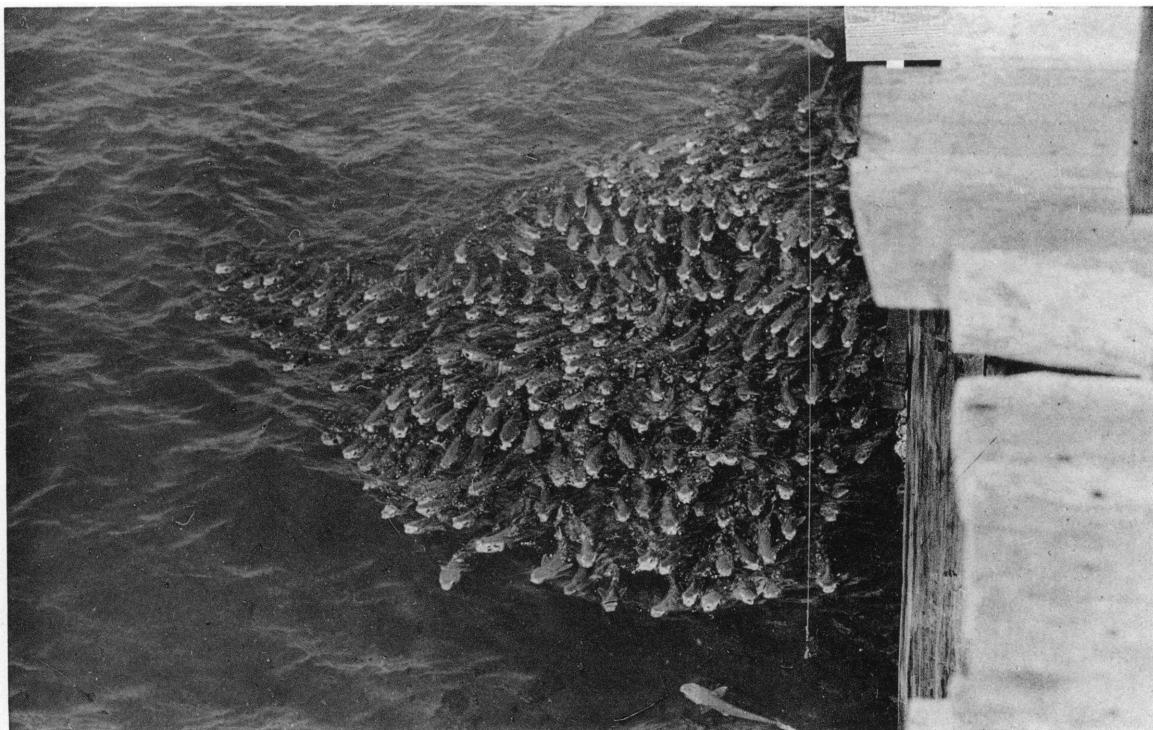


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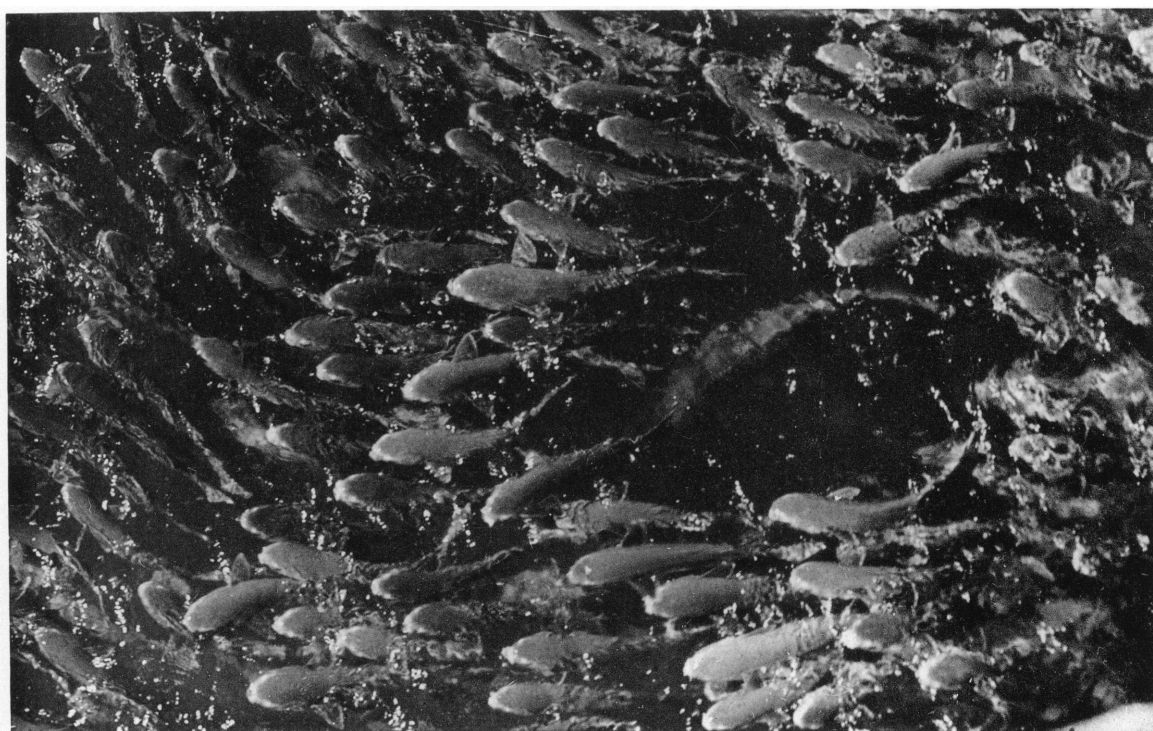


3

Groups of *Mugil*. 1. A pre-spawning pod of *Mugil cephalus* as seen at some distance. Cape Haze Laboratory. 2. A closer and more agitated pre-spawning pod of *Mugil cephalus*. Cape Haze Laboratory. 3. A typical feeding school of half-grown *Mugil trichodon*. Lerner Marine Laboratory



1



2

Post-spawning contact schools or pods of *Mugil cephalus* feeding at the surface. Fort Myers Beach, Florida.  
1. Head-on view. 2. The group disturbed and loosened by an *Archosargus probatocephalus* rising from below





1



2

Small groups of *Mugil cephalus*, feeding at surface in late spring. 1. A group on the move as typically elongated. 2. A more chunky group hovering about a dock



1



2

Off-colored fish in normal schools. 1. Two white *Carassius* "leading" a school of yellow individuals. Mountain Lake Sanctuary, Florida. A third white fish is farther back, surrounded by the barely visible reddish individuals. 2. A whitish *Sardinella macropthalma* in a school of normal individuals, with no apparent effect. Lerner Marine Laboratory

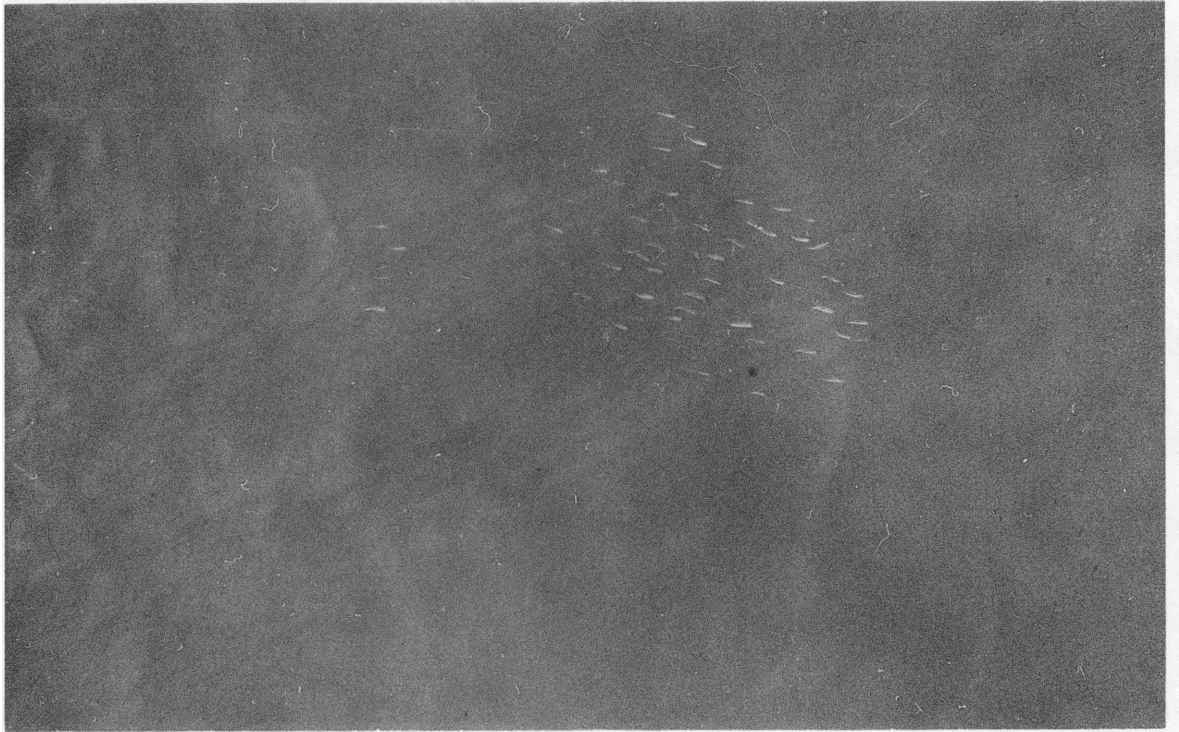


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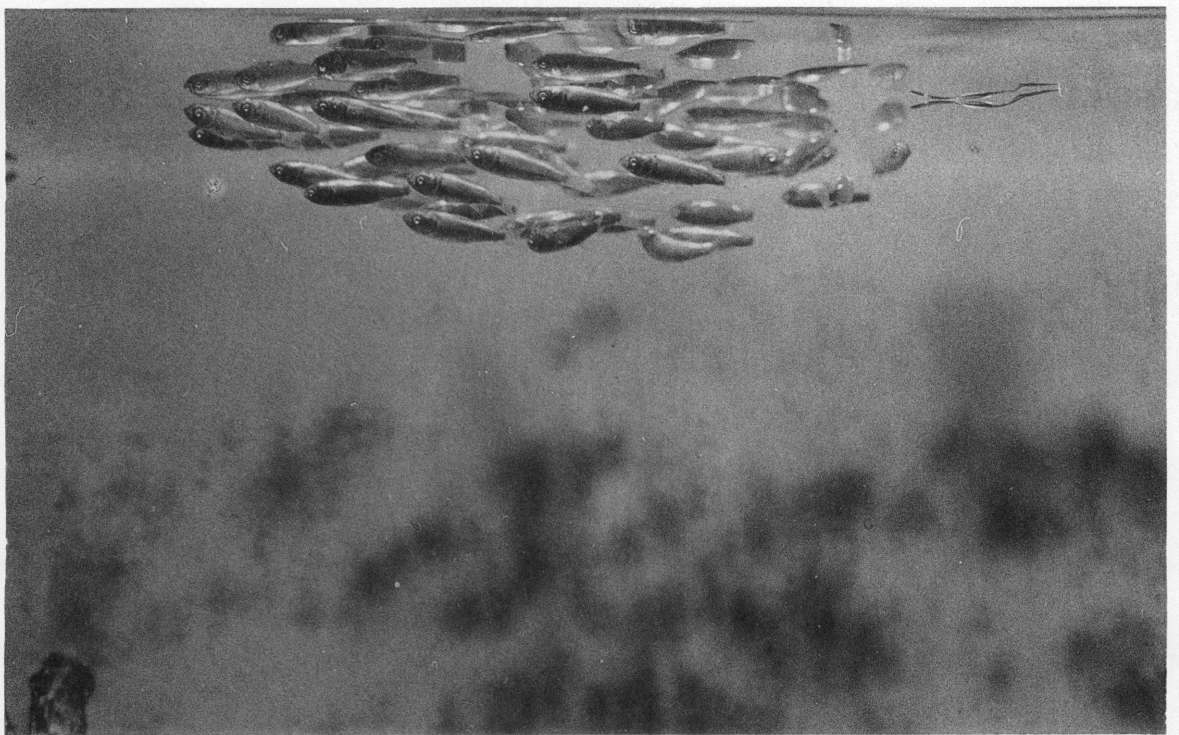


2

Special social behavior in *Salmo gairdneri*. 1. In "orderly files" in a stream with riffled bottom. After Gudger (1949). 2. In a hatchery pool, showing tendency to swim by twos. New Jersey State Hatcheries, Hackettstown



1

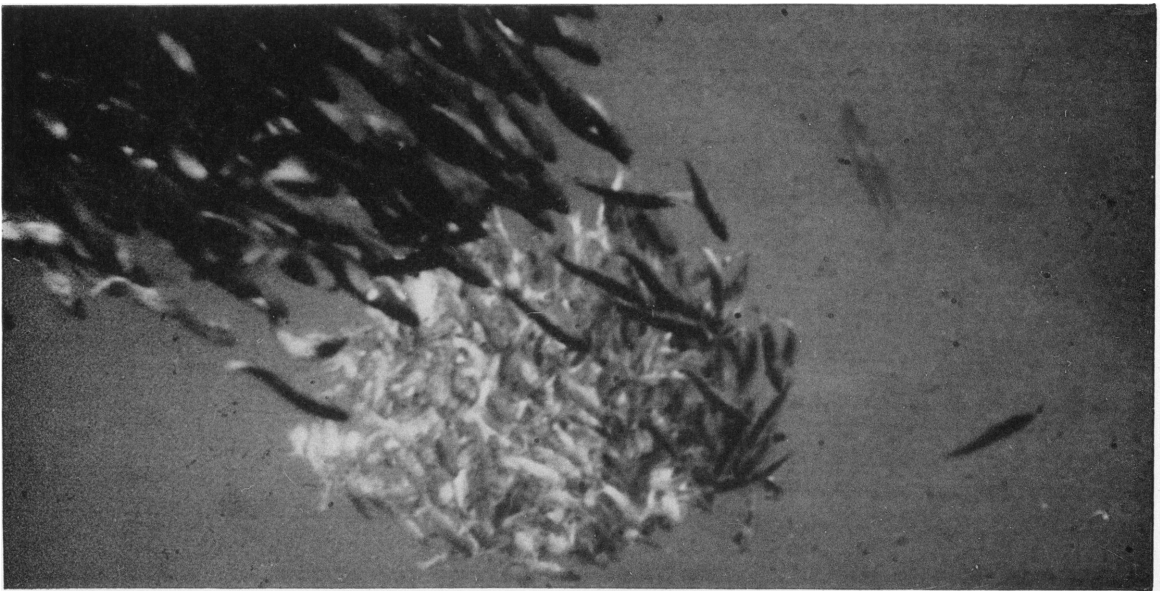


2

Juvenile *Mugil cephalus*. Cape Haze Laboratory. 1. Young *Mugil* in an aggregation at the sea surface. 2. The same *Mugil* in a "fright" school after transfer to an aquarium



1

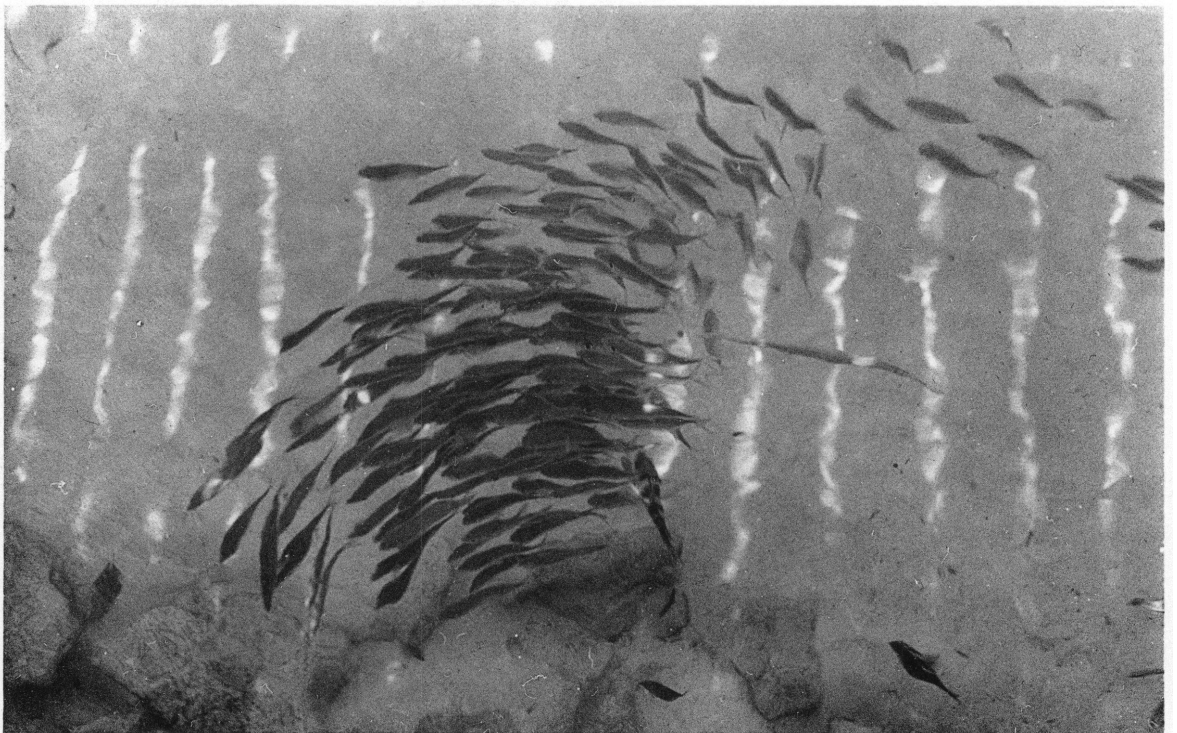


2

Group activity of young *Sebastodes paucispinis*. 1. A fully formed ball under the stern of a small boat. 2. The beginning of the formation of a ball. Photographs taken by Mr. Logan O. Smith near Catalina Island, California

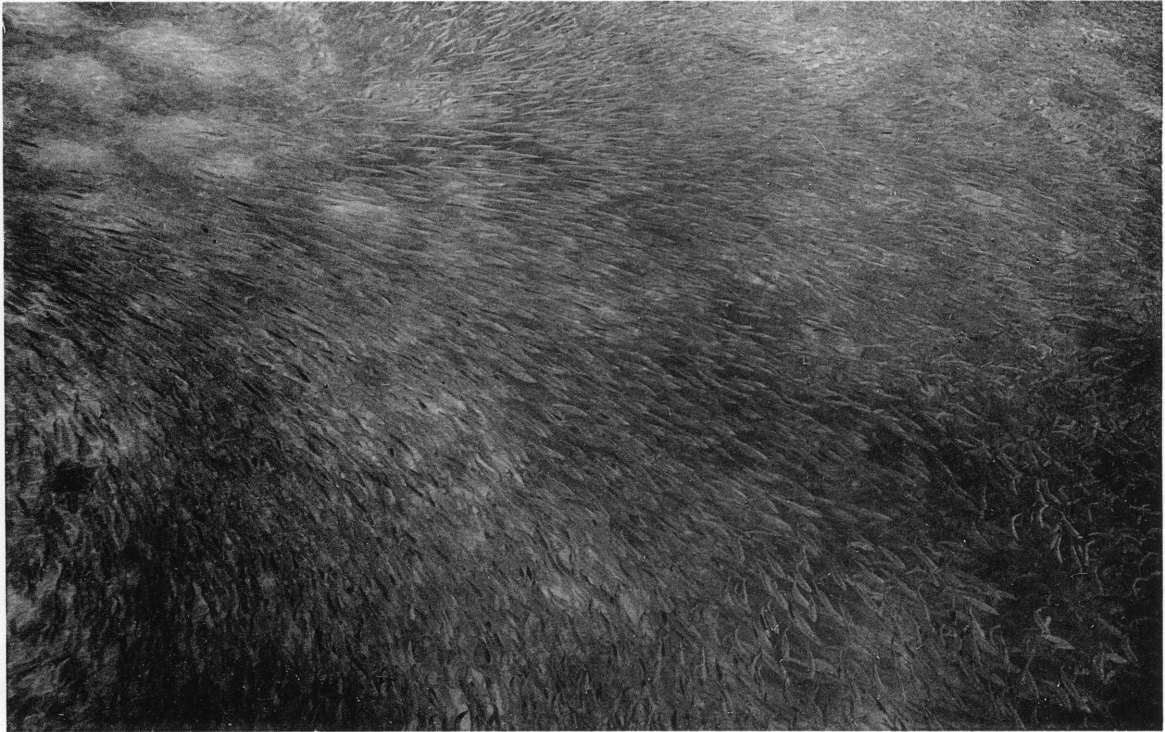


1



2

Carangid schooling. Lerner Marine Laboratory. 1. *Selar crumenophthalmus* swirling under a dock. 2. *Caranx ruber* attacking a school of *Sardinella*



1



2

Isospondyle schooling. Lerner Marine Laboratory. 1. A large school of *Sardinella*. 2. A mill formed by *Jenkinsia* from evidently intrinsic factors



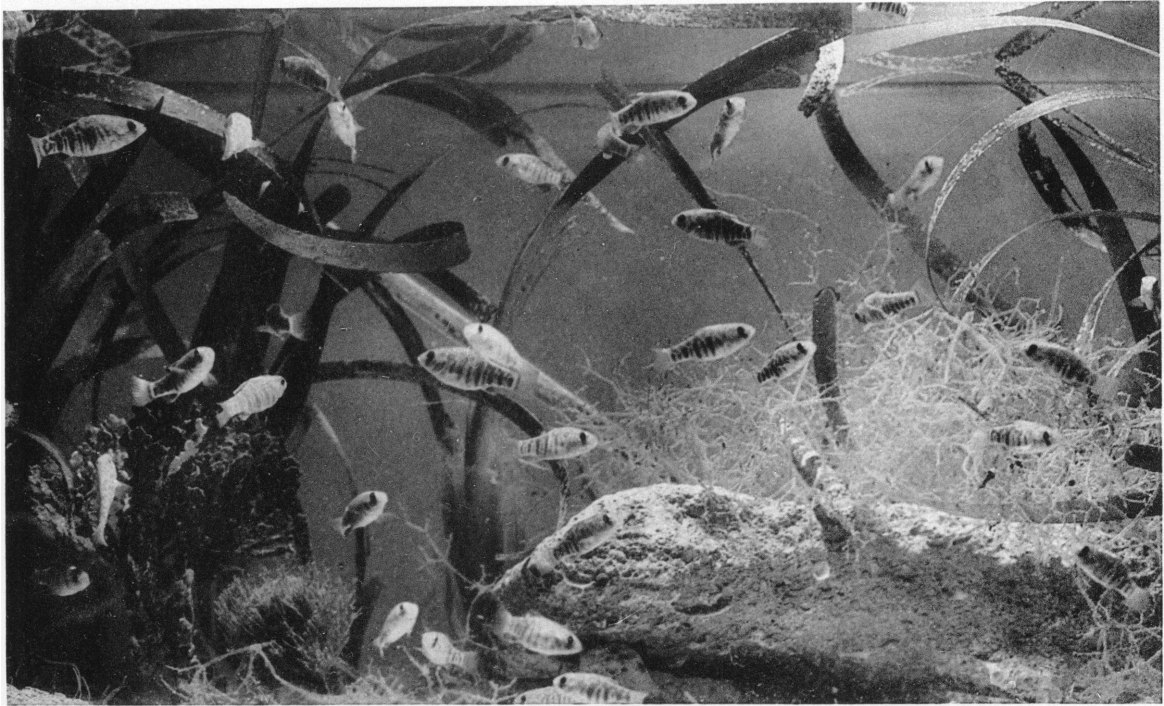
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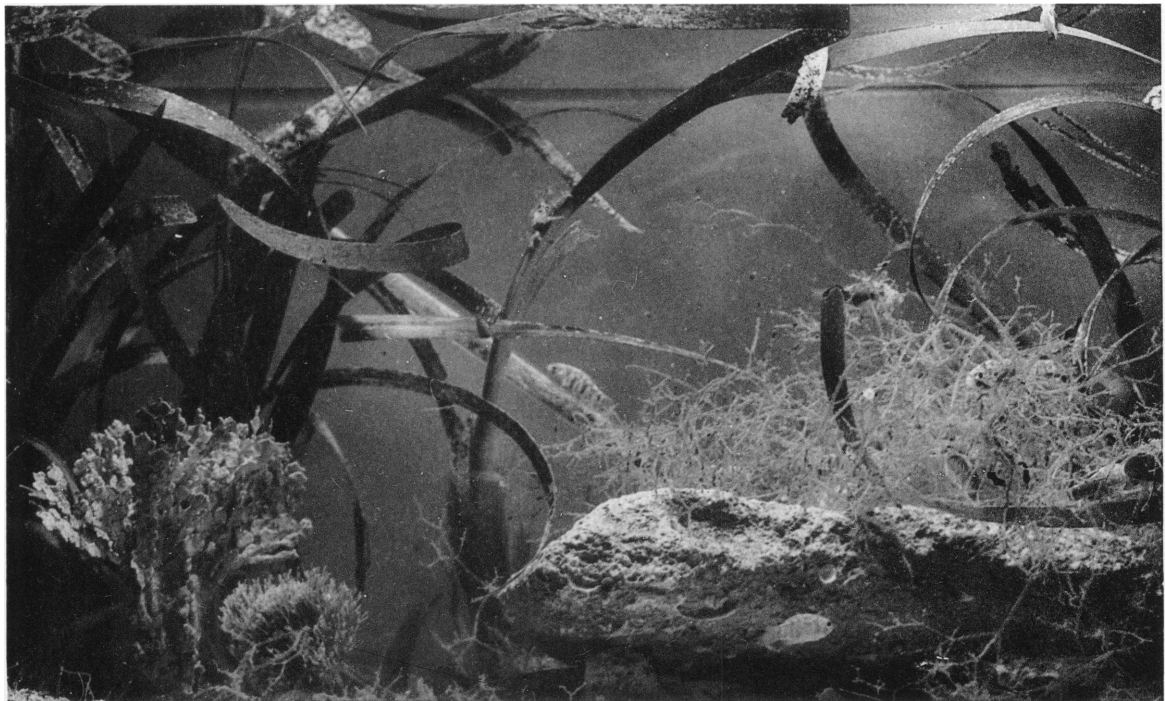
2

Social behavior of *Notemogonus* and *Erimyzon*. In New Jersey. 1. A common aggregation of the two forms as seen in the daytime, in an aquarium. 2. The same group photographed at night by photoflash, with the camera left in the same position, showing the catostomids separated from the cyprinids. The former rest on the bottom and change their pattern to one of blotches





1



2

Diurnal reactions of *Cyprinodon baconi*. Lerner Marine Laboratory. 1. An aggregation as seen in daylight in an aquarium. 2. The same group photographed at night by photoflash, with the camera in the same position, showing very few fishes, as most are out of sight because of their "roosting" habits. In both pictures a single *Bathygobius* is seen, the only other occupant of the aquarium, a practically aperiodic form





