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A contribution to the theoretical analysis of the schooling behavior of fishes

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PREFACE

While watching the movements, especially the milling of a small school of chub mackerel (Scombrus colias), in captivity in the tanks of the New York Aquarium, the author perceived the possibility of a comparatively very simple set of reactions, which would explain the apparently complicated and mysterious behaviour of the fishes in question. It is most unfortunate that the species showing the schooling performances most clearly, as for instance herrings, spratts and mackerels, usually are of such delicate nature that it is practically impossible to keep them alive for any great length of time or in any numbers in captivity, and the opportunities to make observations in the field, though not infrequent, are too dependent upon chance to be especially pursued by a single student not otherwise occupied in the same field.

Though entirely borne out by the author's recollections of numerous former observations in the field and by the more recent observations and experiments made in the New York Aquarium and during the third oceanographic expedition of the "Pawnee," the explanations must therefore still be presented to the readers on a mainly theoretical basis, as a working hypothesis for further investigations and experiments, in the hope that it may arouse the interest of those who by good fortune or occupation will be able to gather further information concerning the very interesting phenomenon of schooling among fishes. The problems involved are of special interest to human society because several of the most typically schooling species are also among the economically most important ones, partly gaining their economical importance through the very schooling habit itself, which is the necessary basis for most of the fishing methods adopted for the exploitation of the species in question.
INTRODUCTION

By a comparison of the various ways in which schools are formed by different species of fishes it immediately appears that the phenomena may naturally be classified into two apparently very different groups. One is the occasional traveling in bands kept together as a reaction to impulses created by a temporary situation. Another is the apparently permanent living in schools. Phenomena of the first group are mainly observed among fishes living and feeding at the bottom or along the shores, and may be due to different causes, as for instance simply that similar needs or fears make the fishes swim in similar directions.¹ The bands formed in this way certainly are of slight stability and will again be dispersed as soon as the conditions for their gathering disappear. The gathering and dispersing of the schools of the first group thus seems to be determined by the immediate environmental factors.

Quite different are the schools of the second group, which are characterized by great stability through the most varied of environmental conditions. Such schools will only disperse under influence of rather violent stimuli, as for instance the splashing or dropping of a stone in their midst, and will immediately reassemble. Schools of this type are chiefly and most typically formed by pelagic fishes such as mackerel, sprat and herring. The independent character and great stability of these schools seems to indicate that their existence must be dominated by internal factors of the school as a whole or of the single individuals, and not by direct influence from the changing environment.

In the present paper we will mainly consider the phenomena of this second group only, and for practical reasons it will therefore be convenient for present purposes to define the term school as the type of fish-“herd,” which has an apparently permanent character and is an habitual spatial relationship between individuals as above described.

At the end we will then return to a discussion of the relationship between the different types of “herds.”

The internal factor keeping together a herd of animals of any type is generally referred to as a social instinct, and this term undoubtedly¹

¹ The difference between the two groups may be explained as merely a difference in the degree of development of the set of reactions usually producing the schooling behavior, as will appear later.
is just as well applicable to the above mentioned internal factor of a school of fishes as to any other phenomenon of a similar nature. The term, however, seems void of any logical definition or analytical description, and the meaning it conveys is therefore very vague. It is indeed mostly used to veil a lack of knowledge of the real psychological or neurophysiological elements and reactions involved in producing the phenomena observed. The meaning of "social instinct" will therefore vary according to the mental inclinations of readers and writers.

In the present case it may, at first thought, seem very natural to interpret the social instinct of schooling fishes in an antropomorphic way, assuming the school to be the result of deliberate activities of the single individuals seeking the protection of great numbers, thus each acting with the school as a whole as their aim. From this point of view, however, the exquisite harmony of individual movement with regard to speed, direction a. s. o. during the maneuvering and movements of the school as a whole, seems rather overdone and evidently does not leave much space or time to the single individuals for deliberating their activities. Under certain circumstances moreover the maneuvering of a school will be automatically converted into the apparently perfectly senseless performance of milling i. e. of the individuals swimming around and around within the narrowest area practically possible while the school as a whole remains in the same place. This phenomenon certainly can not easily be explained in harmony with a theory of deliberate activity of individuals conscious of their purpose, whether social, as in this case, or not. The milling may continue for days in the same spot, as has repeatedly been experienced in the New York Aquarium, especially with schools of chub mackerels and killi-fishes (*Fundulus*), the school apparently being unable to break away from the circular movement except under sufficiently strong stimuli (usually introducing fear) from without. For these reasons one seems justified in suspecting that the apparently social behaviour of schooling fishes may be only an incidental result of mechanically integrated, comparatively simple and automatic reactions of the single individuals.

This suspicion is strengthened by the observations that in many cases even newly hatched fishes will form schools long before they

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2 The tanks of the New York Aquarium are never left in perfect darkness during night.
may reasonably be expected to have experienced the advantage of
great numbers or to have developed conditioned responses of a social
aspect.

It is then the aim of the following discussion by analyzing the
observations to try to find out the possible elementary reactions
involved in the “social behavior” of schooling fishes, and thereby
explain the performances of the school as a whole and of the single
individuals as they are effected by these reactions. Only by analyzing
in this way the sequences of changing stimulations and integral
responses during the performance, not by regarding the entire process
as a unit response to an initial stimulus, can any real understanding
be gained. If the performance should indeed be a unit response,
then this will appear from the analysis, but can not be proved without
it.

It must of course be understood that the reactions will in the real
nature scarcely ever be quite as simple as they might appear from
the following discussion, as the individuals will practically never be
under influence of one stimulus alone, but subjected to diverging
impulses created by a multitude of various internal and external
stimulations. We are, however, at present only concerned with the
particular psychological mechanism responsible for the “social”
element in the behaviour of the fishes considered.

INDIVIDUAL REACTIONS

It is a common experience in any aquarium that if two specimens,
of a species which habitually lives in schools, are put in the same
tank they will not move around separately but will line up beside
each other and keep swimming in practically parallel courses. This
fact, first of all, shows that there is a mutual attraction between single
individuals belonging to the same species of habitually schooling
fishes i. e. the single individual will react to the perception of a prospec-
tive companion by bending its course of swimming towards the
direction from which the perception is received. The fact that the
specimen after having made the approach will also adjust its position
to one parallel with that of its companion, certainly must be regarded
in relation to the fact that this action is necessary to keep the companion
within the desired close range, when the fishes are swimming, as
these schooling types nearly always do, even when they are “not
going anywhere.” The adjustment of direction may therefore very well be interpreted as a learned or conditioned reaction, thus being in its development merely a secondary effect of the primary response to the perception of a companion. When, however, the fish has once become conditioned to respond to a diverging or converging course of a perceived companion by adjusting its own direction of swimming, the performance of this reaction may be directly caused by the perception of a difference in directions alone, independent of the presence or absence of a stimulus creating an impulse to approach the companion. It has thus been possible to observe specimens of such species as Mugil cephalus, Menidia menidia, Fundulus majalis and heteroclitus adjust their positions according to the positions of their respective companions, even when they were at rest and close together, so that no approach between the specimens was made.

In so far as we are only concerned with the normal reactions of the single individuals, not with the ontogenetic or phylogenetic relations between these reactions, we may therefore regard the approach and the adjustment of direction as two separate responses to the separate stimuli of a distant, prospective, companion and a close, but not parallel one. The neuro-physiological independency of the established reactions is also evident from the fact that they are entirely antagonistic, the adjustment of direction checking the approach.

THE SCHOOL.

By our analysis of the behaviour of two individuals, only, in relation to one another we found that two very simple reactions, which may easily be considered as automatic responses originating from a specialized tropism, affected their joint swimming instead of separate movements in arbitrary directions. We will now endeavour to make out how far the performances peculiar to an entire school as a whole and to the individuals therein may also be merely due to the same simple reactions of the single individuals under the special conditions contributed by their great number, without necessarily demanding for their explanation processes of more complicated stimulations and responses.

In regard to the problems of the school as a whole a fundamental difference exists between the states of psycho-physiological equilibrium relative to only one or to two companions. When influenced by the
stimulus of only one companion the individual, as we have already seen, responds by approaching it until a sufficiently strong antagonistic stimulus is called forth to balance the impulse to approach (or until this impulse is sufficiently weakened). When two companions are present, one on each side, the individual is, from the start, under the influence of two antagonistic stimuli, and it is therefore not necessary that it shall respond by outwards reaction, as long as the stimuli may balance each other beforehand. In other words it is not theoretically necessary that an individual, when placed between two companions shall approach either one of them, as long as it perceives them both under the same conditions i.e. from the same distances and so on. This again means that so far as all but the extreme peripheral individuals are concerned, a given number of specimens may be equally distributed over an indefinitely great area in spite of their mutual attraction for one another. The condensed appearance of fishes in a limited school can therefore not a priori be explained by the reactions of the individuals in its interior.

In any number of specimens, however, some will always have to be at the sides of the columns. These peripheral specimens certainly are under constant stimulation from one side only i.e. from the next individuals towards the centre of the school, as they have no companions on the other side. In the peripheral files on the two sides of a school one should therefore expect to find a constant tendency to seek towards the centre. The consideration of a simple theoretical case will illustrate how the reactions caused by this tendency may serve to explain the condensation of the school as a whole and the subsequent maintenance of a constant density of the individuals in space.

The figure 1 represents a theoretical single column of 7 individuals, all swimming on the same level. Originally all the individuals may be supposed to have been at equal distances from each other (A), 2, 3, 4, 3', 2' therefore in stable psycho-mechanical equilibrium with their respective companions on the two sides. The individuals 1 and 1' at the ends of the column are, however, under the influence of a onesided attraction only, and must therefore approach their

A condensation originating in the interior part of the school might however also take place through maintenance and integration of occasional approaches, combined with reactions against occasional dispersals due to the attraction between the individuals. Observations of the re-gathering of dispersed schools does, however, not indicate that this process is of any great importance, although it must always be regarded as a possible element of the performances observed.
Fig. 1. Successive condensation of a theoretical, single column of fishes. Explanations in the text.

respective companions, 2 and 2', just as they would have done if these were the only prospective companions present. But this approach by the extreme individuals will necessarily disturb the equilibriums of the next ones (2 and 2', fig. 1 B) because the latter will no longer be
at equal distances from one companion on each side. The attraction between the individuals 1 (or 1') and 2 (or 2') is certainly a perfectly mutual relation. When 1 (or 1') has adjusted itself to the onesided stimulation from 2 (or 2') by approaching the latter until the impulse has become eliminated or inactivated by antagonistic stimulations, it will therefore by the same process also have eliminated or inactivated itself as a source of attraction for the individual 2 (or 2'). With the perceptions of their distal companions, 1 and 1', thus inactivated as stimuli (fig. 1 B) the individuals 2 and 2' must now automatically respond to the perceptions of their companions on the proximal side, 3 and 3', which are still at active distances, by starting to approach the latter. The individuals 2 and 2' will of course in any such movement be closely followed by the individuals 1 and 1' (see fig. 1 B, right side 2' and 1') as these are continually under onesided attraction only. In this way the column must subsequently reach the stage when the individuals 3 and 3' must start to approach 4 from both sides, followed by 1 and 2 on one side and by 2' and 1' on the other, and the entire school must finally reach a state, when the average distance between the individuals will correspond more or less to the inactive or neurophysiologically balanced distance between two companions.

The theory of these simple reactions, not complicated by "social aims" of any kind thus offers a perfectly rational explanation for the persistently uniform density exhibited by the various schools of the same species, which is one of the most prominent features of the undisturbed schools. The author has repeatedly had opportunity to watch for a considerable period at a time the movements of single schools of various species of fishes, especially herring (Clupea harrengeus), sprat (Clupea sprattus), mackerel (Scombrus scombrus) and chub-mackerel (Scombrus colias), both in the field and in captivity, without ever being able to observe any changes in the density of the individuals in the school, except such changes as were plainly referable to disturbing factors of the environment. It may also be mentioned that according to the author's observations the central part of a dispersed school seems to be the last to regain its normal density, in perfect concordance with the above explanations for the gathering of a school. The ideal conditions illustrated in fig. 1 A, with all individuals except the peripheral ones in perfect equilibrium with their companions on both sides will, of course, never exist in nature. The gathering of the school may in reality therefore not be expected to take
place, as in above example, by subsequent reactions of the single individuals but under simultaneous activity of all of them, and may under certain circumstances even be expected to lead to the disruption of the column into smaller and denser groups, which may or may not subsequently become united to a larger school. This must therefore be kept strictly in mind, when actual observations are compared with the above theoretical explanations of the general principle governing the condensation of the school as a whole.

So far the assumption of a simple, automatic “attraction” towards a perceived companion as the only basis for the schooling behavior of fishes has proved a very satisfactory explanation of the phenomena, considered, and therefore of advantage compared with the theory of a more complicated general “social” or even “altruistic”

instinct involving the entire school, as such, as a stimulus for the responses observed.

**MILLING**

Under certain circumstances the phenomenon of milling will to the best of the author’s knowledge be observable in any type of truly schooling fishes, and sometimes among fishes which only occasionally or intermittently travel together in bands.

As mentioned already in the introduction, the performance of milling consists in a ceaseless swimming in circles on part of the single individuals, while the school as a whole remains stationary and apparently retains its normal density. No purpose seems conceivable for this performance and it is correspondingly difficult to find an explanation thereof on the assumption of a “purposeful” “social instinct.” On the following pages we will therefore try to determine if the theory of a simple automatic attraction between single individuals only, as formerly described, does not yield a far better basis for explanation also of this peculiar phenomenon and, thereby itself receives its crucial test.

From observations especially of a small school (about 60 individuals) of chub mackerel (*Scombrus colias*) kept for some time in the New York Aquarium and also from earlier observations on herrings, sprats and mackerel in the field the following facts have been discovered concerning the formation of a mill.

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4 The social instincts of fishes are defined or classified by David Starr Jordan (Fishes (p. 41). New York 1925. Appleton and Co.) as “altruistic instincts which are concerned with the mass of individuals of the same species.”
Milling will practically invariably follow when a school (as a whole, not the single individuals separately) tries to make a sharp turn of more than 180°, provided no disturbing stimulus of sufficient violence to break the performance is present. Ideal conditions for the formation are found when the school is forced to turn by meeting a solid obstacle to its straight-forward movement, but otherwise remains undisturbed, as for instance when it swims against the wall of an aquarium-tank\(^5\) in which there are no other inhabitants or special conditions yielding disturbing stimulations to the individuals.

It must not be understood from the above description that the performance of milling is an easily disturbed process. On the contrary the mill, like the ordinary school, exhibits a surprising persistency. Once formed it has in aquarium tanks been observed to persist for days, even weeks in the same place,\(^6\) without being in any way by physical, environmental conditions mechanically limited to the narrow space occupied. Only a strong stimulus, like a splashing close by or the sight of a dangerous enemy, is certain to break the mill. In experiments with the above mentioned school of chub mackerel it was found that even a onesided feeding of a mill will usually only produce some irregularities at the point where the food is introduced, but most of the fishes will continue to follow the circular course around picking up some food as they pass by it, while only a few individuals will actually break from the mill to feed. The strength of the stimulus necessary to break the mill will, however, certainly vary according to the species considered and the conditions of the school and its environment.

We will now try to make out what may theoretically be expected to happen on the assumption of only the simple reactions of individual approach and adjustment of direction, when the school tries to make a turn of more than 180° as above described. By comparing our theoretical conclusions with actual observations we will then be able to test the value and validity of the theory involved.

Before going into the details of our problem it is, however, necessary

\(^5\) The milling has nothing to do with the limitation of the space in the tank, as the length of the latter, in the cases considered, was about ten times the diameter of the mill, which, in addition, according to its origin, was never found in the center of the tank but always close to the walls.

\(^6\) The author has moreover had opportunity to observe both herring, sprats and mackerel milling in the sea, but always only when close to the shore or to other obstacles (fishermen's nets and so on).

\(^6\) The aquarium not being left in perfect darkness during night.
first to evolve some general psycho-physiological principles concerning
the varying effects of the same stimulus under changing conditions.\(^7\)
First we will consider the different effect of a stimulus before and
after the individual has responded to it, provided the stimulus is not
removed by the response. It is logically evident that the ultimate
result of a reaction must always be the inactivation of the stimulus
by which it was called forth, because the organism must continue to
react until this state has been reached, as already mentioned on p.
6. When an organism has been allowed a sufficient opportunity to
respond, we will therefore always find that it has brought itself into
a state of psycho-physiological equilibrium to the stimulus concerned,
so that the latter is no longer active. Thus the sight of food is no
longer an active stimulus after the organism has responded by feeding
till it was satisfied.

If an organism, as just described, has adjusted itself to a certain
stimulus, it will, according to the nature of this adjustment, also have
to react to a second even directly antagonistic, and under equal con­
ditions weaker stimulus, because the first stimulus does not again be­
come active i. e. create impulses, until the organism is brought out of its
adjustment, that is until it has already, to some extent at least, reacted
to the second stimulus.

Another principle of great importance to our present problem is
contributed by the fact that as far as visual stimulation is concern­
ed, and we may as well mention at once that most of the schooling per­
formances probably are based upon visual perception of the com­
panions (see discussion and experiments p. 22), a body in movement
relative to the perceiving organism generally has a much greater effect
i. e. a greater power for bringing forth responses than has the percep­
tion of a body at relative rest.

Having recognized these principles we may now return to our
problem. The fig. 2, is a diagrammatic drawing of a small school in
the act of making a turn of about 200\(^\circ\), and thereby forming a mill.
When a turn of more than 180\(^\circ\) is made this means that the anterior
part of the school (at the right in fig. 2) after the turn is moving away
at a course which is converging with the course still being followed by

\(^7\) This certainly is not a quite logical expression as the stimuli are in reality not
identical under changing conditions, because they are not the objects themselves but
the perceptions of these, and therefore will change with the conditions of perception
(distance, speed a. s. o.).

The expression is however common usage and convenient for the present con­
siderations.
the posterior part (at left fig. 2) before the turn. The anterior and
posterior parts of the school will therefore tend to cross in opposite
directions of swimming. We may now investigate how this can be
expected to influence the reactions of the single individuals and
consequently, by integration, the behavior of the entire school.

The individuals of the interior file\(^8\) at the turn certainly will be
the first to come under the influence of the still oppositely directed
specimens, and we will therefore consider them first. Previous to the
turn this file constitutes one flank of the school, and its individuals
are therefore adjusted to a onesided stimulation, only, from the per­
ception of companions towards the center of the school, as described
on p. 6. After having made the turn, however, these individuals
(for inst. no. 2 in fig. 2) will also be stimulated by the perception of
companions on the other side (no. 1 in fig. 2) swimming in the opposite
direction. According to the first principle discussed above they will
now have to respond to this new stimulation in spite of the stimulus
from old companions on the other side (no. 3 in fig. 2) because they
have already adjusted themselves to the latter. According to the
second principle the stimulation from the opposite individual (1) must
moreover, in itself, be much stronger than the stimulation from the
old companion (3), because the former is in very rapid movement
relative to the perceiving individual (2) while the latter (3) is in
relative rest, moving with the same speed in the same direction. In
other words the individuals of the interior file must be expected to
react to the perception of the opposite specimens by their normal
responses of approach and parallelization. Thus in our example
individual no. 2 must try to approach no. 1 and to turn to the
same direction in spite of the stimulus from no. 3, because the latter
stimulation is comparatively weak and not immediately active.

This relation between opposite individuals of the interior file as
stimulating and responding subjects certainly is of a mutual nature.
The individual in the position of no. 2 (fig. 2) evidently must influence
the movements of the individual in position 1 in just the same way
as its own movements are influenced by the latter. This means
that when an individual of the interior file (for instance in position
2, fig. 2), in response to the stimulation from the opposite side, has
turned and joined the latter (in our example fig. 2 reaching the, in
the meantime vacuated, position 1), it will subsequently be stimulated

\(^8\) In a real school there certainly are several interior files, one above the other, but
for simplicity's sake we may consider one single level, only, of the school, as the
stimulations and reactions will be the same at all levels.
in just the same way (by the individual now in position 2) to turn around again and rejoin the side it just left. In other words the individuals of the interior file at the turn will come under the influence of a constant and conquering stimulation to join the opposite side of that on which they are swimming, and must therefore respond by constantly swimming in circle after each other. The nucleus of the mill will thus have been formed.

This explanation of the circular movement of the central file does, however, evidently not necessarily demand that the turn must be more than 180°, as long as it is only sharp enough to make the opposite individuals appear at a sufficiently close range to assert their stimulating influence as above described. In perfect concordance with this theoretical conclusion a more or less well defined milling of the central file will actually be observable at nearly any sharp turn of the school, inasmuch as the individuals at the centre may usually be seen to turn around and around several times before they finally swim off in the new direction. And when a mill is formed by the entire school, the central file will always be the first to fall into the circular movement. When the turn is less than 180° the rest of the school will however generally not follow example. To find the full explanation for the milling we must therefore also consider the special conditions of the other files under the different circumstances.

It is now easy to see why only a turn of more than 180° is certain to bring about the formation of a complete mill, because the second, third, fourth file a. s. o. from the centre will then successively come under the influence of oppositely directed individuals, and will therefore be forced to turn on exactly the same principles as those causing the circular movement of the central file. Looking at our example in fig. 2 we find that, after the first (central) file (nos. 1, 4, 2 a. s. o.) has fallen into circular movement, the second file (nos. 6, 5 a. s. o.) becomes exposed to the stimulus of the oppositely directed individuals, still approaching at the old course, (no. 6 of the second file has already responded by starting to turn), after which the third file (no. 7 a. s. o.) and then the fourth (no. 8 a. s. o.) gets into similar situations. If the turn is less than 180° this series of situations will evidently not develop, because all outer files instead of approaching their opposites will then be rapidly diverging from them, and, being from the start separated by the width of the ring formed by the interior file, they will very quickly pass out of the effective range of the stimulus from the oppo-
sitely directed specimens. We thus understand why the milling performance is only found in the central part of the school or in the central file alone when a turn of less than 180° is made.

When we get away from the central file there are, however, also other factors than the influence from the oppositely directed individuals to be considered, because in all files outside the central one the individuals will have companions also on their central side and will therefore be influenced by the perceived maneuverings of these companions.

Before the turn all individuals except those on the flanks may normally be considered as being adjusted to the perception of one companion on each side, swimming at balanced distances from these and in a parallel direction. When now the companion on the inner side starts turning away towards the centre, the adjustment of the perceiving individual in the case is disturbed, as moreover the companion on the outer side is still parallel and in the proper proximity, the perception of the latter is, at the moment, not an active stimulus and therefore not immediately opposing the response to the new stimulation from the other companions. The perceiving individual must therefore automatically start reacting to the turning away of its inner companion, as it would do to the perception of any individual to which it had not adjusted itself, i.e. by trying to approach it and turn to a parallel direction, in spite of the fact that it is thereby separating from its outer companion. If the outer companion would still keep a steady course of swimming it would now, in turn, become active as a stimulus tending to make the turning individual turn back again, and a shifting course between the inner and outer companion could thus be expected as the response of the individual in question. Such a result would be logically quite similar to the constant swimming in circle in the central file. As soon as the individual starts turning towards its inner companion it will, however, in turn, influence its

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9 For simplicity's sake we do not in the present discussion consider the complications arising from having several companions within the field of perception on each side (for instance 2 above each other on one side balanced by 3 in different positions on the other side, a.s.o. in an infinite number of combinations). The number of companions acting as stimuli on each side of the perceiving specimen is of no interest for our general theoretical conclusions, as long as we regard the movements as responses to separate stimulations from the perceptions of single individuals, only, not related to the school as a whole, "the mass of individuals" or any number thereof as a unit. Our "two companions," one on each side, may in reality be regarded as theoretical representatives for the combinations of individual stimuli present on each side in any actual case.
outer companion in exactly the same way as it was itself influenced by the inner one, and the outer companion must therefore immediately start turning after it, thus reducing the stimulation for the perceiving individual to return. As the primary reaction of each individual, starting from the central file, will be a turning inwards after the inner companion, and as furthermore the impulse to turn back again will, in all normal cases, be reduced or effaced by the similarly induced approach of the outer companion, the turning movement may thus be automatically transmitted through the entire school. Comparing this theoretical conclusion with observations we find that it is well borne out by the fact that, after the central file has fallen into circular movement, the individuals of the outer files will rather frequently start turning in a curve already before they have been exposed to the stimulus from oppositely directed specimens, as for instance illustrated by no. 5, fig. 2. The theory of an automatically transmitted tendency to turn inwards further nicely explains why, in a small school, the individuals of the peripheral files will generally join the mill, even if the ends of the files do not meet during its formation, as in the case of nos. 10 and 11, fig. 2.

By the assumption of this transmission of the impulse to turn, it does, however, at first thought appear as if the angle of the turn would be an inessential circumstance for the formation of a mill, inasmuch as a mill should then be expected to develop automatically as soon as the central file had fallen into circular movement, as it will generally do to some extent at nearly any sharp turn, even of considerably less than 180°. It therefore seems as if there should be a discrepancy between the said assumption and actual observation. This apparent discrepancy however disappears by a closer logical analysis.

The transmission of the turning impulse is dependent upon the already developed angular difference and increased distance between every individual and its inner companion, as these are the conditions necessary for calling forth the individual responses by which the transmission is brought about. This means that the process is not a momentary one, but in the contrary involves, from individual to individual, the time necessary for a sufficient increase of distance and angular difference before it is carried further on. It further means that the turning of the school, caused by this transmission of the impulse from a central file of individuals in circular movement, can
not follow by concentric courses of swimming but must result in a curved fan-like dispersion of the files, leaving sufficient room and angular difference between them to cause the transmission. Now, the angular difference created between two companions by every integral turn of the inner one of them in its equally curved course, rapidly decreases with the increasing radius of the curvature. The time demanded for the increase of distance necessary to call forth a response will moreover increase in correspondence with the just mentioned decrease of integral divergencies. The transmission must therefore become gradually slower away from the central file, while the stimulation transmitted becomes more vague and less violent. We must consequently expect to find that the impulse to fall into circular movement after the centre file will rapidly fade out towards the outer parts of the turning school, unless it is reinforced by stimulation from individuals in oppositely directed movements. Our theoretical conclusions are thus perfectly concordant with the fact that a complete mill is only certain to be formed when the angle of the turn is more than 180°, while a similar maneuvering will generally only be observed in the most central parts of a school when the angle is less than this.

It will carry us too far to go into all the details concerning the influence of the size and proportions of the school upon the formation of mills. According to the recollections of the author the milling is much rarer in large schools than in the smaller ones. In a school of great size a turn of more than 180° will certainly be very apt to bring about a perfect confusion from which no regular performance may be expected to result. The author has repeatedly had opportunity to observe such momentary chaotic conditions from which one (sometimes several) normal schools would again emerge, after a school of herrings or sprats had been forced to make a sharp turn through meeting the fishermen's net. In other cases however normal mills are formed under the same conditions. It is evident that in a greater school the anterior returning part will force the posterior part aside to make room for the mill, thus more or less forcing the posterior individuals to enter into a circular (curved) course even before they have actually reached the initial turning point of the school. This can also generally be observed.

So far we have only considered the process of forming a mill. The factors causing the milling activity to be maintained by the school until it is disturbed by adventitious antagonistic stimulations
certainly will be essentially the same as those causing the initial formation of the mill. The circular movement of the central file has the nature of a perpetual, autonomic process, as above described, and the tendency to turn will be continually transmitted outwards. In the established mill there are, however, special conditions to be considered, which are different from those prevalent while the mill was still in the stage of formation.

As the reader will probably have understood already from the preceding considerations and descriptions, the mill is not always circular but on the contrary starts with an ovoid outline in vertical view, being extended along the area of meeting between the approaching and returning parts of the school. In this area the critical stimulations and responses take place; and its geometrical character is certainly a mechanical consequence of the nature of the turn, but is also an aid to the formation of the mill, and may be necessary as such, by providing increased distances between the turning companions and sharper turns, in addition to the stimulation from the oppositely directed specimens. Now, the peripheral file of the mill is acting under exactly analogous conditions to those of the flanking files of the normal school, being under onesided attraction, only, towards the centre of the mill. The peripheral file must therefore also exert a condensing influence upon the mill in exactly the same way as the normal school is condensed from the flanks, as described on p. 6-8. The first effect to be expected from this condensation is the disappearance of the extended area, because the increased distances between the files in this region are providing just the conditions necessary for bringing about the processes which will eliminate them. (See description p. 15.) And it may be stated from actual observations that the initial ovoid outline usually changes to a circular (or sometimes regularly elipsoid) shape, as soon as the entire school has fallen into milling or even before that. As the school will usually have attained its normal density before forming the mill there will not be instigated by this operation any new condensation-processes except that just mentioned, but after the circular outline has been developed, the density (diameter and transverse section) seems just as constant as was the density of the normal school, and these phenomena may certainly be similarly explained as mainly due to the direct and indirect effect of the onesided attraction upon the peripheral file or upon the flanks as already made out on p. 6-8. In an estab-
lished mill there will, however, be more shifting in the relative positions of the single individuals than there will be in the normal school, the constant density of the former is therefore more to be regarded as a total average result of centrifugal and centripetal tendencies in the mill than as a sum of fixed spatial relations between the individuals. This, however, does not affect the importance of the peripheral file as this will be the main source of the centripetal tendencies as above described.

Now it is evident, that in a mill of constant density the distances between the single individuals must also be essentially constant. With circular, concentric courses there are moreover no areas where a general divergence between the files is found, as in the extended region during the formation of the mill. It is therefore probable that the responses to the stimulation of an increased distance between the single individual and its companions are of very small if any importance in the maintenance of the mill. The adjustment of direction alone in response to nonparallel companions must therefore be considered as the predominating of the internal factors for keeping the individuals to their course, in addition to the exterior centripetal tendency of the peripheral file.

As already discussed, however, the integral angular differences between the individuals, which serve as transmitting stimuli for the impulse to follow the circular course of the central file, quickly fade away towards the periphery, because the integral turns of the individuals at every point of their circular courses decrease in proportion to the increase of the radius. Fig. 3 is a diagrammatic illustration of an established mill with examples of the individual situations to be found therein. In this figure we may readily recognize how the angular difference between 4 and 5 and the consequent stimulation of 5 is much greater, on account of the smaller radii of their courses, than is the angular difference between 9 and 10 and the corresponding stimulation of the latter. The impulse transmitted from the circular central file must therefore gradually lose its grip upon the individuals, and we thus become interested in trying to find out whether there are not, in addition to the positive impulses for maintaining the milling activity, also circumstances indirectly bringing about the same effect by preventing the individuals from breaking away, when the positive impulses fail. First of all we must remember that the mill is to its extreme periphery surrounded by a file of fishes swimming under
one-sided attraction, only, and therefore seeking towards the centre. This peripheral file will in itself act as a wall, and even if individuals from the interior files should break through, these will in turn themselves come under the same onesided attraction, and will therefore automatically join the peripheral file, as illustrated by the position of no. 14 in fig. 3. It is, however, not necessary that the individuals, when the transmitted impulse from the centre fails to control their movements, shall have to break through the peripheral file, and come under onesided attraction, to join the mill again. When an individual leaves its circular file and swims off at a tangent it will for purely geometrical reasons have to pass the other files at an increasing
angle the farther it gets away from the centrum of the mill. Sooner or later this angular difference between the straying individual and the files it passes will therefore become great enough to call forth the response of adjustment of direction, and the fish will again fall into a circular course, only farther off from the centrum than the course it left. Thus for instance no. 6 in fig. 2 has just left its file and its angular difference from no. 7 (and 8) is small compared with the angular differences between no. 12 (and 13) and no. 11, which left the same file as no. 6, but has gotten farther away from the centre.

The individual situations and reactions made out as theoretical possibilities involved in the formation and maintenance of a mill may all be commonly observed in any milling school of fishes more or less in accordance with the different incidents indicated in the diagrammatic figures 2 and 3, which are just as much based upon actual observations as upon theoretical conclusions. It must, however, be remembered that only a small percentage of the individuals will, at any given moment, be called upon to perform independently the reactions on which the existence of the school or mill is based according to the above explanations, because the reaction of any single specimen will generally more or less mechanically force a varying number of others to similar performances by "crowding them in" and so on. Thus for instance the turning of no. 15, fig. 3 will also compel the three individuals interior to it to a similar maneuvering, even if the stimulus to change direction on account of angular difference should not be strong enough to produce a corresponding original impulse in these individuals. (In this case it would be perfectly evident that there was no stimulation to approach at all.) Likewise no. 11, in the same figure, will be forced to turn, simply because its way out is blocked, even if other "normal" stimulations should fail. This crowding in is very apparent in any school or mill, inasmuch as the great majority of the individuals, but for occasional openings, have no opportunities at all for breaking from their files.

We have now found that the theory of a very simple set of responses to the stimulation received from the perception of individual companions only, not of the school as a whole, has given a perfectly satisfactory explanation for the characteristics of the normal school. We have further seen that the performance of milling, which is a ridiculous inconsequence from the point of view of a social instinct yielding more or less desirable responses to stimulations from the school as a
whole and its needs, is not only explainable, but is in fact the only result to be logically expected from our theory on the conditions under which it is actually observed to develop in nature. We may therefore say that our theory is well borne out by the facts of observation as far as they have been available.

THE NATURE OF THE STIMULATING PERCEPTIONS.

On the preceding pages it has been shown how the perception of the individual companions may in general be regarded as the normal stimulus of the individuals partaking in the performances of a school. For simplicity's sake the descriptions and considerations have already been formed more or less in accordance with the view that the perceptions in question are mainly visual, but so far we have not approached the problem of their real nature. It has not been possible for the author to conduct any extensive and detailed investigations on this point, but some general considerations and simple experiments will suffice to make out the normal nature of the stimulating perceptions.

The entire characteristics of the schooling performances observed among pelagic fishes, the way the individuals approach and follow each other and so on, already at first thought seems to indicate very clearly the probability of a control of the individual maneuverings by visual stimulation. This impression is greatly strengthened by a general review of the sensory equipment of the different systematic groups of pelagic fishes, by which the permanent type of schools is habitually formed. They are all characterized by great and very well developed eyes, compared with the general average of fishes. It will suffice to mention the different schooling species of Clupeidae, marine Salmonidae (Mallotus villosus), Scombresocidae, Atherinidae, Mugilidae, Scombridae, Carangidae a. s. o. Schooling pelagic fishes with in any way reduced eyes have to the best of the author's knowledge not been observed. Conclusive evidence of the visual nature of the stimulation was finally obtained, as far as the chub mackerel (Scombrus colias), at least, is concerned, by experiments upon the small school kept in the New York Aquarium.

Some specimens were taken out of the tank and, after the eyes had been dried with clean cotton and then covered with a layer of vaseline mixed with lamp-black, they were again returned to the tank wherein the rest of the school was constantly milling. After the first few
moments of excited rushing about, the excitement subsided and the movements of the blinded specimens were then just as calm and slow, as were those of the undisturbed individuals. 3 specimens lost the vaseline-cover within 2 minutes and then joined the mill, but in 4 other specimens the cover adhered for a longer time and these gave very convincing results. These individuals did not at any moment join in the milling activities of the school, but kept moving separately around in all directions over the entire tank, striking its walls, even in spite of the fact that they would very often pass directly through the mill, sometimes even colliding with the milling specimens, but always without showing traces of a tendency to join them. One specimen thus kept separate for 17 minutes, a second one for 32 minutes, a third for 55 minutes and a fourth for even 75 minutes. As soon as the pupils of the eyes became visible again the specimens would start joining the mill, independent of the length of the time elapsed, but in no case did they do this while the eyes were still covered. As a control 10 other specimens were taken out of the water, were submitted to the same treatment, except the covering of the eyes and were then returned. Immediately after their release these individuals showed the same excitement as did the blinded ones during the first few moments of their separate swimming, but 9 of the ten had all joined the mill within 1 minute, while the tenth had in some way become hurt and quickly died. According to these experiments there can scarcely be any doubt about the visual nature of the stimulations controlling the schooling maneuvers of the individual chub mackerels, and there seems to be no reason why we should not be justified in generalizing this result for all fishes with similar sensory equipment and exhibiting similar performances.

It has been made out already that the characters of the school are not alone dependent upon the impulse to approach, but also upon the fact that, at a certain distance between the companions, this impulse must either fade away or be actively checked by antagonistic stimulations. When a visual perception of the companions is regarded as the stimulus for the approach, we may perhaps find the causes checking the original response in the changes, caused by the very approach, in the features of the visual perception itself. It may be that the increasing size of the image with the shorter distance, at a certain point reverses the positive response. Or it may be that the accommodation of the eyes becomes strenuous and therefore causes an
antagonistic internal stimulation, when the perceived companion is
approached beyond a certain focal distance. These are, however, not
at all the only logical possibilities. A reaction instigated by a visual
perception may certainly be changed or checked by an adventitious
stimulation of any kind possible to the sensory equipment of the
responding individual. This may simply mean that the approach
has brought the individual within range of stimulations from the
companions, which were not active at the greater distance, as for
instance smells, sounds a. s. o. The presence of such stimulations seems
rather improbable, however. To the best of the author's knowledge
there has been advanced theories of only one single type of sensations,
except the visual ones, which might really have any bearing upon the
present problem. In his treatise of the fishes in: "Reptiles, Amphibians
and Fishes," J. T. Cunningham expresses the view, based upon experi­
ment published by A. H. Parker,\(^{10}\) that the lateral line in natural con­
ditions serves the perception of the low-frequency waves emitted from
bodies moving through the water, especially from other fishes. If this
view is correct, it seems very probable that the approach in response
to the visual perception of a distant companion might ultimately be
checked by the increasing force of such lateral-line perceptions of the
movements of the same companion at closer range. In the above
described experiments, however, the blinded mackerels did apparently
not recognize the presence of swimming companions at the usual
distance between the individuals of a school, inasmuch as they, when
accidentally approaching another specimen, would generally not
turn away until they came in actual contact or at least so near, that
such contact (for inst. by the pectorals) seemed most probable.
Such collisions were observed, even when the fishes were both swim­
mimg in the same direction with only slightly different courses. In
many cases a collision was certainly prevented by the seeing speci­
men, but not so often when the blinded one was more or less behind.
It may finally be added that the pelagic types of fishes in question are
not in any way especially distinguished by the development of the
lateral line, but on the contrary, in many cases at least, seems to be
rather scantily equipped in this respect (Clupea, Scomber) compared
with other fishes. In the author's opinion it is therefore most probable
that the response of approach is not only stimulated by visual per-

\(^{10}\) George Howard Parker; The functions of the lateral-line organs in fishes.
ceptions, but is also in turn checked by the changes of these same perceptions,\textsuperscript{11} automatically produced by the primary response itself, as described on p. 23.

When we are thus regarding the performances of the typical pelagic schools as entirely controlled by visual stimulations only, we must, however, not forget that other stimulations may very well be responsible for other types of schooling, when such are observed.

For the present, the author is only aware of one special case in which the visual perception is probably not the dominating factor. In the catfishes (\textit{Ameiurus}) the vision is ostensibly very much reduced. These fishes are mainly orientating themselves by the tactile sense and are equipped with long, sensitive barbels for the tactile perception of the environment. They find their food by means of these feelers, and when a solid obstacle is not first touched by one of them, the fish will apparently unavoidably collide with it. Nevertheless the young of \textit{Ameiurus nebulosus} will gather in schools and perform maneuverings, which are evidently analogous with the normal milling. These herds are however characterized by their very great density, being nearly compact, and the mills are not cylindrical, with horizontal courses of the single individuals, but usually more or less globular, with the individual circular courses in all planes between the horizontal and the vertical. These observations are perfectly concordant with the view that the schooling and milling, like the separate movements, of the catfishes are dominantly\textsuperscript{12} controlled by tactile stimulations, every individual perceiving the presence and movements of its companions by touching them with its feelers.

To understand the details of the performances we have then only to return to the preceding descriptions and discussions taking into due consideration the special qualities and characteristics of the tactile perception. The essential difference between visual and tactile stimulations will be contributed by the fact that the latter only gives orientation relative to single points, not to the sum of objects present in the immediately surrounding space or to their projections on a plane, and therefore may influence the perceiving individual independently of level or direction. The significance and effect of relative motion and relative rest is, however, for purely mechanical reasons, the same in both cases.

\textsuperscript{11} In their motor (related to the accomodation of the eye) or purely sensory aspect, or both combined.

\textsuperscript{12} The catfishes are not perfectly blind so that an interference by less effective visual stimulations is also possible.
THE ECOLOGIC SIGNIFICANCE OF A VISUAL BASIS FOR
THE SCHOOLING BEHAVIOR OF PELAGIC FISHES.

If the above conclusions are correct, that the aggregation of schools among the pelagic fishes is mainly or entirely based upon visual perceptions of the companions, then these schools, which are the most perfectly developed (harmonious) and also the economically most important ones to the human beings, must be in a peculiar way dependent upon environmental factors, as the presence of light becomes a necessary condition for their existence. The conclusion, in other words is inevitable that these schools can not exist during darkness, but must gradually disperse as soon as the light disappears. It lies in the very nature of the case, that direct evidence pertaining to this theoretical conclusion is difficult to obtain. In an article by Edward Newman in Zoologist 187613 we do, however, find the following observations recorded on the behavior of a school of young herring in captivity. During the day the herrings were swimming quietly around in the tank, united in a school, but at night the school was broken up, each fish taking an independent course for itself, darting about from side to side and striking against the rockwork often with fatal effects. When a dim light was placed near the tank, the fishes were saved from striking against the rocks, but still followed independent courses, and their behavior was interpreted as due to nocturnal feeding habits. It is not stated whether this interpretation is purely hypothetical or based upon actual observations, but, however this may be, the observed behavior of the herrings is perfectly concordant with the above theoretical conclusions, in as much as a dispersion of the school takes place in darkness or insufficient light, while it remains quietly together in the daylight. It is further evident that the herrings in the darkness, when they are not even able to escape striking the rocks, must be still much less able to pursue their minute prey. The breaking up of the school under such conditions can therefore not be due to anything but the darkness itself. It is on the other hand quite possible that the herrings may be twilight-feeders, as indicated by their behavior in the dim light, though the author does not feel satisfied that this has been sufficiently proved. If the indicated possibility is confirmed by further investigations it

will, however, according to the above advanced theories only mean that the perception of the companions in the fading light has lost sufficient of its "attraction" to permit the movements of the individuals to be controlled by the perceptions of prospective preys, which, in that case, must have been gaining in attraction by the sustained hunger during the quiet schooling in the daylight. The existence of an elementary twilight-feeding instinct, which would leave the fishes unresponsive to the perception of a prospective prey during daytime, while the perception of the same prey in twilight should call forth the strongest responses, seems utterly improbable to the author. The interaction between independent "instincts," gaining or losing in strength with the changing external and internal conditions of the individual, on the other hand, seems to give a very natural explanation of the phenomena in question. The feeding instinct may be supposed to be permanently present, but the corresponding reactions inhibited in the broad daylight by the greater strength of the impulses created by the perceptions of the companions. (Compare also with the following discussion (p. 29) of the relations between the different types of fish "herds").

The scanty evidence so far obtainable on this point thus seems to bear out the theory of a purely visual basis for the schooling behavior of the typical pelagic fishes. Further confirmation or the conception of still more satisfactory explanations is however highly desirable and may mainly be contributed by those who are permanently occupied in the exploitation or scientific investigation of the fishes in question. The main purpose in publishing the theory has therefore been to call attention to the possibilities involved, so that further information may be gathered.

If the schools are dispersing during every sufficiently dark night, their regathering during the next day ought to be recognizable in the catches and observations of the fishermen. The average size of hauls, which are based upon the capture of single individual schools (as for instance purse-seine catches) ought to show a gradual increase during daytime, corresponding to the gradual aggregation of individuals into small schools and of the smaller schools into larger and larger ones. Positive evidence of this kind would be extremely valuable, negative evidence however less significant for reasons, which it would carry us too far to enter into at this early stage.

The possibility of a nightly dispersion of the schools is also of the
greatest interest to those engaged in the statistical investigations of the biology of the schooling commercial fishes. These investigations are based upon limited samples collected at random from the various schools captured within the faunistic region considered. It may be taken for granted that the samples are usually representative of the single schools from which they have been taken. Another question is the relation between the single schools and the total population present in the region. The close agreement as regards the composition in point of age and other features between samples from different schools of the same common stock has been especially emphasized by Einar Lea and Johan Hjort in their reports on the Norwegian herring investigations. This close agreement is rather difficult to understand on the assumption that the schools are more or less permanently segregated units of the population, because such segregation should most naturally be expected to result in the development of individual peculiarities in the compositions of the various schools. If a nightly dispersion takes place, however, the schools will have to aggregate anew every day from the stock of individuals present in the region, and it is then perfectly clear that the various schools must usually be essentially concordant with each other as truely representative units of the same common stock, because they must then be just as random selections from the latter as are the investigators samples from the captured single schools. There is of course a greater probability for every single individual of a dispersing school to be reunited the next day with other individuals from the same and neighboring schools, than with representatives from schools, which had broken up in more distant places. The exchange can not be complete, but the aggregate effect will be a composition of the entire stock as a whole, which is uniform or uniformly changing in time and space, thence giving rise to correspondingly uniform schools every day, within any biologically continuous region of occurrence.

This view is not at all essentially discordant with the theory advanced by Einar Lea that the selection of the “shoals” doing seasonal migrations toward certain geographical regions “goes on according to some scheme or some rule.” The concept “shoal” will merely have to be exchanged with that of “stock,” it being the entire

migrating stock, or part of the total population of the species, to which this selection pertains, and which performs the migration, while the schools are only diurnal phenomena on the way.

For the reasons above given the author regards it as highly desirable both from a theoretical and a practical point of view, that further investigations should be made concerning the nocturnal and diurnal habits of schooling fishes and the reasons for their schooling performances, and the above advanced theory seems sufficiently probable to furnish a very useful working-hypothesis for such investigations.

THE RELATION BETWEEN DIFFERENT TYPES OF "HERDS."

On the preceding pages the schooling performances of the type most generally found among pelagic fishes have been analyzed and discussed as perfectly automatic results of simple reactions by the single individuals, and the explanations obtained on this basis seem to be entirely satisfactory. In real life the reactions will certainly be continually interfered with by internal or external stimulations of other kinds than those specific for the responses on which the entire performances appear to be based. The performances actually observed can therefore never be as automatically smooth as in the theoretical cases; and in the real degree of smoothness, in a broader sense, we may perhaps find the explanation of the differences between the types of fish-herds mentioned in the introduction. According to the above it is evident that the smoothness of the performances must depend upon the strength of the impulse due to the perception of a companion compared with the strength of the interfering impulses, created by other stimulations. In fishes exhibiting the perfect type of school as the herring and mackerel the corresponding impulses must therefore be of an all-dominating strength and always active in the presence of the adequate stimulus and environmental conditions. As the impulses invoked by the perception of the companions grows weaker, the herds will be more and more easily scattered and take on the character of occasional gatherings, interrupted in response to the stimulations of sex, hunger a. s. o. A good example of this class is rendered by the European Stickleback (Gasterosteus aculeatus), which will travel in rather perfectly formed schools, but will
scatter for feeding and breeding. Similar behavior also seems to be found among the American killies (*Fundulus*) and many other fishes. At the next stage the impulse no longer appears by the perception of the companions alone, but will only develop when this stimulus is presented in combination with certain other stimulations, which are generally creating responses of a visceral ("emotional") nature, especially fear. Cases of this kind are not easily observed among fishes, but are well known from the behavior of higher vertebrates and the human beings as the huddling together of frightened individuals. In the small *Gobius ruthensparii* of Europe the author has had opportunity to observe reactions which may possibly belong to this type. The adults of this species generally do not school at all, but when splashing among the algae where they are scattered, one may very commonly observe that they do not dart off in all directions, but converge to form a school of very short duration, spreading again after a short flight. Finally there are cases where the perception of companions do not under any circumstances call forth responses of the kind with which we are here concerned. In this way we may have a complete series of gradually changing types from the entirely solitary fishes to the most perfectly schooling pelagic species.

Concerning the history of the reactions with which we are here concerned it may be questionable whether they are to be regarded as ontogenetically acquired elements of behaviour or as real phylogenetic traits. The latter possibility seems the most probable one, as it gives the best explanation for the systematic fixedness of the performances, for instance, why they are always found among the herrings but, on the other hand, never among the Cottidae.\(^{16}\) Assuming therefore that the "schooling instinct" is a phylogenetic character it becomes of great interest to find out which is the primitive state; the solitary one or the schooling. The possibility has been suggested that the attraction towards a similar companion was the original property of all fishes (and for that matter most animals), but had to be broken down in the benthonic types by the necessity for these to unherd for propagating and feeding, while it could be maintained in the pelagic fishes which had the opportunity to breed and feed in schools. The systematic distribution of the "schooling

\(^{16}\) The author hopes to be able to approach this question by experimental measures in the future.
instinct" among fishes might also be regarded as correlated to the general defenselessness of the forms in which it is found. The Clupeidae for instance are probably among the most defenseless fishes and even the powerful mackerels have scarcely any other defense than their speed in a combat or competition with enemies of their own or greater size. If for instance the individuals of a much sought species like the sprat or herring would travel around separately, scarcely a single one of them would escape the enemies sufficiently long to be able to propagate, while the occurrence of a great number of specimens united in schools among scattered enemies may give a certain percentage a chance to survive and continue the existence of the species.

The essential problem, however, remains untouched by these theories. One might explain why the schooling performances are usually not observed among the benthonic fishes, the other why comparatively few pelagic species of a defenseless type are found to exist without the assumed protection of a schooling habit, but neither theory is able to shed any light at all upon the origin of the schooling behavior itself.

**SUMMARY.**

Among fishes two descriptively very different types of herds are found. One represented by the permanent and very uniform schools mainly formed by pelagic species. Another represented by the occasional and intermittent traveling in less regular bands, as commonly observed among benthonic and shallow-water fishes.

Two detached individuals of a species normally living in schools of the first type will, when brought together within range of perception, approach each other and subsequently adjust their directions of swimming to parallel courses at close proximity.

These simple reactions may be regarded as automatically controlled by a special kind of tropism giving the responses of approach and adjustment of direction to the stimulus of a perceived prospective companion.

By the recognition of such tropism or set of automatic responses to the separate perceptions of single individuals, only, all peculiarities of the normal school may be satisfactorily explained without necessitating the assumption of deliberate purposeful activities or general "social instincts," giving complicated responses to stimulations from the entire school as a unit.
Under certain circumstances any school of fishes may fall into the apparently purposeless performance of "milling," which is difficult or impossible to explain as anything but the mechanically integrated result of automatic individual responses. An automatic impulse to approach a perceived companion and to adjust the direction according to the direction of the latter, does however, on general psycho-physiological principles satisfactorily explain the phenomenon on exactly the conditions under which it is actually observed to develop in nature.

Experiments on the chub mackerel, \textit{(Scombrus colias)} and general comparisons between the various schooling forms have proved that the stimulating perceptions, on which the schooling performances are based, are probably of a purely visual nature.

The conclusion is therefore inevitable that the schools must be only diurnal phenomena, dispersing again during every sufficiently dark night. This conclusion is borne out by a few observations on a school of herrings in captivity, and by the statistically uniform compositions of the individual schools originating from a common stock.

From the strength of the automatic impulses, above described, compared with the strength of other interfering impulses the character of the herd will be determined. The stable, diurnal schools of many pelagic fishes are based upon the great predominance of the impulses stimulated by the perception of companions over impulses created by other stimulations. In fishes forming intermittent herds the impulse is easily and repeatedly conquered by hunger, sex etc. In the least established (stabilized) type of occasional bands the stimulus of perceived prospective companions may not alone be enough to call forth a sufficiently strong impulse, but has to be combined with other stimulations usually of a character giving an emotional (visceral) response, especially fear.

The set of reactions by which the schooling performances are brought about may be phylogenetic heritage (based on inherited nervous organization) or it may be ontogenetically acquired by the single individuals. The former possibility seems the most probable one, but no theory can be advanced, offering a satisfactory explanation for a phylogenetic origin of the schooling behavior.