PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXIX, No. 15, pp. 509–548, 23 figs. May 29, 1959

BEHAVIOR AND REACTIONS OF THE PACIFIC SARDINE, *SARDINOPS CAERULEA* (GIRARD), UNDER THE INFLUENCE OF WHITE AND COLORED LIGHTS AND DARKNESS*

By

ANATOLE S. LOUKASHKIN and NORMAN GRANT

California Academy of Sciences

INTRODUCTION

From the field observations and laboratory experiments of the students of fish behavior it has been abundantly shown that almost all the schooling and aggregating fishes, both freshwater and marine, disperse at night as a rule. If blinded, these fishes have been found not to school at all. The results of investigations reported by Allee (1931), Atz (1953), Bateson (1889), Bowen (1931, 1932), Breder (1929, 1951), Breder and Nigrelli (1935, 1938), Eddy (1925), Escobar, Minahan, and Shaw (1936), Hardy (1924), Hasler and Bardach (1949), Johnson (1940), Keenleyside (1955), Krefft and Schüller (1951), Morrow (1948), Newman (1876), Noble (1939), Noble and Curtis (1939), Parr (1927), Puchkov (1954), Reinhardt (1935), Richardson (1952), Sato (1938), Scharfe (1951), Scott (1955), Sette (1950), Shlaifer (1938, 1939, 1940, 1942), Spooner (1931), Spoor and

---

* Submitted for publication on February 15, 1958.

Schloemer (1938), and Verheijen (1953) made certain that vision in fishes is definitely a dominant sensory modality involved in integrating and maintaining the schools and aggregations.

Parr (1927), who analyzed schooling behavior theoretically, states "if the above conclusions are correct, that the aggregation of schools among 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."

As far as pelagic fishes are concerned, the role of vision and the effect of light and darkness have been studied in only a few species such as the Atlantic herring, *Clupea harengus,* by Newman (1876), Hardy (1924), Johnson (1940), Verheijen (1953), and others; the dwarf herring, *Jenkinsia stolifera,* by Breder (1929, 1951); the chub mackerel, *Pneumatophorus grex,* by Parr (1927) and Schlaifer (1942); and the Atlantic mackerel, *Scomber scombrus,* by Sette (1950).

The Pacific sardine, *Sardinops caerulea* (Girard), one of the most economically important species in the California oceanic fisheries, has never been subjected to investigation along these lines. To fill this gap, an experimental study has been carried out in the Steinhart Aquarium of the California Academy of Sciences. The first phase of the study conducted covers a series of experiments on the effect of white and certain monochromatic lights and of darkness on the schooling behavior of the sardine. The second phase involves experiments intended to determine the ability of the sardine to discriminate colors of light of different wave-lengths. The results of this study are presented below.

THE EFFECT OF LIGHTS AND DARKNESS ON SCHOOLING BEHAVIOR

In the experiments of the first phase, a thousand-gallon aquarium tank with salt water running at the rate of 85 gallons per hour was used. It contained approximately 185 sardines which had been kept in captivity in this tank for four months. The aeration was provided by suction through an opening in the water-inlet tube. The water turnover produced an insignificant current in the tank, which, however, had no influence on the schooling behavior of the fish. To isolate the tank from the effect of outside illumination, a light-tight plywood structure five feet high with an opening on top for installing the source of light (figure 1) was built around and above the tank.

During the entire period of the sardines' captivity, this tank was illumi-

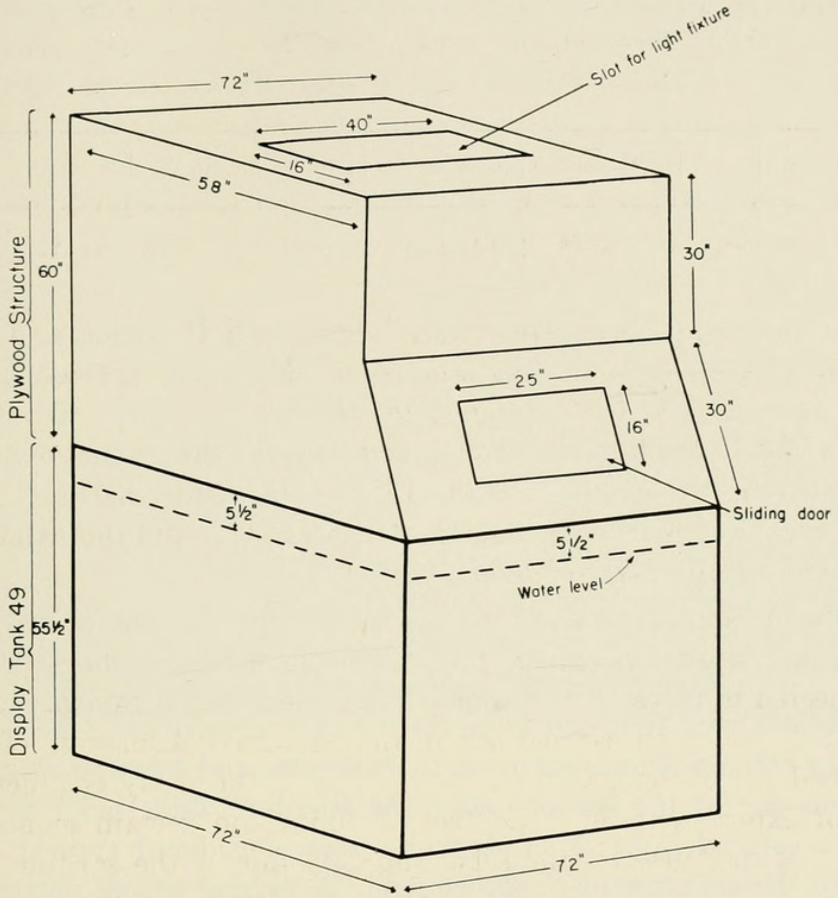

Figure 1. Diagram of tank with superstructure of plywood for studying schooling behavior of sardines under various controlled light conditions.

nated by a 300-watt incandescent bulb suspended two feet above the water surface. Therefore, the sardines used in the study can be considered "light-adapted" animals. For application of the colored lights, a four-tube fluorescent fixture, 48 inches long, was installed in the opening on top of the structure. Following F. A. Linsday (1948), combinations of color tubes and gelatin filters to produce pure blue, green, and red lights were used in the tests. The 40-watt color tubes were of General Electric manufacture and had the manufacturer's symbols as follows: F40T12/B for the blue light, F40T12/G for the green, and F40T12/PK for the pink. The filters, acquired from the Rascoe Laboratories of Brooklyn, N. Y., had the following numbers and descriptions: No. 37 (urban blue), No. 40 (medium green), and No. 15 (light red). Linsday recommends these color tubes and filters to photo-engravers for examining color proofs. The spectral energy distribution of the light sources plus their corresponding filters is shown in figure 2. All observations, recordings, and photographs were made

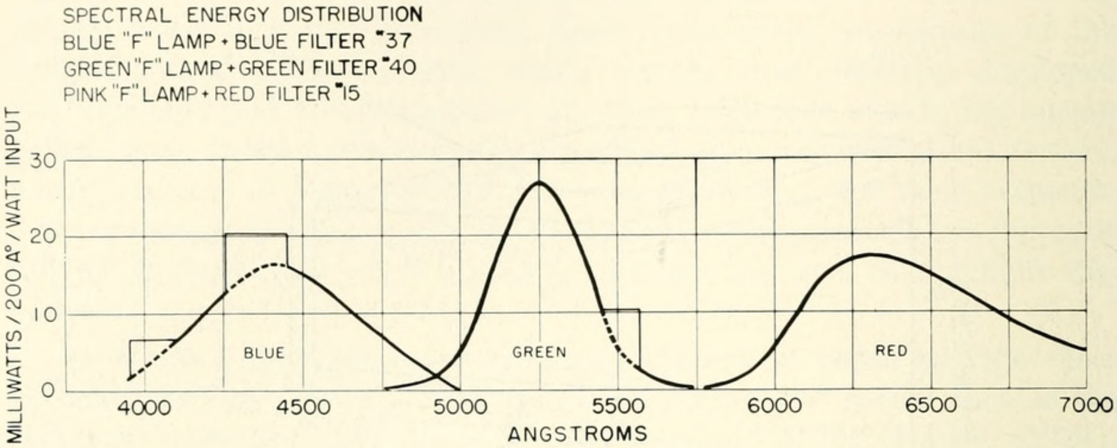

Figure 2. Spectral energy distribution of light sources used (After E. A. Linsday, 1948).

through the glass wall of the tank at night with all lights in the building turned off. The light intensities of each type of illumination applied were measured at water level at the center of the tank. In every test the sardines were kept for an hour under the light being tested, and all reactions of the school as a unit were recorded from the moment of switching the light from standard to colored illumination or to darkness, and back to standard.

The behavior of the school under the standard light prior to application of the colored light or of darkness was considered typical and was classified in the experiment as the control. A typical school pattern under standard illumination was usually a clockwise circling in loose formation in the shape of a complete ring. However, at the commencement of the study it was disclosed that this behavior, for some unknown reason, had markedly changed. For several days in a row the school discontinued circling; instead it occupied a rear part of the tank close to the back wall, remaining almost motionless in a shapeless aggregation. At times this group assumed either a cluster-like, compact configuration as shown by Breder and Nigrelli (1935) for the sunfish, *Lepomis auritus*. At other times the fish arranged themselves into a pyramidal formation very much resembling that of the young black bass, *Micropterus* sp., while wintering in a quiescent state in the New York Aquarium and as photographed by C. H. Townsend (1916). On still other occasions the school formed an aggregation of the vertical columnar shape typical of the young spotted bass, *Micropterus pseudaplites* Hubbs, observed in one of the ponds of the Ohio State Fish

Farm and reported by Langlois (1936). Only during feeding time and for a short period thereafter, would the sardines resume normal circling. To stimulate their circular movement, a predator fish, the kelp bass, *Paralabrax clathratus* (Girard), 38 cm. in standard length, was placed in the tank,

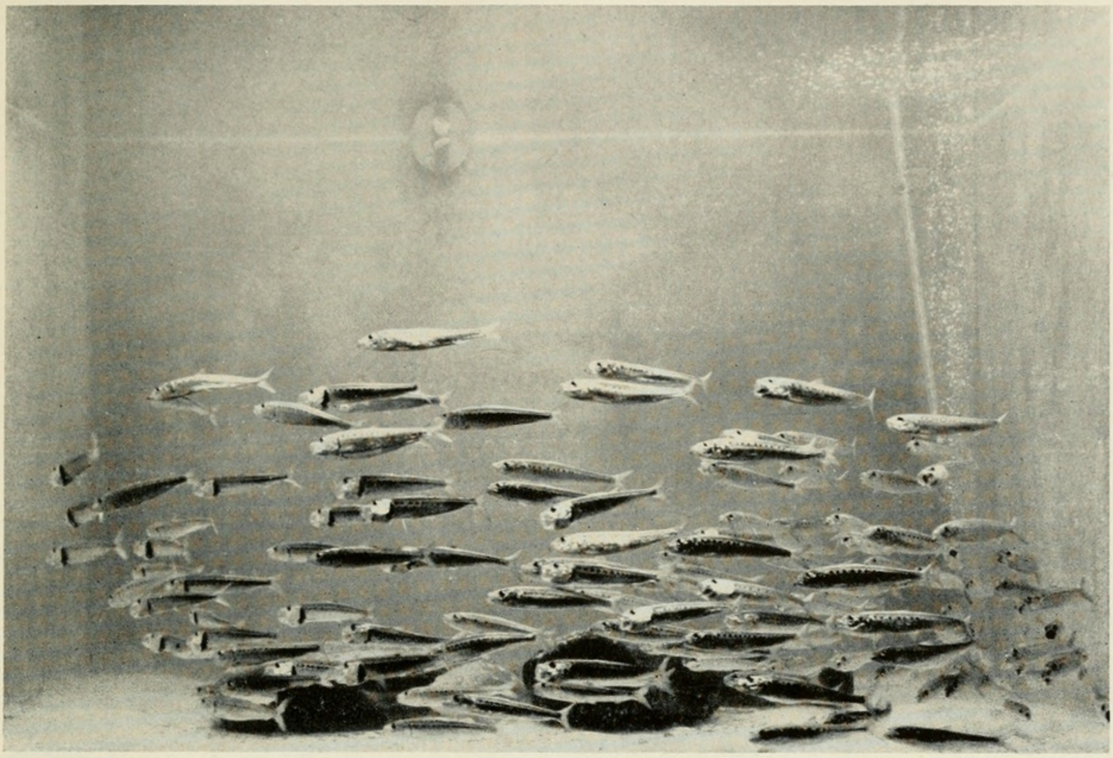

Figure 3. School of sardines freely circling in the tank illuminated by standard white light (control) prior to switching to the red light.

whereupon the school immediately re-formed, resuming circling but avoiding close contact with the bass which, however, made no attempt to attack the sardines during the entire course of the experiments. The bass spent most of its time lying still by the rock on the bottom, exerting neither a positive nor a negative effect upon the natural responses of the sardines to the lights applied in this study.

In the first series of observations of this first phase of the study, a complete set of four tubes for each type of colored light tested was used. The light intensities in this case, therefore, were different for each particular illumination, and these intensities were recorded as follows: 12.9 foot-candles for green light, 9.6 for red, and 0.5 for blue, while the intensity of the standard white-light (control) was 20.0 foot-candles. In the second series of experiments the standard light in intensities equivalent to those of the colored lights used in this study was tested. The third series of experiments was made with the application of a uniform 0.5 foot-candle light intensity for all types of illumination including the standard (incandescent) light.

As the experimental records show, the behavior of the school subjected to the green or blue illumination, regardless of light intensity, remained essentially the same as under the standard light. At the moment of switch-

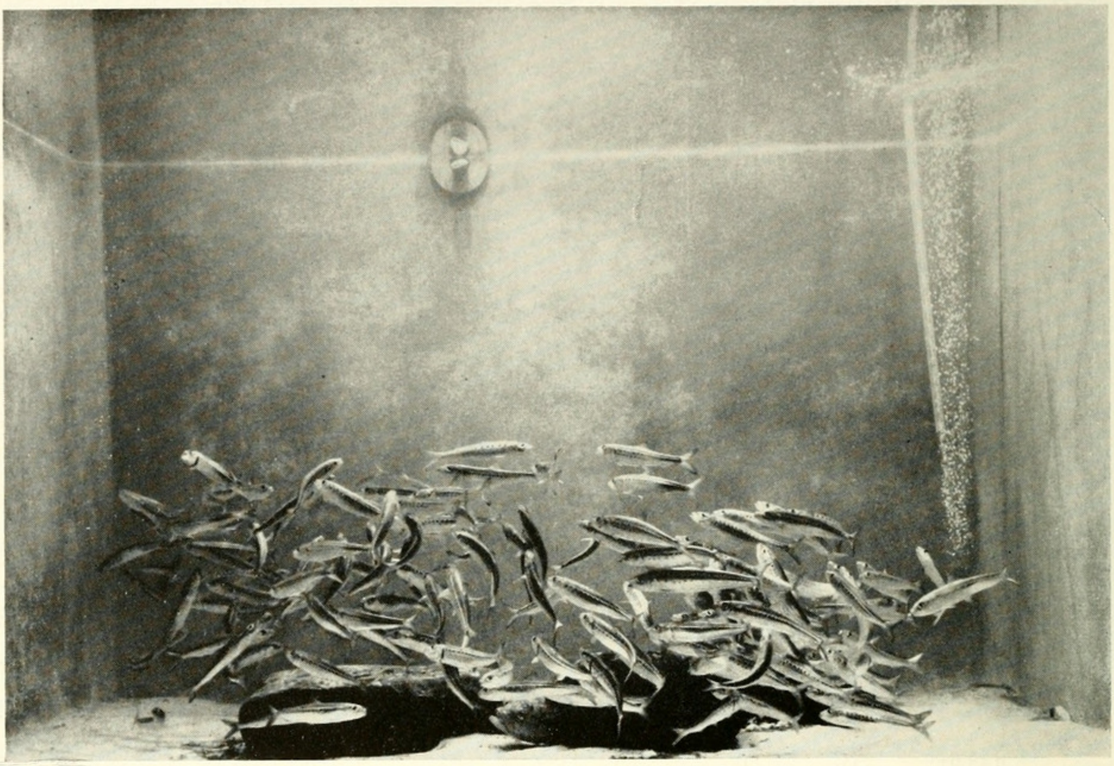

Figure 4. Breaking up of the school at the sudden change from standard white light to the red.

ing the light from standard to green or blue, the school continued its clockwise movements, displaying no fright reaction nor any discomfort. Occasionally, the school would increase or decrease the speed of movement, or change direction for a few minutes.

The exposure of the sardines to the red light of either 9.6 or 0.5 foot-candle intensity produced each time a definite effect on the behavior of the school (figures 3 to 8). At the switching from standard light to red light, the typical school pattern was invariably broken up for a few seconds each time. The fish seemed to experience a kind of shock resembling that of the school in total darkness, described in the next paragraph. This distinctive fright reaction would gradually subside but not to the point of complete relaxation. During the 60-minute tests the effect of the red light on the school pattern and behavior remained pronounced. On no occasion was the typical circular movement resumed. Alarm or tension on the part of the fish was sometimes evidenced by frequent changes of movement from one direction to another or by attempts to hide at the rear corners of the tank. On other occasions they formed a compact ball-shaped aggregation,[1] dispersed vertically fan-wise, darted from one end of the tank to the other,

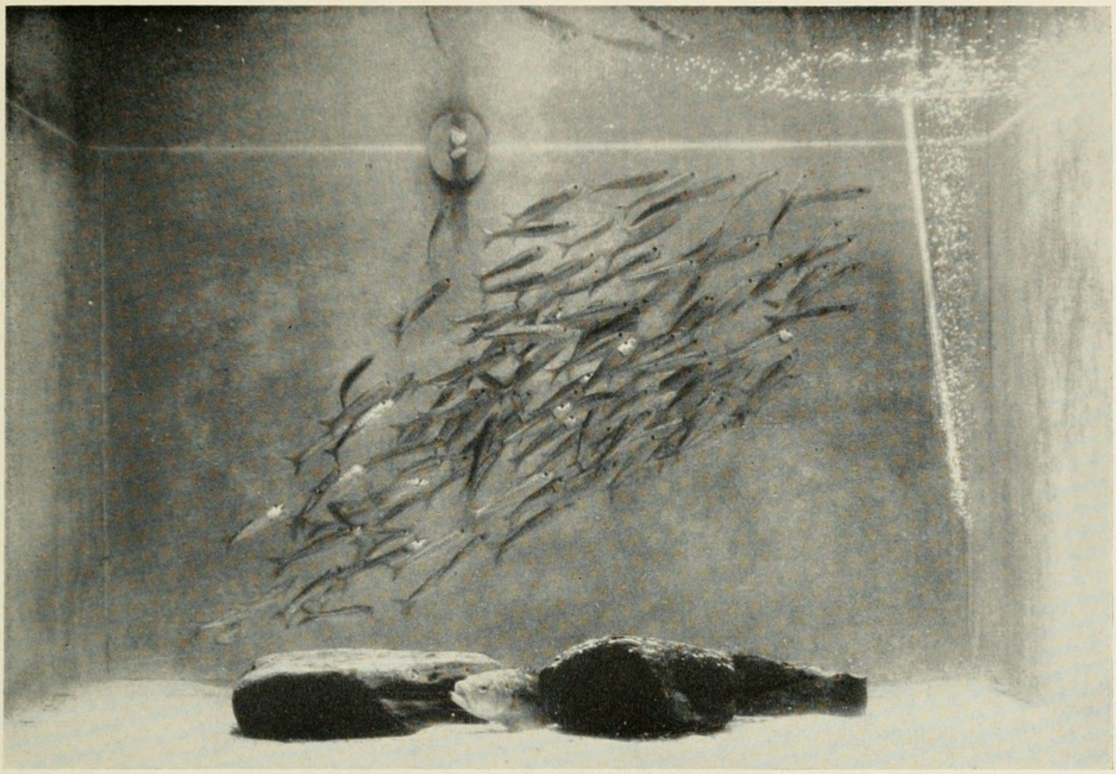

Figure 5. Aggregation pattern after 8-minute exposure to the red light.

or rose to the surface. In contrast to the typical behavior under the standard light, when they were circling along the walls close to the bottom, the sardines exposed to the red light occupied the upper horizon of water in the center of the tank. The speed of movement of the school in the majority of cases was greatly increased in comparison with normal speed under standard illumination. In a few cases recorded the speed was slowed down considerably. At all times the sardines displayed restlessness. After the end of each test a standard light was turned on, and usually within 10 to 15 minutes the school calmed down and resumed typical circling close to the bottom.

The effect of total darkness on the behavior of the school was much more striking than that of the red light. Because of the impossibility of making visual observations in the darkness, the flash photographic recording alone was applied in these tests. At the sudden change from standard light to

1. See DISCUSSION, paragraph 4.

total darkness, the school exhibited each time a sharp reaction, its movement being completely halted and the school being broken up. Most of the fish in a school would assume a vertical body position, head up, tail down, slowly rising toward the surface.[2] Such a phenomenon usually lasted for

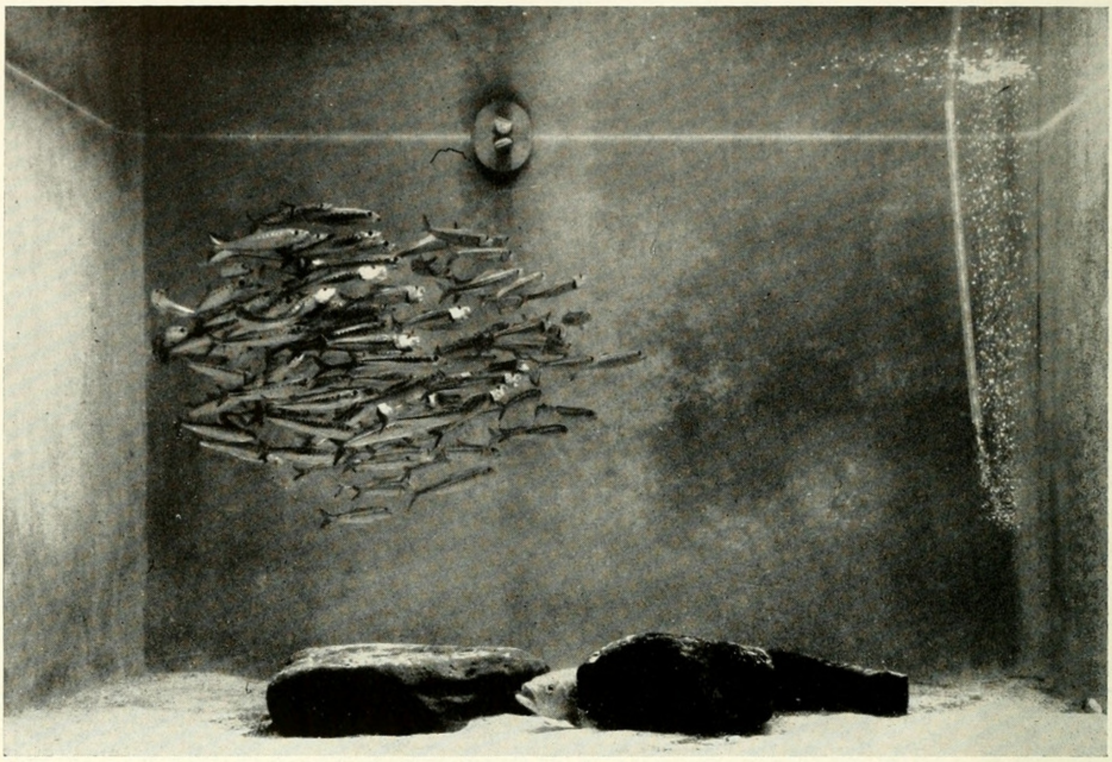

Figure 6. Ball-shaped aggregation beginning to dissipate after 15-minute exposure to the red light.

three to five minutes. Gradually the fish recovered their equilibrium but the school remained broken up. The sardines were scattered throughout the tank, moving slowly and aimlessly in all directions. The school as a typical unit was not re-formed and normal circling was not resumed.[3] With the turning on of the standard light the sardines restored their schooling pattern within five to ten minutes. A set of photographs (figures 9 to 15) shows the behavior of the sardines in darkness. To check the results of observations obtained in total darkness after a sudden turning off of the light, gradual darkening was tested on the same school of sardines. However, an application of a gradual change of standard white illumination (using 300-watt flood-light lamp and an iris diaphragm) from 38.9 foot-candles at the surface to almost 0, produced no such striking effect as did the sudden change from bright light to total darkness described above. The

2. See DISCUSSION, paragraph 3.
3. See DISCUSSION, paragraph 1.

school was not broken up even at the end of an hour-long observation when the diaphragm had a pin-point opening five feet above the water surface, and illumination was reduced to below 0.01 foot-candle. With growing darkness the school circled in a rather compact formation. When the light was finally turned off and the sardines were no longer able to see each other,

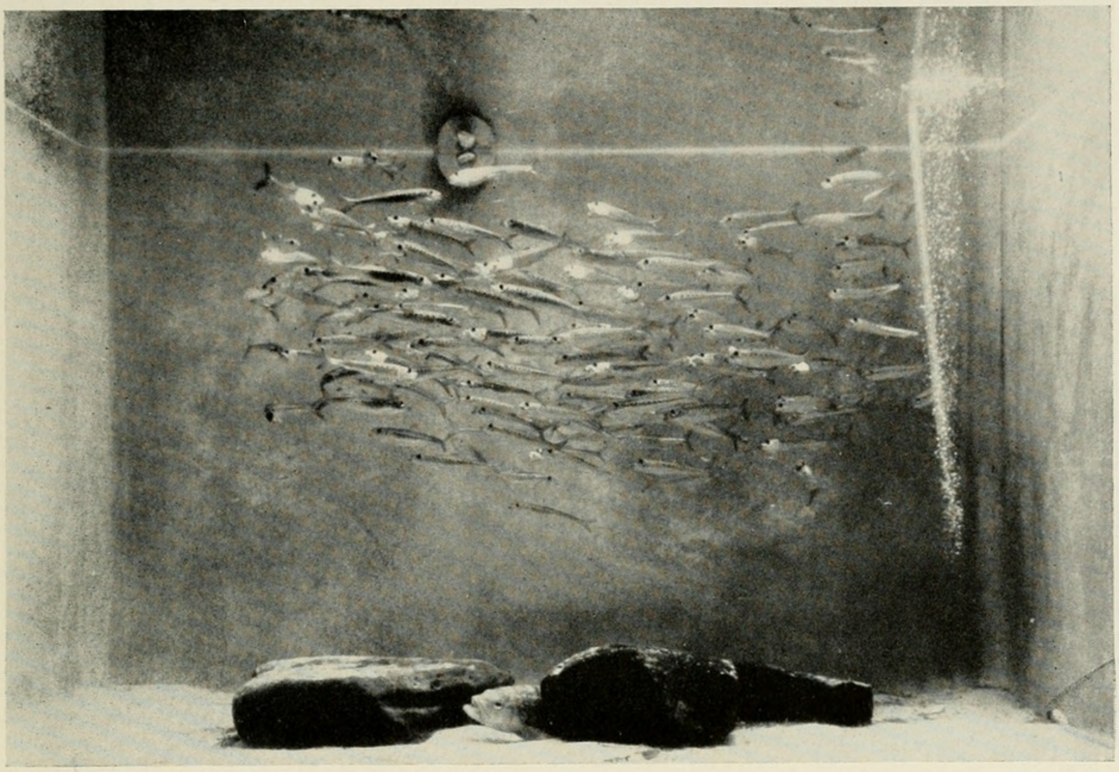

Figure 7. The aggregation of sardines moving from one end of the tank to the other after 30-minute exposure to the red light.

schooling immediately ceased and the school broke up as at the sudden switching from light to total darkness. This was followed by the application of the standard white light in the exact values of the intensity of colored lights used (12.9, 9.6, and 0.5 foot-candles). This failed to elicit any differential response on the part of the sardine school. School pattern and behavior with all normal reactions characteristic of control illumination (20.0 foot-candle intensity of standard white light) remained unchanged during the course of the experiments.

To find out how soon the organs of sight of the sardines became adapted to colored lights, the effect of these lights, which were standardized in their intensity at 0.5 foot-candle level, was tested on the sardine's feeding response, this measurable reaction having been selected by the experimenters as the best possible indicator of the response of the fish to the lights. In the first series of tests the school was exposed to each of the three primary colored lights for five minutes before their favorite food, live brine shrimp (*Artemia salina*) was added to the tank in the usual manner. Sardine reaction in this case, in comparison with normal, instantaneous feeding response under standard white illumination, was slightly retarded: in green light, for a few seconds; in red, for 35 seconds; and in blue, for about a

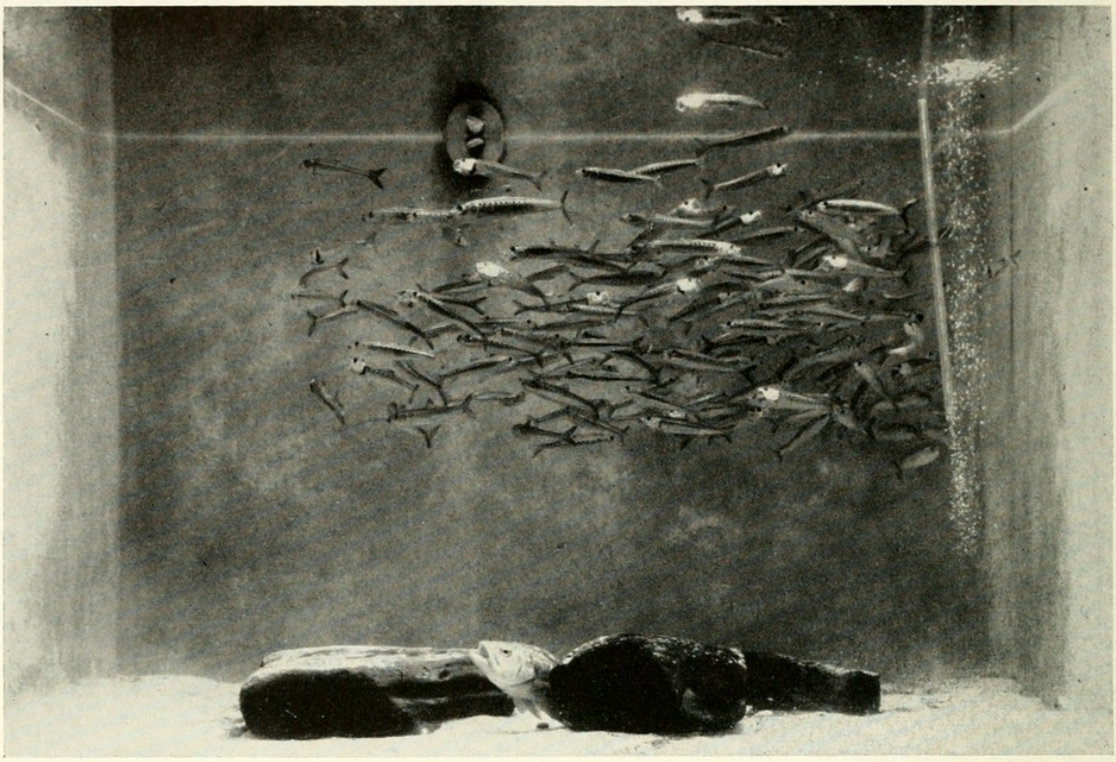

Figure 8. "Boiling" aggregation with fish moving up and down, and toward each other after 60-minute exposure to the red light.

minute. In the second series, the school was exposed to the colored lights for half an hour before the brine shrimp were added. In these tests, the feeding response was immediate and very similar in intensity to that displayed under standard illumination (figures 16 and 17). In both series, as soon as the familiar food was detected, the sardines displayed their typical fast and efficient chasing of the brine shrimp. The feeding response of the school under white light used in the same standardized intensity of 0.5 foot-candle in both cases (after 5- and 30-minute exposures) was found to be as instantaneous and vigorous as under control illumination of white light of a 20 foot-candle intensity.

In closing the first phase of the experimental study of the effect of light on schooling behavior of the sardine, the effect of a flashing and a continuous beam of standard white light in otherwise total darkness was tested (figures 18 to 20). This time a source of light was installed at the right side of the glass wall on the outside. A 35-watt incandescent bulb was incased in a metal container with changeable openings of one-eighth, three-eighths, and one-half inch, and tightly attached to the glass. A mechanical interrupter to produce flashing light was attached to the device. The light was interrupted up to 60 times per minute. To make the beam of light con-

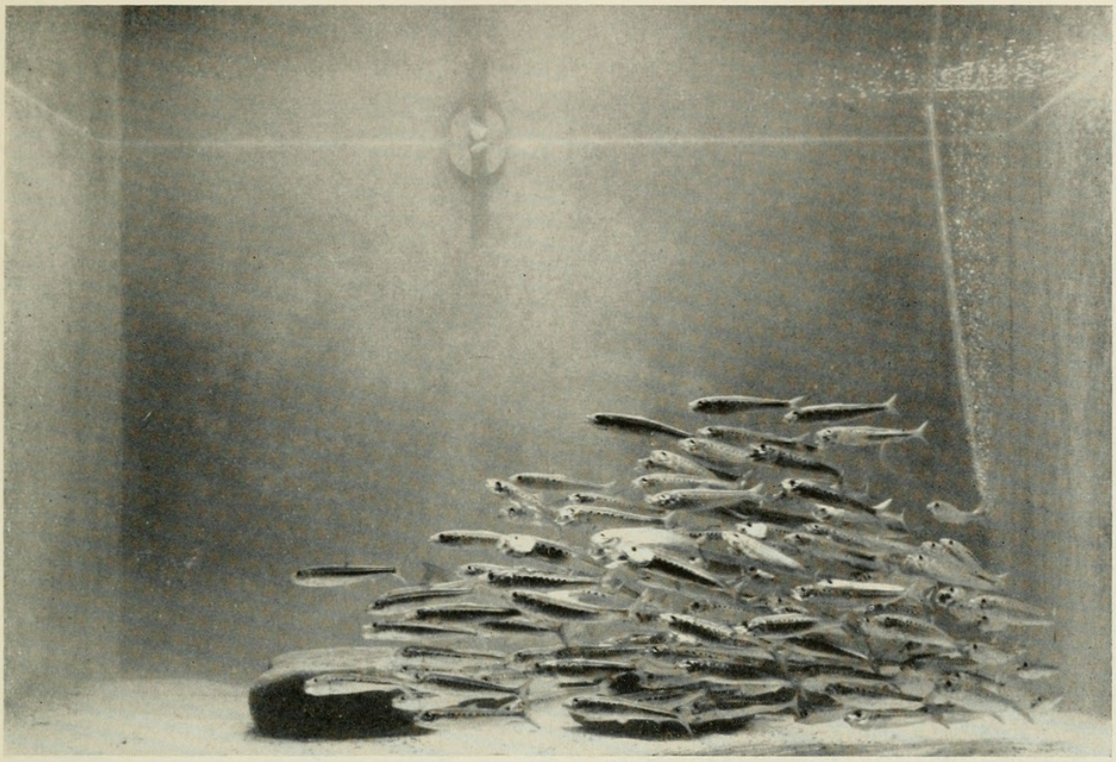

Figure 9. School of sardines freely circling in rather compact formation in the tank illuminated by the standard white light (control) prior to the turning off of the light.

tinuous, the interrupter was omitted from the circuit. Before application of either one of the two types of light beams, the school was kept in total darkness for about 15 minutes. As the records indicate, the flashing beam of light, regardless of its intensity (all three openings produced light of low intensity, below 1 foot-candle), elicited a very distinct fright reaction, causing the fish to aggregate in a shapeless "boiling" mass in the darker side of the tank. Individual sardines would enter the illuminated zone, but retreat immediately to the main body of the aggregation. Circling was not maintained.[4]

The application of a continuous beam of light produced no fright reaction but rather helped the sardines, which were scattered throughout the tank in the darkness, to reassemble into a normal school and to start typical circular movements and enter the illuminated zone of the tank.

4. See DISCUSSION, paragraph 2.

PREFERENTIAL RESPONSES OF THE SARDINE TO CERTAIN TYPES OF COLORED LIGHTS

The preceding experiments, as direct observations and photographic records show, demonstrated the definitely negative effect of both darkness and red light on the schooling behavior of the sardine. The facilities used did not offer a possibility for the application of more than one type of illumination at a time in order to elicit a preferential response of a positive or negative nature to a certain type of light tested in combination with one or two contrasting lights. Therefore, for the purpose of the solution of this

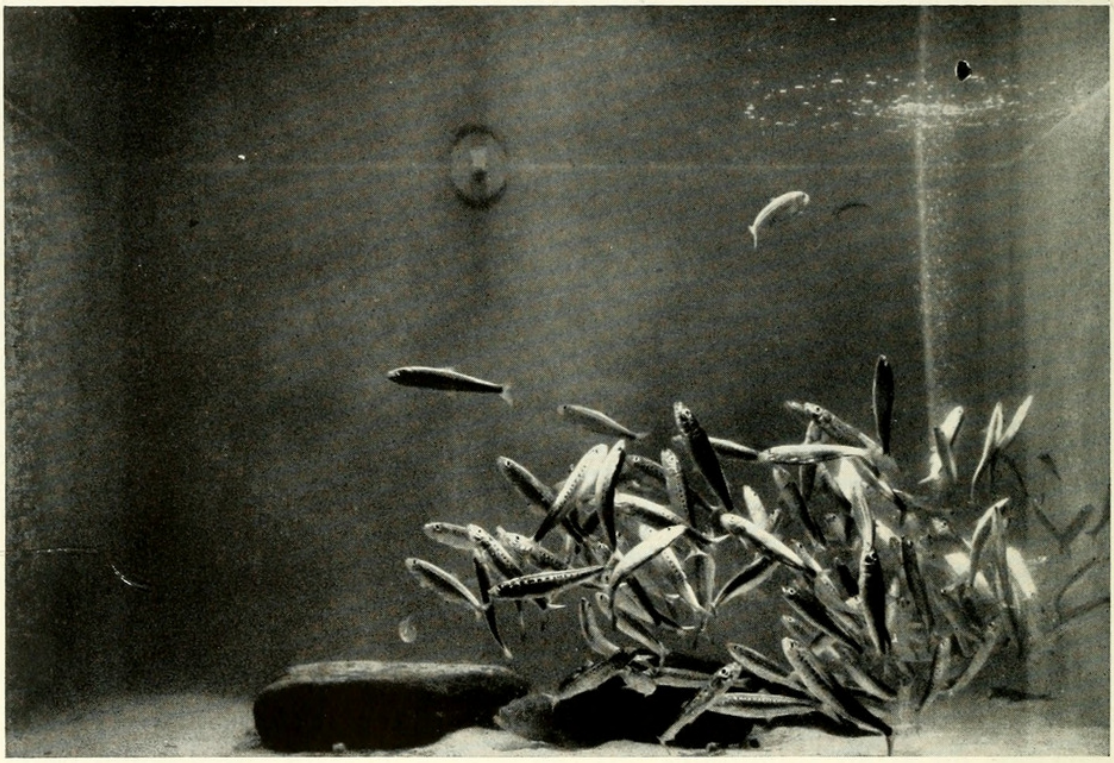

Figure 10. Breaking up of the school at the sudden switching from standard white light to total darkness. Fish seem to lose equilibrium, and act as if "floating" head up, tail down.

problem, a second phase of the experimental study was conducted in a dark room (specially built in the Aquarium) in which an experimental wooden tank 12′ 6″ long, 21.5″ wide, and 10″ high was installed. This tank was filled with sea water to a depth of 6 inches and was divided into either two or three zones of even length (75″ and 50″ respectively) depending on the number of light sources used in any particular experiment. The sources of light were 20-watt fluorescent tubes, 24″ long, with gelatin light filters of colors and of a manufacture already described. For regulating the intensity of light at a desired level, the electric fixtures were attached to adjustable scaled supports which were clamped to the sideboards of the tank at even distances and always in the centers of light zones. In order to prevent the intermixture of contrasting illuminations at the borders of zones, these zones were separated one from another by plywood partitions 27″ high (from water level) and 32″ wide. For neutralization of the effects of

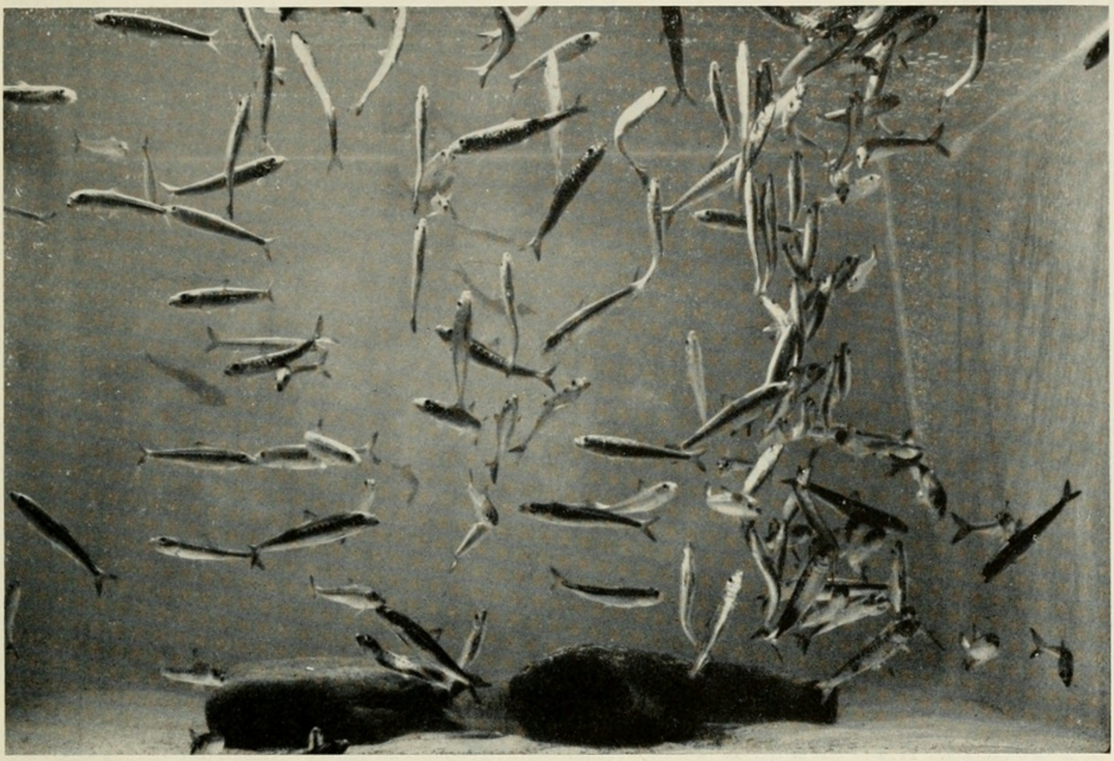

Figure 11. After seven minutes in total darkness. The school is completely broken up. The loss of body equilibrium reached its peak.

reflected light from the white-painted ceiling of the building, a sheet of plywood 32″ wide was placed on the partitions and supports above the tank (figure 21). Before each test, the water was drained out and the tank cleaned. Then a fresh supply of sea water was added and three aerators turned on to keep an uninterrupted supply of air in the water. This was followed by the introduction of six sardines from a display tank. They were left alone in the tank for two and a half hours for acclimation, and then the observations of their behavior began with the recording at fixed intervals of the number of fish present in each of the differently illuminated light zones. Throughout the course of these experiments, which were intended to elicit a sardine's preferential reactions to different lights as evidence of the ability to discriminate colors of light, the intensity of light for all types of illumination was uniformly maintained at a 10-foot-candle level at the water surface along the sides of the tank. During preliminary tests it was disclosed that the sardines, when undisturbed and behaving normally, could swim from one end of the tank to the other in 10 seconds. When disturbed and agitated, they could cover the same distance three times in 10 seconds. Therefore, a recording of the numerical distribution

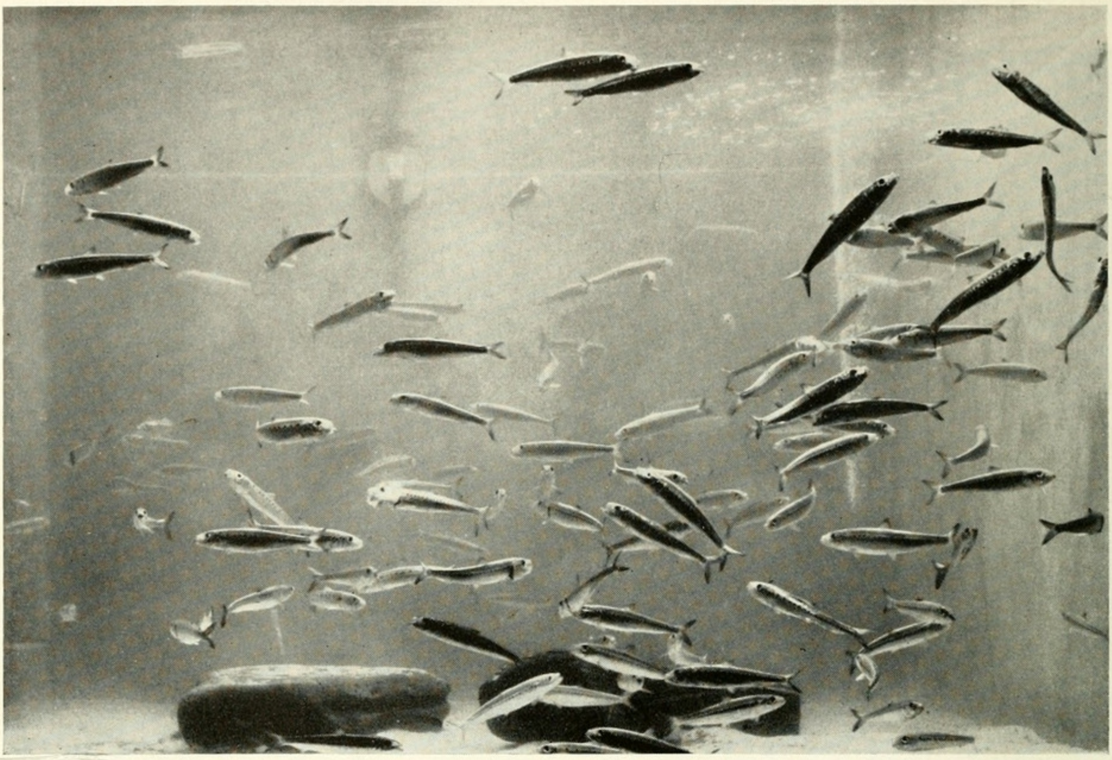

Figure 12. After fifteen minutes in total darkness. Body equilibrium restored, but the sardines are dispersed, swimming aimlessly in all directions at greatly reduced speed.

of sardines zonally was made every 10 seconds. All records of these tests with excited sardines are ignored and excluded from the tables as presenting distorted results. Five hundred recordings were made, with cumulative totals of 3,000 fish for each separate test. Four tests in each light-combination experiment resulted in 2,000 recordings with 12,000 fish.

For quite a long time it was difficult to establish a cause for the sardines' restlessness and excitement in the experimental tank. Sometimes one of the fish, becoming excited, would begin racing from end to end, thus stimulating the others to follow its example. Sometimes, the entire school would exhibit a high degree of restlessness from the start; in other cases, the normally behaving school suddenly, and seemingly without provocation, would begin wild racing. The experimenters took all possible care and precautions to avoid undesirable disturbance among the fish, using special nets for removing them from the display tank, and a large bucket for transferring them, one fish at a time, to the experimental tank. The effects of foreign sounds and vibration were reduced practically to zero, and yet the cases of excitement among the sardines happened quite frequently. After a while it was noticed that the sardines, after having been fed early in the morning,

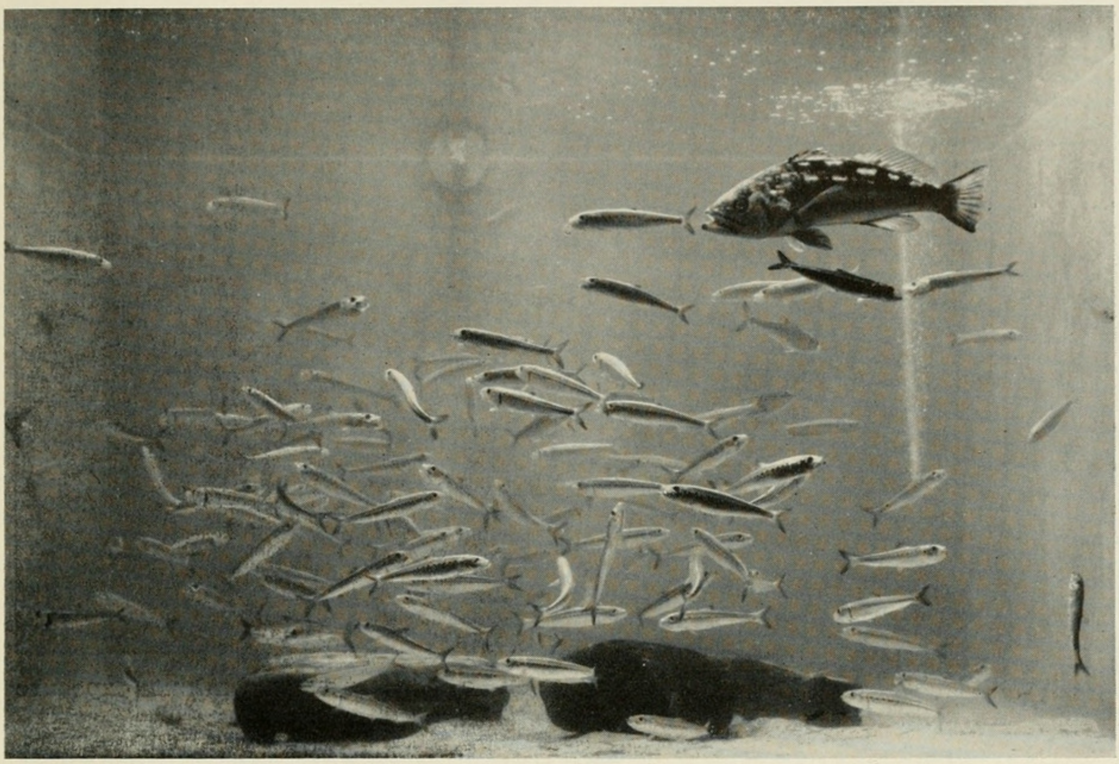

Figure 13. After thirty minutes in total darkness. Sardines still remain scattered throughout the tank. Two fish continue "floating" in vertical body position.

always behaved normally throughout the test with no sign of restlessness. From then on, on the day of testing (three times a week), the sardines were given an ample supply of brine shrimp an hour prior to transfer to the experimental tank. Also, turning off of the testing lights for a few minutes was found to be a good remedy, and after 5 to 10 minutes in darkness the sardines would calm down and resume normal behavior when the lights were turned on again; this measure, however, did not prove to be a complete guarantee that the restored order would last until the end of the test. The resumption of wild racing by one of the sardines could have distorted the results of the test or even spoiled the test entirely by exciting the other fish again. At the time of ascertaining the cause of frequent restlessness and excitement among the sardines, the stock of live fish which had been kept in captivity over a year was reduced to 20, and toward the end of the experiments there were only 8 sardines left, of which 2 had impaired organs of sight (very often they hit the aerators or sides of the tank, and therefore they were not used in further tests). The experiments were discontinued when only 5 healthy sardines were left.[5]

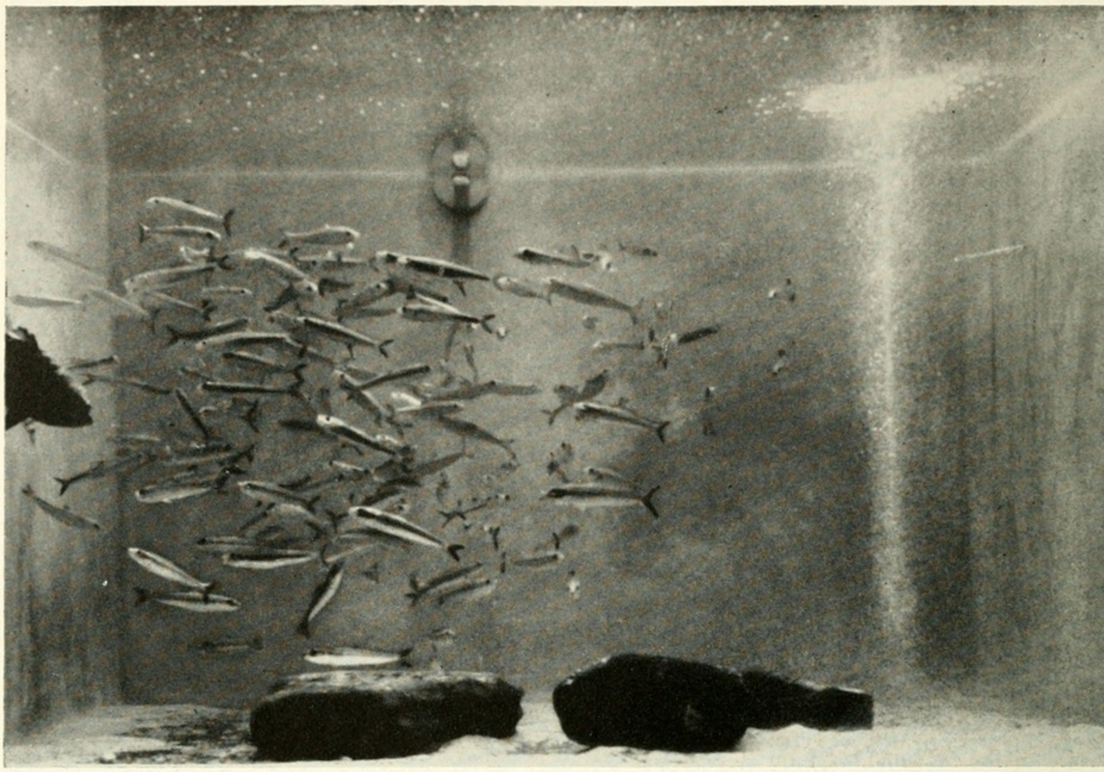

Figure 14. "Piling-up" aggregation at the end of the test after 60-minute exposure to total darkness.

The count of the recorded observations of each test was made by summing up the numbers of sardines that had entered each light zone. For example, test A of table I is presented below:

	Fish recorded in groups of								Per
Description	*0*	*1*	*2*	*3*	*4*	*5*	*6*	*Total*	*cent*
Red Light Zone									
Number of entries	304	162	30	2	0	0	0	—	
Number of fish	0	162	60	6	0	0	0	228	7.60
White Light Zone									
Number of entries	54	126	126	106	74	12	2	—	
Number of fish	0	126	252	318	296	60	12	1,064	35.47
Blue Light Zone									
Number of entries	6	28	100	120	130	96	20	—	
Number of fish	0	28	200	360	520	480	120	1,708	56.93
								3,000	100.00

5. On these grounds the present study has been confined to 2,000 recorded observations for each type of light combination instead of 5,000 as originally planned. In spite of this accidental limitation, the results obtained nevertheless reveal a definite tendency of the sardine to react differently to different types of light regardless of their combination or sequence.

Turning now to the description of the results of these experiments, it should be noted that the aim of the investigation conducted was the attempt to reveal the sardines' reaction mainly to the red light, which, as the preceding series of experiments in the display tank showed, had a negative effect upon schooling behavior. The present series of experiments was divided into two parts. In the first part the tank had three compartments or zones, each illuminated with a different type of colored light. In these experiments the red light was tested against white[6] and blue, white and green, and blue and green. While these three combinations of lights were being tested four times each, the position of light sources was subject to change each time, as for instance in the case of the red–white–blue group shown below:

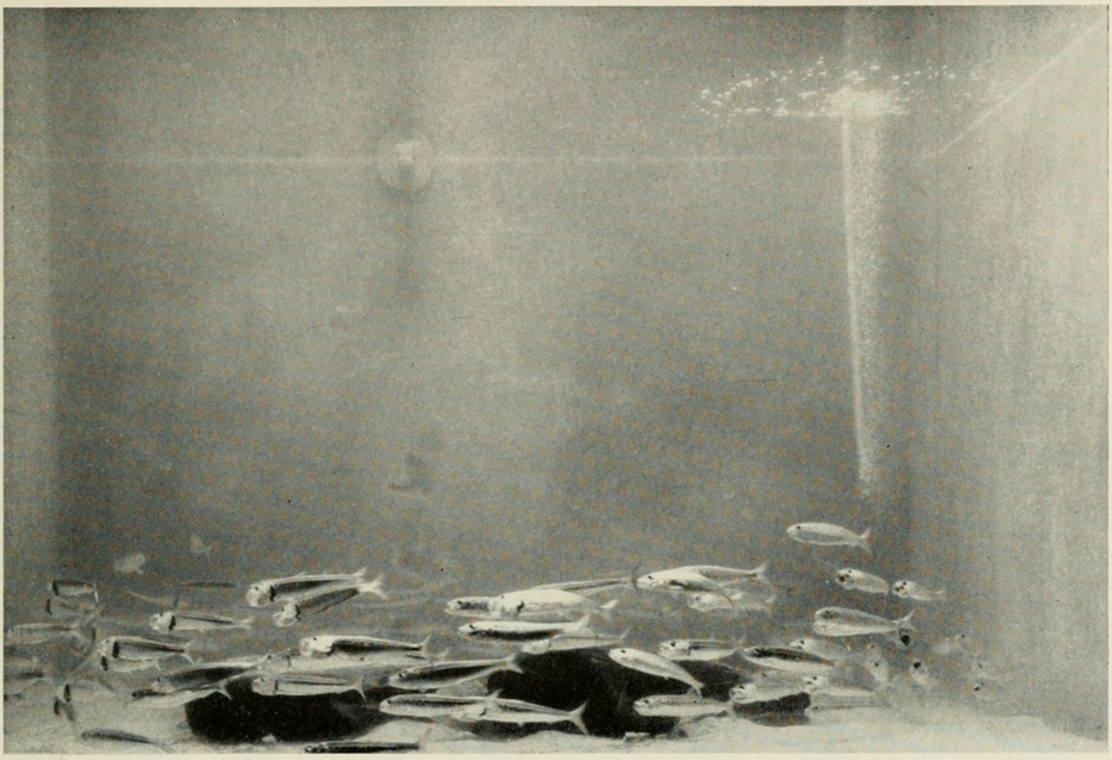

Figure 15. In fifteen minutes after turning on of the standard white light (control) the school is re-formed and typical circling resumed.

Left End Zone	*Center Zone*	*Right End Zone*
Red Light	White Light	Blue Light
Blue "	White "	Red "
Blue "	Red "	White "
White "	Red "	Blue "

6. General Electric 20-watt tube, Symbol F20T12/SW, Soft White.

The results of these four tests are summed up and presented in tables I–III showing the frequency of occurrence by zone and relationship in per cent to the total.

(a) Reaction of the sardines to the red light in combination with white and blue lights.

As seen from table I, the least average number of occurrences falls in the zone illuminated with red light (8.82%), and the largest in the blue

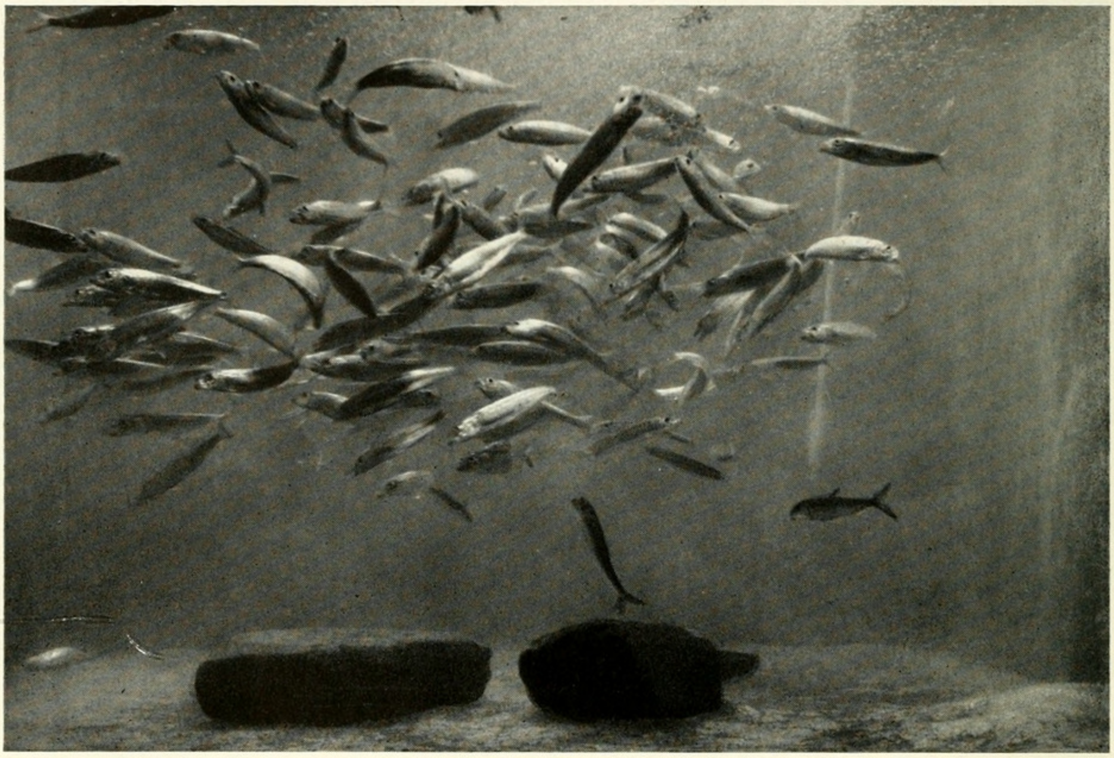

Figure 16. An instant feeding response of the school to the cloud of brine shrimp under the blue light. Food was introduced after a 30-minute exposure of the school to the light tested.

zone (52.94%). The white zone occupies an intermediate position (38.24%). The frequency of occurrence of the fish in the red zone varies from 1.07% to 16.53%, while the corresponding figure for the blue zone remains more or less constant except for test D, at the end of which test one of the sardines had become excited and stimulated the others to follow him from the blue zone through the red one into the white zone, where they remained until the end of the test and made no attempts to return to the blue zone. It is of interest to note that the sardines, swimming normally within the blue or white zone, developed exceptionally high speed while moving through the central zone illuminated with red light. Upon entering the blue or white zone they immediately slowed down and began circling about in a school pattern at normal speed. Usually after 500 scheduled observations on the effect of prolonged exposure to the red, white, and blue lights, tests were made to determine the immediate effect of a rapid change in the distribution of the light sources or on the turning off of the light in one or two zones.

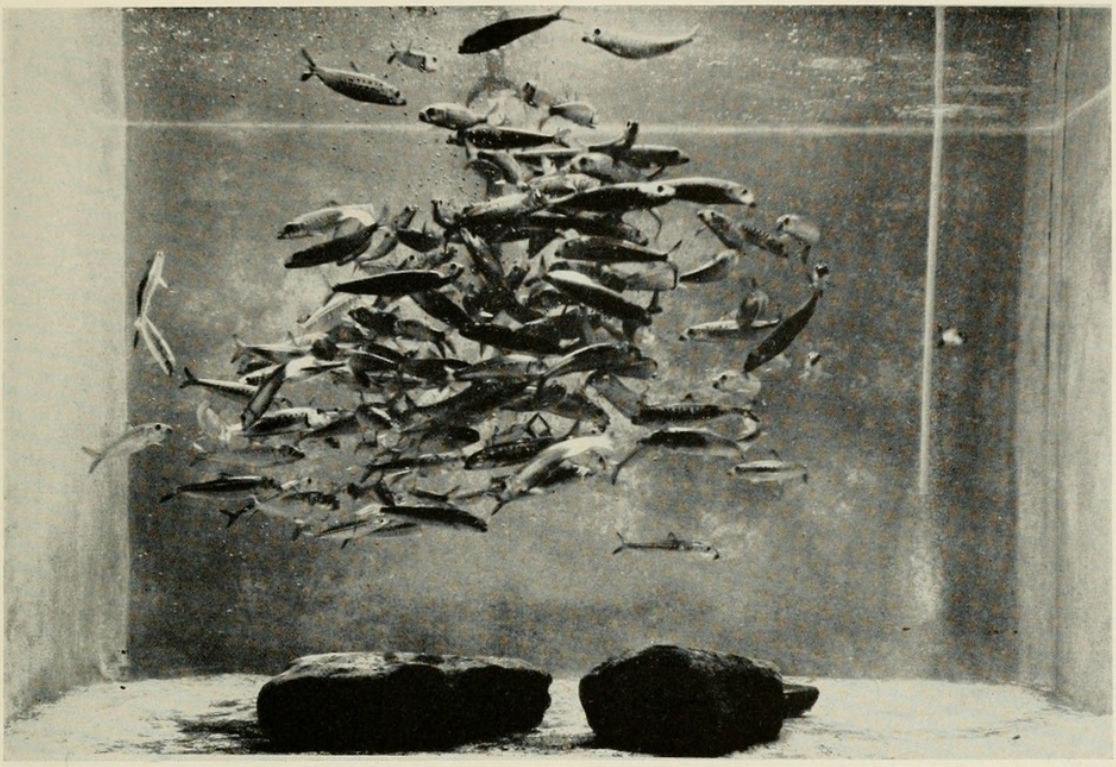

Figure 17. An instant and vigorous response of the school to the brine shrimp after being exposed to the red light for 30 minutes.

In each of these tests the experimenters observed immediate reactions of the sardines similar to those displayed by them on prolonged exposure to the same lights. If the red light in the left end of the tank was changed to the blue, and the blue light in the opposite end changed to the red, the sardines instantly deserted the new red zone, moving through the central zone illuminated with white light into a new blue zone at the left end of the tank. If the white light in the central zone was changed to the red, thus forming two adjacent red zones, the sardines aggregated in the blue zone alone. When the blue light was turned off, the sardines from this darkened zone moved into the white zone. The same was true when the test was reversed. When the blue and white lights were turned off simultaneously or one after another, the sardines deserted the darkened zones and swam about within the red illuminated zone alone. However, their behavior was different from normal: they increased their speed of movement, the school pattern being broken, and their swimming acquired a disorganized character. By all visible signs the fish experienced some agitation and inconvenience. As soon as the blue or white light at the opposite end of the tank was turned on again, the fish one after another swam out of the red zone, crossing the darkened central zone, and reached the blue or white zone and remained

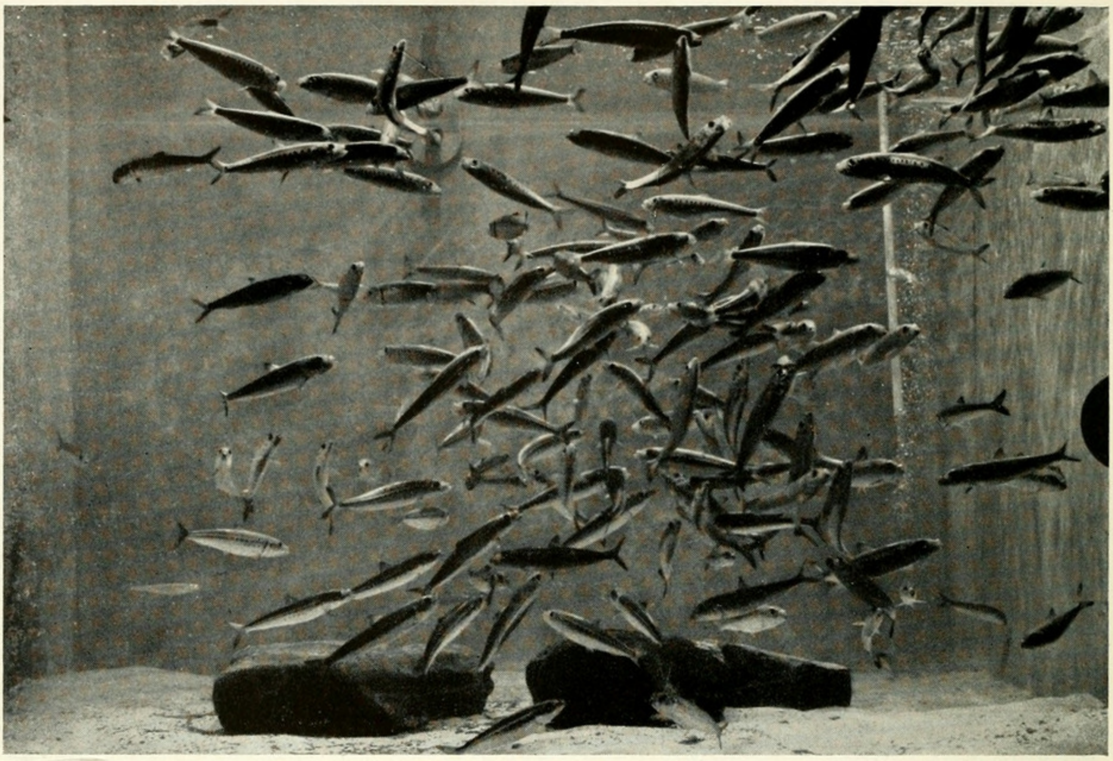

Figure 18. Broken-up school of sardines in total darkness fifteen minutes after turning off of the standard white light, to show a pattern of fish distribution in the tank prior to application of flashing beam of light.

there. Whenever the red light was turned off and the green light was turned on, the sardines began to frequent this zone as well as the blue one, showing special preference to neither. Again, the turning off of the green light and the restoring of the red illumination usually forced the sardines to leave this zone and avoid it thereafter.

Summing up the above records, the statement can be made that the numerical data and direct observations of the experiment with prolonged exposure of the sardines to the red light opposed by white and blue lights, and the records of the effects of the immediate change in illumination, indicate for the fish a decided preferential reaction in favor of the blue light, a lesser response in favor of the white light, and a very minor response in favor of the red light. *For the purposes of this paper such a minor preferential reaction is hereafter arbitrarily designated a negative* *response.* The red light zone was occupied by the sardines mostly when the other two zones were kept in darkness.

(b) Reaction of the sardines to the red light in combination with white and green lights.

Table II repeats practically the same results as presented in table I. The least number of occurrences were in the zone illuminated with red

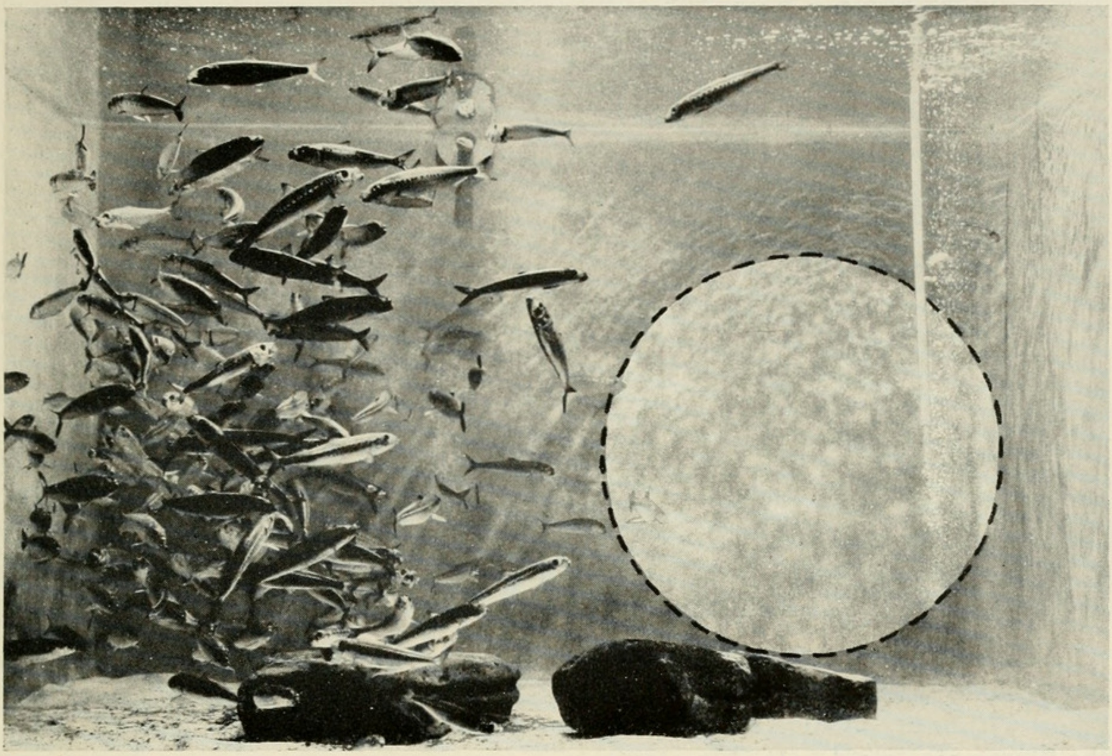

Figure 19. Avoidance reaction of the sardines to a flashing beam of standard white light of low intensity in total darkness. Source of light was placed on the right side of the picture. The light field is shown by broken line.

light (10.10%); the greatest, in the green-light zone (55.80%). As before, the reactions to white light occupy an intermediate position (34.19%). However, the frequency of occurrence in the red zone this time was much greater, varying from 0.60% to 21.40%, thus resulting in a comparatively higher indicator for the total in comparison with that of the previous experiment. Some distortion in distribution of the sardines was observed in test H owing to the comparatively long presence of the group of sardines in the white zone before they crossed the central red zone and entered the green one. As in the previous experiment, at the end of each test of prolonged exposure of the sardines to the red, white, and green lights, the positions of the light sources were changed, the red light was replaced by the blue, and the light was turned off in one or two zones for the observation of the immediate response of the sardines to the sudden change of the types of illumination. The reactions of the fish to the change of lights were found to be similar to those described in paragraph (a). Again, the sardines entered and remained in the red zone only when lights in the other

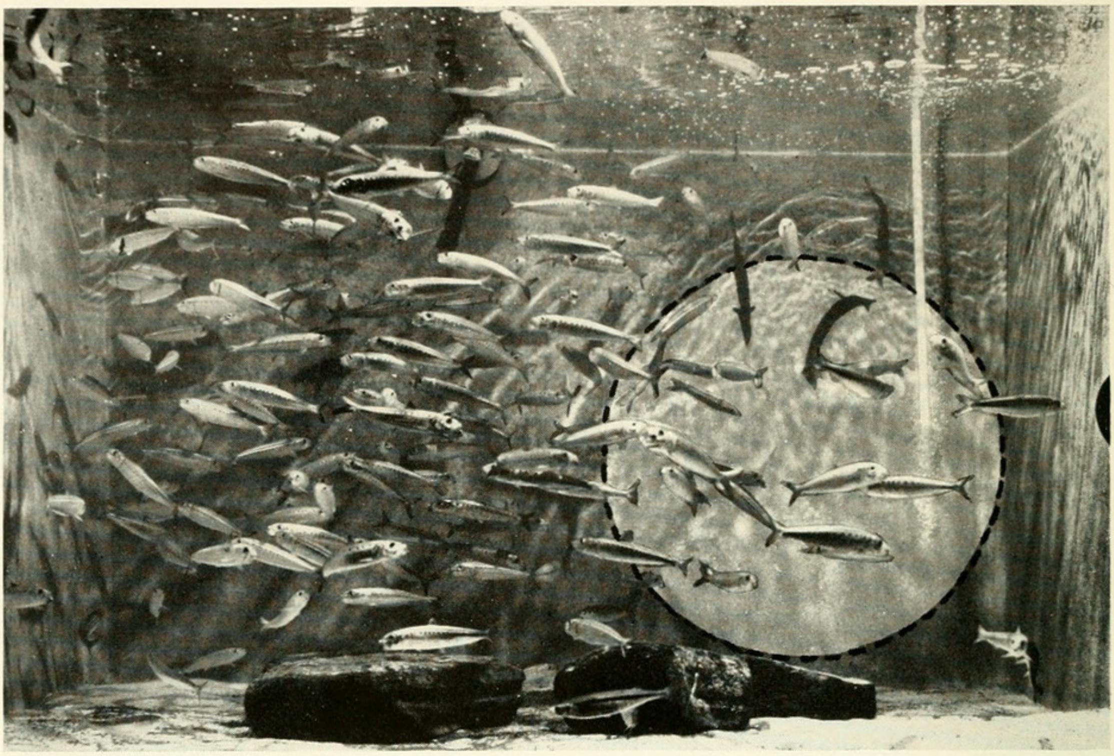

Figure 20. A continuous beam of the standard white light from the same source produced no fright reaction on the sardines. It rather helped the fish to re-form a school within five to eight minutes, to resume their circular movement, and to enter the illuminated right half of the tank.

two zones were turned off. The element of confusion and some agitation among the fish were recorded this time as before. In conclusion it can be stated that the numerical indicators obtained, together with the direct observations recorded during the prolonged exposure of the sardines to the red light opposed by white and green lights and supplemented by the records of the effects of the immediate change in illumination, definitely show a negative preferential reaction to the red light, and a positive preferential reaction in favor of the green light, while the reaction toward the white light lies between the two extremes. In general, tolerance for the red illumination, as in the previous case [paragraph (a)], was displayed by the sardines only when the other two zones were in total darkness.

(c) Reaction of the sardines to the red light in combination with blue and green lights.

Table III shows the results of the experiment with the application of the three primary colored lights: red, blue, and green. This time the sardines' tendency to avoid the red light zone was manifested much more clearly than in the two preceding experiments, and the frequency of occurrence for individual tests varied from 0 to 1.60% only, averaging 0.67% for the entire experiment. The positive preference for the opposing lights

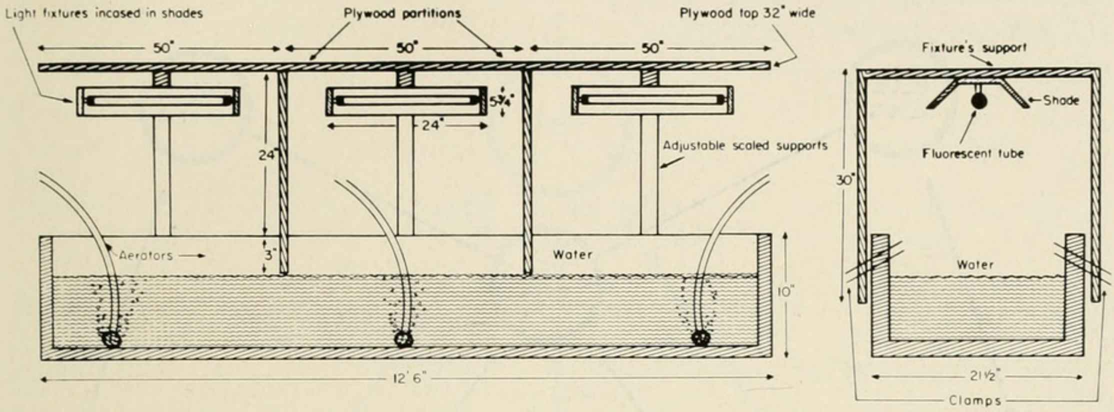

Figure 21. Sketch drawing of the experimental tank divided into three light zones for testing sardines' ability to discriminate colors of the light.

was shared by the sardines almost equally: 48.97% for the green, and 50.36% for the blue. However, in individual tests the frequencies of occurrence varied considerably in comparison with the relative stability observed for each of these types of light in the presence of the white light in the three-zone experiments (tables I and II). The frequency of occurrence fluctuated from 13.87% to 83.33% for the green light, and from 16.53% to 86.13% for the blue light. In regard to these colored lights, the sardines did not seem to have any specific preferential reaction. The lights caused positive responses without eliciting any appreciable difference in the degree of the sardines' preference toward either of the two. The fluctuation of the frequencies of occurrence in individual tests can be explained exclusively by the location of the zones provided with these sources of light. When the sardines were separated by the central zone illuminated by the red light, they aggregated in one of the terminal zones, regardless of the color of the opposing illumination (tests I and J). When the green and blue were adjacent, the readings were more or less similar for the two zones (tests K and L). After each test of prolonged exposure of the sardines to the effect of red, blue, and green lights, the fish were usually subjected to the effects of sudden changes of illumination, darkening of one or two zones, etc. And again, as in previous experiments, the sardines manifested their preferential tendencies of a positive character for the blue and green lights, and of a negative character for the red light. This time the negative preferential reaction to the red light was displayed more markedly than in either of the two preceding experiments. Tolerance for the red light was observed only in cases when the sardines had no other choice of light because of the darkening of the other two zones. Summing up all recorded occurrences of the sardines in the red light zone for the three experiments in the first part of this series (tables I, II, and III), one can see that the

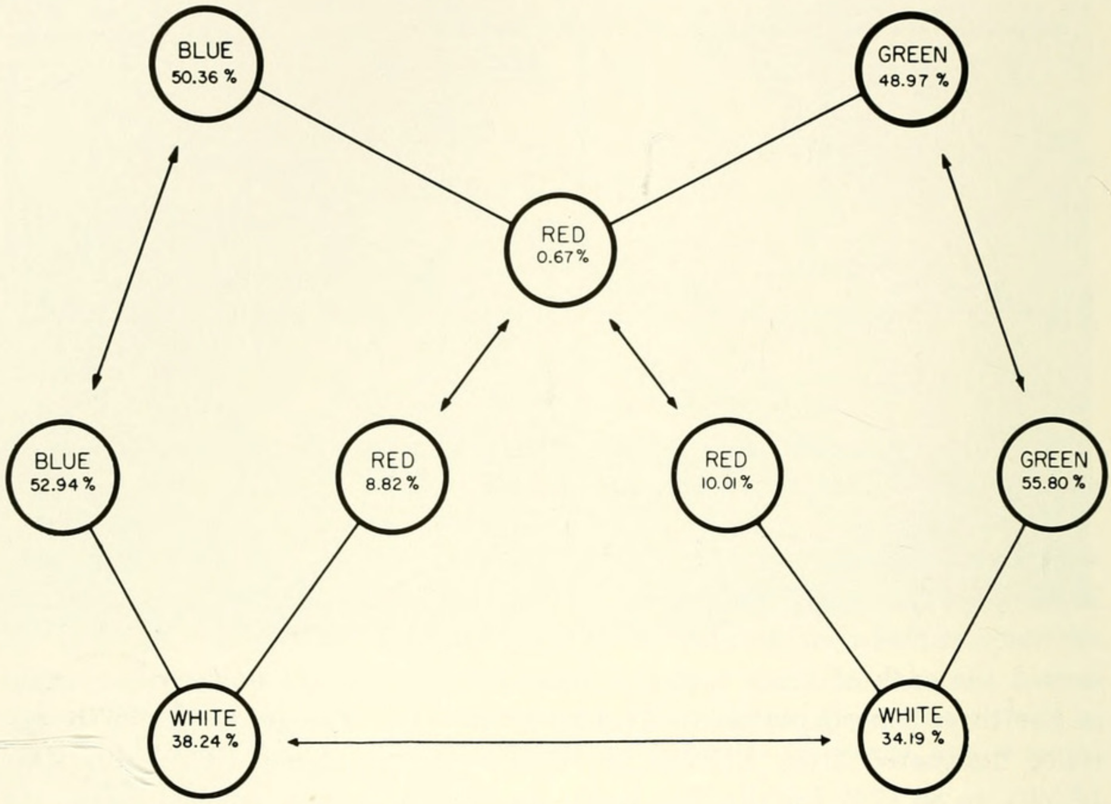

Figure 22. Diagrammatic interpretation of the relationships between the effects of different lights on the sardines' discriminating ability in the three-zone tank.

red zone was frequented by 2,341 sardines only (or 6.50%), whereas the other two zones combined were frequented by 33,569 sardines (or 93.50%) regardless of the type of illumination applied.[7]

For the purpose of checking the results obtained, the second part of this series of experiments was carried out. Each experiment consisted of four tests as in the previous series. The effect of the red light on the sardines was tested in combination with only one of the three other types of

7. Within the scheme of the three-zone experimentation, the white light was also tested against the blue and green. Unfortunately, only two tests were made in the beginning of the present study, and both appeared to be not indicative, because of the restlessness and agitation observed among the sardines used in these tests. The sardines raced wildly from one end of the tank to the other, and because of this fact the distribution of the fish within the tank's zones was as follows: 31.77% for the green, 34.73% for the white, and 33.50% for the blue. Because of the depletion of the stock of live sardines in the Steinhart Aquarium, the experiment with the application of the white, blue, and green lights could not be accomplished.

light. In these experiments the tank was divided into two parts, each 75″ long. One of these parts was illuminated with red light, the other, either with blue, or green, or white light. Procedure and recording of observations, as well as the number of observations, remained unchanged in order to obtain comparable data. Below is given a brief analysis of the results of the experiments as they appear in tables IV, V, and VI, of which table IV

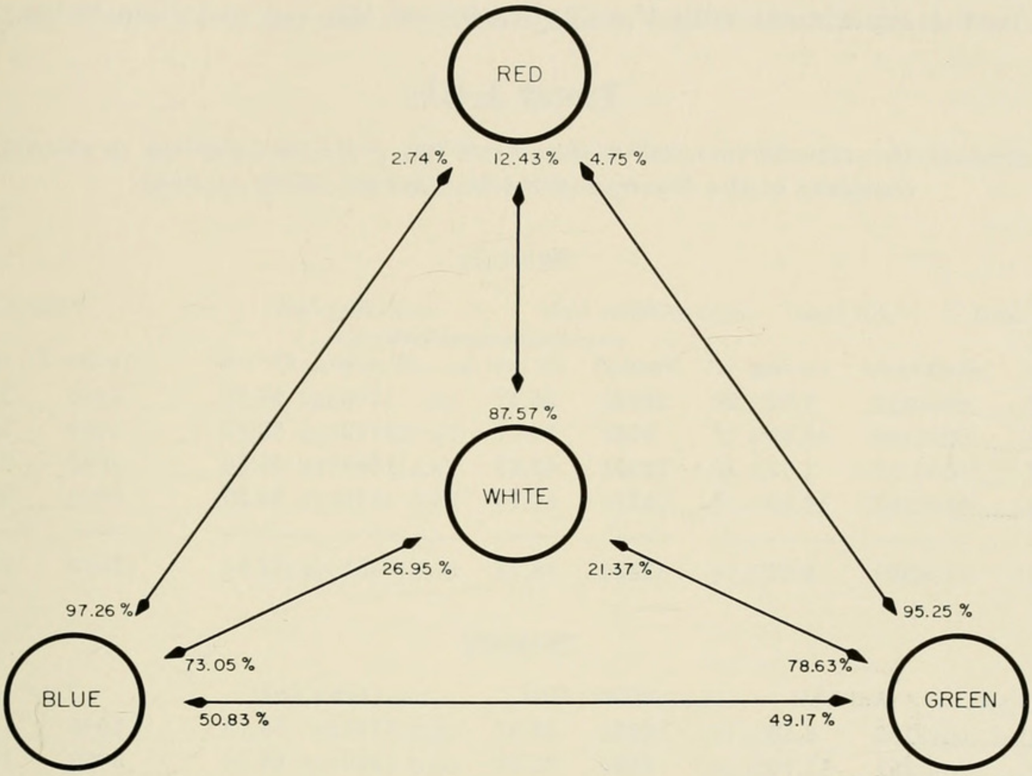

Figure 23. Diagrammatic interpretation of the relationships between the effects of different lights on the sardines' discriminating ability tested "in pairs" in the two-zone tank.

presents the results of the testing of the red light against the white. The frequency of occurrence in the red zone (12.43%) was found to be the highest of all the records obtained for the red light. Nevertheless, the red light still produced an invariably negative reaction, while the white light elicited a highly preferential reaction of a positive character (87.57%). In the individual tests of this experiment the negative reaction to the red light varied from 7.63% to 22.67%. In order to check the sardines' response to a sudden change of illumination, after each test the positions of the light sources were switched, or the light in one of the zones was turned off, or a new light source (blue or green) was introduced. In reaction to the change in position of lights, the sardines remained in the white zone regardless of its position being switched from left to right, or from right to left (the fish did occasionally swim into the red zone). The darkening of one of the zones caused the sardines to aggregate in the illuminated one regardless of the color of light. However, while in the red zone, they very often displayed restlessness leading to the breaking up of the school pattern. When green or blue light was substituted for the red light, the sardines seemed to prefer to remain within the zone illuminated by either of these lights, but they continued to frequent the white zone.

In the experiment with the application of the red and blue lights, as

Tables I–III

Records of the experiments using the three-zone tests for eliciting preferential reactions of the Pacific sardine to different colors of light.

Table I

	Red Light		*White Light*		*Blue Light*		*Total*	
	Frequency of Occurrence							
Test	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
A	228	7.60	1064	35.47	1708	56.93	3000	100
B	496	16.53	725	24.17	1779	59.30	3000	100
C	32	1.07	1279	42.63	1689	55.30	3000	100
D	304	10.10	1521	50.70	1175	39.20	3000	100
	1060	8.82	4589	38.24	6351	52.94	12000	100

Table II

Test	*Red Light*		*White Light*		*Green Light*		*Total*	
E	190	6.33	1019	33.97	1791	59.70	3000	100
F	351	11.70	669	22.30	1980	66.00	3000	100
G	642	21.40	831	27.70	1527	50.90	3000	100
H	18	0.60	1584	52.80	1398	46.60	3000	100
	1201	10.10	4103	34.19	6696	55.80	12000	100

Table III

Test	*Red Light*		*Green Light*		*Blue Light*		*Total*	
I	0	0.00	416	13.87	2584	86.13	3000	100
J	4	0.14	2500	83.33	496	16.53	3000	100
K	48	1.60	1180	39.33	1772	59.07	3000	100
L	28	0.94	1780	59.33	1192	39.73	3000	100
	80	0.67	5876	48.97	6044	50.36	12000	100

TOTAL FOR ALL THREE TABLES

Red Light		*All other lights combined*		*Total*	
2341	6.50	33659	93.50	36000	100

table V shows, the preferential negative reaction to the red light was displayed very markedly by a 100 per cent avoidance of the red zone in two tests (GG and HH). The average frequency of occurrence for the red zone was only 2.74%, the second lowest in the entire series. A repetition of the changes in illumination after the tests with a prolonged exposure of the sardines to the effect of red and blue lights revealed the same peculiar reactions of the sardines as those learned from the foregoing experiments. Table VI illustrates the results of the experiment in which the red

TABLES IV–VI.

Records of the experiments using the two-zone tests for eliciting preferential reactions of the Pacific sardines to different colors of light.

Table IV

Test	Red Light — Number	Red Light — Per cent	White Light — Number	White Light — Per cent	Total — Number	Total — Per cent
	Frequency of occurrence					
AA	235	7.83	2765	92.17	3000	100
BB	680	22.67	2320	77.33	3000	100
CC	347	11.57	2653	88.43	3000	100
DD	229	7.63	2771	92.37	3000	100
	1491	12.43	10509	87.57	12000	100

Table V

Test	Red Light		Blue Light		Total	
EE	89	2.97	2911	97.03	3000	100
FF	240	8.00	2760	94.52	3000	100
GG	0	0.00	3000	100.00	3000	100
HH	0	0.00	3000	100.00	3000	100
	329	2.74	11671	97.26	12000	100

Table VI

Test	Red Light		Green Light		Total	
II	208	6.93	2792	97.07	3000	100
JJ	280	9.33	2720	90.67	3000	100
KK	82	2.73	2918	97.27	3000	100
LL	0	0.00	3000	100.00	3000	100
	570	4.75	11430	95.25	12000	100

TOTAL FOR ALL THREE TABLES

Red Light		All other lights combined		Total	
2390	6.67	33610	93.33	36000	100

light was opposed by the green. The figures obtained confirm once again a striking preferential reaction of a positive character for the sardines in favor of the green light (95.25%), and a minor response toward the red (4.75%). In four tests the indicator of the frequency of occurrence for the red zone varied considerably (from 0 to 9.33%). The sudden change in positions and types of illumination at the end of each test of prolonged exposure of the sardines to the effect of the above-mentioned combination of colored lights elicited responses resembling those already described for the first two checking experiments.

Summing up all the recorded occurrences of the sardines in the red light zone for the three checking experiments in the second part of this series, one can see that the red zone was frequented by 2,390 sardines[8]

Tables VII–IX

Records of the experiments using the two-zone tests for eliciting preferential reactions of the Pacific sardine to different colors of light.

TABLE VII

Test	Blue Light		White Light		Total	
	Frequency of occurrence					
	Number	Per cent	Number	Per cent	Number	Per cent
M	2081	69.37	919	30.63	3000	100
N	1709	56.97	1291	43.03	3000	100
O	2545	84.83	455	15.17	3000	100
P	2431	81.03	569	18.03	3000	100
	8766	73.05	3234	26.95	12000	100

TABLE VIII

Test	Blue Light		Green Light		Total	
Q	432	14.40	2568	85.60	3000	100
R	252	8.40	2748	91.60	3000	100
S	2536	84.53	464	15.47	3000	100
T	2880	96.00	120	4.00	3000	100
	6100	50.83	5900	49.17	12000	100

TABLE IX

Test	Green Light		White Light		Total	
U	2516	83.87	484	16.13	3000	100
V	2202	73.40	798	26.60	3000	100
	4718	78.63	1282	21.37	6000	100

8. Against 33,600 sardines for all the other types of illumination put together.

(or 6.67%), which is almost identical to the figures obtained for the red light in the three-zone experiments.

(d) The effect of other light combinations tested in the two-zone experiments.

In closing the experimental study of the sardines' preferential reactions with the application of the zones of contrasting lights, the blue, green, and white lights were also tested against each other. In table VII the results of the effects of the blue and white lights are included. The sardines manifested their preferential reactions of a positive character (73.05%) for the blue light, and negative (26.95%) toward the white. Table VIII represents the results of the application of the blue and green lights. In this experiment the sardines reacted positively to both of them, but manifested specific preferential tendency to neither. The distribution of the sardines in the zones with contrasting lights was close to a 50:50 proportion, although in individual tests the percentage of frequency of the occurrence varied from 8.40% to 96.0% for the blue light, and from 4.0% to 91.60% for the green light. When the final results and the pattern of variation of this experiment are compared with the data obtained in testing the green and blue lights against the red in the experiments using the three-zone method presented in table III, it can be stated that the picture remains the same, and that the blue and green lights when tested against each other were found to be equally attractive to the sardines. Table IX presents the results of the tests using green and white lights. Because the stock of live sardines was depleted, the experiment could not be completed. Though the experiment was incomplete, the table nevertheless shows a preferentially positive reaction of the sardines in favor of the green light (78.63%), and a negative reaction to the white (21.37%).

On the basis of the results obtained during the present experimental study it can be assumed that the Pacific sardine possesses an ability to qualitatively discriminate the colors of light tested, and that phototactically it is a red-negative animal.

For a visual interpretation of the relationships of sardine reactions toward different lights in various combinations, two diagrams are shown in figures 22 and 23.

DISCUSSION

In respect to the results obtained during the course of the present experimental study, some comparative data on similar behavior of other species of fishes as have been reported by the other students of fish behavior are given below:

(1) It was shown very definitely that in total darkness the sardines

do not school, being widely dispersed throughout the tank. This behavior of a broken school in the dark agrees well in every major detail with the behavior of other schooling fishes under similar conditions in aquaria. For instance, the following species of fish stop schooling if the amount of light falls below a certain threshold value: mullet, *Mugil* sp. (Boulenger, 1929); dwarf herring, *Jenkinsia stolifera* (Breder, 1929, 1951); silver salmon, *Oncorhynchus kisutch* (Dunkan, 1956); golden rudd, *Scardinius erythrophthalmus* (Boulenger, 1929; Keenleyside, 1955); chub mackerel, *Pneumatophorus grex* (Schlaifer, 1942); Atlantic herring, *Clupea harengus* (Newman, 1876; Verheijen, 1953; Puchkov, 1954). The present experiments and the evidence reported by the authors noted above demonstrate clearly that the fish must see each other in order to integrate and maintain the school. Hence, vision in sardines, as in any other schooling fishes, is the dominant sensory modality involved in schooling.

(2) The sardines' avoidance of the beam of intermittent light in total darkness, revealed in the present study, produces positively a deflecting effect, and clearly explains the use of this type of light in California purse-seine fisheries to keep the catch of sardines within the seine until the bottom has been closed. Brett and MacKinnon (1953) evaluated the deflecting effect of intermittent light on a young king salmon, *Oncorhynchus tshawytscha*. Dunkan (1956) found that the fingerling silver salmon, *Oncorhynchus kisutch,* experiences "typical fright reaction with sudden, spasmodic movement and rapid darting away from the light directed on the fish and quickly turned on and off."

(3) Referring to the loss of equilibrium by sardines caused by a rapid switching of illumination from standard white light to red light or total darkness, an observation by Woodhead and Woodhead (1955) on the behavior of herring larvae is worth mentioning. As in the case of our sardines which responded to red light or total darkness by assuming a vertical body position and slowly progressing toward the surface "with heads up and tails down," the herring larvae in the Woodhead experiments behaved in a similar manner when exposed to diffuse white light of low intensity (down to 3 m. c.) and to red light (above 6500 Å). Their fish, kept in a tall glass cylinder with illumination provided from above, swam upward only vertically, "standing on their tails."

(4) In regard to the reorganization of the typical loose ring-shaped school of sardines into a compact ball-shaped formation caused by the change of illumination from standard white light to the red light, it should be noted that the sardines kept under observation in the Steinhart Aquarium since 1949 have never behaved similarly. Wilson (1949) described an identical performance displayed by gobies, *Gobius flavescens,* in the Plymouth Aquarium. This species possesses no schooling proclivity, and usually when

in groups, the fish swim about individually with jerky forward motions. According to Wilson, however, on one occasion about three hundred gobies, each an inch long or less, were placed in a tank, and "instead of dispersing immediately, they kept together in compact rather globular shoals each consisting of fifty or a hundred fishes. For one or two days these shoals moved slowly through the tank keeping more or less in mid-water . . ." Gradually the schools broke up and the gobies dispersed throughout the tank. Wilson assumes that this unusual schooling phenomenon of a non-schooling species was "perhaps a fear reaction induced by capture and by strange surroundings." An analogous behavior of the Pacific sardine in the sea was reported by Allen (1920), who had observed a small school of little sardines in the presence of a large loon, *Gavia immer* Brünnich. This school "was very compact and was in the form of a symmetrical ball approximately six feet in diameter." The loon made several divings through this school but failed to catch a single fish. "The sphere of fish indented like a hollow rubber ball at the point of attack, then scattered slightly, coming together again into a sphere as the bird passed to the other side." Another field record of a compact globular school observed in nature was recently reported by Springer (1957). A school of "majua," *Jenkinsia lamprotaenia* Goose, comprising approximately 7,500 or more fish, assumed a dense ball-shaped formation, occupying not more than a cubic foot and moving at much higher speed than individuals could have moved. This observation was made in Tortugas harbor during night collecting using electric light for attracting the fish.

The present experimenters recently tested this protective adaptation in group behavior of the sardine by the introduction of a predator fish, the striped bass, *Roccus saxatilis* (Walbaum), about 50 cm. in standard length, into a tank containing over 150 young sardines. In the presence of the predator fish, school reaction and behavior were very similar to those described by Allen (1920) and to those recorded here in the experiments dealing with the application of red light. Therefore, the abrupt change in environmental factors, such as illumination by switching from standard white light to the red light, could elicit a strong fright reaction which, in its acuity and intensity, is equivalent to the alarm induced by the presence of an aggressive predator. In other words, this is the most pronounced natural negative reaction of the sardine to the red light so far obtained under laboratory conditions.

(5) As to the preferential reactions of the sardine in the experiments intended to elicit the fish's ability to discriminate light of different wavelengths, it was disclosed that the sardine's reaction to the red light in any combination with other light sources is strongly negative. In recent literature there are records of similar avoidance of the red light. For instance,

all five species of young marine fishes *(Oplegnathus fasciatus, Monocanthus cirrhifer, Cybium niphonium, Spheroides niphobles,* and *Sphyraena japonica)* in the experiments of Kawamoto and Takeda (1951) have shown a very low percentage (from 0 to 5.3%) of gathering in the zone illuminated by the red light, while green and blue lights remained most attractive stimuli for the same species (up to 40.6% and 43.5% respectively.[9] In the experiments with young vendace, *Coregonus albula,* Privolnev (1956), using apparatus and methods very similar to those described in this report, found that this freshwater species reacted negatively to the red light (12.8%), and positively to the green (27.2%) and white (23.4%), and less positively to the blue and to darkness (18.3% for each).[10] In Borisov's experimental catches in the Caspian Sea using white and colored electric lights, the Caspian sprat, *Clupeonella delicatula caspia,* reacted negatively to the red light. Only 0.5% of the total experimental catches were made using red light (Privolnev, 1956). Many more data of the earlier reports on this subject are abundantly presented in the reviews of the literature on color-vision in fishes by Reeves (1919), Warner (1931), Brown (1937), Walls (1942), Herter (1953), and others.

Another peculiarity of the sardine's reactions to colored lights is that it seemed unable to show a preference for either green or blue lights when they were offered in pairs. Similar difficulties were experienced by the mud-minnow, *Umbra limi,* in the studies conducted by White (1919), and by the black bass, *Micropterus salmoides,* in Brown's experiments (1937). These fishes could not distinguish blue from green.

(6) The red light causes most of the duplex teleost fishes already investigated to respond vigorously in one way or the other. Usually, the light-adapted, or photopic species, will rather avoid the red light, as is the case in the present study, while the dark-adapted, or scotopic forms, such as the Japanese eel, *Anguilla japonica,* will be attracted by it (Kawamoto and Takeda, 1951). On the basis of the instinctively strong negative reactions of *Charax puntazzo, Atherina hepsetus,* and *Box salpa* to red light, Bauer (1910, 1911) called this phenomenon "Rotscheu" or red-shyness, red-fear. A display of red-negative response by photopic fishes and red-positive pho-

9. Kawamoto and Takeda (1951) tested the discriminating ability of their experimental marine fishes in an apparatus divided into eight zones and illuminated with filtered light of different wave-lengths of 50 luxes each. The color filters were arranged in two ways, one in order of wave-lengths and the other at random. The average results of the gathering of the fish for the entire group are as follows: in the red compartment 2.18%, in the orange 5.56%, in the yellow 10.58%, in the green 30.18%, in the blue 31.58%, in the indigo 7.52%, in the violet 2.32%, and in the white 10.6%.

10. Kurien *et al.* (1952) stated that *Mugil, Hemiramphus, Caranx, Arius, Equula, Stolephorus, Chatoessus, Brachyurus,* Cattle fish, *Penocus, Paloemon, Scylla,* and *Neptunus* responded to green, blue, and red lights, and that these lights were found more effective than white light in attracting the fish, the green light being most effective. However, the authors gave no details as to which particular colored light had been preferred by which particular fish or prawn listed.

totactic response by scotopic ones explains a high attentive value for red, and therefore this display is a *proof* that the fish has *redness perception*, and that this perception is based on a *function of light wave-length*.[11]

SUMMARY

1. The present investigation was conducted in order to study experimentally the effects of various types of illumination on the Pacific sardine, *Sardinops caerulea* (Girard), from the point of view (a) of the behavior of the school as a unit, and (b) the ability of the fish to discriminate different colors of light.

2. The first group of the experiments were carried out in a display tank of the Steinhart Aquarium. In these experiments, the effects on the behavior of the school of the pure green, blue, and red illumination as well as total darkness and flashing and constant beams of white light of low intensity in total darkness were studied.

3. Out of the three colored lights of both different and uniform light intensities, only the red light elicited what are here called negative reactions as explained in the text. These were as follows: (a) at the sudden switching from white light to the red, the school displayed fright reactions with a partial breaking up of the school pattern and the loss of body equilibrium in individual fish; (b) during prolonged exposure to the red light the school continued to display the fright reactions, being in a state of total confusion; (c) the normal harmony of circular movement of the school and the direction of movement were never restored during the hour-long exposures.

4. The sudden switching from white light to the blue or green, or prolonged exposure to either of these colored lights elicited no appreciable difference in the behavior of the school as a unit.

5. The application of white illumination of various light intensities equivalent to those of the colored lights tested caused no change in the typical and normal behavior of the school.

6. The sudden turning off of the light caused a shock effect on the fish, including mass loss of body equilibrium. The total darkening of the tank invariably led to a complete disorganization of the school. During prolonged exposure to darkness the equilibrium was gradually restored, but

---

11. In this respect, it is interesting to recollect a rather anthropopathic observation made by Walls (1942) which is as follows: "Perhaps it is because red, distinctively visible as red, is so unfamiliar to fishes that it gives them such a start . . . Both shunning and pursuit of red mean the same thing—that the fish sees red vividly, that it is strange, and that it fascinates him."

the school as a unit at all times remained broken up, and the sardines swam about slowly and aimlessly in all directions as if they were incapable of forming a school and of resuming a clockwise circling.

7. However, a very gradual reduction of the light intensity of the white illumination from 38.9 foot-candles down to almost zero (below 0.01 foot-candle) by means of an iris diaphragm produced no effect like the one observed at the sudden switching from light to total darkness.

8. The adaptation of the organs of sight to the change in illumination occurred in a comparatively short time. It was established that after the sardines had been exposed for five minutes to the colored lights the feeding responses of the fish to live brine shrimp, *Artemia salina,* in comparison with those under control illumination (white light of 20.0 foot-candle intensity), were delayed as follows: from a few seconds in green light, up to 35 seconds in red, and about a minute in blue. When the sardines were exposed to colored lights for half an hour, the feeding responses were immediate and intensive regardless of the color of illumination.

9. The flashing beam of white light of low intensity (much below 1 foot-candle) elicited fright reactions on the part of the sardines, forcing the school to break up and hide in the dark half of the tank and to avoid entering the field of light. No typical circling was maintained by the sardines.

10. The same beam of light constantly illuminating half of the tank caused no fright reaction, but instead it helped the sardines to re-form the typical school and to resume normal clockwise circling, as under control illumination.

11. In the second phase of the study the discriminative ability of the sardine in regard to different types of illumination was explored in the specially constructed dark room and the experimental wooden tank, which was divisible into two and three contrasting light zones.

12. In the three-zone experiments the following combinations of lights were tested: red–white–blue, red–white–green, and red–green–blue.

13. In the two-zone experiments the following combinations of lights were tested: red–white, red–blue, red–green, blue–white, blue–green, and green–white.

14. In all combinations of lights maintained at the 10 foot-candle level, the effect of the red light on the sardines remained invariably negative in contrast to the preferential positive reaction of these fish toward any other light tested.

15. In the experiments using the tank divided into three zones, when the red light was opposed by the blue or green in combination with white light, the preferentially positive reaction of the sardine was manifested either toward the blue or the green (52.94% and 55.80% respectively),

while a much less positive reaction was displayed in regard to the white light (38.24% in combination with blue, and 34.19% with green), which occupied the intermediate position between the red and blue or red and green lights.

16. In combinations of the red, green, and blue lights, the preferential positive reaction of the sardines was divided almost evenly between the green and the blue (48.97% and 50.36% respectively), with the most marked negative reaction toward the red light (0.67%). The similar relation of the indicators of the sardine reactions to the blue and green lights remained unchanged in the experiments in the two-zone tank (49.17% for the green and 50.83% for the blue).

17. The average indicator of the negative effect of the red light on the sardine for all three combinations tested in the three-zone experiments was found to be 6.50%. The figures obtained by testing the red light against each of the three types of light sources separately show that the average indicator for the red light remained almost unchanged (6.67%).

18. In the experiments with white light against blue or green separately, the sardines displayed negative reactions to the white light (26.95% and 21.37%) and definitely positive responses to the blue (73.05%) and green (78.63%).

19. The experiments revealed three important factors in sardine reactions to the light and darkness: (1) the sardine is a phototactic animal; (2) the sardine is incapable of reacting differently to different intensities of the white light ranging from 0.01 to 38.9 foot-candles; (3) and the sardine is capable of discriminating qualitatively the colors of light of the three primary colors.

20. The Pacific sardine proved to be strongly negative to the red light However, the fish tolerated this type of illumination when it was tested in combination with total darkness.

ACKNOWLEDGMENTS

This work has been carried on with funds provided by the Marine Research Committee as a part of the California Cooperative Oceanic Fisheries Investigations. The authors express their appreciation to Dr. Robert C. Miller, Director of the California Academy of Sciences, for his keen interest in the studies and for encouragement and valuable suggestions during the progress of the research; and to Dr. Earl S. Herald, Curator of Aquatic Biology, California Academy of Sciences, for his willing cooperation and valuable counsel; and to Mr. James W. Atz, Assistant Curator of the New York Aquarium, New York Zoological Society, for helpful suggestions relating to recent literature on the schooling behavior in fishes;

and to Mrs. Lillian J. Dempster, Assistant Curator in Ichthyology, California Academy of Sciences, for valuable assistance in preparing the manuscript. Acknowledgment is made also to Dr. Frank A. Brown, Jr., Morrison Professor of Biological Sciences, Northwestern University; Dr. C. M. Breder, Jr., Chairman and Curator, Department of Fishes and Aquatic Biology, American Museum of Natural History; Mr. John Radovich of the California State Department of Fish and Game; and Mr. Charles P. O'Connell of the U.S. South Pacific Fisheries Investigations, for helpful and constructive criticism of the manuscript.

LITERATURE CITED

Allee, Warder Clyde

1931. Animal Aggregations. A Study in General Sociology, ix + 431 pp., 35 text figs., The University of Chicago Press, Chicago, Illinois.

Allen, W. E.

1920. Behavior of loon and sardines. *Ecology*, 1:309–310.

Atz, James W.

1953. Orientation in schooling fishes. *Proceedings of a Conference on Orientation in Animals, February 6 and 7, 1953, Washington*, pp. 115–130. Office of Naval Research, Department of the Navy, Washington, D. C.

Bateson, W.

1889. Sense organs and perceptions of fishes with remarks on the supply of bait. *Journal of the Marine Biological Association of the United Kingdom*, 1:225–256.

Bauer, Victor

1910. Über das Farbenunterscheidungsvermögen der Fische. *Pfluger's Archiv für die gesamte Physiologie des Menschen und der Tiere, Berlin-Göttingen-Heidelberg*, 133:7–26.

1911. Zu meinen Versuchen über das Farbenunterscheidungsvermögen der Fische. *Ibidem*, 137:622–626.

Boulenger, E. G.

1929. Observations on the nocturnal behaviour of certain inhabitants of the Society's aquarium. *Proceedings of the Zoological Society of London*, 1929, part II, pp. 359–362.

Bowen, Edith S.

1931. The role of the sense organs in aggregations of *Ameiurus melas*. *Ecological Monographs*, 1 (1):3–35, 1 text fig.

1932. Further studies of the aggregating behavior of *Ameiurus melas*. *Biological Bulletin*. The Marine Biological Laboratory, Woods Hole, Massachusetts, 63(2):258–270.

Breder, C. M., Jr.

1929. Certain effects in the habits of schooling fishes, as based on the observation of *Jenkinsia*. *American Museum Novitiates*, The American Museum of Natural History, New York, no. 382, pp. 1–5, 2 text figs.

1951. Studies on the structure of the fish school. *Bulletin of the American Museum of Natural History*, 98(1):1–28, 9 text figs., 4 plates and 3 tables.

Breder, C. M., Jr., and R. F. Nigrelli

1935. The influence of temperature and other factors on the winter aggregations of the sunfish, *Lepomis auritus*, with critical remarks on the social behavior of fishes. *Ecology*, 16(1):33–47, 3 text figs.

1938. The significance of differential locomotor activity as an index to the mass physiology of fishes. *Zoologica*, The New York Zoological Society, 23 (Part 1, Nos. 1–4):1–29, 8 text figs.

Brett, J. R., and D. MacKinnon

1953. Preliminary experiments using lights and bubbles to deflect migrating young spring salmon. *Journal of the Fisheries Research Board of Canada*, 10(8):548–559, 5 text figs.

Brown, Frank A., Jr.

1937. Responses of the large-mouth black bass to colors. *Illinois Natural History Survey Bulletin*, 21(2):33–55, 1 color plate, 10 text figs. and 11 tables.

Dunkan, Rea E.

1956. Use of infrared radiation in the study of fish behavior. *Special Scientific Report—Fisheries, no. 170*, U. S. Department of the Interior, Fish and Wildlife Service, 16 pp. and 9 text figs.

Eddy, M. W.

1925. Metabolic rate and bunching in catfish. *Anatomical Records*, 31:332–333 (Abstract no. 79).

Escobar, Raul A., Roger P. Minihan, and Ralph J. Shaw

1936. Motility factors in mass physiology: locomotor activity of fishes under conditions of isolation, homotypic grouping, and heterotypic grouping. *Physiological Zoology*, 9(1), 66–78, 1 text fig.

Hardy, A. C.

1924. The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the coast of England. *Fisheries Investigations*, Ministry of Agriculture and Fisheries, London, series II, 7(3).

Hasler, Arthur D., and John E. Bardach

1949. Daily migrations of perch in Lake Mendota, Wisconsin. *Journal of Wildlife Management*, 13(1):40–51, 7 text figs.

Herter, Konrad

1953. Die Fischdressuren und ihre sinnesphysiologischen Grundlagen, 326 pp., 147 text figs., 1 color plate. Akademie-Verlag, Berlin.

JOHNSON, W. H.

1940. Effect of light on movements of herring. *Journal of the Fisheries Research Board of Canada*, 4(5):349–354, 1 text fig.

KAWAMOTO, N. Y., and M. TAKEDA

1951. The influence of wave lengths of light on the behavior of young fish. *Report of the Faculty of Fisheries, Prefectural University of Mie*, 1(1): 41–53, 8 text figs. and 11 tables.

KEENLEYSIDE, MILES H. A.

1955. Some aspects of the schooling behaviour of fish. *Behaviour—An International Journal of Comparative Ethology, Leiden*, 8(2–3):183–247, 18 text figs., 16 tables.

KREFFT, G., and F. SCHÜLLER

1951. Beobachtungen über die Tiefenverteilung von Heringsschwarmen in der nordlichen und mittleren Nordsee in August 1950. *Fischereiwelt Jahrgang*, 3(6):93–95.

KURIEN, C. V., V. K. PILLAI, and G. S. NAIR

1952. Use of light of different intensity and colour in luring fish. *Current Science*, 21(6):130–131. Bangalore, India.

LANGLOIS, T. H.

1936. Survival value of aggregational behavior of bass under adverse conditions. *Ecology*, 17(1):177–178.

LINSDAY, E. A.

1948. The use of fluorescent lamps for examining color proofs. Reprint from *Photoengravers Bulletin*, November 1948, American Photoengravers Association, by the General Electric Engineering Div., Lamp Dept. in a pamphlet LS-122, May 1949, Cleveland, Ohio; original pagination not indicated.

MORROW, JAMES E., JR.

1948. Schooling behavior in fishes. *Quarterly Review of Biology*, 23(1):27–38, March 1948.

NEWMAN, EDWARD

1876. Mr. Saville Kent's lecture, at the Society of Arts, on "The aquarium: construction and management." *Zoologist*, Second Series, 11:4853–4858. London.

NOBLE, G. K.

1939. The experimental animal from the naturalist's point of view. *American Naturalist*, 73(#745, March–April 1939):113–126.

NOBLE, G. K., and BRIAN CURTIS

1939. The social behavior of the jewel fish, *Hemichromis bimaculatus* Gill. *Bulletin of the American Museum of Natural History, New York*, 76(1): 1–46, 6 text figs., 1 plate.

Parr, Albert Eide

1927. A contribution to the theoretical analysis of the school behavior of fishes. *Occasional Papers of the Bingham Oceanographic Collection*, no. 1, 32 pp., 3 text figs.

Privolnev, T. I.

1956. Reaction of fish to light. *Voprosy Ihtiologii* (The Problems of Ichthyology), published by the Academy of Sciences of the U.S.S.R., Division of Biological Sciences, Ichthyological Commission, issue 6:3–20, 5 text figs., in Russian.

Puchkov, N. V.

1954. The Physiology of Fishes, 369 pp., 108 text figs. Moscow, in Russian.

Reeves, Cora D.

1919. Discrimination of light of different wave-lengths by fish. *Behavior Monographs, London*, 4(3), serial number 19:i–iv + 1–106, 17 text figs.

Reinhardt, F.

1935. Über Richtungswahrnehmung bei Fischen, besonders bei der Elritze *(Phoxinus laevis* L.) und beim Zwergwels *(Ameiurus nebulosus* Raf.). *Zeitschrift für vergleichende Physiologie*, 22:570–613. Berlin.

Richardson, I. D.

1952. Some reactions of pelagic fish to light as recorded by echo-sounding. *Fisheries Investigations, Ministry of Agriculture and Fisheries, London*, series II, 18(1):1–20.

Sato, M.

1938. The role of the visual sense organ in aggregation of *Plotosus anguillaris* (Lacepède), with special reference to the reactions to mirror. *Science Report of the Tohoku Imperial University, Fourth Series (Biology)*, 12(4):629–638.

Scharfe, J.

1951. Fischwanderungen im Grossen Ploner See wahrend einer Tagesperiode, dargestellt in Echogrammen. *Archiv für Fischereiwissenschaft*, 3:138–145.

Scott, D. C.

1955. Activity patterns of perch, *Perca flavescens*, in Rondeau Bay of Lake Erie. *Ecology*, 36(2):320–327, 6 text figs.

Sette, Oscar Elton

1950. Biology of the Atlantic mackerel *(Scomber scombrus)* of North America. Part II — Migrations and habits. *Fishery Bulletin of the Fish and Wildlife Service*, 51(no. 49):249–358, 21 text figs.

Shlaifer, Arthur

1938. Studies in mass physiology: effect of numbers upon the oxygen consumption and locomotor activity of *Carassius auratus*. *Physiological Zoology*, 11(4):408–424.

SHLAIFER, ARTHUR—Cont.

1939. An analysis of the effect of numbers upon the oxygen consumption of *Carassius auratus*. *Physiological Zoology*, 12(4):381–392.

1940. The locomotor activity of the goldfish, *Carassius auratus* L., under various conditions of homotypic and heterotypic grouping. *Ecology*, 21(4): 488–500, 6 text figs.

1942. The schooling behavior of mackerel: A preliminary experimental analysis. *Zoologica*, New York Zoological Society, 72(Part 2, nos. 9–16): 75–80, 3 text figs., 1 plate.

SPOONER, G. M.

1931. Some observations on schooling in fish. *Journal of the Marine Biological Association of the United Kingdom*, new series, 17(2):421–448, 12 text figs. Plymouth, England.

SPOOR, WILLIAM A., and CLARENCE L. SCHLOEMER

1938. Diurnal activity of the common sucker *(Catostomus commersonnii* Lacépède), and the rock bass *(Amplopites rupestris* Rafinesque), in Muskellunge Lake. *Transactions of the American Fisheries Society*, 68:211–220.

SPRINGER, STEWART

1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. *Ecology*, 38(1):166–171.

TOWNSEND, C. H.

1916. Hibernating fishes. *Zoological Society Bulletin*, 19(2):1344–1345, 1 text fig. New York.

VERHEIJEN, F. J.

1953. Laboratory experiment with herring, *Clupea harengus*. *Experimentia*, 9(5):193–194.

WALLS, GORDON LYNN

1942. The vertebrate eye and its adaptive radiation. *Cranbrook Institute of Science Bulletin*, no. 19, xiv + 785 pp., 197 text figs., 1 plate.

WARNER, LUCIEN H.

1931. The problem of color vision in fishes. *Quarterly Review of Biology*, 6(3):329–348, 4 text figs.

WHITE, GERTRUDE MAREAN

1919. Association and color discrimination in mud minnows and sticklebacks. *Journal of Experimental Zoology*, 27(4):443–498, 10 text figs.

WILSON, DOUGLAS P.

1949. Notes from the Plymouth Aquarium. *Journal of the Marine Biological Association of the United Kingdom*, 28(2):345–351.

WOODHEAD, P. M., and A. D. WOODHEAD

1955. Reactions of herring larvae to light: a mechanism of vertical migration. *Nature*, 176(4477):349–350, 1 text fig. London.