R. J. B.

SOCIAL BEHAVIOR AND INTERSPECIFIC COMPETITION IN TWO TROUT SPECIES

MURRAY A. NEWMAN

Reprinted for private distribution from
PHYSIOLOGICAL ZOOLOGY
Vol. XXIX, No. 1, January 1956
Printed in U.S.A.

SOCIAL BEHAVIOR AND INTERSPECIFIC COMPETITION IN TWO TROUT SPECIES[1]

MURRAY A NEWMAN[2]

Institute of Fisheries, University of British Columbia

The eastern brook trout, (Salvelinus fontinalis) (Mitchill), and the rainbow trout, (Salmo gairdneri) Richardson, are fishes which have been extensively stocked in suitable waters throughout the world but which occur naturally in cool fresh waters on opposite coasts of North America. Such related species which have evolved in isolation and which live as ecological equivalents are potentially their own greatest competitors, since they have not necessarily evolved mechanisms for interspecific toleration, yet they are so similar biologically that they make the same demands of their environment.

The most direct, although not necessarily the most effective, method of competing is interindividual aggressive behavior, whereby the less successful individual is deprived of an essential need, such as food or cover. This type of aggressive behavior among individuals of a single species frequently results in territoriality or social hierarchy. The former involves a dispersion in space, while the latter consists of a precedence order. Similar social organizations may result from interspecific aggressive behavior of related species.

The concepts of territoriality, hierarchy, and home range are seldom discussed together, and their relationship, particularly to the non-sexual periods of animal life, is by no means clear. Although many kinds of territoriality are recognized (Allee, Emerson, Park, Park, and Schmidt, 1949, p. 412), the most definite and typical is the mating territory in which the nest is defended against all intruders by one or both members of an established pair. Among fishes this type of territory is well illustrated by some of the cichlids (Noble, 1938, 1939; Baerends and Baerends-Van Roon, 1950).

1. Contribution from the Sagenhen Creek Project and Department of Zoölogy, University of California.

2. The author wishes to record his appreciation to Professor Paul R. Needham for his invaluable advice and assistance and for use of the facilities of the Sagenhen Creek Project. Dr. Earl S. Herald provided space and materials at the Steinhart Aquarium. Dr. P.A. Larkin and Dr. C.C. Lindsey, of the Institute of Fisheries, University of British Columbia, read the manuscript and suggested improvements.

Other species of fish establish spawning territories of lesser stability in accordance with the peculiarities of their innate reproductive patterns. Territoriality among immature and adult green sunfish has been described in detail by Greenberg (1947). In this species "partial" territories are established in which residents defend their areas against subordinates but not against dominants. Such behavior is to be expected in nature, where fish of different sizes live together, but there is little field information on the subject. Hoar (1953) believes that prolonged residence of juvenile salmon and trout in streams depends primarily on their territorial behavior, and he demonstrated that coho salmon fry and Kamloops trout defend areas within laboratory tanks (Hoar, 1951; Hoar, MacKinnon, and Redlich, 1952; Stringer and Hoar, 1955).

The idea of "home range", used primarily by mammalogists (Burt, 1943), has recently been employed by Gerking (1950, 1953) in discussing the stability of fish populations in streams. Home range is the area over which an animal normally travels, and it differs from territoriality in that aggressiveness and defense are not necessary corollaries. Gerking (1953) maintains that territoriality is a more useful interpretation of interaction among members of a population than the home range, because it stresses aggressive competition; but the existence of a strong homing tendency in many fish suggests some basic attraction of the home site which has nothing to do with aggressiveness.

Domination-subordination relations have been shown to exist in various kinds of fishes (Noble and Borne, 1938; Braddock, 1945, 1949; Greenberg, 1947; Allee, 1952) in which nipping characterizes social interaction and aggressiveness is intermediate between the low level required for schooling and the intense level required for territoriality or isolation. Dominance relations among Kamloops trout, (Salmo gairdneri kamloops) Jordan, are discussed by Stringer and Hoar (1955). Even less is known about these relations in nature than about territoriality and home range, since direct observation is required to ascertain their existence.

MATERIAL AND METHODS FOR AQUARIUM STUDIES

Most of the observations were carried out in the Steinhart Aquarium in San Francisco during the winter of 1950 and 1951. During July, 1953, field observations were made at the University of California Sagenhen Creek Project near Truckee, California. The methods and materials employed in this stream study are described in another section.

One hundred and fifty rainbow trout 10-17 cm. in total length, were obtained from the East Bay Reservoir, a fish-rearing pond operated by the California Department of Fish and Game, in Napa, California. A comparable number of similar-sized brook trout was donated by the Steinhart Aquarium, in which they had been hatched and reared. All fish of both species were in the "parr" stage of development, characterized by a series of eight to twelve dark, oval marks on the sides.

These fish were studied in small glass tanks and in a large, concrete exhibition tank with a glass front. The small tanks had the following dimensions: 76 x 32 x 36 cm., 61 x 32 x 32 cm., and 51 x 27 x 32 cm. The exhibition tank was 183 x 191 x 127 cm. Each of the small aquaria was illuminated by a 25-watt incandescent bulb with a circular reflector suspended about 20 cm. from the surface of the water. The exhibition tank was lighted by a 250-watt bulb similarly reflected. Observations were made behind a blind which concealed the observer. Most of the observations were made in the evening, when least disturbance occurred. The lights over the tanks were turned on at least an hour before each observation, because the fish appeared to be inactive in the dark and sudden illumination disturbed them. Water temperature varied between 9 and 12 ^{o}C.

Qualitative social behavior was recorded and described as observed. This included threat displays, fighting, nipping, chasing, retreating, defense of territory, and the formation of dominance-subordination orders.

Certain aspects of the social relationships among aquarium fish were investigated quantitatively by tabulating nipping. The first quantitative

observation on each new group of fish followed an adjustment period of at least 24 hours, during which time the fish became habituated to the tank and established relatively definite social patterns.

Observations of trout in the small tanks were each 15 minutes in duration. The intraspecific groups consisted of four fish of the same species and approximate size, each of which had its fins differentially clipped to enable recognition. Interspecific groups contained two marked fish of each species. The number of aggressive contacts or "nips" in terms of the total permutations was tallied for each fish in each group. This type of tabulation was made for each group before feeding and then somewhat later in the same evening after feeding. In this way the effect of feeding on aggressive behavior could be studied. Brine shrimp (Artemia sp.) were used as food and were usually introduced in greater numbers than could be consumed.

Since the effect of food on activity lagged behind the introduction of the food, the shrimp were introduced 15 minutes prior to observation in the small tanks.

Except for the first three groups of rainbow trout (twelve fish) on which four series of observations were made, each group was observed on three evenings. The total length of time that trout underwent confinement in an aquarium was from 1 to 2 weeks. After their behavior had been recorded, the trout were killed, measured, weighed, and dissected to determine sex.

Observations in the exhibition tank consisted of tallying the nips made among twenty unmarked fish over half-hour periods. It was not possible to distinguish individuals. Here, again, observations were made before and after feeding. The diffusion of shrimp and consequently of the trout increased the lag between introduction of the food and its effect on behavior. Hence feeding was continued for an hour before a tally was made. Both intraspecific and interspecific groups were studied. The various types of observations and the numbers of confined trout used are listed in Table 1.

TABLE 1 M

NUMBER AND TYPES OF OBSERVATIONS IN WHICH QUANTITATIVE INFORMATION WAS OBTAINED FOR AQUARIUM FISH

	SMALL TANKS		EXHIBITION AQUARIUM	
	Before Feeding	After Feeding	Before Feeding	After Feeding
No. of observations on brook trout...	36	36	4	4
No. of observations on rainbow trout.	30	30	4	4
No. of interspecific observations.....	36	36	4	4
Duration of observations (min.).....	15	15	30	30

M Each series of observations in the small tanks consisted of twelve groups of four fish. Only one group (twenty fish) per series was observed in the exhibition aquarium.

INTRASPECIFIC BEHAVIOR

INITIAL CONTACTS AND THREAT DISPLAYS

When four trout of either species were introduced into a small tank, they first rested motionless on the bottom. At this time they were pale and undifferentiated in color pattern, and their fins were usually expanded. They were exceedingly sensitive to movement and were easily made to dash wildly about. Within 10 or 15 minutes they began swimming about the tank, up the sides, and into the corners as though attempting to escape. After 1/2 hour to 1 day this asocial activity was replaced by aggressive social activity. In general, the less the handling and disturbance, the more rapid was the initiation of social behavior.

The first social interplay between two fish in an aquarium group consisted of reciprocal threat displays and fighting which resulted in one fish becoming dominant over the other. These threat displays were the most highly stylized behavioral patterns observed during the study. They were essentially the same in both species but were more elaborately developed in the brook trout. The rainbow trout tended to fight or retreat in the initial contact without undergoing threat display, but omission was not observed for brook trout.

The initial contact depended on an aggressive awareness involving two closely approximated fish. Brook trout fully expanded all their fins, lowered the hyal bones, and extended the branchiostegal membranes, stiffly undulated their parallel bodies, and then struck each other's sides with their flanks. The body of each fish was bent into an inverse arch, with the head and tail elevated and the belly extended downward. This corresponds to the "lateral threat display" of arctic char (Fabric 1953). Hyal depression was not conspicuous in the rainbow.

The lateral threat display usually preceded, but sometimes followed, reciprocal circling. Each fish attempted to turn, mouth open, upon the other. Occasionally one succeeded in turning upon its opponent sufficiently to grasp the pectoral or dorsal fin of the other. Ultimately, one fish

managed to move away from the other in such a way as to face the side of its opponent from a distance of 6 or 7 cm. This "frontal threat display" (Fabricius, 1953) was generally followed by attack.

When one fish faced the flank of the other, the latter retreated or rapidly undulated its body. It sometimes assumed a subordinate condition and swam rapidly away. Regardless of the behavior of the victim, attack usually followed. The attacker rushed swiftly, with its mouth open, upon the flank of its opponent, and the two fish whirled about, biting each other.

During threat display brook trout became more brightly colored, but rainbow did not. Various peripheral areas, such as the fin margins, the dorsal surface, the throat, and the supper surfaces of the maxillaries, became very dark. The parr marks darkened but did not achieve maximum intensity, while the pinkish color of the sides appeared to become more red. At this time the greatest color contrast existed.

In the course of the fighting, one of the fish would lower its dorsal fin, become darker, and retreat, generally pursued by the dominant. The darkening of the subordinate occurred in both species. As it was chased and repeatedly attacked, it became increasingly dark and more erratic in movement. It tended to rest between attacks in a corner near the surface with its head up and its caudal fin down, rapidly beating its pectoral fins. All its vertical fins drooped.

The dominant fish appeared to be aggressively activated by success. It vigorously pursued the subordinate and increased its tempo of attack as the defeated fish took on the pattern of subordinance. If it succeeded in defeating the other two fish in the group, its threat displays ceased, and its color gradually faded to a lighter shade. In the large exhibition tank there existed sufficient space to enable the loser of an initial contact to retreat and escape. Among twenty fish, threat displays were common after a period of a week. After a week they were observed only rarely among four fish in the small tanks.

THE INFLUENCE OF FEEDING ON NIPPING

After the initial encounters had taken place, nipping, chasing, and retreating characterized social behavior in small aquaria and, as in sunfish (Greenberg, 1947), the full fighting pattern was not common. Aggressive actitivity was not continuous. Long rest periods usually separated periods of nipping and chasing. The factors responsible for this discontinuity were not always apparent. One such factor was food.

Food stimulated aggressive activity among individuals of both species (Tables 2, 3, 4). The initial activity following the introduction of food in the large exhibition aquarium was directed solely toward its capture. Individuals swimming toward the same shrimp would bump into each other and immediately turn away to seek more food. Nipping was seldom seen at this time. As feeding continued, nipping and threat displays became increasingly frequent. At from 20 to 40 minutes following the introduction of brine shrimp, these patterns became common. There was no connection between this heightened aggressiveness and underfeeding, since food was still present after the commencement of fighting. A small amount of food did not appear to produce an effect different from a large amount of food. All the after-feeding observations, except the first one for the rainbow trout in the exhibition tank, were performed following the introduction of more food than the fish could eat within one hour.

The relation between feeding and nipping in the exhibition tank is shown in Table 2. In a series of paired observations the frequency of nipping was in every case greater after feeding than before feeding, and, on the average, it was doubled.

In the small tanks the frequency of nipping increased after feeding, but the lag between the introduction of food and the appearance of aggressiveness was shorter. If the subordinate fish were subject to severe domination, they frequently failed to feed at all. Usually the dominant fish began feeding first and ceased feeding last. The dominant interrupted its

TABLE 2 W

NIPPING BEFORE AND AFTER FEEDING DURING
HALF-HOUR PERIODS IN EXHIBITION
AQUARIUM CONTAINING TWENTY FISH OF ONE SPECIES

RAINBOW TROUT		BROOK TROUT	
Nips Before Feeding	Nips After Feeding	Nips Before Feeding	Nips After Feeding
57	202	48	195
55	203	73	219
138	206	107	208
144	235	96	211
394 TOTAL	846 TOTAL	324 TOTAL	833 TOTAL

M Each group was observed 8-10 days. After-feeding observations were begun 1 hour after the food was introduced.

TABLE 3 M

DIFFERENTIAL EFFECT OF FEEDING UPON NIPPING OF DOMINANT AND SUBORDINATE FISH IN SMALL TANKS CONTAINING FOUR FISH OF ONE SPECIES PER TANK

	RAINBOW TROUT		BROOK TROUT	
	Before Feeding	After Feeding	Before Feeding	After Feeding
No. of observations	30	30	36	36
Observations having greatest no. of nips	3	27	8	26 ±
No. of observations in which dominant is nipped	9	12	2	9
Total no. of nips	944	2,494	610	1,687
No. of nips on dominant	32	48	33	56
Percentage of nips on dominant out of total nips	3.1	1.9	5.4	3.3
No. of nips by dominant	851	2,212	508	1,568
No. of nips by subordinates	143	282	102	119
Percentage of nips by dominant .	85.6	88.6	83.3	92.9
Percentage of nips by subordinates	14.4	8.8	16.7	7.1
Av. no. of nips per dominant per hour	113.6	294.8	56.4	170.0
Av. no. of nips per subordinate per hour	6.4	12.5	3.8	4.4

M Each observation was 15 minutes in duration. After-feeding observations were begun 15 minutes after introduction of food.

± No difference in number of nip s after feeding on two occasions.

feeding to nip and chase the subordinates. Occasionally the introduction of food was not followed by an increase in nipping frequency (Table 3). In most such cases the fish did not feed and thus were not stimulated to aggressiveness. The statistical sign test (Dixon and Mood, 1946) applied to all paired observations on the frequency of nipping before and after feeding indicates a significant difference at the probability less than .01.

SIZE OF TANK AND NIPPING FREQUENCY

The number of nips per fish per hour was much higher in the small tanks than in the exhibition tank (Table 4). Most nipping in the small tanks was performed by the dominant fish (Table 3), but nipping appeared to be more evenly distributed in the large one.

DOMINANCE-SUBORDINATION RELATIONS

In small tanks the cessation of threat display marked the establishment of a despotic dominance-subordination relationship in which "nip-right" prevailed and reciprocal aggressiveness ended. Nip-right is the relation in which the subordinate passively submits to being nipped and chased by the dominant without nipping in return (Braddock, 1945; Allee, 1951, p. 130). It implies some kind of recognition of dominance either of the individual fish or of the dominant state as expressed by the color and behavior of the dominant fish. Nip-dominance, the relation in which the dominant wins a majority of encounters, was observed but was not characteristic of either species in small aquaria. Nipping of the dominant fish by subordinates did sometimes occur, however (Table 3).

Out of 3,488 nips, the dominant rainbow was nipped 80 times, or 2.3 per cent of the total. The dominant brook trout was nipped 89 times out of 2,297 nips (3.9 per cent). Return nips were recorded in 35 per cent of the rainbow observations and 15 per cent of the brook-trout observations. In spite of the fact that the rainbows attacked the dominant in more observation periods, they attacked the dominant a smaller total number of times. In other words, there were fewer nips per encounter. The fact that the

TABLE 4

AVERAGE NIPPING FREQUENCY PER FISH PER HOUR IN INTRASPECIFIC GROUPS BEFORE AND AFTER FEEDING FOR BOTH SMALL TANKS AND EXHIBITION AQUARIUM

		Before Feeding	After Feeding
SMALL TANKS	Brook trout	16.9	48.8
	Rainbow trout	33.1	83.1
EXHIBITION AQUARIUM	Brook trout	8.1	20.8
	Rainbow trout	9.9	21.1

brook trout nipped more times per encounter suggests that each such encounter was likely to represent a revolt of a subordinate against the dominant rather than, as in the rainbow, perhaps a failure to recognize the dominant.

The heightened aggressiveness of all members of a group following feeding increased both the number of observations in which the dominant fish was nipped and the actual number of times it was nipped (Table 3), but the greatly increased aggressiveness of the dominant fish resulted in a lower percentage of return nips.

Since it was not possible to recognize individuals for any length of time in the exhibition tank, where twenty fish were present, no exact data on nip-type could be obtained. However, by observing one fish at a time over a few minutes, a sequence of aggressive encounters could be observed. Return nips were common, and small fish sometimes nipped larger ones.

The presence of nip-dominance and threat display suggests an indefinite social organization among the twenty fish in the large tank. However, the social organization among four fish of either species in a small tank was stable and definite. Nine out of twelve groups of rainbows had a single fish remain dominant as long as they were observed (7-14 days). Two of the three changes in dominance occurred between the first and second observations. Ten out of twelve groups of brook trout possessed an unchanged dominant, and both the recorded changes took place between the first and second observations. The defeat of a dominant after the first observation may indicate that these were continuations of unresolved pair-contacts rather than successful revolts of established subordinates.

Feeding altered the structure of the hierarchy. Before feeding, the three subordinates in each group of four fish did little nipping and chasing (Table 3). There were only two ranks, one occupied by the dominant, the other by the remaining members of the group. Feeding stimulated fighting among the subordinates and caused more or less complete nip-orders to manifest themselves, which then were gradually suppressed by the activated dominant.

SEX AND SIZE AS FACTORS INFLUENCING DOMINANCE

Many factors are involved in the determination of a particular individual as a dominant among members of its own species. Some established factors are sex, size, previous experience, health, and age (Collias, 1944). The age of all the fish was the same within each species, and all the fish of both species were in their second year. All had had similar handling, and previous to observation they had been kept in large numbers in tanks of similar size. No diseased or misshapen individuals were used.

All the rainbow trout, with one exception, were undeveloped sexually. The sex of these fish could be determined only by microscopic examination of the gonads. Thus it is improbable that the testes were secreting androgens.

No conclusive difference in aggressiveness between the sexes was discovered. Since determination of sex depended upon dissection following observation, groups containing equal numbers of males and females could not be organized. Only five groups in each species contained two males and two females. Of these males were dominant in three groups of brook trout and no groups of rainbow trout. Ten of the twelve intraspecific brook-trout groups and eleven of the twelve rainbow groups contained both sexes. Although more male brook trout were dominant than females and more female rainbow trout were dominant than males, the numbers are too low to be significant. It is difficult to separate the effect of sex from that of size. Most of the male dominants were heavier than the heaviest females in their groups, and most of the dominant females were heavier than the heaviest males in their groups.

The most important information to be derived from the relationship between sex and aggressiveness is that both sexes exhibit aggressiveness and that either sex may dominate heterosexual groups.

Larger size confers a positive advantage in establishing dominance in various kinds of fishes (Noble and Borne, 1938; Noble, 1939; Noble and Curtis, 1939; Braddock, 1945, 1949; Greenberg, 1947; and Stringer and Hoar, 1955). Eight out of twelve dominant brook trout were as heavy as, or

heavier than, the heaviest subordinate in the group, and nine out of twelve dominant rainbow trout were equal to , or larger than, the heaviest subordinate. Slight differences in weight may be less significant than other factors in the determination of dominance, but if a fish is very much smaller than the others in a group, it can never achieve dominance. Dominance of a small fish over a large one gives the impression that the large fish is not very aggressive rather than the alternate hypothesis that the small fish is exceedingly aggressive. Thus the larger fish mught be unhealthy or physiologically unresponsive to evokers of aggressive behavior.

TERRITORIALITY

No rainbow trout was observed to defend a subdivision of an aquarium in accordance with Greenberg's (1947) criterion of territoriality. In the large exhibition tank these fish tended to swim indiscriminately throughout the water, not restricting themselves to any particular area and not orienting in relation to the bottom. No single fish was seen repeatedly, day after day, in the same place. Dominant rainbow trout did not chase subordinates from particular parts of the small tanks but nipped and chased them without relation to place. The only restriction of domain involved subordinate fish severely driven by the dominant. Under these circumstances the subordinates remained in a corner (not always the same one) near the surface in a tight aggregation.

Flat rocks were placed in some small aquarium so as to divide it into four interconnected compartments. Four rainbow trout remaining in this tank for 2 weeks failed to become territorial, despite the defensive advantage conferred by the rocks.

Some territorial tendency was observed in confined immature brook trout, but it was not a frequent pattern. Consistent defense of a single area over a long period as in cichlids (Noble and Curtis, 1939) and green sunfish (Greenberg, 1947) did not take place.

The brook trout associated more intimately with the substrate than did the rainbow trout. They frequently rested on the bottom and remained in

particular places for periods of several hours, during which time they would nip other fish which approached. They seldom swam in the middle depths of the exhibition tank, and movements to the surface were in rapid darts with a quick return to the bottom. Even in the small tanks, brook trout, except for badly driven subordinates, tended to remain on the bottom.

On one occasion a brook trout was observed to defend a partial territory between a rock and the right side wall of the exhibition tank. It remained most of the time on the bottom in a threat display. Whenever a fish of the same size or smaller came within about 25 cm., the resident fish curved its body (head and tail up, belly down) and swelled out its throat as in an initial contact. It then slowly and stiffly circled the intruding fish, showed both lateral and frontal threat display, and chased it away. Following the chase, the fish returned to approximately the same place between the rock and the side of the aquarium. If the intruding fish was larger, the resident frequently remained quiescent and failed either to threaten or to attack. Several times it was chased from its territory by larger fish but returned within several minutes.

This particular example was observed for several hours. On the following day the territory was not occupied, nor was it ever subsequently occupied.

INTERSPECIFIC BEHAVIOR IN AQUARIA

GENERAL BEHAVIOR RELATIONS

Immature brook and rainbow trout behaved toward each other essentially as though they were the same species. They threatened each other, developed nip-right relations, and established incomplete interspecific hierarchies. Qualitatively the behavior of the two species was similar, but differences in degree appeared.

Upon introduction of two rainbow trout and two brook trout into a small tank, all underwent the sequence in activity described for a single species. They rested on the bottom of the tank, gradually began asocial, exploratory swimming, and finally directed their movements aggressively toward each other. The rainbow trout was generally less persistent in the

TABLE 5

NIPPING DISTRIBUTION IN RELATION TO SPECIES IN SMALL TANKS CONTAINING TWO FISH OF EACH SPECIES PER TANK

	Before Feeding	After Feeding
Brook against brook	110	661
Brook against rainbow	425	945
Rainbow against rainbow	353	674
Rainbow against brook	256	353
Total	1,144	2,633
Av. nips per brook trout per hour	29.7	89.2
Av. nips per rainbow trout per hour	33.8	57.0

original pair-contact and frequently withdrew without fighting.

Little species segregation occurred in either the exhibition tank or the small tanks excpet in terms of different depth preference.

Even in the small tanks the rainbows tended to swim mid-water above the brook trout, but this tendency did not prevent aggressive interaction.

On several occasions the tendency for the rainbows to remain near the top and the brook trout near the bottom caused a dual-dominant sort of hierarchy. A brook trout dominated all the fish, yet a rainbow maintained a secondary dominance near the surface. The dominant brook trout drove the subordinate rainbow to the surface, and the dominant rainbow drove it repeatedly to the bottom. The mechanical movements of the two dominant fish resembled the behavior of two territorial sunfish driving a subordinate back and forth (Greenberg „) in that the tension between the dominants was reduced. The subordinate brook trout in such a situation was usually not attacked by the rainbows.

FEEDING, NIPPING, and DOMINANCE

As in the intraspecific groups, the frequency of nipping was increased by the feeding and inversely related to the size of the tank (Table 5). The presence of food induced feeding activity, which, in turn, induced aggressive activity following the fulfilment of hunger.

Nipping was fairly evenly divided between the two species in the large exhibition tank (Table 6). The rainbow trout were more indiscriminately roaming than the brook trout. Moving in this way, a rainbow would nip any unobservant fish not in a threat display and then swim away. The brook trout, on the other hand, tended to limit their movements and attack other fish coming near them. These differences in behavior may have compensated for the nip-eliciting effect of rainbow movement.

Aggressive relations were somewhat different in the small tanks (Table 5). Rainbows were nipped more often than brook trout. One statistical complexity involved in Table 5 should be clarified, however. When two fish of each species are confined, a dominant of one species will have twice as many fish of the other species to attack; thus one dominant brook trout has one subordinate trout and two subordinate rainbows to nip. If

it attacked them at random, twice as many rainbows would be nipped as brook trout. This table shows that brook trout attacked rainbows more often than they did their own species but that rainbows more frequentoy attacked their own species. Brook trout were more often dominant in the social order and therefore less often nipped.

The proportion of complete hierarchies was higher when two species were present. A typical interspecific complete hierarchy had a brook-trout dominant and a relatively inactive brook trout in the second position. The third status was maintained by an aggressively active rainbow, and the fish subordinate to all was a severely chased rainbow.

Brook trout were dominants in nine out of twelve groups in the small tanks. In intraspecific groups of either species it was shown that, where other conditions are similar, weight is an important factor in the determination of dominance. Each of the three rainbow dominants wegthed over 10 per cent more than the heaviest brook trout in its group. Six of the brook trout dominants were within or below 10 per cent of the weight of the heaviest rainbows within their groups.

TERRITORIALITY IN INTERSPECIFIC GROUPS

In the large exhibition tank three different defended areas were established along the rear wall by brook trout on one day. There was one in the left corner (A), one in the center (B), and one in the right oorner (C). These areas were not seen to be occupied until after the fish had been fed. The trout at A was more secure than the one at B, which, in turn, was more secure than the one at C. Fish at A and B threatened all intruding fish, while the trout at C threatened only the smaller ones. One one occasion, trout A was observed to chase trout B out of its territory. Trout B then moved into close contact with trout C and chased it out of its area. Shortly thereafter all three returned to their respective stations. Nevertheless, trout A was not sufficiently aggressive to repel some of the larger fish that approached. Several times all three territorial fish were attacked and driven to other parts of the aquarium by larger rainbow trout.

TABLE 6 M

NIPPING DISTRIBUTION IN EXHIBITION AQUARIUM CONTAINING TEN FISH OF EACH SPECIES

	Before Feeding	After Feeding
Brook against brook	5	5
	7	38
	1	32
	27	65
Total	40	140
Brook against rainbow	3	8
	14	29
	1	46
	6	26
Total	24	111
Rainbow against rainbow	15	11
	55	42
	4	70
	15	37
Total	89	160
Rainbow against brook	14	21
	35	42
	3	77
	9	45
Total	61	185
Av. nips per brook trout per hour ...	3.2	12.5
Av. nips per rainbow trout per hour ,	7.5	17.2

M Four 1-hour observation periods are analyzed.

Prior to feeding, 4 days later none of the territories was occupied. At this time most of the fish were aggregated facing the water inlet. Following feeding, however, three brook trout took up stations at the sites of A, B, and C, and again the trout at C was the least stable. On the third day after this the center area, B, was occupied prior to feeding. After feeding, no territorial fish were observed, nor were they on the following day. Thereafter no more observations were made on this group.

INTERSPECIFIC BEHAVIOR IN THE STREAM

MATERIAL AND METHODS

Both species were watched through the windows of an observation tank submerged in Sagehen Creek. This tank is illustrated by Needham (1953). It is 152 cm. tall, 122 cm. wide, and 183 cm. long and is thus sufficiently large to permit the observer to lie down within it. At the time of observation, the deep side of the tank was in water 36 cm. deep at the up-stream end abd 40 cm. deep at the down-stream end. The two windows faced a pool, 72 cm deep, at the base of a pine tree. The distance from window to tree was 100 cm., and maximum visibility at an angle upstream was about double this. The stream bottom consisted of small, round stones (8-15 cm. in diameter) grading into smaller particles along the stream margins. The stones afforded some cover, but the roots of the tree and the overhanging adjoining bank provided much more.

Nocturnal minimum temperatures varied from 7 to 10 C. and daytime maximum temperatures from 15 to 20 C.

Unfortunately, the fish could not be captured and marked, but the presence of similar-sized individuals of the same species in the same places enabled recognition of the six principal fish. There were four rainbows (estimated length; 25, 20, 11, and 9 cm.) and two brook trout (about 17 and 15 cm. long).

The fish were observed every day for 15 days during July.

POSITION OF FISH IN RELATION TO TOPOGRAPHY OF STREAM

The pine tree and its roots, which provided the principal environment for the trout, constituted the upstream end of a small island. The current had eroded deeply beneath the tree, and the limits of the resultant dark

pocket could not be seen.

Trout were seldom seen in the open current upstream of the tree. When moving from one place to another during the day, they swam in relation to cover, either among the tree roots or along the observation tank. There were four positions in which fish remained oriented into the stream for long periods at a time. Position A was the deepest, and the others were progressively shallower. Positions C and D were not so discrete as A and B but were roughly divided according to greater depth and superior cover at the downstream end (C).

There was no observable difference in habitat selection between the two species, nor was there any species segregation. Both species competed for the same positions in the stream, apparently on the basis of depth and darkness, but probably also in relation to an optimum current. They both tended to remain closer to the bottom during the day than in the evening and always remained near the edge of shadow. The differences in vertical distribution and indiscriminate movement seen in the aquarium were not apparent in the stream.

DOMINANCE AND ROTATING TERRITORIES

Six recognizable individuals were seen at least once every day for 15 days. These fish had definite aggressive social relations which involved elements of both a dominance-subordination order and territoriality. Each of the four occupied positions constituted a partial territory (Greenberg, 1947), which was defended by the resident fish against all smaller fish and occasionally against a fish one size larger than the resident. Thus the 15-cm. brook trout nipped and chased the 9-cm. and 11-cm. rainbows, occasionally threatened and nipped the 17-cm. brook trout, and always retreated before the 25-cm. and 20-cm. rainbow. The 25-cm. rainbow and 17-cm. brook trout were apparently resident in adjoining parts of the stream not visible from the observation tank.

The larger rainbow was frequently seen for short periods generally on its way either up- or downstream, during which time it would stop a moment in the deep pocket. The 20-cm. rainbow was observed to retreat before it five times and to threaten and exchange nips with it once. Usually the smaller resident moved aside and remained motionless near the bottom while

the larger fish held position, unresponsive to its presence.

The 17-cm. brook trout was also often seen and usually competed with the 15-cm. brook trout for position B. The size difference between these fish was not great, and dominance beteeen them fluctuated. During the first week the larger fish tended to nip and chase the smaller, but during the remainder of the observations the 15-cm. brook trout successfully defended its position.

Although the same fish tended to be in the same position each day, the absence of a larger resident usually resulted in its being replaced by a smaller one. When the 20- and 25-cm. rainbow trout were missing, the deep pocket was occupied by the brook trout, whose position was then taken by the 11-cm. rainbow, whose position, in turn, was filled by the 9-cm. rainbow. If a smaller fish intruded while a fish was occupying its new territory, the small one was nipped and chased as usual. The intensity of defense remained the same, regardless of the territory in which interaction took place. Thus the territories were not only partial but also rotating.

Dominance-subordination relations were based on size differences, in that there was a complete nip-order from the largest to the smallest member of the interspecific group. The two rainbows had nip-right over the brook trout and the small rainbows. Similarly, the brook trout had nip-right over the small rainbows. Between the members of each pair, however, there was occasional threat displays and fighting, probably signifying ambivalence and unsettled dominance. Small fish usually avoided larger ones, and such avoidance was more common than nipping and chasing.

Although no subordinate appeared to be severely drivin by a dominant, there were both light-colored and dark-colored individuals. The larger fish of each pair tended to be lighter colored than the smaller one. This may imply that the greatest conflict exists between fish of nearly the same size.

DIURNAL CYCLES IN BEHAVIOR

While holding position, trout feed by moving slightly from one side to the other after suspended bits of matter carried in the current. This

mouth-sampling of visually screened particles went on fairly continuously when not interrupted by other fish, predators, or fishermen. But the distance which a trout moved after a particle varied with the time of day. During most of the day the feeding amplitude was slight. Even around sunrise the fish were not seen to move far for a particle. Toward evening, however, this movement increased, and the fish darted back and forth and up toward the surface, returning each time to their positions. The intensity of feeding and aggressive activity were clearly related, and, as feeding movements increased, the amount of nipping and chasing of small fish by large ones and the frequency of reciprocal threat displays between the members of each pair also increased. Fright responses to any gross movement and to the activity of larger fish were not so evident as during the day, and all the fish widened their areas of activity.

As the distance they moved continued to increase, they ceased returning to their territories and began disappearing from view in the direction of shallower water. With the advent of darkness, none remained in the deeper water in view of the windows, nor were any observed there during the night when checked with a light. They began returning in the morning, but all did not come back before the middle of the day.

DISCUSSION

Requirements for the existence of interspecific competition at the level of social behavior are (1) that the species occupy the same or overlapping habitats, (2) that the species aggressively respond to each other, and (3) that the periods of rhythms of aggressive activity overlap.

Brook trout and rainbow trout are frequently stocked in the same streams, but brook trout generally occur in the Sierra Nevada at higher elevations. In Sagenhen Creek the two species overlap in range for about a mile. Perhaps a single species would have a more extended range in the absence of the other.

Some vertical separation of the species was observed in the aquarium. Brook trout remained quietly close to the bottom much of the time, while

rainbow trout tended to swim indiscriminately in mid-water. This difference was not observed in the stream, where individuals of both species remained in close contact. It may indicate that separation occurs in deeper water such as lakes or rivers but that in shallow streams the populations are forced together.

Individuals of the two species aggressively responded to each other much as though they were of the same species. Their behavior was not identical, however, for the brook trout had a more elaborate threat display, involving a lowereng of the hyal bones, brightened color pattern, and more exaggerated movements. Rainbow trout nipped more and threatened less except when subordinated by a brook-trout dominant. Individuals in the stream displayed, nipped and chased without regard to species, just as they did in the aquarium.

Although not specifically analyzed from an ethological point of view, the aggressive behavior can be interpreted in terms of the ideas of Lorenz (1950) and Tinbergen (1951). According to them, an animal is motivated by an accumulation of energy which can be discharged by a relatively simple set of specific sign stimuli. The motivated animal undertakes certain activities which increase the probability of its encountering approximate sign stimuli. When found, these sign stimuli release a stereotyped behavior pattern as characteristic of the species as is its morphology. In social relations individuals interact, and their behavior patterns become reciprocal sign stimuli in the development of complex relationships, such as dominance-subordination orders.

The oblique posture, undulation of the body, and expansion of the fins during threat display were signals which released comparable behavior in aggressively motivated adjacent trout or retraating behavior in a subordinate. Threat display, so long as it was fully expressed, inhibited attack by an adjacent fish. The diminution of threat by one partner brought about attack from the other. In established groups or among fish of unequal size, nipping, chasing, and retreating took the place of threat display. The dominant fish responded to the dark, retreating subordinate by chasing and

nipping. The subordinate responded to the approach of the light dominant by retreating. Both dark color and retreating have been shown to be releasers of chasing behavior in Kamloops trout (Stringer and Hoar, 1955).

The greatesr use of threat by the brook trout and its lower nipping frequency may indicate a more advanced social behavior in which injurious fighting is replaced by stereotyped non-injurious threat ceremonies (Tinbergen, 1953) having the same function.

Periods of aggressive activity can be considered from a seasonal and diurnal point of view. Stream-living salmonids are characterized by aggressive behavior during the seasons when they are associated with particular locations (Hoar, 1953). At various times they may lose their aggressiveness and migrate. Brown trout remain in the same stream location during the summer but may move over a mile upstream during October and November to spawn. Such migrants have subsequently been caught in the original tagging locality (Schuck, 1945). Needham (1943) reports a non-reproductive migration of brown trout downstream in May in a high mountain stream of California In Michigan, brook trout did not travel during June, July, August, and early September but were observed to migrate an average of $\frac{3}{4}$ mile upstream in the autumn (Shetter, 1937). During the winter there was a downstream migration of the bulk of the population for as far as 18 miles. This was followed by a return to the tagging locality in the next year.

In milder climates the winter migration downstream may not occur, since Allen (1951) reports exceedingly stable populations of brown trout in a small stream in New Zealand.

The parr-smolt transformation accompanies downstream migration of anadromous salmonids and is associated with reduced aggressiveness in the coho salmon (Hoar, 1953). Stringer and Hoar (1955) present preliminary data showing a reduction in nipping among juvenile Kamloops trout in the spring. A similar transformation might account for the aggressive inferiority and greater mid-water swimming tendency of the rainbows in the present study, but the high nipping frequency is contradictory.

Rainbow trout spawn in the early spring, while brook trout spawn in

the autumn. At these times the species would not maintain their aggressive social contacts but would migrate to other areas appropriate for spawning. During a considerable portion of the year, however, particularly during the summer, the two species must show aggressive interspecific social behavior in overlapping sections of a stream.

Movements after food and other fish varied in frequency and amplitude throughout the day, but no differences were observed in this respect between the species in the stream. The greatest activity occurred toward evening, after which the fish left their daytime positions and moved out of view. Feeding and nipping probably continued in shallower water until incident illumination fell below a critical level. This critical level is 4 foot-candles for the Kamloops trout (Stringer and Hoar, 1955). The Atlantic salmon and the brook trout can feed in total darkness, yet do not feed at night and hence may have a physiological rhythm regulatiog diurnal activity, according to Hoar (1942). In this study, however, trout were fed at various times at night under artificial illumination and responded as actively as in the day.

Stream-dwelling salmonids settle to the bottom and remain inactive throughout the period of darkness (Hoar, 1953). Sagehen Creek trout returned to their positions throughout the morning. During the day they were quite inactive. High temperature depresses feeding in the middle of the day (Hoar, 1942), and strong light may depress feeding and social behavior by increasing shade-seeking reactions and fright responses.

Although certain factors interfere with feeding, if feeding takes place, aggressive activity follows. Spencer (1939) found the effect of feeding goldfish to be so great that the rhythm could be reversed by feeding at night. He maintains that there is "a definite relationship of activity to feeding. When the fish are well and regularly fed there is an intense activity period lasting from one to three hours after the food is placed in the tank. The fish actually consume the food in 15 minutes or less and the intense activity far exceeds this time." In the aquarium increased aggressive behavior followed a period of non-aggressive feeding in both

species of trout.

During feeding the fish attacked brine shrimp, using some of the exaggerated movements associated with aggressive behavior, such as undulating the body, darting swiftly, and biting. Similar behavior in adjacent fish gradually induced a change in the object of attack from food to fish. Both internal and external factors were involved (Tinbergen, 1953). The fish became more aggressively motivated, as indicated by their movements, and at the same time the movements themselves constituted sign stimuli eliciting attack from other fish.

In the stream, feeding and aggressive behavior were not so separated as in the aquarium, and both activities increased as the factors which depressed feeding waned toward evening.

The significance of this increased aggressiveness is obscure, but it constitutes an interesting exception to the frustration-aggression hypothesis of psychologists (Scott, 1948). One possible function is dispersion of the fish and consequently an exploitation of a larger area. It may also bring about the movement of the smaller fish into shallow water, where they settle down during the night. In terms of interspecific competition, a less aggressive species might be so severely chased that it would fail to feed. Subordinated rainbows in small tanks sometimes failed to feed in the presence of dominant brook trout.

The requirements for interspecific competition between brook and rainbow trout are thus met. They occupy overlapping habitats, they aggressively respond to each other, and they are active in overlapping periods of time.

Competition at the behavior level takes place within a dominance order among trout which occupy the same home range. These societies of trout probably develop among individuals which are similarly attracted to a particular locality in a stream rather than to each other. Initial contacts between trout involve reciprocal threat displays and fighting. The larger fish is likely to dominate. If one fish exceeds the other by an undetermined amount, there is no threat display but only attack and retreat. This results in the establishment of a predominantly nip-right hierarchy in which

dominance is based on size. The greatest conflict exists between fish of the same size, and dominance relations between such fish may never be secure. High status in a social hierarchy conveys definite values, and, conversely, low status in such a social organization may increase the difficulties of survival. Dominant green sunfish (Lepomis cyanellus) have been shown to eat more and grow faster than do those subordinate to them in an aquarium (Allee, Greenberg, Rosenthal, and Frank, 1948). Moreover, the dominant green sunfish tended to establish territories and to defend them against those fish subordinate to them (Greenberg, 1947).

In the stream the reward of dominance is territory selection within the home range. The largest fish maintains position in the territory having the best cover conditions, and the others remain in progressively poorer territories. The small subordinates do not have so great a need for first-clsss cover as do the large ones, and such a division of territories is not necessarily harmful to the weaker members of a single-species group. Where two species are present and aggressiveness varies, equal-sized fish will require equally good cover, but the more aggressive species may dominate and thus force the other species into poorer areas of the stream, where predation pressure is more intense. The great number of brook-trout dominants in the laboratory indicates an aggressive superiority in that species, but the rainbow trout appeared aggressively adequate in both the large exhibition tank and the stream. This suggests that in confinement or under conditions of concentration the brook trout is more aggressive and more likely to dominate within a hierarchy than is the rainbow trout.

The primary spatial fixation is toward the general area, the home range, within which are defended a series of positions against subordinates during the day. These partial territories are generally occupied by specific individuals, but if a large fish is absent, the subordinates tend to move into the better positions. Thus the positions may be termed "rotating" territories. "Prior residence" (Braddock, 1949) may not be a primary issue among the members of the group, since they are habituated (Thorpe, 1950) to the home range, which includes all the territories. Small fish or sub-

missive fish (dark-colored, retreating fish with contracted median fins) are nipped and chased from the territory that a member of the group happens to be occupying.

Prior residence may be more significant to a fish out of its home range than to one out of its territory. Miller (1952) maintains that the very high mortality of hatchery-reared cutthroat trout in a stream can be ascribed partly to unsuccessful competition, leading to starvation. He says: "On many occasions a tagged trout was observed to start out after a morsel in the current, only to be turned aside and the food taken by a wild trout." Mortality of introduced 3-year-old trout was lower than that of 2-year-olds because the older ones were larger than the wild trout and could therefore compete better. The introduced fish drifted downstream as far as the inclosing fence (up to $\frac{3}{4}$ mile) and did not normally disperse for 2 weeks. The inability to obtain a position in the stream may be related to the aggressive behavior of the residents and the lack of a home range to which the new fish could orient.

SUMMARY

1. The social behavior of immature eastern brook trout, (Salvelinus fontinalis (Mitchill), and coastal rainbow trout, (Salmo gairdneri Richardson), was studied in intraspecific and interspecific groups in the aquarium. Both species were later studied in a stream from a submerged observation tank.

2. The social behavior of both species was qualitatively similar, and they behaved toward each other as though they were one species. No schooling was observed. Social behavior was aggressive and consisted of threatening, fighting, nipping, chasing, and retreating. The brook trout exhibited more elaborate behavior than did the rainbow trout.

3. Following the initial contacts, a stable dominance-subordination order developed, in which nip-right prevailed and a single dominant did most of the nipping. The dominant fish of either species was light colored, and the subordinates were darker colored.

4. The presence of food elicited feeding activity, which, in turn, elicited aggressive activity following the fulfilment of the hunger drive. Feeding primarily increased the aggressive activity of the dominant fish but also increased nipping among subordinates and revealed complete hierarchial relations.

5. The frequency of nipping was much higher in small tanks than in a large one.

6. Large fish tended to dominate smaller ones, but maleness was not demonstrably significant in the determination of dominance.

7. In the stream six trout formed a complete interspecific, nip-right hierarchy in which status was determined by size. Four of these fish defended territories against subordinates. The other two apparently had territories just out of sight. The position having best cover was defended by the largest fish, and the subordinates had territories of decreasing cover value There was continuous competition for better positions. In the absence of a larger fish a smaller one occupied and defended the vacant territory. Such defended areas can be called "rotating territories."

8. Feeding and nipping were seen at all times during daylight, but the least movement took place in the middle of the day. Toward evening both increased in frequency and intensity.

9. All the fish moved out of their territories in the evening and returned the following day.

10. Brook trout dominated even slightly larger rainbow trout in small tanks, but rainbow trout appeared aggressively adequate in a large exhibition tank and in the stream.

LITERATURE CITED

ALLEE, W.C. 1951. Cooperation among animals, with human implications. New York: Henry Schuman.

_____. 1952. Dominance and hierarchy in societies of vertebrates. In: Colloques internationaux du Centre national de la Recherche scientifique, Vol. 34: Structure et physiologie des societes animales, ed. PIERRE-P. GRASSE, pp. 157-81.

ALLEE, W.C., EMERSON, A.E., PARK, O., PARK, T., and SCHMIDT, K.P. 1949. Principles of animal ecology. Philadelphia: W.B. Saunders Co.

ALLEE, W.C., GREENBERG, B., ROSENTHAL, G.M., and FRANK, P. 1948. Some effects of social organization on growth in the green sunfish, (Lepomis cyanellus.) Jour. Exper. Zool., 108: 1-19.

ALLEN, K.R. 1951. The Horokiwi stream. New Zealand Marine Dept. Fish. Bull.No. 10, pp. 1-321.

BAERENDS, G.P., and BAERENDS-VAN ROON, J.M. 1950. An introduction to the study of the ethology of cichlid fishes. Leiden: E.J. Brill.

BRADDOCK, J.C. 1945. Some aspects of the dominance-subordination relationship in the fish (Platypoecilus maculatus). Physiol. Zool., 18: 176-95.

_____. 1949. The effects of prior residence upon dominance in the fish (Platypoecilus maculatus.) Ibid., 23: 161-69.

BURT, W.H. 1943. Territoriality and home range concepts as applied to mammals. Jour. Mammal., 24: 346-52.

COLLIAS, N.E. 1944. Aggressive behavior among vertebrate animals. Physiol. Zool., 17: 83-123.

DIXON, W.J., and MOOD, A.M. 1946. The statistical sign test. Jour. Amer. Statis. Assoc., 41: 557-66.

FABRICIUS, E. 1953. Aquarium observations on the spawning behavior of the char, (Salmo alpinus). Rept. Institute of Fresh Water Research, Drottiningholm, 34: 14-48.

GERKING, S.D. 1950. Stability of a stream fish population. Jour. Wildlife Management, 14: 193-202.

_____. 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology, 34: 347-65.

GREENBERG, B. 1947. Some relations between territory, social hierarchy, and leadership in the green sunfish (Lepomis cyanellus). Physiol. Zool., 20: 267-99.

HOAR, W.S. 1942. Diurnal variations in feeding activity of young salmon and trout. Jour. Fish. Res. Board Canada, 6: 90-101.

____. 1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. Ibid., 8: 241-63.

____. 1953. Control and timing of fish migration. Biol. Rev., 28: 437-52.

HOAR, W.S., MACKINNON, D., and REDLICH, A. 1952. Effects of some hormones on the behavior of salmon fry. Canad. Jour. Zool., 30: 273-86.

LORENZ, K.S. 1950. The comparative method in studying innate behaviour patterns. Symp. Soc. Exper. Biol., 4: 221-68.

MILLER, R.B. 1952. Survival of hatchery-reared cutthroat trout in an Alberta stream. Trans. Amer. Fish. Soc. (1951), 81: 35-42.

NEEDHAM, P.R. 1943. Movement of trout in Convict Creek, California. Jour. Wildlife Management, 7: 142-48.

_____. 1953. The mortality of trout. Scient. Amer., 188: 81-85.

NOBLE, G.K. 1938. Sexual selection among fishes. Biol. Rev., 13: 81-85.

_____. 1939. The experimental animal from the naturalist's point of view. Amer. Naturalist, 73: 113-26.

NOBLE, G.K. and BORNE, R. 1938. The social hierarchy in Xiphoporus and other fishes. Bull. Ecol. Soc. America, 19: 14.

NOBLE, G.K. and CURTIS, B. 1939. The social behavior of the jewel fish (Hemichromis bimaculatus).Gill. Bull. Amer. Mus. Nat. Hist., 76: 1-46.

SCHUCK, H[illegible]45. Survival, population dens[illegible]
of the w[illegible]brown trout in Crystal Creek. Tra[illegible]
73: 209-30.
SCOTT, J.P. 1948. Dominance and the frustration-ag[illegible]
Physiol. Zool., 21: 31-39.
SHETTER, D.H. 137. Migration, growth rate, and populati[illegible]
brook trout in the north branch of the Au Sable River,
Amer. Fish. Soc., 66: 203-10.
SPENCER, W.P. 1939. Diurnal activity rhythms in freshwater fishes.
Ohio Jour. Sci., 39: 119-32.
STRINGER, G.R., and HOAR, W.S. 1955. Aggressive behavior of underyear-
ling Kamloops trout. Canad. Jour. Zool., 33: 148-60.
THORPE, W.H. 1950. The concepts of learning and their relations to
those of instinct. Symp. Soc. Exper. Biol., 4: 148-60.
TINBERGEN, N. 1951. The study of instinct. Oxford: Clarendon Press.
_____. 1953. Fighting and threat in animals. New Biol., 14: 9-24.

P.R.N.

STUDIES ON SOCIAL GROUPINGS IN FISHES

C. M. BREDER, JR.

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 117 : ARTICLE 6 NEW YORK : 1959

STUDIES ON SOCIAL GROUPINGS IN FISHES

STUDIES ON SOCIAL GROUPINGS IN FISHES

C. M. BREDER, JR.
The American Museum of Natural History

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 117 : ARTICLE 6 NEW YORK : 1959

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Volume 117, article 6, pages 393–482, text figures 1–28,
plates 70–80, tables 1–20

Issued June 22 1959

Price: $1.50 a copy

CONTENTS

INTRODUCTION 399

DEFINITIONS AND EXPLANATIONS 400

SPECIAL FORMS OF SOCIAL GROUPINGS 406
Pods and Spawning 406
The Problem of Leadership and Hierarchy 407
Fishes in Orderly Files 410
Fishes in Balls 411
Collective Protective Behavior 412
Heterotypic and Homotypic Groups 416

SPECIAL ENVIRONMENTAL INFLUENCES ON FISH GROUPINGS 419
The Influence of Light and Temperature 419
Pigmentary Reactions 419
Locomotor Reactions 421
Visual Reactions 421
Effects of Light Quantity and Quality 421
Reactions to Light Intensity 423
Reactions to Wave Length 434
Reactions to Polarized Light 436
Photoperiodism 437
Interrelations of Light and Heat 438
The Influence of Past History of Individuals 444

STRUCTURAL NATURE OF FISH GROUPS 449
Circular Movements in Animate and Inanimate Objects 449
Internal Structure of Schools 449
Centrifugal and Centripetal Forces 458
Cybernetics and Fish Groups 459
Effects of Groups on Population Density 470

EVOLUTION OF FISH GROUPS 472

SUMMARY 473

BIBLIOGRAPHY 475

TABLES

Table 1. Reactions of Species not Especially Treated in Subsequent Tables 422
Table 2. Reactions of Blind Cave Fishes to Various Comparative Light Values . . 424
Table 3. Individual Readings of Fishes Used in Groups of Four in Table 2. 424
Table 4. Behavior of Four *Brachydanio rerio* in Reference to Various Light Values . 426
Table 5. Reactions of *Gambusia* Sp. to Light of Various Intensities in Reference to Sex, Time of Day, and Season 427
Table 6. Behavior of Blind and Pinealectomized *Astyanax* and *Anoptichthys* 429
Table 7. Behavior of Four *Atherina stipes* in Reference to Various Light Values . . 430
Table 8. Behavior of *Phoxinus laevis* in Reference to Light and Darkness under Various Restrictions 430
Table 9. The Reactions of *Cyprinodon baconi* to Light by Day and by Night . . . 431
Table 10. Behavior of Certain Individuals of *Atherina stipes* 431
Table 11. Responses of Fishes to a Choice of Colored Lights 435

Table 12. Responses of Fishes to Ultra-Violet Radiation 437
Table 13. Responses of Goldfish to Light and Temperature in a Pool in Springtime . 440
Table 14. Calculations of Reactions of Gray and Yellow Goldfish to Light and Temperature 441
Table 15. Effects of Past History on the Photosensitivity of *Jenkinsia lamprotaenia* . 445
Table 16. Effect of Past History on the Photosensitivity of *Atherina stipes* 447
Table 17. The Influence of Adrenalin on the Attitudes of Fishes Towards Light and Darkness 448
Table 18. Matrixes of Transition Probabilities of the Diagrams of Immediate Effects Shown in Figure 26 462
Table 19. Relationships of Various Possible Fish Groups 466
Table 20. Protocol for Trajectories of Three *Jenkinsia* 468

INTRODUCTION

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

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

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

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

3. SPECIAL ENVIRONMENTAL INFLUENCES ON FISH GROUPINGS: This part considers primarily new data that involve direct environmental influence on individuals in reference to their social attitudes.

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

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

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

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

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

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

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

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

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

DEFINITIONS AND EXPLANATIONS

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

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

A study of the distribution of the dominoes might start with the individuals very far apart, so that each domino would satisfy anyone's definition of "solitary." These could be brought together from these sites to any degree of nearness, say, a complete set of dominoes within the area of a circle with a 3-foot radius. Compared with the rest of the surface, they might be considered as "clumped," "crowded," or some other word indicating some kind of approach to one another. At this point the effect of relative magnitude must be taken into consideration. Dominoes of ordinary size evenly distributed within a circle 6 feet wide would hardly be "crowded," or fish as small as dominoes in a similar condition could be considered only as localized or, at most, loosely grouped. Thus the spacing between objects is most conveniently expressed in terms of the size of the objects. This feature of absolute size need not be considered in this discussion of terminology but appears below in more important connections.

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

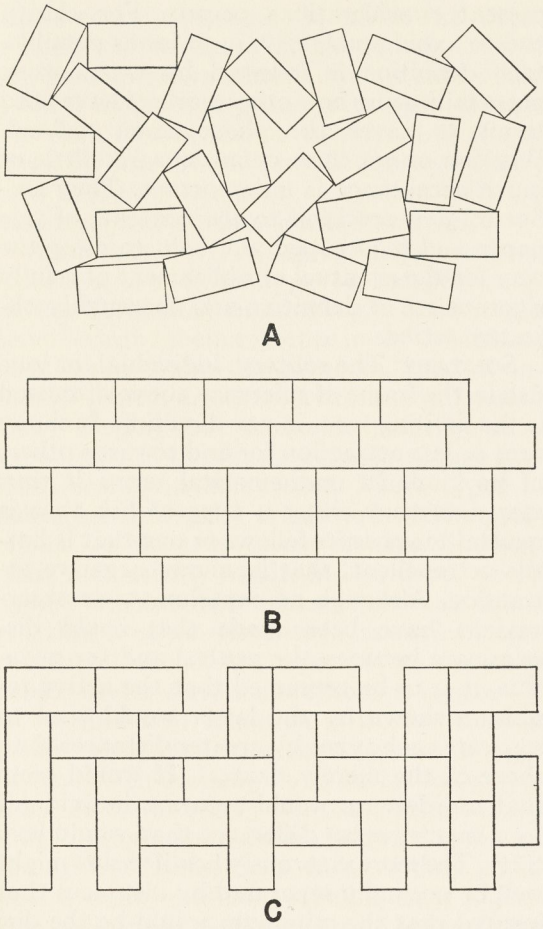


FIG. 1. Deployment of dominoes. A. Randomly distributed dominoes pushed to contact, showing typical interspaces. B. Systematically distributed dominoes, all in full contact. This type of distribution permits of two types of array, that shown being with the long sides forming continuous lines. The other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

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

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

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

Definitions follow that have been framed with the above concepts as their bases. In their framing, recognition of the dynamics of motile fishes has been made, and adherence to past usage has been continued so far as the present considerations permit. For clarity and to avoid ambiguity, in so far as possible, each definition is followed by explanatory notes indicating how other workers have used terms to cover the phenomenon defined. Whether or not these definitions find little or much acceptance is unimportant. They suffice to give precision to the contents of this paper and it is hoped will help to clear the way for the eventual establishment of a fully rigorous set of definitive and thoroughly objective terms.

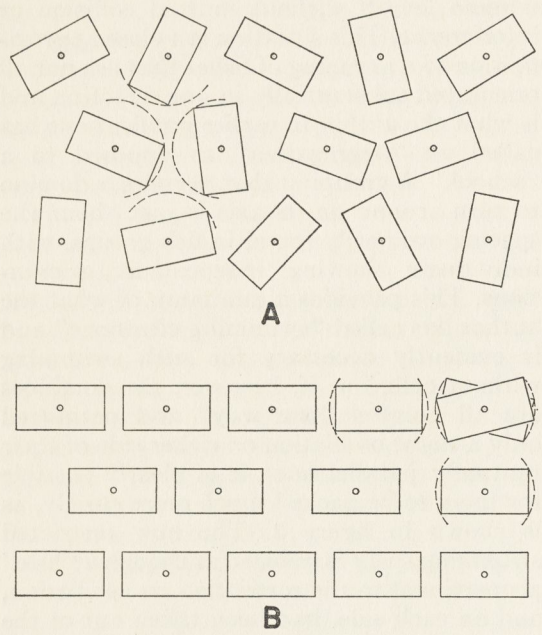


FIG. 2. Deployment of dominoes. This figure differs from figure 1 in that the dominoes are permitted a certain amount of rotation about their centers. A. Here the dominoes are permitted full rotational clearance and are packed as closely as possible with the small clearance. Dashed lines indicate amount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

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

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

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

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

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

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

longer courses than those that swim a simple straight course.

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

In a very compact school, fishes have two choices of movement in relation to their fellows. They may line up, nose by nose, with their nearby companions and synchronize their swimming strokes, a feature that is conspicuously different from less precise schooling and obvious at a glance. The other way is not to line up, nose by nose, but to hang back alternately and let the yaw of their heads come opposite the mid-part of the body, the place of least lateral movement, in a quincunx pattern. In this second way, synchronization is not of any importance, and the difference in the appearance of the group, compared to that of the first, is marked.

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

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

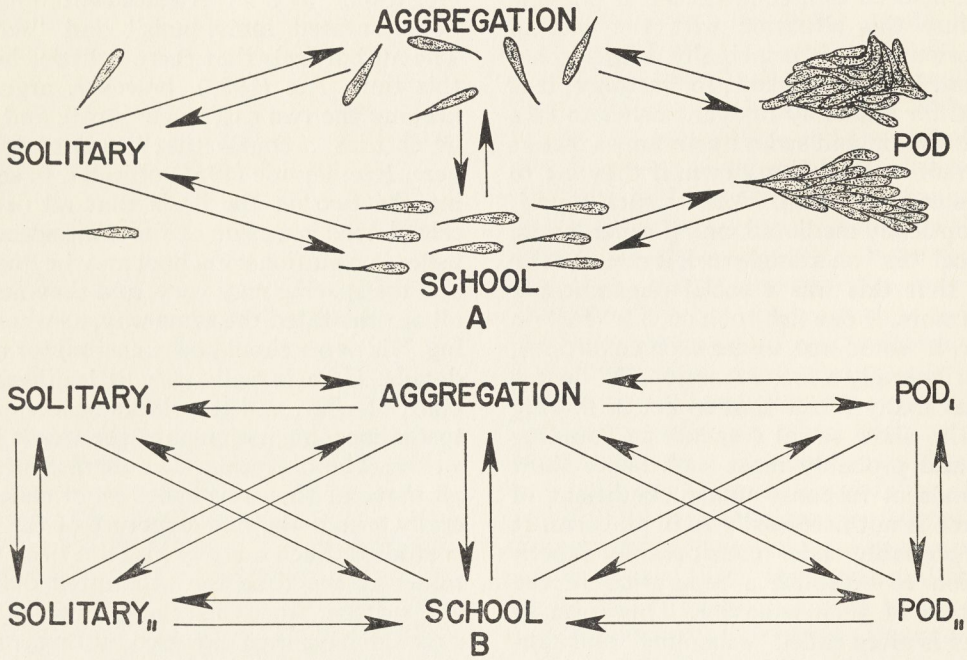


FIG. 3. Diagram of relationships between various forms of fish grouping. A. The usage in which the solitary and pod formations are each considered as a single type, while the intermediate ones are considered different, depending on the form of the orientation. B. The usage that considers each type of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

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

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

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

SPECIAL FORMS OF SOCIAL GROUPINGS

BEFORE THE GROUPINGS of fishes are further analyzed, a variety of special cases that have not been reported or have been little noted in connection with present interests is presented and discussed separately, in order to permit a more satisfactory continuity in the later portions of the discourse. This section is followed by another in which special environmental influences are similarly treated. While this treatment may appear to be a purely arbitrary arrangement, it was found to be the only one practicable. Because of the vast amount of interdependence of the various items of behavior and environment brought into this study of fish groupings, these two sections are intimately interconnected in many ways, and their separation, for purely practical reasons, should not obscure this fact.

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

PODS AND SPAWNING

Mugil cephalus Linnaeus, on the Gulf coast of Florida at least, is ordinarily found in schools of greater or less size. The mature fish change their habits from simple schooling to one of pod formation in September or October and show this condition until at least late February. This behavior continues with interruptions through and after the spawning period, so that spent fish may be found in pods well after the peak of the spawning season has passed. That is to say, during the period of the three to four coldest months these extremely tight groups of fishes in physical contact may be found. The peak of the spawning appears in late November or early December, varying with the latitude and the particular year. This information is based on personal observations and commercial fishermen's activities, records, and statements. It agrees fully with the published data of Broadhead and Medford (1954). These groups of mullet are for the most part in close physical contact, as is shown in plates 70 and 71 of pods under different conditions. The photographs clearly indicate that they are advancing groups of fishes which, unlike what is here called a school, have disregarded the maintenance of "swimming clearance." These fishes are feeding on dense plankton which has accumulated just under the surface of the water. Usually this species browses on the bottom. See Hiatt (1947) and Ebeling (1957) for data on the feeding methods involved. The single fish ahead of the pod and facing it in figure 1 of plate 71 has been literally squeezed out by the press of its fellows and is returning to the group. Often single individuals will be seen to leap ahead when the pack becomes unusually dense. Looser and smaller schools are more common in April and May, as shown in plate 72.

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

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

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

Schiche (1921) and Bowen (1931 and 1932) were well aware of the contacts made between young and old *Ameiurus nebulosus* (LeSueur) and *Ameiurus melas* (Rafinesque) and discuss the senses involved. As the siluroids are notably thigmotactic and cryptic, it is not in the least surprising that among them there is more of a tendency to form pods than in fishes that are generally not thigmotactic. That such forms as *Mugil* would form pods evidently calls for some further explanation and may be connected with some unknown peculiarity of their reaction to cold or of their reproductive act, or both. Evidently, what Breder (1940) thought to be courtship in *Mugil cephalus* may have been some elementary stage in pod formation in a rather confined place and may or may not have had reproductive significance.

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

THE PROBLEM OF LEADERSHIP AND HIERARCHY

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

Instances of such extreme forms as a small carangid's "schooling" with the dorsal fin of a large shark have already been commented on by Breder (1954), in which the large member is probably not even aware of the presence of the smaller. Less extreme is the situation described by Medcof (1957) for the behavior of *Alosa sapidissima* (Wilson) on its spawning grounds. Whether or not the behavior described by this author was part of the reproductive act or in some secondary way connected with it was not determined. However, it was clear that a single fish was the leader of a more or less single-file procession. The fishes, sometimes in contact, would form a tight circle, in which the same one fish was at the head of the group as much as when the tight circle gave way to an open figure. This fish may, of course, have been a female and the rest males in some prenuptial performance, as suggested by the observer. Such a situation is, nonetheless, from the standpoint of fish associations a leadership in which one individual has an influence much greater than any of the rest, all of which are evidently equipotential at their level of influence.

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

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

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

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

Cases in which the "leadership" is of a nonsexual order are to be found in goldfishes, in and out of their reproductive periods. In instances in which goldfishes are kept in pools of sufficient size so that they may form bands and wander about together through otherwise "empty" water, partial leadership is evidently based on color or markings. Thus, in a group of plain yellow goldfish in which a few pure white individuals are included, the latter may usually be found at or near the head of such an aggregation when it moves forward more as a school. This feature disappears when the group stops and fans out randomly. This was first noted in goldfishes in Mountain Lake Sanctuary, Florida (pl. 73, fig. 1). While it was not possible to make statistical measurements, it was obvious that the white fishes were in the van of these processions almost all the time. This detail of school structure was checked in a pool on the author's property, with similar results. It would appear that this is probably nothing more than a difference in visibility of the white compared with the yellow fishes and that there is a stronger reaction on the part of the other fishes to move towards the most conspicuous members, which in this situation are presumed to be the white ones. The converse was also noted, in that dark gray goldfish kept disappearing against the background of the bottom and were most often not to be found in small groups of which every individual could be counted. Such an interpretation would check well with the data of Breder and Halpern (1946) and Breder and Roemhild (1947), who demonstrated that the social behavior of goldfishes differed in a locomotor sense with differences in the pigmentation of the individuals that were involved. This tendency of white fish to be followed more than yellow ones in a group predominantly of the latter color would thus be a gross appearance of the results of the behavior that was statistically measured by the above workers in a more refined manner.

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

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

Closely related to the above considerations is the problem of hierarchy. The approach of one fish to another may be considered positive or negative if it results, respectively, in a pacific swimming along together or in aggression on the part of the approaching fish. The latter, if the activity is general and violent enough, leads inevitably to a status of isolation and solitary behavior or to the establishment of a peck order within an aggregation. A school, as here used, is automatically reduced to an aggregation on a very slight appearance of aggressiveness by relatively few individuals. From this it follows that when both an aggressiveness and a tendency to form groups are present, a hierarchy may be established. Basically when these are just balanced, they may persist for some time, but unless there is some special extrinsic influence that is responsible for the balance, which is usually temporary at best, one falls below the other in value, and the fish move either to a properly aggregating condition or to one of solitary existence. Such extrinsic influences may be limited feeding areas, or restricted breeding sites, involving conflict brought on primarily by territoriality or crowding caused by overpopulation or other matters. In the first case, limited feeding areas, there is often a cessation of hostilities among solitary fishes, such as barracuda, when they strike individually into a school of food fishes, and the schooling habits of the prey itself make a "restricted feeding area." The predators usually simply avoid one another. Bottom-feeding fishes, such as many kinds of gobies, will often drive another off before striking a quiescent food object. This would seem to be little more than an extension of their territoriality which notoriously weakens when the individuals are off their home territory. The peck order, with crowding, has been extensively studied in laboratory aquaria, for here such crowding may be produced quite incidentally or unavoidably, and not infrequently leads to destruction of the lower members of the hierarchy. In a state of nature this type of relationship is not often seen, because usually there are other effects that depress the activity of the fishes. For example, mild suffocation, as happens in a drying pond, will reduce the aggressive activity, as was demonstrated on *Aequidens latifrons* (Steindachner) by Breder (1934). Eddy (1925) indicated that the young *Ameiurus melas* and adult *Schilbeodes insignis* intensified their aggregating on stimulation, by caffeine and strychnine sulphate, and reduced it on suppression, by chloretone and potassium cyanide, all in very small concentrations. Both excessive heat and cold produced similar results. These data, taken with the many casual references in a host of experimental papers, as well as personal observation in the field and in aquaria, seem to indicate the simple physiological condition that organisms sickened or otherwise subdued by unusual environmental conditions fail to respond in their typical fashion. Their social responses, hostile or social, evidently are among the first to drop out under these conditions.

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

all times, are discussed by Tavolga (1954).

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

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

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

FISHES IN ORDERLY FILES

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

On the downstream side of these sand ridges a slight eddy is formed, which presents a line of comparatively still water in which such fishes usually come to rest. Fish in other situations downstream of a small rock or fallen log rest similarly and can be seen regularly in suitable locations. This fact alone can easily account for the transverse parallel rows of fishes which follow the riffle marks closely. Grant (1951), commenting on the situation, was well aware of the mechanics involved.

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

In connection with all such cases of the

form of standing "schools" in flowing water, it must be remembered that it is possible to arrange the distribution and form of the schools into almost any outline desired by suitable adjustment of the amount of flow and its direction, together with whatever other influences happen to be involved in the forming of a specific group. Such an arrangement is seen in perhaps its simplest and purest form in winter groups of fishes under such conditions, as, for example, has been discussed by Breder and Nigrelli (1935). Anyone with access to a trout-hatchery trough of fingerlings can cause the fish to line up in a manner similar to that shown in plate 74, figure 1, by wedging strips of wood of suitable size and cross section across the troughs at the bottom.

FISHES IN BALLS

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

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

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

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

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

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

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

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

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

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

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

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

COLLECTIVE PROTECTIVE BEHAVIOR

Fritz Haas (1945) postulated "collective mimicry" for insects (grasshoppers) that in small tight groups resembled nearby whole caterpillars. This concept was evidently new in the area of protective resemblance, involving not an individual effect but a large, multi-individual component. Cases that various students have thought to be more or less similar to it in fishes have been described by Breder (1948) for small groups of *Eucinosto-*

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

With the above considerations comes the question of what relationship to grouping the individual fish bears which is found solitary but in close association with and resembling some other object, such as a leaf. A list of the known cases of this sort was given by Breder (1946), with a discussion of their biological implications. An especially interesting case is that of young *Lobotes surinamensis* (Bloch), which have been shown by Breder (1949b) to aggregate with a swirl of mangrove leaves and so much resemble them, both as to form and color and manner of floating, as completely to disappear before one's eyes. Such questions occur as, whether this behavior arose directly and the species was always solitary, or whether this is a further extension of the aggregating habit, or whether at one time the ancestors of the present-day form once schooled with one another instead of leaves. In such cases one could imagine that on a simple selection basis it became more "profitable" for a fish to school with leaves and so widely scatter the individuals. Without the invoking of a predator to account for this behavior, it could conceptually be derived by assuming that these fishes had aggressive tendencies, and in the establishment of a hierarchy it became more useful to individuals to aggregate with inert "individuals," i.e., leaves, than with the active individuals, i.e., other fishes. The question would then become, Is the present-day behavior a result of protective response against a predator only or is it that only in part and primarily against fellow fishes? There are no data on the subject for this species, but in the case of *Chaetodipterus faber* (Broussenet), which when small operates in a similar way with mangrove seed pods, it is known that it is destructively aggressive if placed with its fellows. At a little larger size these fish school together and are entirely passive. Bearing on this is the report by Yabe and Mori (1950) of finding the normally schooling *Katsuwonus* and *Neothunnus* accompanying drifting timber.

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

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

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

To return to the more central parts of this section, it may fairly be inferred that groups of animals being preyed on obtain a certain amount of security from predation by the totality of all conceivable items of behavior of the individuals involved which interact with the limitations of the predators. Then it should follow that the more important this type of behavior became to a species the greater the likelihood is that there would evolve, on a straight basis of selection, special forms of schooling or pod formation, such as are described above.

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

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

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

An approach to this problem might start with a survey of the details of the feeding habits of these fishes and the manner in which those that feed upon them actually do take their food. J. J. Graham (1957) notes that there is a difference in the feeding behavior with different foods as is indicated by his following statement: "Mills formed in laboratory tanks offered opportunities to observe the feeding movements of the alewife school. These observations and those taken in the field showed that the alewife does not take its food by random straining of water. When *Daphnia* were introduced into the laboratory tank along the course of the mill, the milling ceased and each alewife pursued its prey. Strained liver, which formed a cloud when introduced into the tanks, also had the same effect excepting that it was consumed by swimming through the cloud and the breakdown of the mill was not into individuals but into numerous small groups. A possibly similar relationship between the compactness of a school and the size of the food upon which it feeds has also been shown for the mackerel (Sette, 1950)." While it is tempting to suppose that the feeding mode of such creatures is a function of the ratio of size of food to feeder, it is nonetheless possible that on survey the relationship will be found to be much more complex. Tending to bear this relationship out is the fact that the even relatively small *Polyodon* strains daphnia by dropping its lower jaw and using its mouth very much in the manner of a "pushed" tow-net (personal observation) or the manner of feeding of large oceanic forms, such as plankton-feeding whales and *Manta*. The descriptions of the feeding of *Rhineodon typus* Smith on both small and large fish by Gudger (1941) and Springer (1957) are also in agreement with this view.

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

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

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

HETEROTYPIC AND HOMOTYPIC GROUPS

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

At one time in January, 1952, a group of *Anchoa hepsetus* (Linnaeus) became available which when established in the pool formed a large school. These fishes so nearly resembled the *Jenkinsia* in size, shape, and general deportment, that it was sometimes difficult to be certain which species was under observation. Neither species of fish was confused in the slightest. Each maintained a separate group as soon as the schools formed. Frequently when the two schools were halfway across the pool from each other they would swim towards each other, but when the distance had been reduced to about $1\frac{1}{2}$ feet, they would turn away and refuse to approach

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

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

Also placed in the pool was a school of small *Harengula* nearly twice the size of the other two species. These also maintained a monotypic group except at low temperature. Actually it was obvious, moreover, that there was less repulsion between the *Harengula* and the anchovy than between the other two combinations. The above observations all refer to situations in very clear water, with the fishes fully visible to one another at all the inter-fish distances involved. Considerations invoking other sensory modalities are discussed elsewhere.

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

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

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

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

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

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

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

SPECIAL ENVIRONMENTAL INFLUENCES ON FISH GROUPINGS

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

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

THE INFLUENCE OF LIGHT AND TEMPERATURE

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

PIGMENTARY REACTIONS

Pigmentary response to environmental stimuli in teleost fishes, accomplished primarily by means of an adjustment of the positions of the granules in the various chromatophores, has been the subject of study by many researchers. The most obvious and widespread reaction of this kind is that in which fishes tend to match the tone, and often the color, of the background against which they are seen. Until recently this kind of reaction has received almost the entire attention of researchers in the field and has been summarized by Parker (1948). That this reaction to background is not inevitably present, varying only in extent from a condition of nearly no ability to that of the most marked and rapid background matching, has been shown by Breder (1946, 1958, 1949a, and 1955) and by Breder and Rasquin (1950 and 1955b). They have indicated that various fishes from the most diverse groups showed responses to both environmental stimuli and hormonal treatment precisely contrary to the background matching of others.

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

"POSSIBLE PIGMENTARY REACTIONS"
"A. In reference to the background"
"i. Matching background"
Direct responses
"1. In general tone"
General direct response
"2. In pattern detail"
Detailed direct response

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

"ii. Opposing background"
Inverse response

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

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

All the fishes in the above list are acanthopterygians and have light-protected pineal areas, and the two tested, *Haemulon* and *Chaetodipterus*, were found by Breder and Rasquin (1950) to react to adrenalin by blanching their normally dark irises only. Rasquin (1958) greatly extended these studies on a number of species and included both the morphology and the histology of the pineal organ and the pigmentary reactions to a variety of hormones. She demonstrated that the blanching of the iris is caused by the reaction of the perineural system of the melanophores to adrenalin, the iral melanophores belonging to that system. The fishes tested were arranged in three groups: forms in which all the melanophores reacted, forms in which only the perineural system reacted, and forms in which none of the melanophores reacted. The last group is represented by two species of Chaetodontidae, and one each of the Acanthuridae and Monacanthidae. Some relationship, not completely clear as yet, exists between this circumstance and the degree of exposure of the pineal organ. No fish listed after the Sphyraenidae, in classifications arranged with the Persoces first in the acanthopterygians, has been found with other than a permanently covered pineal area. No member studied in this assemblage reacts wholly to adrenalin. All have been found to show either no reactions whatever or, at most, a blanching of the iris. The peculiar details found in the scombriform fishes are surely secondary specializations. Various aspects of these features are discussed by Rivas (1953) and by Rasquin (1958) for *Gymnosarda* and *Thunnus*.

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

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

"iii. Indifference to background"
No response

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

"B. In reference to emotional state"
"i. Unvarying with state"
No intrinsic response
"ii. Varying with state"
Intrinsic response

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

The relationship of the other items of be-

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

Locomotor Reactions

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

Visual Reactions

In addition to adjusting the state of their chromatophores to match or contrast with background many fishes will swim only over a matching (or contrasting) background. This may be frequently observed in the field, where schools of clupeids swimming over light sand refuse to pass over a dark weed bed unless there is absolutely no way to avoid it and vice versa. Various studies have been made on the special features of such behavior by Brown and Thompson (1937), Breder and Halpern (1946), Breder (1947b, 1951, 1955), and Breder and Rasquin (1955a). The significance of these studies in present connections is that they can be invoked to explain, in many instances, why schools, on approaching one another, will at times merge and at other times refuse to merge. The difference in pigmentation, especially of clupeids that have been living over dark and light backgrounds, respectively, is rather difficult to detect under usual field conditions. However, in the few cases in which the author was clearly able to distinguish a difference between the fishes, the behavior was found to be in accordance with the above view. Jones (1956) found that *Phoxinus* would not cross a dark background band when illuminated by from 0.17 to 0.08 meter-candles. Related to this is the work of Kanda and Koike (1958a, 1958b) and of Kanda, Koike, and Ogura (1958a, 1958b) who demonstrated that a variety of fresh- and salt-water fishes were more repelled by vertical nets that reflected long wave lengths than by those that reflected short ones. That is, the fishes would pass through the meshes in the following order: the fewest through red, more through yellow and orange, and the most through green and blue. This apparently has to do with visibility and contrast with the background. Color (wave length) was found to be more important than intensity (brightness), which is in good general agreement with the foregoing data based on other considerations and experiments.

Effects of Light Quantity and Quality

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

TABLE 1

REACTIONS OF SPECIES NOT ESPECIALLY TREATED IN SUBSEQUENT TABLES

(In each experiment the choice was between a dark and a lighted chamber. Explanatory details of each case are given in text. The means are those for the lighter chamber in each case. In each case 4 fish were used and $N = 500$.)

Means	Standard Error	Means Expressed as Percentage
Sardinella macropthalmia (Ranzani)		
3.988	0.029	99.8
Leptocephalus sp.		
2.52	0.035	26.0
2.86	0.055	43.0
Anoptichthys (Arroya)		
2.122	0.014	6.1
Carassius auratus (Linnaeus)		
0.884	0.060	−55.8
Strongylura notata (Poey)		
2.024	0.049	1.2
2.000	0.044	0.0
Lebistes reticulatus (Peters)		
4.000	0.000	100.0
3.440	0.050	72.0
Mollienesia sphenops (Cuvier and Valenciennes)		
2.416	0.083	20.8
Mugil trichodon (Poey)		
0.93	0.067	−53.5
Synodus synodus (Linnaeus)		
1.04	0.085	−30.7
3.000	0.000	100.0
2.74	0.019	82.7
Betta splendens (Regan)		
1.074	0.039	−46.3
Haemulon melanurum (Linnaeus)		
1.862	0.046	− 6.9
1.52	0.040	−24.0
0.13	0.016	−93.5
0.028	0.009	−98.6
Eucinostomus gula (Cuvier and Valenciennes)		
0.032	0.009	−98.4
0.418	0.038	−79.1
0.97	0.025	− 3.0
2.638	0.021	31.9
1.646	0.039	−17.7
3.978	0.006	98.9
3.15	0.037	57.5
2.87	0.052	43.5
0.934	0.028	−53.3
3.228	0.032	61.4
2.578	0.038	28.9
Tilapia macrocephala (Bleeker)		
1.204	0.032	−39.8
Apogonichthys stellatus (Cope)		
3.478	0.082	73.9
2.61	0.039	30.5
Pseudupeneus maculatus (Bloch)		
4.000	0.000	100.0
Abudefduf saxitilis (Linnaeus)		
1.552	0.066	−22.4
2.670	0.074	33.5
Abudefduf analogus (Gill)		
2.706	0.058	35.3
2.342	0.062	17.6
Thalassoma bifasciatum (Bloch)		
0.744	0.039	−62.8
1.325	0.044	−33.75
1.34	0.024	−33.0
0.228	0.027	−88.6
Scarus croicensis (Bloch)		
0.000	0.000	−100.0
2.200	0.055	10.0
Sparisoma radians (Cuvier and Valenciennes)		
4.000	0.000	100.0
0.904	0.052	−54.8
Carapus bermudensis (Jones)		
1.000	0.000	100.0
Monacanthus ciliatus (Mitchill)		
4.000	0.000	100.0
3.916	0.039	95.8
0.906	0.042	−54.7
2.492	0.030	24.6
Histrio histrio (Linneaus)		
2.042	0.029	36.1

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

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

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

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

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

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

Reactions to Light Intensity: The origin of these studies was merely an attempt to determine if certain blind cave fishes were light sensitive (Breder and Gresser, 1941a, 1941b). Later, Breder and Halpern (1946) extended the method to other species. The present part of this paper is to be considered a still further extension of those studies. Table 1 lists experiments that are concerned purely with a choice between a bright and a dark chamber, for which there is no further breakdown. The remainder of the tables pertinent to this work cover fishes that were studied in greater detail. Various refinements were added to these studies which appear in later tables. Tables 2 and 3 list later experiments with cave fish, in which in addition to the light-dark choice, the fishes were tested against light ratios in the two chambers of intensity of 1 to 2 and of 1 to 4.

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

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

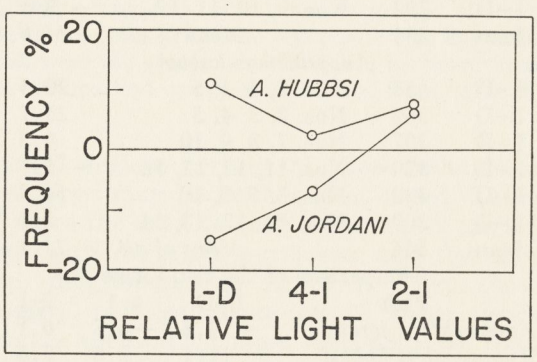


Fig. 4. Reactions to various differences in light intensity. In horizontal index, "L-D" indicates light and darkness, and the numerals "4-1" indicate the difference if the greater was four times the lesser, and so on. Readings were always made in the brighter chamber. Two forms of *Anoptichthys*. Data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

TABLE 2

REACTIONS OF BLIND CAVE FISHES TO VARIOUS COMPARATIVE LIGHT VALUES

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

Light Ratio	Foot-Candles	Fishes and Their Individual Nos.	Per Cent Positive
		Anoptichthys jordani	
2–1	495	Nos. 1, 4, 6, 11	2.2
2–1	270	Nos. 1, 4, 6, 11	10.1
		Mean of all	*6.1*
		Anoptichthys hubbsi	
2–1	405	Nos. 2, 3, 4, 5	18.7
2–1	420	Nos. 2, 3, 4, 5	− 3.4
2–1	245	Nos. 11, 12, 13, 14	3.3
2–1	217	Nos. 3, 5, 8, 10	13.0
		Mean of all	*7.8*
		Anoptichthys jordani	
4–1	457	Nos. 1, 4, 6, 11	− 6.2
4–1	259	Nos. 1, 4, 6, 11	− 2.7
4–1	280	Nos. 1, 4, 6, 11	−18.6
4–1	285	Nos. 1, 4, 6, 11	0.6
		Mean of all	*− 6.7*
		Anoptichthys hubbsi	
4–1	360	Nos. 2, 3, 4, 5	− 9.0
4–1	482	Nos. 2, 3, 4, 5	1.0
4–1	280	Nos. 2, 3, 4, 5	0.9
4–1	285	Nos. 2, 3, 4, 5	5.2
4–1	243	Nos. 3, 4, 8, 10	14.9
		Mean of all	*2.6*
		Anoptichthys jordani	
L–D	372	Nos. 1, 2, 3, 4	−15.8
L–D	380	Nos. 5, 6, 7, 8	−39.6
L–D	252	Nos. 1, 4, 6, 11	3.9
L–D	250	Nos. 1, 4, 6, 11	−18.3
L–D	460	Nos. 1, 4, 6, 11	−10.4
L–D	392	Nos. 9, 10, 11, 12	− 8.6
Mean	351	*Mean of all*	*−14.8*
		Anoptichthys hubbsi	
L–D	453	Nos. 2, 3, 4, 5	20.5
L–D	362	Nos. 2, 3, 4, 5	25.7
L–D	307	Nos. 7, 8, 9, 10	9.3
L–D	320	Nos. 11, 12, 13, 14	− 5.5
L–D	320	Nos. 3, 5, 8, 10	14.5
L–D	302	Nos. 11, 12, 13, 14	2.2
Mean	344	*Mean of all*	*11.1*

Comparison of the two forms

Fish	L–D	4–1	2–1
Anoptichthys jordani	−14.8	−6.7	6.1
Anoptichthys hubbsi	11.1	2.6	7.8

Statistical comparison

	d/σ_d	
A. hubbsi L–D — *A. jordani* L–D	20.0	Significant
A. hubbsi 4–1 — *A. jordani* 4–1	1.3	Not significant
A. hubbsi 2–1 — *A. jordani* 2–1	0.6	Not significant

TABLE 3

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

(All readings made with only one end lighted.)

	Foot-Candles	Fish No.	Per Cent Positive
		Anoptichthys jordani	
	377	1	9.6
	361	2	12.0
	362	3	9.6
	372	4	16.8
	365	5	− 1.2
	367	6	10.0
	363	7	0.4
	357	8	− 3.6
	385	9	−12.0
	387	10	−17.2
	352	11	13.2
	345	12	− 6.8
Mean	*366*		
		Anoptichthys hubbsi	
	—	1	4.4
	345	2	12.8
	363	3	36.8
	384	4	14.4
	361	5	41.6
	295	6	11.6
	290	7	12.0
	302	8	46.0
	302	9	6.8
	290	10	16.8
	322	11	13.6
	312	12	8.4
	320	13	11.6
	318	14	8.0
Mean	*323*		

Means of groups of four compared with sum of same individuals as isolates

	Group of Four Fish	Sum of Four Isolates	Difference
	Anoptichthys jordani		
	−15.8	12.0	27.8
	−39.6	1.4	41.0
	− 8.6	−5.7	2.9
	3.9	4.8	0.9
	−18.3	4.8	23.1
	−10.4	4.8	15.2
Mean of all	*−14.8*		
	Anoptichthys hubbsi		
94 89–92	20.5	26.4	5.8
96 89–92	25.7	26.4	1.3
109 105–108	9.3	20.4	11.1
114 110–113	− 5.5	20.4	25.9

TABLE 3 (*Continued*)

	Group of Four Fish	Sum of Four Isolates	Difference
117			
90, 92, 106, 108	14.5	35.3	20.8
119			
110–113	2.2	20.4	18.2
Mean of all	*11.1*	*21.5*	

Statistical comparison

	d/σ_d	
A. jordani in groups — Random	6.11	Significant
A. hubbsi in groups — Random	4.61	Significant
A. jordani as isolates — Random	0.58	Notsignificant
A. hubbsi as isolates — Random	3.43	Significant
A. jordani isolates — *A. hubbsi* isolates	3.53	Significant
A. jordani groups — *A. hubbsi* group	20.06	Significant

implications of these data are discussed in another place.

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

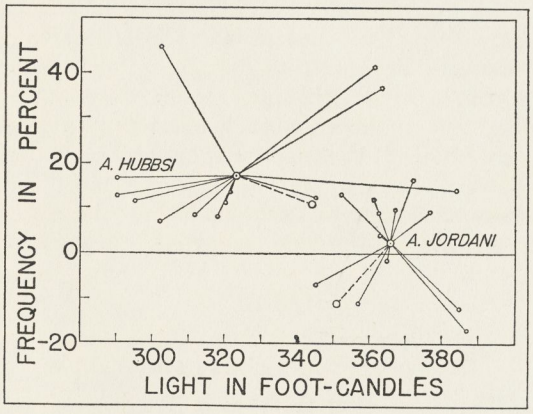


FIG. 5. Comparisons of behavior of *Anoptichthys hubbsi* and *A. jordani* to various light intensities when alone and in groups of four. The small circles indicate individual values of solitary fishes. The larger circle with which they are connected by a fine solid line represents the mean of these values.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

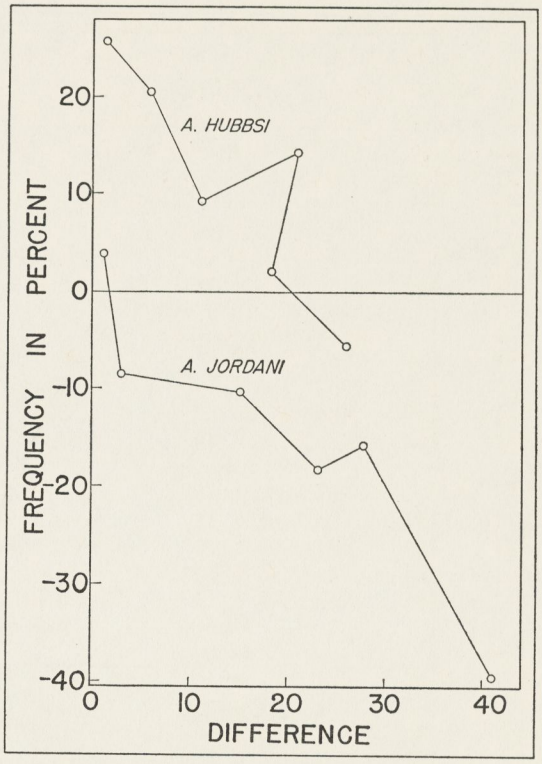


FIG. 6. Measurement of the group effect in the attitude of two forms of *Anoptichthys* towards light. The horizontal index represents the difference between the same individuals read separately and then averaged from the readings of them measured in groups of four. In each case the fish proved to be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

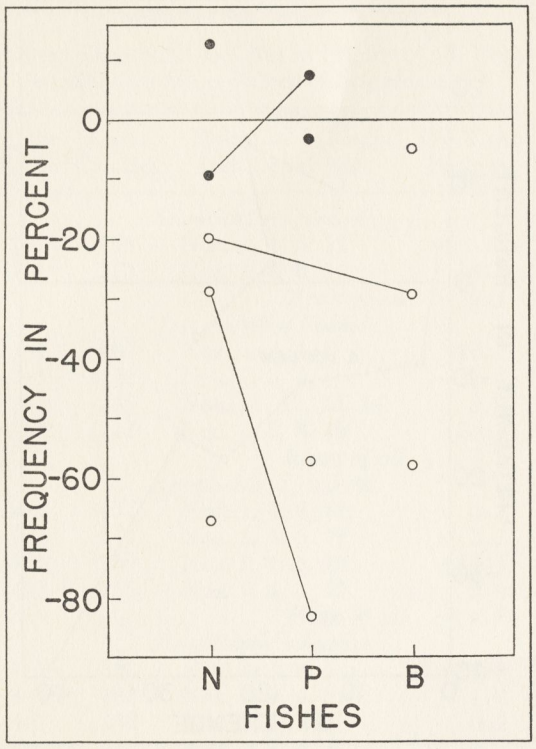


FIG. 7. The effects of pinealectomy on *Anoptichthys* and of pinealectomy as well as blinding on *Astyanax*. Dark circles indicate *Anoptichthys*, and light circles indicate *Astyanax*. Values from fish measured before and after operation are connected by a thin line from normal (N) to pinealectomized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

this reaction largely disappears. Naturally, unwanted visual stimuli are easily eliminated during these experiments by screens, but others, principally jars to the building which are unavoidable, induce retreat to the dark chamber. Blinding eliminates the retreating reaction, and such blinded fish show no response to a jar other than a slight twitch. These fish are nevertheless light negative when blinded, just about as much so as the cave fish *Anoptichthys jordani*. Both normally have the pineal area protected from direct light. The fish here listed in table 6 were blinded by optic nerve section, unlike those reported by Breder and Rasquin (1947) which had only the lenses removed and consequently remained strongly light negative. Here again no correlation could be established between the intensity of illumination and the degree of light positiveness in either the normal or the operated animals. The comparatively light-positive blind fish from Sótano de la Tinaja evidently become slightly more so on removal of the pineal. The differences are slight, but significant. The case of *Phoxinus laevis*, the fish on which von Frisch did early work concerned with the influence of the pineal on pigmentation, is interesting in present connections. This fish is normally optically controlled to a considerable extent. The intact animal is slightly light negative and behaves not greatly unlike *Astyanax* in regard to hiding under things such as leaves or overhanging rocks. On being blinded, it becomes strongly light positive, as it has a well-exposed pineal. Capping this area in either a blind or intact animal makes it even more light negative than blinding alone makes it light positive. The figures are given in table 8 and in figure 8.

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

TABLE 4

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

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

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

TABLE 5

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

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

Time of Day	Sex	Per Cent Positive	Condition of Fish
		March, 1950	
Day	Female	−41.4	Normal
Day	Female	− 3.6	Normal
Night	Female	−25.6	Normal
Day	Male	−38.2	Normal
Night	Male	−18.2	Normal
Day	Male	−74.6	Pineal uncovered
Day	Female	−43.6	Pineal uncovered
Night	Male	−92.6	Pineal uncovered
Night	Female	−95.8	Pineal uncovered
Day	Male	−43.3	Head blackened
Day	Female	90.0	Head blackened

July, 1951

Light Ratio	Foot-Candles	Sex	Experiment Number	Per Cent Positive
L–D	120	Female	190	−93.6
2–1	120	Female	192	12.9
L–D	80	Male	193	91.2
2–1	100	Male	194	18.2
L–D	80	2 f, 2 m	195	34.5
2–1	80	2 f, 2 m	196	0.0

Statistical comparison

	d/σ_d	
Night, pineal exposed, male and female	2.2	Probably not significant
Night, normal, male and female	1.9	Not significant
Female 2–1	0.9	Not significant
Female 2–1 — Random	2.7	Probably significant
Male 2–1 — Random	4.8	Significant

May, 1952

Time of Day	Sex	Per Cent Positive	Condition of Fish	Set No.
Night	Female	− 71.4	Normal	1
Night	Female	− 5.8	Head blackened	1
Night	Male	− 71.3	Normal	2
Night	Male	− 49.8	Head blackened	2
Day	Female	− 62.6	Normal	3
Day	Female	65.8	Adrenalin injected	3
Day	Female	− 95.3	Normal	4
Day	Female	5.4	Blinded	4
Day	Female	− 0.4	Black head + adrenalin	4
Day	Female	−100.0	Normal	5
Day	Female	− 22.4	Blinded	5
Day	Female	− 2.0	Black head + adrenalin	5
Day	Female	− 99.5	Normal	6
Day	Female	14.3	Adrenalin injected	6
Day	Female	−100.0	Normal	7
Day	Female	98.0	Black head + adrenalin	7

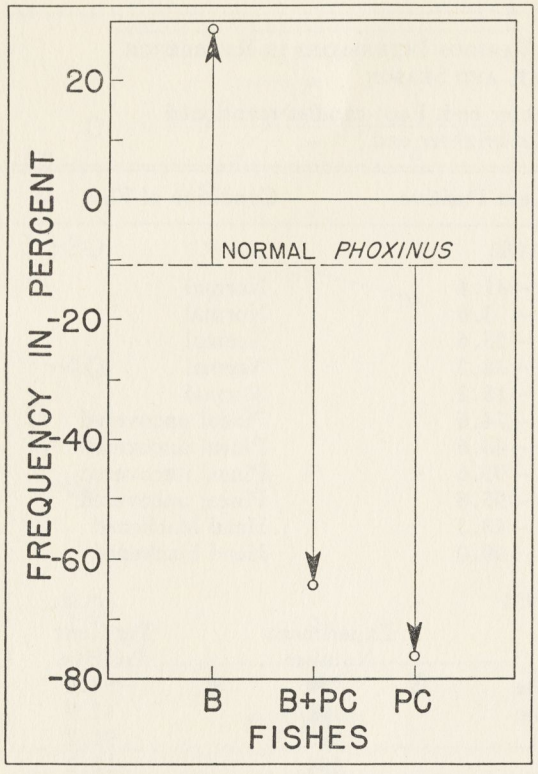


FIG. 8. The effects of blinding and covering pineal on *Phoxinus*. The reaction of the normal fish is indicated by the dashed horizontal line, and the departures therefrom, following experimental procedures, are indicated by the light circles to which arrows point, to blinded (B) and covered (C). Data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

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

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

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

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

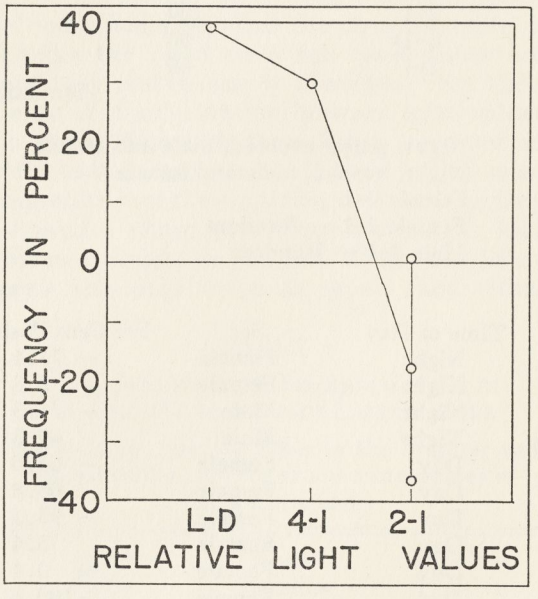


FIG. 9. Reactions to various differences in light intensity. In horizontal index, "L-D" indicates light and darkness, and the numerals "4-1" indicate the difference if the greater was four times the lesser, and so on. Readings were always made in the brighter chamber. Normal *Brachydanio rerio*. Data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

TABLE 6

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

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

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

The work described above was done in March, when the light values are less, the days are shorter, and the water is cooler than in the summer time. It was found that during July and August the males are extremely light positive, while the females are light negative. At this season the fish are most active, both sexually and otherwise. This situation was taken advantage of in the checking of their response to light of various values. The data are given in the lower part of table 5. Males tested in groups of four were nearly fully light positive, while females similarly tested were just as light negative. Under conditions of light in the ratio of two to one, the behavior of each became completely indifferent and could not be distinguished from

TABLE 7

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

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

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

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

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

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

TABLE 8

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

(All readings were made in the light chamber.)

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

TABLE 9

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

(All readings were made in the light chamber.)

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

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

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

The observations on the other species listed in table 1 are in close agreement with those of Breder and Rasquin (1950). *Sardinella*, Leptocephalus sp., *Anoptichthys* (Arroya form), *Lebistes*, *Mollienesia*, *Apogonichthys*, and *Carapus* are all distinctly light positive, *Histrio* is practically neutral, while *Synodus* and *Eucinostomus* show variations falling on either side of the line of neutrality. The remainder (*Carassius*, *Betta*, *Haemulon*, and *Tilapia*) are all distinctly light negative. None of them suggested sufficient difference from expectation to warrant the carrying of this type of analysis further in their cases.

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

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

TABLE 10

BEHAVIOR OF CERTAIN INDIVIDUALS OF *Atherina stipes*

(All readings were made in the light chamber.)

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

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

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

A related matter was observed on some aquarium-kept *Cypselurus heterurus*, of from about 15 to 50 mm. in length. These are notoriously difficult to keep in aquaria and are extremely sensitive to handling and incident shock. The fishes in question, however, had thrived for three weeks and were showing a good growth rate, being fed continuously with *Artemia*, which they took avidly. In mid-January, 1951, because of some completely unrelated experimental work, the lights normally on in the aquarium room in which the *Cypselurus* were located had been left off until well after dark. When the lights were turned on, raising the illumination on the tanks instantly from 0 to 26 foot-candles, the fish showed strong shock reactions. Several spiraled around and down and lay upside down on the bottom. One died, but the others recovered. The aquarium had been blackened on four sides except for a narrow band around the top, so that as the fish fell they passed into a region of much dimmer light. If this had not been so, it is probable that more would have died. The fact that some of them lay upside down on the bottom also contributed to their protection, but it is doubtful if this reaction was deliberate on the part of the fish.

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

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

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

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

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

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

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

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

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

In one experiment *Abudefduf saxatilis* (Linnaeus) entered the dark compartment, stayed a while, and then swam freely in and out, with a score of −22.4 per cent. Subsequent tests on this species showed that these fish gave either positive or negative scores, evidently depending on some subtle influence we have not yet been able to designate. The related *A. analogus* (Gill) gave only positive scores.

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

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

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

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

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

Reactions to Wave Length: A considerable amount of work has been done on the influence of wave length on the movement of fishes since Walls (1942) summarized earlier controversy: Mookerjee (1934), Kawamoto and Takeda (1950 and 1951), Kawamoto and Konish (1952), Maeda (1955), and Ozaki (1951 and 1952). Their conclusions all point to the blue-green region of the spectrum as being most attractive and red and violet the least. This is clearly on a basis of wave length as apart from intensity. Kawamoto and Takeda (1951) thought they could establish that certain species were attracted to red. This is almost certainly not the case, at least for the fish they used (*Anguilla*), which is thoroughly light negative, and, by the nature of the physical characteristics of their choice box, light-negative animals would most surely gather under the red or violet, as no dark compartment was provided.

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

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

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

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

TABLE 11

RESPONSES OF FISHES TO A CHOICE OF COLORED LIGHTS

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

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

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

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

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

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

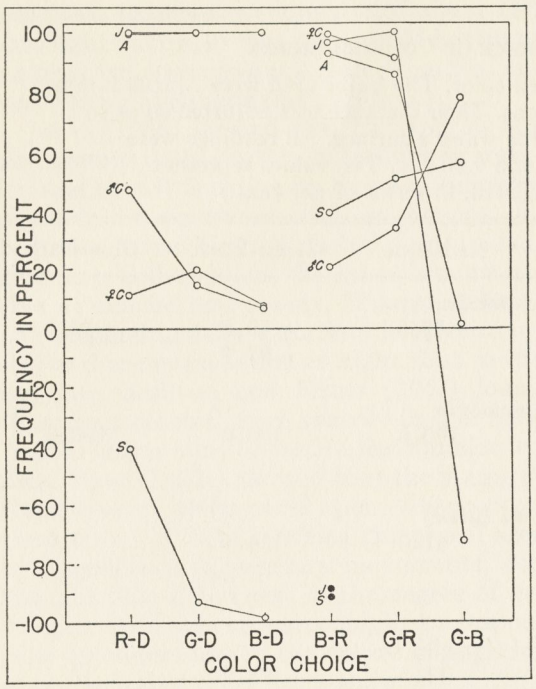


FIG. 10. Reactions to lights of various colors and to darkness of various species of marine teleosts. The letters on the horizontal index represent the choice with which the fishes were confronted, as follows: R, red; G, green; B, blue; D, darkness. The chamber in which the reading was made is mentioned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

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

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

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

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

TABLE 12

RESPONSES OF FISHES TO ULTRA-VIOLET RADIATION

(All readings made in the ultra-violet chamber except as noted.)

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

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

PHOTOPERIODISM

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

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

Interrelations of Light and Heat

It has been shown experimentally that the ambient temperature has an important bearing on the sign of the reaction of the response to light when varied beyond certain limits. Andrews (1946) showed that *Catostomus commersonii* (Lacépède) at the age of two years was light negative in shallow water but positive in deep water. This situation he referred to the lower light values found in deeper water. Sullivan and Fisher (1947) showed that trout selected temperature more sharply in dim light than in bright light. Andrews (1952), working with young, but mature, goldfish, found that they became insensitive to light if the temperature was raised to a certain value, which varied with the temperature of the water to which they had become accommodated. Thus, if conditioned to 12° C., they became insensitive to light at a little less than 22° C., but, if conditioned to 24° C., they became insensitive at a little over 30° C. These figures were found to vary with the age of the fish, as well as with the temperature to which they had been accustomed, with the general conditions that the insensitivity appeared higher in ratio to the temperature of the conditioning water. He showed that the heat receptors involved were distributed along the lateral line system. Barlow (1958) in a study of the behavior of *Cyprinodon macularius* in the Salton Sea showed that these fishes moved into cool shallow water with the coming of darkness and into the warmer and deeper places with the coming of daylight.

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

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

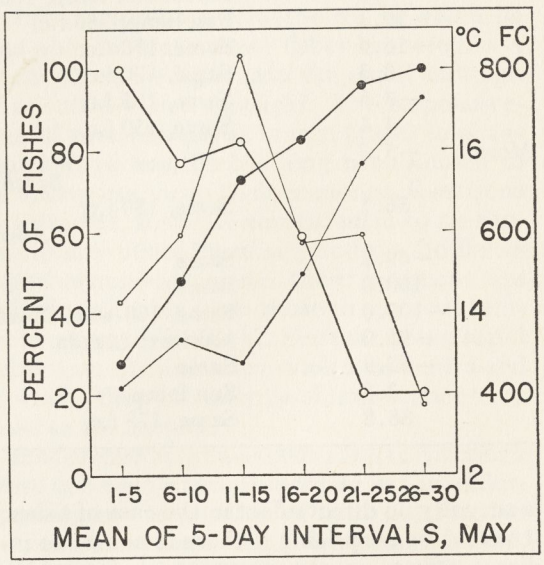


Fig. 11. Behavior of five goldfish during May in terms of five-day means. Large dark circles: mean number of fishes not buried, in per cent. Large light circles: per cent of fishes resting on bottom, but not buried. Small dark circles: mean water temperatures. Small light circles: mean foot-candles.

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

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

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

To extend this line of study, experiments were carried out in aquaria on young fish as follows. Four goldfish of a single brood at about an inch in length, two slate gray and two yellow (transparent-scaled type), were distributed two each to two aquaria, each 2 feet by 1 foot by 1 foot. Temperature differences were maintained by a thermostat-heater in one and an ice bag in the outside filter of the other. These two tanks were connected by pipes and a pump, as described by Breder (1957), so that there was chemical identity, which was maintained except during the course of the experiments. Even when the pump was not operating, there was some interchange because of the thermal difference between the two tanks. One-half of each tank was shaded with a cover and side shades of dark paper.

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

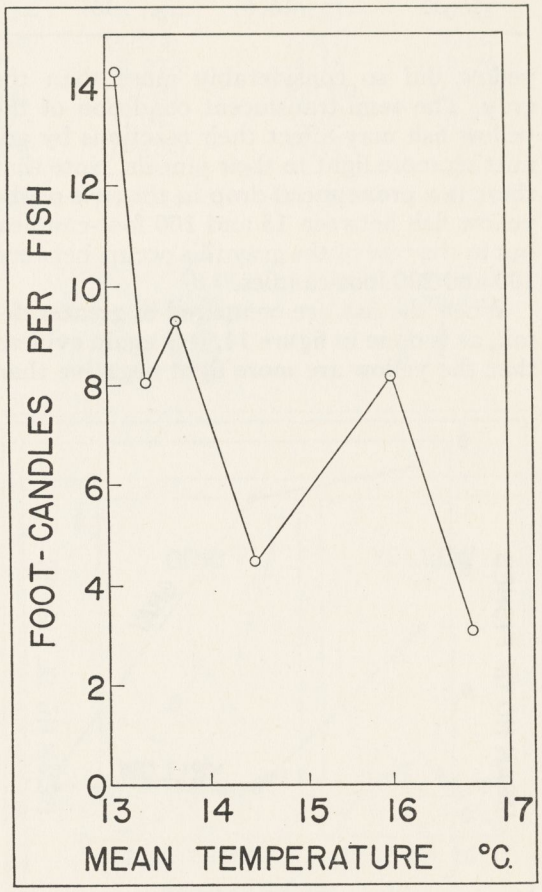


FIG. 12. Relationship of light reactions of five goldfish in reference to mean temperatures. The vertical index, foot-candles divided by number of fish not buried, gives a measure of light reaction. This indicates that the fishes were less light positive at low water temperature than at high, within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

TABLE 13

RESPONSES OF GOLDFISH TO LIGHT AND TEMPERATURE IN A POOL IN SPRINGTIME

(Data taken in 1952 on five fish under conditions of rising temperature and expressed in means of five-day periods.)

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

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

When the fish are compared in greater detail, as is done in figure 14, it is again evident that the yellow are more light negative than the gray. No case is shown for the former in which the mean values reach higher than 0.88, whereas in the case of the gray fish there are three instances in which the mean values exceed 1.00, which indicates these to be light-positive values. In the case of the yellow fish, there is a general trend for the fish to become more light negative the higher the water temperature. The values for the gray fish are more erratic, which indicates again a greater independence from the temperature-light relationship, at least in this range.

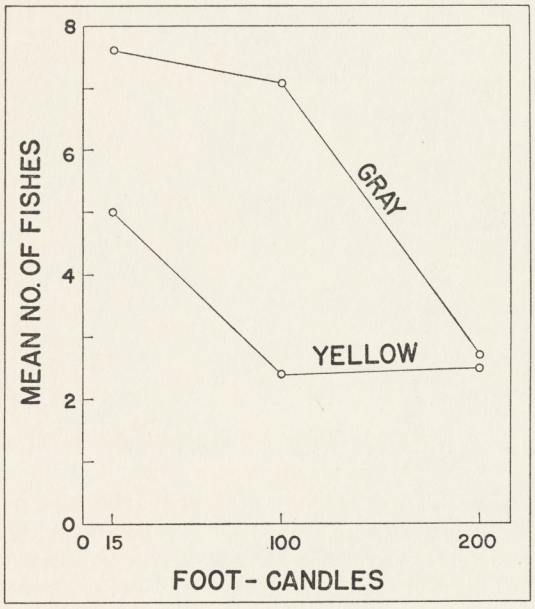


FIG. 13. Behavior of gray and yellow goldfish in reference to light intensity and use of shelter from direct light. Light in foot-candles is compared with mean number of fish out of shelter.

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

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

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

TABLE 14

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

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

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

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

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

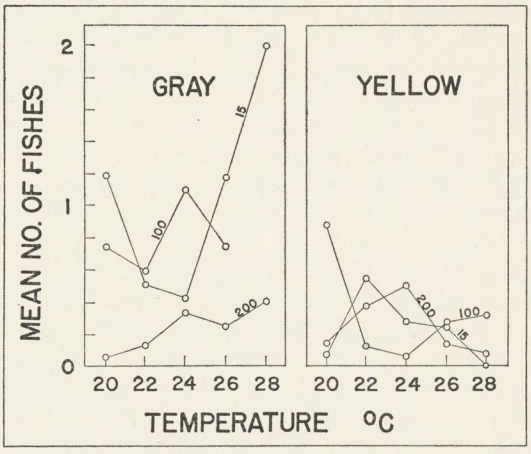


FIG. 14. Behavior of gray and yellow goldfish in reference to light and heat. Water temperature is compared with mean number of fish out of shelter with reference to the light intensity. The numbers indicate the higher limit of two-degree intervals. Lines connect points with a common light intensity,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

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

In order to attain a clearer understanding of the reasons involved in the changes in attitude of schooling fishes towards aggregation with differences in light and temperature, the preliminary studies of Breder (1951) on *Jenkinsia* were extended by the utilization of more refined instrumentation. A Leeds and Northrop "Micromax" recording unit provided with two pens was so arranged as to plot a graph of temperature in degrees Centigrade direct by use of that company's "Thermohm" and to plot the incident light by means of a Weston photocell in milliamps directly convertible to foot-candles. This was calibrated and checked at intervals by concurrent readings taken with a photovolt foot-candle meter. Incidental notes were made directly on the paper roll of the recording device. This was in continuous operation for considerable periods of time, interrupted only by such servicing as was occasionally necessary. The thermocouple was immersed in a test tube containing water and sealed in. This was built into a small stand which was placed at a given point in a pool 12 feet in diameter. The test tube was immersed nearly to its lip. Thus there was ready transfer of heat, but no metal came in contact with the water in which the fishes swam. A small shade was provided so that direct sunlight could not reach the thermometric element. The photo-cell mounted on a board was placed at the edge of the pool near the thermometer. It was protected from rain by a clear glass cover. No difference in reading could be detected by the presence of this cover. Readings taken from the machine-drawn graph, every hour on the hour, for two sample periods in November and January are given in figure 15. This shows at a glance, for instance, that during November the water temperature dropped rather sharply and that during January it was rising rather uniformly while the incident light did not vary greatly. The daily behavior of these two variables is in clear relief. Still further analysis is given in figures 16 and 17 which show the maximum, mean, and minimum of temperature and light by days and also the time of day of the occurrence of maximum temperature and light. The tides taken at this time from a Bendix water level recorder appeared to bear no relation to the behavior of the fishes.

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

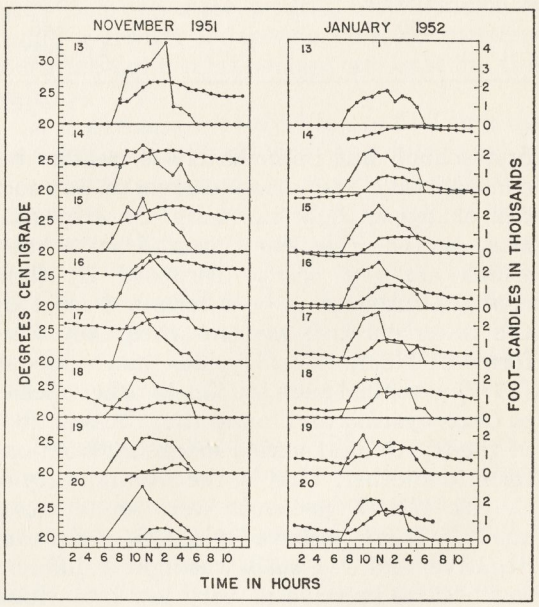


FIG. 15. Temperature and light conditions in a circular pool during comparable periods of November and January. Data picked from continuous temperature and light records made by a Leeds and Northrop "Speedomax" recorder. Each point represents recording as each hour passed. Black circles refer to temperature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

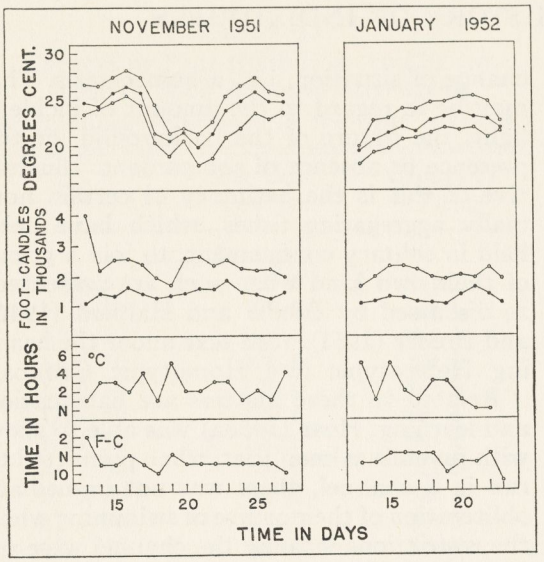


FIG. 16. Time and magnitude of maxima and minima of temperature (top graph) and light (second graph) from the same source as in figure 15. There is no minimum indicated for the light readings, as each night it fell below the instrument's threshold. The dark circles indicate mean values. These were obtained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

cially fig. 16). In figure 16 also is shown the return of the temperature to the levels of November 13 to 15. During this period the school reconstituted itself. Contrariwise, with the very low temperature of January 13, the fishes were in loose groups or merely diffuse. By the twentieth of January the school had reformed, although the temperature was no higher than the November temperature on which the school broke up, which seems to indicate that there is a considerable amount of accommodation to the general level of temperature of the period immediately past. Comparable reactions appear in behavior influenced by light and concerned with the immediate past history of the individuals. Furthermore, it seems that fishes in many cases are generally reluctant to change from a physiological or a psychological condition to a new one, even if the change is "for the better." General homeostasis and the avoidance of shock and stress in both the physiological and psychological sense may be attained by such reluctance. Such behavior could easily be thought of as having a very high survival value. The heat-regulating mechanism of birds and mammals should give a very considerable relief from at least the physiological importance of avoidance of shock and stress. The above considerations, based on fishes that live in a school continuously and are not subjected to extreme temperature variations, are perhaps not so clearly expressive of these changes in attitude as are those of more northern forms which evidently have more strongly marked differences relative to light and temperature differentials. It was partly for this reason that the preceding studies on goldfish under the influence of springtime increase in light and temperature in the latitude of New York were undertaken.

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

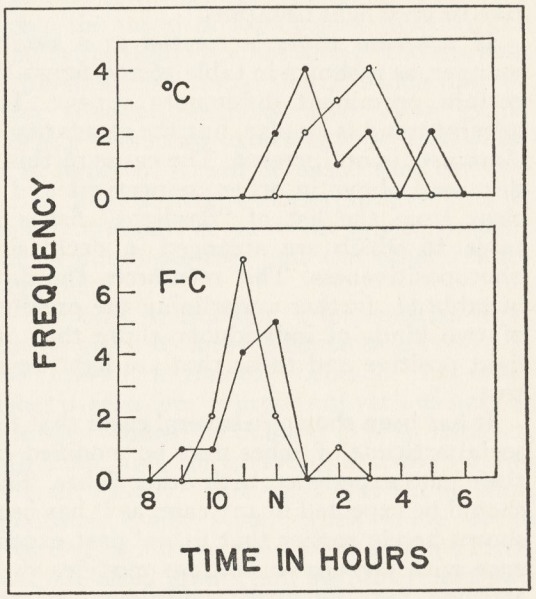


FIG. 17. Distribution of hours of maximum light and heat. Light circles represent November 13 to 23; dark circles, January 13 to 23.

THE INFLUENCE OF PAST HISTORY OF INDIVIDUALS

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

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

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

It has been shown in several cases that the social attitude of fishes may be modified by their past experience with other fishes. This should be expected in any case, as it has been shown herein earlier that fishes' past experience with physical conditions modifies their attitude towards such conditions. All the experiments so far seem to indicate a "preference" for a *status quo* or a resistance to a change of situation, i.e., a homeostasis. This may be in regard to the amount of incident light, the nature of the background, or the presence or absence of companions. Illustrative of this is the hesitancy of certain normally aggregating fishes, which have been held in solitary confinement, to join a group of their own kind when such are presented, as discussed by Breder and Halpern (1946) and Breder (1951). (See text under the heading Heterotypic and Homotypic Groups.)

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

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

TABLE 15

EFFECTS OF PAST HISTORY ON THE PHOTOSENSITIVITY OF *Jenkinsia lamprotaenia*

(All readings were made in the light chamber.)

Date	Per Cent Positive	Groups of 4 Fishes
	Sunlight	
1/28/50	100.0	Set 1
1/28/50	100.0	Set 1
1/29/50	100.0	Set 2
1/30/50	100.0	Set 3
1/30/50	100.0	Set 3
1/31/50	100.0	Set 4
1/31/50	100.0	Set 4
2/ 2/50	100.0	Set 5
2/ 2/50	100.0	Set 5
2/ 7/50	100.0	Set 6
6/ 7/50	100.0	Set 7
1/31/50	95.5	Set 4
	Shadow outdoors	
1/30/50	99.6	Set 4
7/11/49	99.0	Set 4
2/16/50	2.0	Set 8
1/29/50	−100.0	Set 2
	Dull day outdoors	
7/14/49	99.7	Set 8
2/ 5/50	−100.0	Set 7
	In laboratory room	
1/30/50	99.1	Set 3
1/29/50	− 50.0	Set 2
1/30/50	−100.0	Set 2
	At night	
1/31/50	100.0	Set 4
2/ 7/50	93.4	Set 10
2/ 7/50	50.8	Set 8
2/ 5/50	35.0	Set 9
2/ 5/50	− 99.3	Set 6
1/30/50	− 99.7	Set 2
6/ 7/50	−100.0	Set 9
1/29/50	−100.0	Set 2
1/30/50	−100.0	Set 3
	From darkroom	
2/ 7/50	− 26.8	Set 10
2/12/50	−100.0	Set 11

Synopsis

Environment	No. of Tests	Maximum	*Mean*	Minimum
Sunlight	12	100.0	*99.6*	95.5
Shadow	4	99.6	*23.6*	−100.0
Dull light	2	99.7	*− 0.2*	−100.0
Laboratory room	3	99.2	*−16.9*	−100.0
At night	9	100.0	*−24.7*	−100.0
Darkroom	2	−46.9	*−73.4*	−100.0

Mean of all outdoor values: 91.6

Mean of all indoor values: −30.0

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

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

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

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

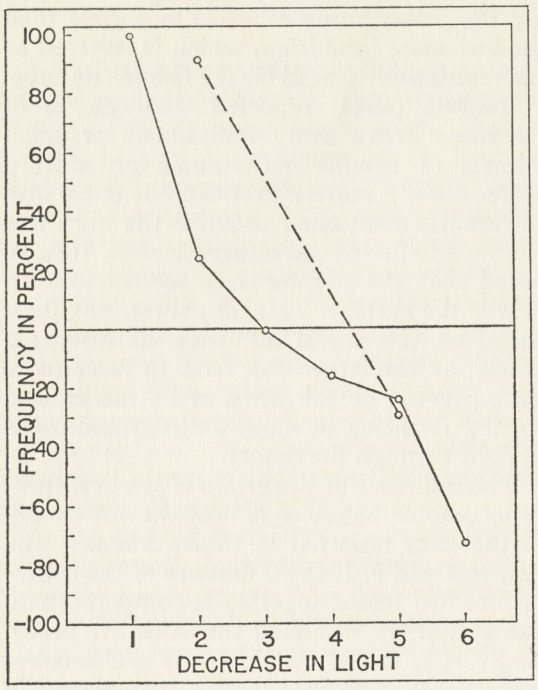


FIG. 18. The effect of the immediate past on *Jenkinsia*. The numbers on the horizontal index indicate the following light conditions previous to the tests: 1. Fish from outdoors in open sunshine. 2. Same as 1 but fish in shade. 3. Same as 1 but on dull overcast day. 4. Fish in laboratory for 24 hours.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

chance of regaining it by wide ranging and fast swimming. Overcrowding may, of course, be overcome by the same kind of activity, initially at least. Observations in the field, with such considerations in mind, clearly indicate that when such a "lost" fish speeds up its activity it also is less susceptible to other stimuli that at other times it would react to, such as food or quick movements on the part of the observer. All that need be assumed in interpreting figure 6 is, therefore, that the solitary fish is reacting to that state as do many other species, i.e., "paying less attention" to general external stimuli of a non-violent sort than it would when in a group of companions. Expressed another way, the more cohesive the group the more it tends to be controlled by the reactions of the individual most sensitive to external stimuli. Thus the light-negative *Anoptichthys jordani* might be expected to be more so in a group than when alone. However, the light-positive *Anoptichthys hubbsi* also becomes more so when in a group. This matter is not too easily explained away. Actually both forms become more light positive when alone, for reasons which are not fully explainable at this time.

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

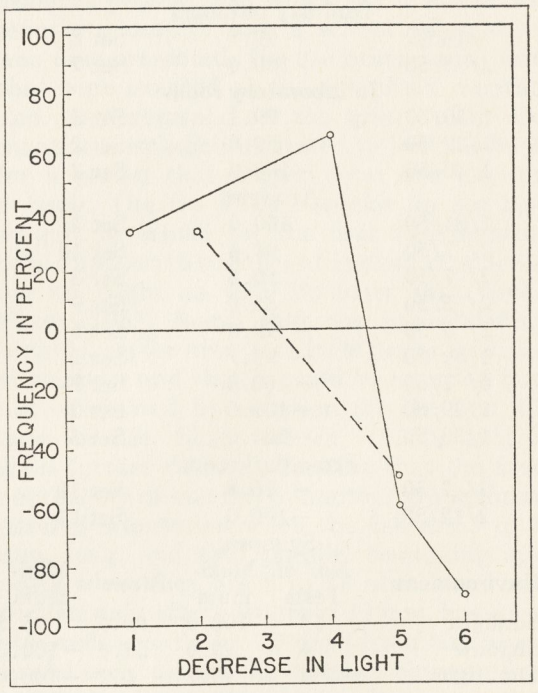


FIG. 19. The effect of the immediate past on *Atherina*. Horizontal index same as in figure 18, with which this is to be compared. The dashed line compares the outdoor values with the mean of the indoor values. Data from table 16.

TABLE 16

EFFECT OF PAST HISTORY ON THE PHOTOSENSITIVITY OF *Atherina stipes*

(All readings were made in the light chamber.)

Date	Per Cent Positive	Groups of 4 Fishes
	Daylight	
1/25/50	100.0	Set 1
2/27/50	100.0	Set 2
2/27/50	100.0	Set 3
6/ 4/50	99.5	Set 4
1/25/50	99.3	Set 1
3/26/50	97.9	Set 5
3/26/50	92.1	Set 5
2/ 8/50	89.8	Set 6
6/ 5/50	88.6	Set 7
2/ 2/50	85.0	Set 8
3/27/50	87.5	Set 9
2/12/50	80.0	Set 10
2/18/50	92.9	Set 7
2/12/50	42.6	Set 10
1/26/50	− 50.2	Set 11
1/25/50	8.0	Set 12
1/26/50	− 70.9	Set 11
2/ 2/50	− 72.9	Set 8
1/27/50	− 87.5	Set 13
2/ 8/50	− 91.2	Set 7
1/26/50	− 97.6	Set 11
1/26/50	− 99.0	Set 11
1/27/50	−100.0	Set 13
1/27/50	−100.0	Set 13
	In laboratory room	
6/ 4/50	65.6	Set 4
	At night	
1/25/40	0.4	Set 1
1/25/50	− 8.0	Set 12
1/27/50	− 33.8	Set 13
6/ 3/50	− 57.3	Set 7
1/26/50	− 74.6	Set 11
1/25/50	− 82.6	Set 1
1/27/50	− 82.9	Set 13
6/ 3/50	− 94.0	Set 4
1/26/50	− 96.9	Set 11
	From darkroom	
2/12/50	− 91.0	Set 14

Synopsis

Environment	No. of Tests	Maximum	*Mean*	Minimum
Daylight	24	100.0	*33.1*	−100.0
Laboratory room	1		*65.6*	
At night	9	0.4	*−58.9*	− 96.9
Darkroom	1		*−91.0*	

Mean of all outdoor values: 33.1
Mean of all indoor values: −50.4

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

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

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

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

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

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

TABLE 17

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

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

Species	Per Cent Positive: Before Injection	After Injection	Difference
Cyprinodon baconi (female)	−96.5	15.8	112.3
Cyprinodon baconi (male)	−69.5	−23.5	46.0
Gambusia sp. (female)	−62.6	65.8	128.4
Gambusia sp. (female)	−100.0	98.0	198.0
Mugil trichodon	−34.3	−95.4	−61.1
Haemulon flavolineatum	−100.0	−90.4	9.6
Abudefduf saxitalis	−99.4	−99.8	−0.4
Sparisoma radians	96.4	49.7	−46.7
Scarus croicensis	−67.3	−94.9	−27.6
Scarus croicensis	85.9	18.0	−67.9
Monacanthus ciliatus	100.0	80.8	−19.2

Arranged in order of mean increase

163.2	*Gambusia*
79.1	*Cyprinodon*
9.6	*Haemulon*
−0.4	*Abudefduf*
−19.2	*Monacanthus*
−46.7	*Sparisoma*
−47.7	*Scarus*
−61.1	*Mugil*

Experiment with blind *Gambusia*

Normal	Blind	After Injection
−95.3	5.4	−4.0

Experiment with *Gambusia* on black and white backgrounds

% on white background

Normal	Injected
−99.5	14.3

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

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

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

As should be expected, adding adrenalin to a blinded *Gambusia* does not change its light neutrality.

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

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

STRUCTURAL NATURE OF FISH GROUPS

THE PRECEDING FOUR SECTIONS (Introduction, Definitions and Explanations, Special Forms of Social Groupings, and Special Influences on Fish Groupings) cover mostly new data necessary to a more general consideration of fish assemblages. The present section, under its various subheadings, considers the more theoretical aspects of this study, and because, taken together, they present the views and conclusions arrived at, it has been unnecessary to present a separate Discussion. Throughout this section reference is made to various aspects of fish groups in terms of cybernetics. The cybernetic point of view so far as it concerns the present studies is taken up in detail below under the subheading Cybernetics and Fish Groups. The terminology of Ashby (1954 and 1956) has been followed throughout, and it is recommended that readers not familiar with the subject consult these two works in the case of any seeming lack of clarity or ambiguity.

CIRCULAR MOVEMENTS IN ANIMATE AND INANIMATE OBJECTS

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

Translatory influences often serve to disrupt rotational manifestations, as in wind movements and where hair whorls give way to smooth pelage. Where such destruction of rotational movement does not follow, the combination of the two may appear as harmonics, or, viewed the other way, harmonics are present except where either translatory or rotational influences are reduced to zero. These changes may be produced by either intrinsic or extrinsic influences. The studies on *Jenkinsia*, *Brevoortia*, and *Ameiurus* strongly suggest the former; the latter are obvious.

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

INTERNAL STRUCTURE OF SCHOOLS

The movement of the school as a whole is the "composition of velocities" of each individual in it, or is the "geometrical sum" of their individual trajectories and speeds in which each fish represents a vector. The individuals in such a group influence their neighbors, to equalize the speed of each fish. In a well-knit school there is little change of position of fishes, but in a looser one there is a constant shifting as individuals accelerate or decelerate. This condition could be thought of as similar to turbulent flow, where the fishes are continually changing the arrangements of the individuals, as is commonly found. Laminar flow could be similarly compared to fishes that hold fixed positions in their group and, in its full form, is probably just about as rare an occurrence in nature as is the true laminar flow of fluids.

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

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

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

Fishes in a tight school are automatically constrained to face in the same general direction, for otherwise the school would break up, with individuals moving in all directions as in a simple aggregation. Certain structural features of the locomotor equipment of the individuals are of considerable basic importance in this connection. Most, if not all, of the fishes that normally live in "permanent" schools display no, or very limited, abilities to back up. This is especially notable in the mackerels and herrings with strong schooling habits. The forms with more mobile pectorals, such as goldfish and many other Ostariophysi, while forming schools at times do not retain the formation for long, merging freely into mere disorientated aggregations or breaking up into isolated smaller groups or individuals. It would seem that this marked ability and tendency to back up freely may be instrumental in disrupting the schooling tendency. On the other hand, there is no compulsion on fishes with rather rigid pectorals to form schools from such reasons. The notable inability of sharks to back up does not prevent them, in many cases, from being solitary or traveling in very loose packs. Here their rather poorly developed optical equipment may well be a schooling inhibitor. In other words, mobile and flexible pectoral fins may tend to discourage permanent school formation in many fishes, while stiff pectorals with no backing ability present no such impediment towards the maintenance of such formations.

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

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

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

Because sound travels in water at a rate somewhat over four times its speed in air, a sound would be expected to disturb fishes in a school with such unanimity that it would be practically impossible to detect which fish heard and responded first to such a disturbance. Observations and field experiments do not yield this effect except under very special and exceptional conditions. Usually there is a well-marked "wave" of movement which passes over such a school at a much slower rate than the speed of sound even in air. The movement noted is usually in the form of a small "start" of each fish which appears as a "flurry" of activity that passes from one end of the school to the other, in a short but measurable time, which varies widely from a large fraction of a second to a few seconds, depending on the size of the school, the direction of the sound in reference to the shape of the school, and cross interference from other stimuli. If no other factors are at work within an average, more or less elongated school, and the sound source lies on the projected axis of the group, at least two phenomena prevent an almost instantaneous response of each fish in the group. The presence of the mass of fishes between the sound source would seem clearly to interfere with the hearing of those individuals that are on the far side of the school. This would be proportional to the mass of intervening fish, the nature of its disposition in the space occupied, and the nature of the sound itself. The sound-absorptive effect of fish muscle and other structures would be reënforced by the fact that the fishes are separated by small distances, and their arrangement in a school with its many reflecting surfaces should make the group act as a very effective silencer, somewhat after the principle of a Maxim silencer on a gun. The reality of such an effect is attested to by the reflected sound from a school of fishes which registers so clearly on an echo sounder. It is, of course, the remainder, not reflected back, that penetrates, or is absorbed by, the fishes, only the attenuated residue reaching the far side of the school. It appears, then, that the speed of transmission of the disturbance under such conditions is near the rate at which each agitated fish transmits its agitation to its nearby neighbors and therefore much slower than the speed of sound. In a few cases in which a sound was produced on the broadside of a school, the "flurry" was so fast as to be nearly beyond detection. Response to sound is thus based on direct perception of sound and on the perception of the response of neighbors. The relative amounts of these two cues may vary from 100 per cent to zero, the second increasing while the first decreases as the stimuli pass from one side of a school to the other. Another feature that increases the difficulty in studying this subject is the rapid conditioning that fishes show and the short time it takes for them to pass to a refractory condition in which they simply fail to react at all to a sound which has become familiar and is therefore one to be disregarded. Precise and formalized experiments are difficult to establish for the reasons discussed above, and the data on which these views were based consist of an accumulation of observations from docks and similar places in which fishes could be made to show the "start" reaction by sharp sounds made on the dock itself or the hull of a small boat.

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

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

The reactivity of various small fishes to the body juices of their own kind or of other fishes is well known and need not be discussed here. However, one experiment concerned with that type of behavior, which was undertaken by Verheijen (1956), has special pertinence to the present study. By placing two aquaria close together but mechanically and otherwise separated, except for the possibility of clear vision from one to the other, he was able to cancel all but the optical stimuli between two equal groups of *Phoxinus laevis*. A drop of tissue juice from the same species caused the fishes in one aquarium to show the typical "fright" reactions, which in such small tanks take the form of the huddling together on the bottom of all the fish in a tight "fright" school. The fish in the other tank showed essentially the same behavior but were about 10 seconds slower in forming their "fright" group. This delay was taken to represent the loss of the effectiveness of transmission of information when only the sight of a reacting companion was permitted and there was no possibility of the fishes' receiving any direct chemical stimulus. There is thus evidently a large element of "following the behavior of the other fish" in these reactions within a school or aggregation. The data of this experiment would seem to be analogous to the reactions to sound as previously described, i.e., disturbance, and reaction to it by those that could receive it, but otherwise reaction to the behavior of companions. In this connection it should be emphasized that the sense of smell is evidently very acute, as is witnessed by the studies of Walker and Hasler (1949) who showed that *Hyborhynchus notatus* (Rafinesque) was able to distinguish very delicate differences in the odors of various aquatic plants.

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

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

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

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

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

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

Thus far schools have been studied more or less as mass effects, with but little regard to the movements of individuals that make up the aggregation. By a simple means of cinematographic analysis, the movements of one fish in reference to the movements of its companions may be conveniently traced. Motion pictures taken from directly above may be used as follows. Projected a frame at a time on a drawing board, the motion pictures may be used to trace the path and speed of any or all individuals in a school. The technique simply calls for placing a dot on the "nose" of the chosen fish or fishes, a frame at a time, and then connecting these dots with a line which becomes the trajectory of the fish. Taken at silent speed, each sixteenth dot marks the passage of one second. By this means the following data were collected for analysis.

Figure 20 shows the change in locomotor

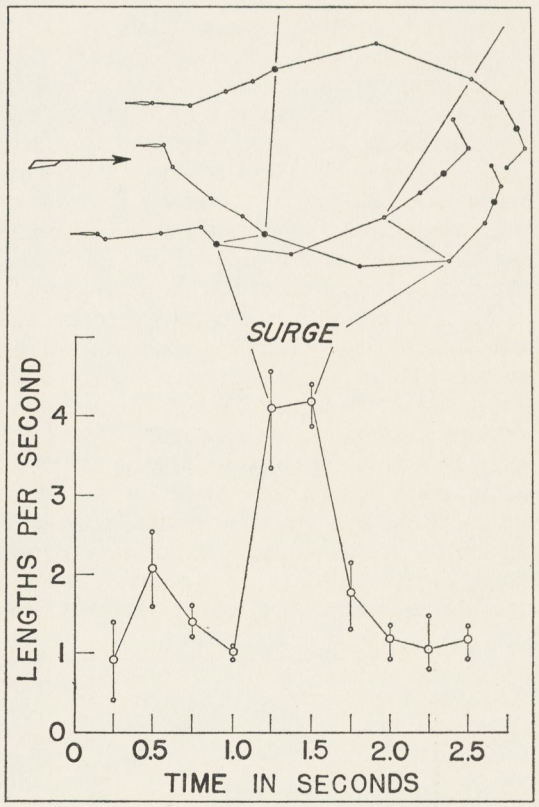


FIG. 20. Change of speed and paths of three fish in a school of *Jenkinsia* over which a shadow has passed. The arrow in the upper left indicates the direction from which the shadow, of a hand, approached. Each point on the paths of the three fishes represents 0.25 second and the larger dark ones represent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

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

The individual reactions to a thermal wall, which have been studied by Breder (1951) in terms of the whole school, as shown in figure 21, based on the paths of three advance members of a school meeting a mass of water of slightly lower temperature, are typical of the group as a whole. The time marks on the paths of the fish are as in figure 20, and the numerals note elapsed simultaneous seconds. Figure 22 is a graphic representation of the above paths. The index "distance from start" refers to the curve that runs from the lower left to the upper right, while the index "lengths per second" refers to the other curve running from the upper left to the lower right. The elapsed time is numbered the same as the diagram on the abscissa. The mean distance from the starting point measured in a straight line is indicated, together with the maximum and minimum of the three fish, connected by vertical lines to smaller circles. It will be noted that the fish up to and including the sixth second are progressing at a steady pace. This has been calculated to show a mean rate of 1.26 lengths per second. The angle with X to 51° 40′ and the deviations from it are small in spite of the irregular path of one of the fishes. Inasmuch as the lines represent the tracks of the three lead fishes, they give a fair approximation of the behavior of the school as a whole, as it was moving along smoothly in the usual manner of fish schools. This smooth flow of the school changes rapidly after the sixth second, as the influence of the cold water causes the fishes to turn back. Actually the termination of the fifth second is the final one in which no influence of the cold wall is indicated. In figure 22 the turning is quite apparent. In this graph are also indicated the distances per second traveled in the succeeding seconds. The extremes which were very small are not indicated. It may be noted that there is a marked decline in the rate of speed from the first second on. The fifth second shows a sharp

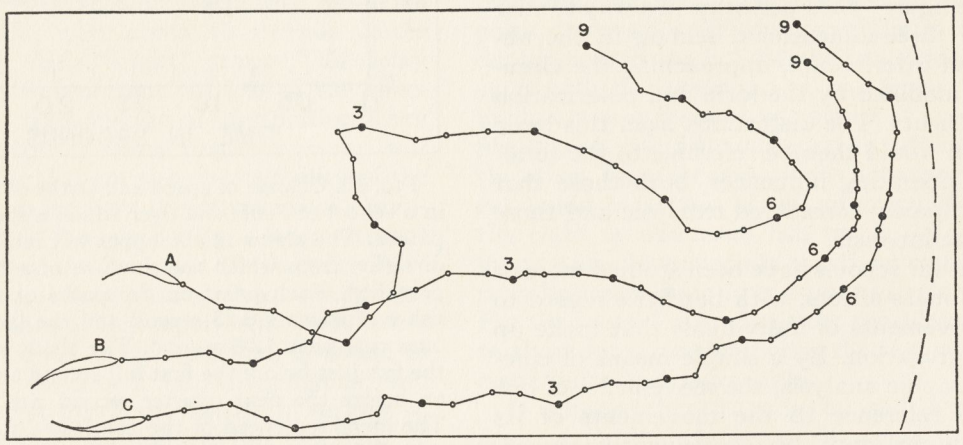


FIG. 21. The paths of three individuals in a school of *Jenkinsia* as it approaches a mass of water a fraction of a degree below that within which the fishes are swimming. The points are as in figure 20. The dashed line at the right represents the extreme advance of any of the school members into the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

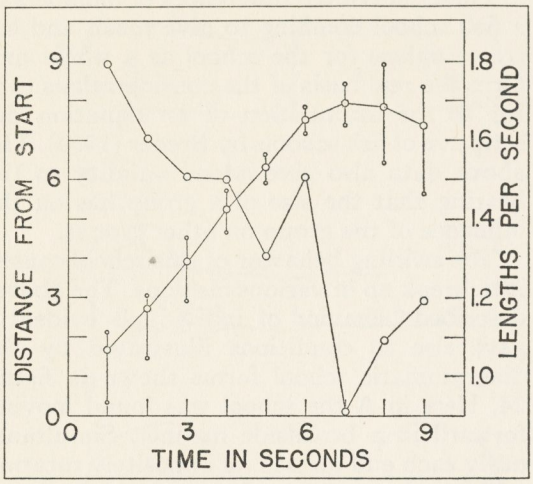


FIG. 22. A graphic analysis of the data in figure 21. The horizontal index employs the same numerals on the paths as in that figure. The vertical index, distance from start, refers to the curve, which rises from the lower left to the upper right, where it starts to descend as the fish turn back on themselves.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

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

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

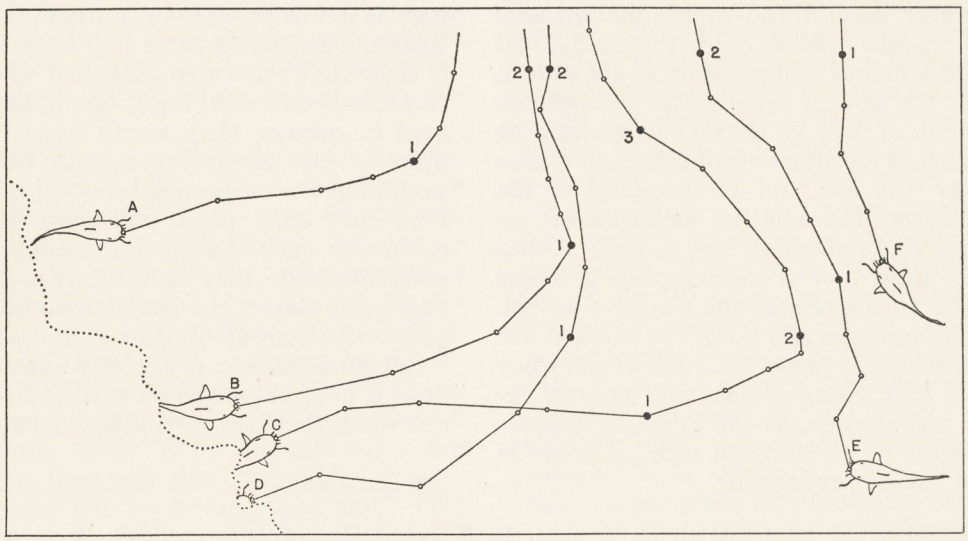


FIG. 23. Behavior of six individuals in a school of young *Ameiurus*. The four entering from the left are emerging from a mud cloud the school had stirred up, indicated by a dotted line, and the two from the right are part of a portion of the school that had become separated and is here rejoining the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

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

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

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

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

	A, B, D	E, F	C	All Fish
Maximum	5.73+	3.28+	5.60	5.73+
Mean	*2.72−*	*2.24−*	*2.79−*	*2.67+*
Minimum	1.33+	1.72+	0.80	0.80

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

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

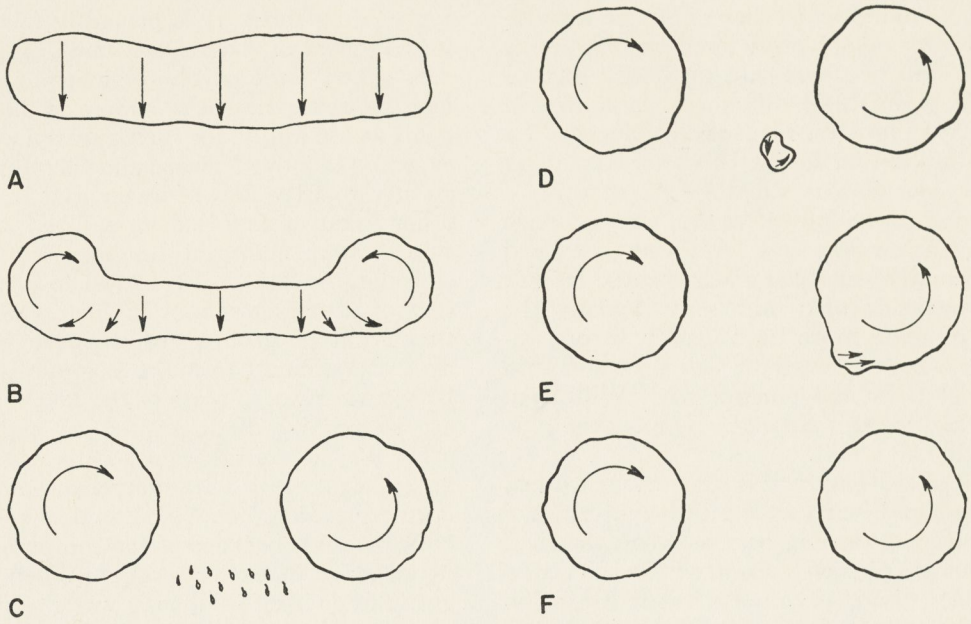


FIG. 24. Diagram of one way in which a school of young *Ameiurus* may break up. See text for explanation.

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

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

It has become apparent, however, that not all mills form in this fashion and some, for want of a better term, appear to be intrinsic, which they may indeed be in a very proper sense of the word. Such spontaneous mills have been described in *Jenkinsia* by Breder (1951), in young *Oncorhynchus keta* (Walbaum) by Hoar (1953), and are herein described for *Brevoortia tyrannus* (Latrobe) and *Ameiurus nebulosus* (LeSueur). Hoar wrote of his salmon that, "They will mill for a few minutes; they will then move off for some reason that I do not know, in a school." That statement also applies to the present author's observations, except for those described for some of the *Ameiurus* activity, which may be intrinsic only in the sense that the particular shape that the school happens to take may trigger off the mill formation, while those mills that seem to form for no evident reason may well be caused by some transient chemical or temperature moiety not available to instrumental measure at the time of observation, or might be associated with some physiological change in sufficient numbers of the school members to set off the reaction. This behavior, which it would seem possible to place under experimental control, is still not reproducible at will, but attainment of such control would seem to be a first sound step in the direction of its analysis.

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

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

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

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

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

CENTRIFUGAL AND CENTRIPETAL FORCES

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

The equation was given as

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

in which d = distance between individuals or groups; f = numbers of individuals; p = potential of each individual; fp = repulsive force; a = attractive force; and c = a measure of the cohesiveness of the group.

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

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

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

In equation 1, a may be considered as

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

It was thought that there was probably no case in nature in which p equals zero except as a very transient phenomenon, as noted in the earlier paper. The behavior of *Mugil cephalus*, which had not been studied from this standpoint at that time, has been shown earlier to be clearly a case of this sort. In it p has a value of zero for extended periods in the life of this species. It should be noted that the expression fp is an expansion of r, for repulsion, used in the primary equations of Breder (1954).

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

CYBERNETICS AND FISH GROUPS

If each fish in a school be considered as a Markovian machine, which is isomorphic with every other unit, the school itself becomes a homeostatic device composed of absolute ultrastable subsystems. The regulation implied in such a situation would necessarily be Markovian, but, as regulation blocks the flow of variety, the uniformity of behavior of fishes in schools suggests that the whole system rapidly approaches, but, of course, never reaches, a determinate one. In this view a mere loose aggregation would be a system with a larger stochastic probability and more information. The seried and regular ranks approximated by a fish school, so strikingly different in an optical sense from an unpolarized aggregation, are evidently a consequence of close packing. This decay of variety, which so constrains the individuals in a fish school, may nonetheless have important consequences to the stability of the system, and the sharp transition from aggregation to school may well be controlled by some parameters, acting as step-functions. There is an obvious reason apparent that can account for the passing of individuals from random orientation to parallel swimming when the crowding reaches a certain condition of density. It is merely that no swimming could be possible without collisions in fishes so closely packed unless they all moved in an orderly fashion, as seen in schools where there is typically just about "swimming room" between individuals. The step-functions evidently operate at this point.

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

fish, clearly the operation of a part-function.

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

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

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

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

Breder and Halpern (1946) compared various inanimate systems, such as swirling leaves and iron filings in a magnetic field, with fish mills. These comparisons, if valid, would be considered isomorphic in the present usage, as noted above in the section Circular Movements in Animate and Inanimate Objects.

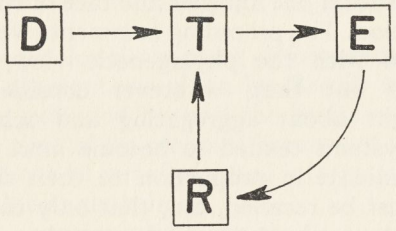


FIG. 25. Diagram of immediate effects in a closed loop regulator or error-controlled servo-mechanism.

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

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

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

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

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

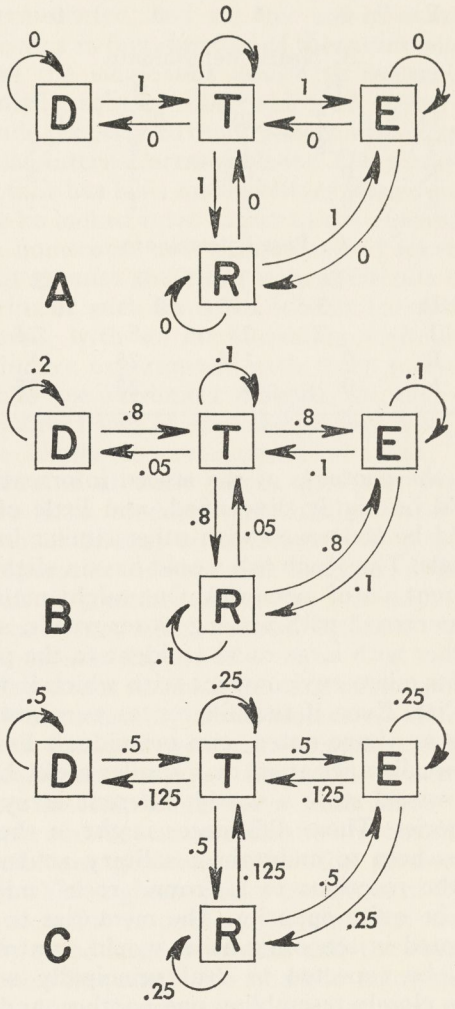


FIG. 26. Diagram of immediate effects in Markovian machine, with probabilities indicated. A. The limiting form, which is a determinate machine, identical with that shown in figure 1. B. A machine with very high probabilities and consequently nearly determinate. C. A machine with much lower probabilities,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

TABLE 18

MATRIXES OF TRANSITION PROBABILITIES OF THE DIAGRAMS OF IMMEDIATE EFFECTS SHOWN IN FIGURE 26

A. Fully determinate

	D	T	R	E
D	0	0	0	0
T	1	0	1	0
R	0	0	0	1
E	0	1	0	0

B. Nearly determinate

	D	T	R	E
D	.2	.05	0	0
T	.8	.1	.8	.1
R	0	.05	.1	.8
E	0	.8	.1	.1

C. Less determinate

	D	T	R	E
D	.5	.125	0	0
T	.5	.25	.5	.25
R	0	.125	.25	.5
E	0	.5	.25	.25

case the contents of the stored information would be highly diversified, and little of it would be concerned with other similar individuals. Thus each fish would have a slightly different set of memories. One might mainly be concerned with waving water weeds, and another with large rocks incident to the particular micro-environment with which it was familiar. Even if the differences were not so gross as above noted, two individuals living a short distance apart on a similar rocky bottom would store a vastly different array of memories. These differences might in themselves help to maintain a solitary attitude, for the reactions to a "round rock" might well be quite opposite. The memories to be expected in schooling fishes would, contrariwise, be expected to deal principally with fishes closely resembling one another, and in which the details of inanimate environment would be definitely reduced. These fishes would then have much more common content in their memories than would solitary fishes. This in itself should tend to hold the group together. For this reason alone schooling fishes would always approach closer to a true Markovian machine than a number of solitary fishes, in the sense that their memory content is so repetitive. It makes little difference whether a fish inside a school remembers only the preceding event or what happened one or two days earlier, for normally they would be the same for all practical purposes. Also, in this sense, the schooling fishes would have "less" memory content than those that lead a more diversified solitary life.

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

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

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

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

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

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

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

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

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

In another way, the searching movements of small bands of fishes in very shallow water described by Breder (1951) would seem again to be referable to excessive feed-back but through a different part of the system which was involved not directly in the maintenance of the school itself but with the need for each individual and the whole group to avoid being stranded. In either case these "searching" or "hunting" movements appear to be closely analogous to similar movements commonly seen in recording potentiometers when the tracing pen oscillates continually because of over-amplification in the feed-back circuit. Stark and Cornsweet (1958) considered such oscillations in both servo-mechanisms and organisms as the equivalent of malfunctioning or pathological manifestations.

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

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

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

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

$$
\begin{array}{lll}
\text{Pods} & & p = 0 \\
\text{Schools} & & a > 0 \\
 & c = a - (f_1 p_1)(f_2 p_2)/d^2 & \qquad (1) \\
\text{Aggregations} & & a > 0 \\
\text{Solitary} & & a = 0
\end{array}
$$

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

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

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

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

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

The above text discusses a series of homeostatic machines, with four easily recognized types and a smaller number of intermediate and generally transient situations. The question of why the four central types of social organization should be situated as they are, along such a scale, presents an interesting problem. The evolutionist or ecologist probably would begin by speculating on the possible survival values of each type of behavior. We can take, however, the more detached attitude of the cyberneticist and consider the functional relationships of this series of machines, which in itself may be considered as a single Markovian machine, of which the observed fish groups are only physical embodiments of parts of the machine. Thus without invoking any biological notions, it is possible to explore more critically the fundamental nature of the operation of these homeostatic groups. Primarily the situation is approximated by the classification in table 19.

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

TABLE 19

RELATIONSHIPS OF VARIOUS POSSIBLE FISH GROUPS

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

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

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

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

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

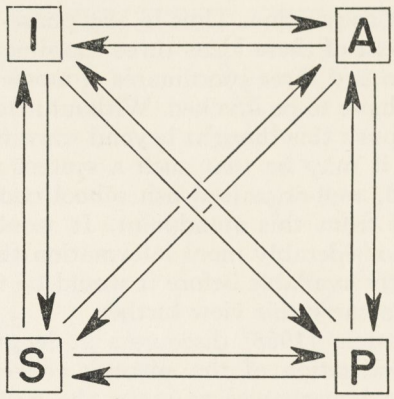


FIG. 27. Diagram of immediate effects in transitions between four nodal types of fish social structures. I, isolated (solitary); A, aggregation; S, school; P, pod.

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

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

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

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

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

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

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

TABLE 20

PROTOCOL FOR TRAJECTORIES OF THREE *Jenkinsia*

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

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

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

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

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

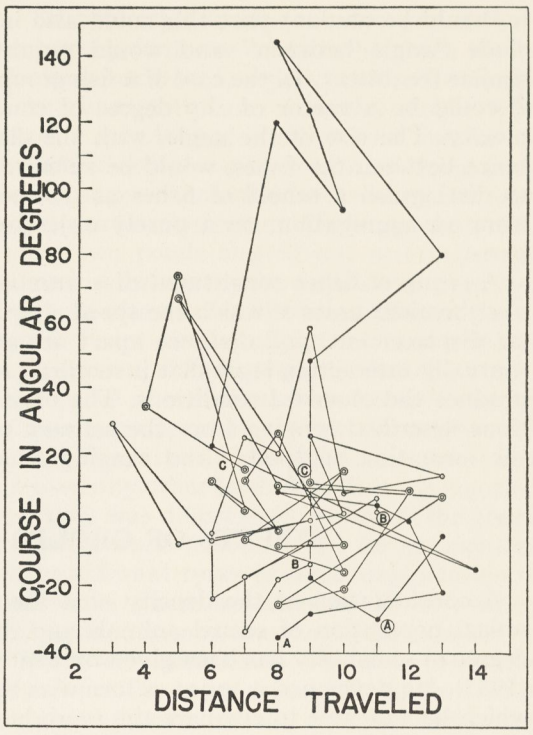


FIG. 28. Phase-space diagram of protocol of table 20. The start of each trajectory is marked by a circled letter, the end by the same letter. Repeated transfers between points are not indicated; for which, see table 20. See text for explanation.

symbols, which are described below for present purposes:

E = Essential variables. Distance apart. 0.146 to 0.174 of a fish length apart, i.e., standard error of mean of 0.16.
η = Range within which E must be kept.
T = Environment (including parts of organisms involved). Locomotor mechanism.[1]
D = Distances. Other fish increasing or decreasing distances.[2]
R = Mechanism (R and T coupled keep E within η). Decreases distance (Regulator) on increase and vice versa, light, eyes.

As E has been given as distance apart only,

[1] Environmental functions of null value, such as water temperature and so on, understood.

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

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

A group of fishes constituted of a number of equivalent units of which the speed, angular displacement, and distance apart are all mutually interacting is all that is required to produce the observed conditions. The variations described ranging from the solitary to the formation of "pods" and ranging from groups of equipotential individuals to those in which some have greater influence, as well as the distances apart the individuals establish and the details of their orientation, are all readily accounted for in this view. Rigorous mathematical treatment would obviously be of very considerable difficulty and, for present purposes at least, would not in any case appear to justify an attempt. This difficulty is common to many approaches to biological problems, but nevertheless the consideration from the mathematical viewpoint often goes far towards clarifying difficult concepts, which otherwise tend to become involved in subjective controversey in which the wrong questions are debated.

EFFECTS OF GROUPS ON POPULATION DENSITY

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

It could be argued that the fish school represents an operation by such populations which might be considered the ultimate development of insurance of reproductive encounters. If a population of fishes moved purely at random, no school would form, and certainly most, if not all, of the individuals would be lost from the reproductive "pool." The maintenance of a schooling habit would insure against this eventuality, and it is conceivable that here is the real operational basis for the existence of such groups, either the so-called permanent or the temporary schoolers. In the first case would be the schooling isospondyles, such as herrings, and in the second those such as salmon and trout. Herring and mackerel, primarily open-water fishes, usually keep in "permanent" schools, while salmon and trout usually form schools when migrating to a place which confines the fishes in small compass. That fishes range from the notably asocial to the extreme social would merely appear to be the long-time interplay of survival advantages. Thus the simple aggregations of many poeciliids evidently are adequate to insure the complete encounters of every female with a male under ordinary circumstances, while in such fishes as the abyssal ceratiods "random" encounters cannot be sufficient, the hazards of which have been guarded against not by schooling closely but by the permanent physical attachment of the males to the females, which in the present sense could be considered as the extreme of pod formation, or one might say as its "limiting form." At the opposite extreme the other "limiting form" could be the case in which purely random movements were sufficient to provide adequate reproductive encounters, a situation that would seem to have no representation in fishes. One effect of a migratory habit which has not been stressed is primarily that it provides an automatic assembly of fishes where sufficient encounters may take place. This would be useful only in the case of fishes in which such encounters would otherwise be too few to insure adequate reproduction. These features and many other similar ones are taken into account in the

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

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

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

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

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

This leaves us only with evidence that can be obtained from the physical structures of the fossils. That is to say, for instance, that a fossil, eel-like form would hardly be expected to school like a mackerel, but might form contact pods, or burrow in the bottom individually. Actually more can be gleaned from such considerations than may be at first apparent. As it has been shown that mobile pectorals, which permit backing, are associated with groups other than the proper schoolers, it seems safe to infer that this was so from the earliest times for the definite mechanical reasons already discussed. Because such mobile pectorals do not antedate the subholosteans, it follows at least that the earlier types of body and fin design associated with open water, such as in the Haplolepidae, would not have the evident impediment to schooling that a mobile pectoral presents. Thus it is not unreasonable to suppose that many of the paleoniscoids, so herring-like in many ways, may well have formed dense schools and may have occupied an ecological niche very like that occupied by the present-day herrings. "Ecological niche" as used here is the equivalent of the cybernetic "area of stability."

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

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

SUMMARY

Definitions and Explanations

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

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

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

Special Forms of Social Groupings

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

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

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

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

Special Environmental Influences on Fish Groupings

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

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

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

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

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

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

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

15. A marked relation exists between the

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

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

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

Structural Nature of Fish Groups

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

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

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

21. The transmission of information through a school, even if the cue is a sound, is ordinarily transmitted at a slower rate, related to the fish-to-fish optical or other transfer, evidently because of the silencing effect of the intervening fishes and their arrangement.

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

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

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

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

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

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

BIBLIOGRAPHY

ALLEE, W. C.

1931. Animal aggregations. Chicago, University of Chicago Press, ix+431 pp., 35 figs.

1938. The social life of animals. New York, W. W. Norton Co., 293 pp.

ALLEE, W. C., AND J. C. DICKINSON, JR.

1954. Dominance and subordination in the smooth dogfish, *Mustelus canis* (Mitchill). Physiol. Zool., vol. 27, no. 4, pp. 356–364.

ALLEN, W. E.

1920. Behavior of loon and sardines. Ecology, vol. 1, no. 1, pp. 309–310.

ANDREWS, C. W.

1946. Effect of heat on the light behavior of fish. Proc. Trans. Roy. Soc. Canada, ser. 3, vol. 40, pp. 27–31.

1952. Sensitivity of fish to light and the lateral line system. Physiol. Zool., vol. 25, no. 3, pp. 240–242.

ASHBY, W. R.

1954. Design for a brain. London, Chapman and Hall, ix+260 pp.

1956. An introduction to cybernetics. London, Chapman and Hall, ix+293 pp.

ATZ, J. W.

1953. Orientation in schooling fishes. *In* Proceedings of a Conference on Orientation in Animals, Feb. 6 and 7, 1953, Washington. Washington, D. C., Office of Naval Research, Department of the Navy, pp. 103–130.

BAERENDS, G. P., AND J. M. BAERENDS-VAN ROON

1950. An introduction to the study of the ethology of cichlid fishes. Behaviour, suppl. 1, pp. 1–242.

BAINBRIDGE, R., AND T. H. WATERMAN

1957. Polarized light and the orientation of two marine Crustacea. Jour. Exp. Biol., vol. 34, no. 3, pp. 342–364.

BALLS, R.

1951. Environmental changes in herring behavior: a theory of light avoidance, as suggested by echo-sounding in the North Sea. Jour. du Conseil, vol. 17, no. 3, pp. 274–298.

BARLOW, G. W.

1958. Daily movements of desert pupfish, *Cyprinodon macularius*, in shore pools of the Salton Sea, California. Ecology, vol. 39, no. 4, pp. 580–587.

BEEBE, W.

1935. Resume of the 1935 expedition of the Department of Tropical Research. Bull. New York Zool. Soc., vol. 38, no. 6, pp. 191–196.

BERWEIN, M.

1941. Beobachtungen und Versuche über das gesellige Leben von Elritzen. Zool. Vergl. Physiol., vol. 28, pp. 402–420.

BIGELOW, H. B., AND W. C. SCHROEDER

1948. Fishes of the western North Atlantic. No. 1, Part 1. Lancelets, cyclostomes and sharks. New Haven, Sears Foundation, Yale University, 576 pp.

BOLSTER, G. C.

1958. On the shape of herring schools. Jour. du Conseil, vol. 23, no. 2, pp. 228–234.

BONNER, J. T.

1952. Morphogenesis, an essay on development. Princeton, Princeton University Press, viii+296 pp.

BOWEN, E. S.

1931. The role of the sense organs in aggregation of *Ameiurus melas*. Ecol. Monogr., vol. 1, pp. 1–35.

1932. Further studies of the aggregating behavior of *Ameiurus melas*. Biol. Bull., vol. 63, pp. 242–270.

BREDER, C. M., JR.

1934. An experimental study of the reproductive habits and life history of the cichlid fish, *Aequidens latifrons* (Steindachner). Zoologica, vol. 18, no. 1, pp. 1–42.

1936. The reproductive habits of the North American sunfishes (family Centrarchidae). *Ibid.*, vol. 21, no. 1, pp. 1–48.

1940. The spawning of *Mugil cephalus* on the Florida west coast. Copeia, no. 2, pp. 138–139.

1942. On the behavior of young *Oligoplites saurus* (Bloch and Schneider). *Ibid.*, no. 4, p. 267.

1946. An analysis of the deceptive resemblances of fishes to plant parts, with critical remarks on protective coloration, mimicry and adaptation. Bull. Bingham Oceanogr. Coll., vol. 10, no. 2, pp. 1–49.

1947a. An analysis of the geometry of symmetry, with especial reference to the squamation of fishes. Bull. Amer. Mus. Nat. Hist., vol. 88, art. 6, pp. 321–412.

1947b. A note on protective behavior in *Gambusia*. Copeia, no. 4, pp. 223–227.

1948. Observations on coloration in reference to behavior in tide-pool and other marine shore fishes. Bull. Amer. Mus. Nat. Hist., vol. 92, art. 5, pp. 281–312.

1949a. On the relationship of social behavior to

pigmentation in tropical shore fishes. *Ibid.*, vol. 94, art. 2, pp. 83–106.

1949b. On the behavior of young *Lobotes surinamensis*. Copeia, no. 4, pp. 237–242.

1951. Studies on the structure of the fish school. Bull. Amer. Mus. Nat. Hist., vol. 98, pp. 1–28.

1954. Equations descriptive of fish schools and other animal aggregations. Ecology, vol. 35, no. 3, pp. 361–370.

1955. Special features of visibility reduction in flat-fishes. Zoologica, vol. 40, no. 8, pp. 91–98.

1957. Miniature circulating systems for small laboratory aquaria. *Ibid.*, vol. 42, no. 1, pp. 1–10.

BREDER, C. M., JR., AND E. H. ATZ

1952. Conditioned restriction of movement of fishes, fancied and real. Copeia, no. 4, pp. 261–265.

BREDER, C. M., JR., AND E. B. GRESSER

1941a. Correlations between structural eye defects and behavior in the Mexican blind characin. Zoologica, vol. 26, no. 16, pp. 123–131.

1941b. Further studies on the light sensitivity and behavior of the Mexican blind characin. *Ibid.*, vol. 26, no. 28, pp. 289–296.

BREDER, C. M., JR., AND F. HALPERN

1946. Innate and acquired behavior affecting aggregations of fishes. Physiol. Zool., vol. 19, pp. 154–190.

BREDER, C. M., JR., AND L. A. KRUMHOLZ

1943. On the locomotor and feeding behavior of certain postlarval Clupeoidea. Zoologica, vol. 28, no. 10, pp. 61–67.

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, vol. 16, no. 1, pp. 33–47.

1938. The significance of differential locomotor activity as an index to the mass physiology of fishes. Zoologica, vol. 23, no. 1, pp. 1–29.

BREDER, C. M., JR., AND P. RASQUIN

1947. Comparative studies in the light sensitivity of blind characins from a series of Mexican caves. Bull. Amer. Mus. Nat. Hist., vol. 89, pp. 319–352.

1950. A preliminary report on the role of the pineal organ in the control of pigment cells and light reactions in recent teleost fishes. Science, vol. 111, no. 2871, pp. 10–12.

1955a. A further note on protective behavior in fishes in reference to background. Copeia, no. 1, pp. 95–96.

1955b. Further notes on the pigmentary behavior of *Chaetodipterus* in reference to background and water transparency. Zoologica, vol. 40, no. 7, pp. 85–90.

BREDER, C. M., JR., AND J. ROEMHILD

1947. Comparative behavior of various fishes under differing conditions of aggregation. Copeia, no. 1, pp. 29–40.

BRIDGE, W. T.

1904. Fishes, exclusive of the systematic account of the Teleostei. *In* Cambridge Natural History. London, vol. 7, p. 452.

BROADHEAD, G. C., AND H. P. MEDFORD

1954. Interim report on mullet research. Special Serv. Bull., Marine Lab., Univ. Miami, no. 8, pp. 1–9. [Mimeographed.]

BROWN, F. A., JR., AND D. H. THOMPSON

1937. Melanin dispersion and choice of background in fishes, with especial reference to *Erycimba buccata*. Copeia, no. 4, pp. 172–181.

BURNETTE, J. F., AND OTHERS

1952. Progress report. California cooperative sardine research program. January 1, 1951, to June 30, 1952. State of California, Department of Fish and Game Marine Research Committee, pp. 1–51.

DANNEVIG, A.

1932. The influence of light on the cod. Jour. du Conseil, vol. 7, no. 1, pp. 53–59.

DAVIDSON, V. M.

1949. Salmon and eel movement in constant circular current. Jour. Fish. Res. Board Canada, vol. 7, no. 7, pp. 432–448.

DRAGESUND, O.

1958. Reactions of fish to artificial light, with special reference to large herring and spring herring in Norway. Jour. du Conseil, vol. 23, no. 2, pp. 213–227.

EBELING, A. W.

1957. The dentition of eastern Pacific mullets, with special reference to adaptation and taxonomy. Copeia, no. 3, pp. 173–185.

EDDY, M. W.

1925. Metabolic rate and bunching in catfish. [Abstract.] Anat. Rec., vol. 31, pp. 332–333.

ELLIS, G. H.

1956. Observations on the shoaling behavior of cod (*Gadus callarias*) in deep water relative to daylight. Jour. Marine Biol. Assoc. United Kingdom, vol. 35, no. 2, pp. 415–417.

EMERSON, A. E.

1939. Social coordination and the superorgan-

ism. Amer. Midland Nat., vol. 21, pp. 182–209.

ESCOBAR, R. A., R. P. MINAHAN, AND R. J. SHAW
1936. Molility factor in mass physiology: locomotor activity of fishes under conditions of isolation, homotypic grouping. Physiol. Zool., vol. 9, no. 1, pp. 66–78.

FISH, M. P.
1954. The character and significance of sound production among fishes of the western North Atlantic. Bull. Bingham Oceanogr. Coll., vol. 14, art. 3, pp. 1–109.

FRISCH, K. VON
1911a. Das Parietalorgan der Fische als funktionierendes Organ. Sitzber. Gesellsch. Morph. Physiol. München, vol. 27, pp. 16–18.
1911b. Beiträge zur Physiologie der Pigmentzellen in der Fischaut. Arch. Ges. Physiol., vol. 138, pp. 319–387.

FRY, F. E. J., AND J. S. HART
1948. Cruising speed of goldfish in relation to water temperature. Jour. Fish. Res. Board Canada, vol. 7, no. 4, pp. 169–175.

GEORGE, F. H.
1958. Machines and the brain. Science, vol. 127, no. 3309, pp. 2169–1274, May 30.

GRAHAM, J. J.
1957. Some observations on the schooling movements of the alewife in Lake Ontario. Canadian Field-Nat., vol. 71, no. 3, pp. 115–116.

GRAHAM, M.
1931. Some problems in herring behavior. Jour. du Conseil, vol. 6, pp. 252–265.

GRANT, C.
1951. Behaviorism in fishes. Copeia, no. 1, pp. 90–91.

GUDGER, E. W.
1941. The food and feeding habits of the whale shark, *Rhineodon typus*. Jour. Elisha Mitchell Sci. Soc., vol. 57, no. 1, pp. 57–72.
1944. Fishes that swim heads to tails in single file. Copeia, no. 3, pp. 152–153.
1945. Amphioxi swimming in a chain. *Ibid.*, no. 2, pp. 113–114.
1949. Fishes that rank themselves like soldiers on parade. Zoologica, vol. 34, no. 10, pp. 99–102.

HAAS, A.
1956. Über die soziale Rangordnung kleinzahliger Gruppen des Malabarbärblings (*Danio malabaricus* Jerdon). Zeitschr. f. Tierpsychol., vol. 13, no. 1, pp. 31–45.

HAAS, F.
1945. Collective mimicry. Ecology, vol. 26, no. 4, pp. 412–413.

HIATT, R. W.
1947. Food chains in Hawaiian fish ponds. Trans. Amer. Fish Soc., 1944, pp. 250–261.

HIRATA, H.
1957. Diurnal rhythm of the feeding activity of goldfish in winter and early spring. Bull. Fac. Fish. Hokkaido Univ., vol. 8, no. 2, pp. 96–107.

HOAR, W. S.
1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. Jour. Fish Res. Board Canada, vol. 8, pp. 241–263.
1953. Discussion. *In* Proceedings of a Conference on Orientation in Animals, Feb. 6 and 7, 1953, Washington. Washington, D. C., Office of Naval Research, Department of the Navy, p. 265.
1954. The behaviour of juvenile Pacific salmon, with particular reference to the sockeye (*Onchorhynchus nerka*). Jour. Fish. Res. Board Canada, vol. 11, pp. 69–97.
1955a. Phototactic and pigmentary responses of sockeye salmon smolts following injury to the pineal organ. *Ibid.*, vol. 12, pp. 178–185.
1955b. Seasonal variations in the resistance of goldfish to temperature. Trans. Roy. Soc. Canada, ser. 3, vol. 49, pp. 25–34.
1956a. The behaviour of migrating pink salmon and chum salmon fry. Jour. Fish. Res. Board Canada, vol. 13, pp. 309–325.
1956b. Photoperiodism and thermal resistance of goldfish. Nature, vol. 178, pp. 364–365.
1958a. Rapid learning of a constant course by travelling schools of juvenile Pacific salmon. Jour. Fish. Res. Board Canada, vol. 15, pp. 251–274.
1958b. The evolution of migratory behaviour among juvenile salmon of the genus *Oncorhynchus*. *Ibid.*, vol. 15, pp. 391–428.
1958c. Effect of photoperiodism on response of juvenile trout to water currents. Nature, vol. 181, pp. 1283–1284, May 3.

HOAR, W. S., M. H. A. KEENLEYSIDE, AND R. G. GOODALL
1957. Reactions of juvenile Pacific salmon to light. Jour. Fish. Res. Board Canada, vol. 14, pp. 815–830.

HORSTMANN, E.
1950. Schwarm und Phalanx als überin-

dividuelle Lebensformen. Forsch. Spiekeroog Univ. Hamburg, Stuttgart, no. 1, pp. 7–25.

1952. Form und Struktur von Starenschwärmen. Verhandl. Deutschen Zool. Gesell. Freiburg, pp. 153–159.

IMAMURA, Y.

1953. Study on the disposition of fish towards the light. Report No. 1. Study on the behavior of *Trachurus japonicus* to light. Jour. Tokyo Univ. Fish., vol. 39, no. 2, pp. 223–229.

JOHNSON, W. H.

1939. The effect of light on herring movements. Jour. Fish. Res. Board Canada, vol. 4, no. 5, pp. 349–354.

JONES, F. R. H.

1956. The behaviour of minnows in relation to light intensity. Jour. Exp. Biol., vol. 33, no. 2, pp. 271–281.

KANDA, K., AND A. KOIKE

1958a. The study on the colour of fishing net. —I. Observations on the passage of fishes through a coloured net. Bull. Japanese Soc. Sci. Fish., vol. 23, no. 10, pp. 612–616.

1958b. The study on the colour of fishing net. —IV. A change in illumination affecting the behaviour of a fish school near a coloured net. *Ibid.*, vol. 23, no. 11, pp. 680–683.

KANDA, K., A. KOIKE, AND M. OGURA

1958a. The study on the colour of fishing net. —II. Behaviours of fish schools in the neighbourhood of a coloured net. Bull. Japanese Soc. Sci. Fish., vol. 23, no. 10, pp. 617–620.

1958b. The study on the colour of fishing net. —III. Effect of the depth of colour of a net on the behaviour of a fish school near a net. *Ibid.*, vol. 23, no. 10, pp. 621–624.

KAWAMOTO, N. Y., AND H. KOBAYASHI

1952. Influence of various light conditions on the gathering rates of fish. Rept. Fac. Fish. Prefec. Univ. Mie, Japan, vol. 1, no. 2, pp. 139–150.

KAWAMOTO, N. Y., AND J. KONISH

1952. The correlation between wave length and radiant energy affecting phototaxis. Rept. Fac. Fish. Prefec. Univ. Mie, Japan, vol. 1, no. 2, pp. 197–208.

1955. Diurnal rhythm in phototaxis of fish. *Ibid.*, vol. 2, no. 1, pp. 7–17.

KAWAMOTO, N. Y., AND S. NAGATA

1952. On the relation between light gradient and fish behavior. Rept. Fac. Fish. Prefec. Univ. Mie, Japan, vol. 1, no. 2, pp. 151–173.

KAWAMOTO, N. Y., AND T. NIKI

1952. An experimental study on the effect of leading fish by fish attracting lamps. Rept. Fac. Fish. Prefec. Univ. Mie, Japan, vol. 1, no. 2, pp. 175–196.

KAWAMOTO, N. Y., AND M. TAKEDA

1950. Studies on the phototaxis of fish. Japanese Jour. Ichthyol., vol. 1, no. 2, pp. 101–115.

1951. The influence of wave lengths of light on the behavior of young marine fish. Rept. Fac. Fish. Prefec. Univ. Mie, Japan, vol. 1, no. 1, pp. 41–53.

KEENLEYSIDE, M. H. A.

1955. Some aspects of the schooling behavior of fish. Behaviour, vol. 8, nos. 2–3, pp. 183–248.

KEENLEYSIDE, M. H. A., AND W. S. HOAR

1954. Effects of temperature on the responses of young salmon to water currents. Behaviour, vol. 7, nos. 2–3, pp. 77–87.

KIMIURA, K.

1934. On the manner of swimming of sardines in a confined space. Bull. Japanese Soc. Sci. Fish., vol. 3, no. 2, pp. 87–92.

KITTEL, R., AND L. KÄMPFE

1955. Verhaltensstudien an Makrelen (*Scomber scombrus* L.) in einem Seewasseraquarium. Zool. Garten, new ser., vol. 20, no. 6, pp. 383–390.

KNIPPER, H.

1953. Beobachtungen an jungen *Plotosus anguillaris* (Bloch). Veröffentl. Überseemus. Bremen, vol. 2, no. 3, pp. 141–148.

LANGLOIS, T. H.

1935. Survival value of aggregational behavior of bass under adverse conditions. Ecology, vol. 17, no. 1, pp. 177–178.

1936. A study of the small-mouth bass, *Micropterus dolomieu* (Lacepede) in rearing ponds in Ohio. Bull. Ohio Biol. Surv., vol. 6, no. 4, pp. 191–225.

LONGLEY, W. H., AND S. F. HILDEBRAND

1941. Systematic catalogue of the fishes of Tortugas, Florida. Papers Tortugas Lab., Publ. Carnegie Inst. Washington, no. 535, vol. 34, pp. i–xi, 1–331.

MAEDA, H.

1955. Statistical analysis of the influences of various lights upon the distribution of fishes in aquarium—1. Bull. Japanese Soc. Sci. Fish., vol. 21, no. 3, pp. 159–163.

MEDCOF, J. C.

1957. Nuptial or pre-nuptial behavior of the

shad, *Alosa sapidissiuma* (Wilson). Copeia, no. 3, pp. 252–253.

MIEHE, VON H.
1911. Über den Okzipitalfleck von *Haplochilus panchax*. Biol. Centralbl., vol. 31, pp. 732–733.

MOOKERJEE, N.
1934. Reactions of goldfish to colours. Indian Jour. Psychol., vol. 9, pp. 69–78.

MORROW, J. E., JR.
1948. Schooling behavior in fishes. Quart. Rev. Biol., vol. 23, pp. 27–38.

MOSIMANN, J. E.
1958. The evolutionary significance of rare matings in animal populations. Evolution, vol. 12, no. 2, pp. 246–261.

MOULTON, J. M.
1958. The acoustical behavior of some fishes in the Bimini area. Biol. Bull., vol. 114, no. 3, pp. 357–374.

NAKAMARA, Y.
1952. Some experiments of the shoaling reactions in *Oryzias latipes* (Temminck and Schlegel). Bull. Japanese Soc. Sci. Fish., vol. 18, pp. 93–101.

NICHOLS, J. T., AND R. C. MURPHY
1918. Long Island fauna IV. The sharks. Brooklyn Mus. Sci. Bull., vol. 3, no. 1, pp. 1–34.

OCHIAI, A., AND H. ASANO
1955. On the relation between the sociality in a school of fishes and the intercepting effect of nets in the Japanese minnow, *Orizias latipes* (Temminck and Schlegel). Bull. Japanese Soc. Sci. Fish., vol. 21, no. 3, pp. 154–158.

OTTERSTRØM, C. V.
1912. Fisk. I. Pigfinnefisk. *In* Danmarks Fauna. Copenhagen, vol. 6, 199 pp. 1,

OWATARI, A., K. FURUYA, AND K. FURUYA
1953. The behaviors of the sardine schools by fish detector. Bull. Japanese Soc. Sci. Fish., vol. 18, no. 12, pp. 669–674.

OZAKI, H.
1951. On the relation between the phototaxis and the aggregation of young marine fishes. Rept. Fac. Fish. Prefec. Univ. Mie, Japan, vol. 1, no. 1, pp. 55–66.
1952. Sur la phototaxie des poissons isoles. *Ibid.*, vol. 1, no. 2, pp. 129–138.

PARKER, G. H.
1948. Animal colour changes and their neurohumors. A survey of investigations 1910 to 1943. Cambridge, Cambridge University Press, x+377 pp.

PARR, A. E.
1927. A contribution to the theoretical analysis of the schooling behavior of fishes. Occas. Papers Bingham Oceanogr. Coll., no. 1, pp. 1–32.
1931. Sex dimorphism and schooling behavior in fishes. Amer. Nat., vol. 65, pp. 173–180.

PEARSON, J. F. W., AND E. M. MILLER
1935. Aggregations of *Ameiurus natalis erebennus* Jordan, the Florida freshwater catfish. Ecology, vol. 16, no. 1, pp. 123–124.

PHILIP, J. R.
1957. Sociality and sparse populations. Ecology, vol. 38, no. 1, pp. 107–111.

PRIVOLNEV, T. I.
1956. Reaksiya ryb na svet. Voprosy Ikhtiol., vol. 6, pp. 3–20.

RASQUIN, P.
1958. Studies in the control of pigment cells and light reactions in recent teleost fishes. Part 1. Morphology of the pineal region. Part 2. Reactions of the pigmentary system to hormonal stimulation. Bull. Amer. Mus. Nat. Hist., vol. 115, art. 1, pp. 1–68.

REIGHARD, J.
1920. The breeding behavior of the suckers and minnows. Biol. Bull., vol. 38, no. 1, pp. 1–32.

RIVAS, L. R.
1953. The pineal apparatus of tunas and related scombrid fishes as a possible light receptor controlling phototactic movements. Bull. Marine Sci. Gulf and Caribbean, vol. 3, pp. 168–180.

ROTHSTEIN, J.
1958. Communication, organization and science. Indian Hills, Colorado, Falcon's Wing Press, xcvi+110 pp.

SATO, M.
1938. The role of the visual organ in aggregation of *Plotosus anguillaris* (Lacépède), with special reference to the reactions to mirror. Sci. Rept. Tohoku Imp. Univ., ser. 4, vol. 12, no. 4, pp. 489–500.

SCHAEFER, M. B.
1948. Size composition of catches of yellowfin tuna (*Neothunnus macropterus*) from Central America and their significance in the determination of growth, age and schooling habits. Fish. Bull. Fish and Wildlife Serv., vol. 51, no. 44, pp. 197–200.

SCHÄFER, W.
1955. Über das Verhalten von Jungerheringsschwarmen im Aquarium. Arch. f.

Fischereiwiss., yr. 6, no. 5/6, pp. 276–278.

SCHARRER, E.
1927. Die Lichtempfindlichkeit blinder Elritzen. (Untersuchungen über das Zwischerhirn der Fische. I.) Zeitschr. Vergl. Physiol., vol. 7, pp. 1–38.

SCHICHE, O. E.
1921. Reflex biologische Studien an Bodenfischen. 1. Beobachtungen an *Ameiurus nebulosus*. Zool. Jahrb., Jena, Zool., vol. 38, pp. 49–112.

SCHUETT, F.
1934. Studies in mass physiology: the activity of goldfish under different conditions of aggregation. Ecology, vol. 15, pp. 258–262.

SETTE, O.
1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part II —Migrations and habits. Fish. Bull. Fish and Wildlife Serv., vol. 51, no. 49, pp. 251–358.

SHANNON, C. E., AND J. MCCARTHY (EDS.)
1956. Automata studies. Ann. Math. Studies, no. 34, pp. i–viii, 1–285.

SHAW, E.
1957. Preliminary studies of the ontogeny of school behavior in the silversides, *Menidia menidia*. [Abstract.] Biol. Bull., vol. 113, no. 2, pp. 354–355.
1958a. The development of schooling behavior in the genus *Menidia*. [Abstract.] *Ibid.*, vol. 115, no. 2, p. 324.
1958b. A study of current orientation as a stimulus to schooling behavior in *Menidia*. [Abstract.] *Ibid.*, vol. 115, no. 2, p. 365.
1958c. A study of visual attraction as a stimulus to schooling behavior in *Menidia*. [Abstract.] *Ibid.*, vol. 115, no. 2, p. 365.

SHAW, R. J., R. A. ESCOBAR, AND F. M. BALDWIN
1938. The influence of temperature and illumination on the locomotor activity of *Carassius auratus*. Ecology, vol. 19, no. 2, pp. 343–346.

SHLAIFER, A.
1942. The schooling behavior of mackerel, a preliminary experimental analysis. Zoologica, vol. 27, pp. 75–80.

SKELLAM, J. G.
1951. Random dispersal in theoretical populations. Biometrika, vol. 38, pp. 196–218.

SPOONER, G. M.
1931. Some observations on schooling in fish. Jour. Marine Biol. Assoc. United Kingdom, vol. 17, pp. 421–448.

SPRINGER, S.
1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. Ecology, vol. 38, no. 1, pp. 166–171.

STARK, L., AND T. N. CORNSWEET
1958. Testing a servoanalytic hypothesis for pupil oscillations. Science, vol. 127, no. 3298, p. 588, March 14.

STEFAN, M.
1958. Physiological analysis of the interrelation between the gas exchange and shoal behaviour of certain marine and freshwater species. Zool. Zhur., vol. 37, no. 2, pp. 222–228. [In Russian; English summary.]

STEINHAUS, H.
1950. Mathematical snapshots. New York, Oxford University Press, 266 pp.

SULLIVAN, C. M., AND K. C. FISHER
1947. Temperature selection and the effects of light and temperature on movements in fish. Fed. Proc., vol. 6, pt. 2, no. 1, p. 213.

TAUTI, M., AND H. HAYASI
1926. On the shoal of fishes crowding toward a lamp. Jour. Imp. Fish. Inst. Tokyo, vol. 21, no. 4, p. 42.

TAVOLGA, W. N.
1954. Reproductive behavior in the gobiid fish *Bathygobius soporator*. Bull. Amer. Mus. Nat. Hist., vol. 104, art. 5, pp. 427–460.

THORPE, W. H.
1956. Learning and instinct in animals. London, Methuen and Co. Ltd., viii+493 pp.

TINBERGEN, N.
1942. An objectivistic study of the innate behavior of animals. Biblioth. Biotheoret., vol. 1, pt. 2, pp. 39–98.
1953. Social behavior in animals. London, Methuen; New York, Wiley, xi+150 pp.

TOKAREV, A. K.
1955. [Untitled note.] *In* Trudy Soveshchaniya po Methodike Izucheniya Kormovoi Bazy i Pitaniya Ryb. Akad. Nauk SSSR. Ikhtiol. Komiss., Trudy-Soveshch., vol. 6.

TOWNSEND, C. H.
1916. Hibernating fishes. Bull. New York Zool. Soc., vol. 19, no. 2, p. 1345.

UTTLEY, A. M.
1953. Information, machines, and brains. Trans. Inst. Radio Engin., Symp. Inform. Theory, London, pp. 143–149.

VERHEIJEN, F. J.
1953. Laboratory experiments with the her-

ring, *Clupea harengus*. Experientia, vol. 9, fasc. 5, pp. 193–194.

1956. Transmission of a flight reaction amongst a school of fish and the underlying sensory mechanism. *Ibid.*, vol. 12, fasc. 5, pp. 202–204.

WALKER, T. J., AND A. D. HASLER

1949. Detection and discrimination of odors of aquatic plants by the blunt nose minnow (*Hyborhynchus notatus*). Physiol. Zool., vol. 22, no. 1, pp. 45–63.

WALLS, G. L.

1942. The vertebrate eye and its adaptive radiation. Bull. Cranbrook Inst. Sci., no. 19, xiv+785 pp.

WALTER, W. G.

1953. Possible features of brain function and their imitation. Trans. Inst. Radio Engin., Symp. Inform. Theory, London, pp. 134–136.

WATERMAN, T. H.

1950. A light polarization analyzer in the compound eye of *Limulus*. Science, vol. 111, no. 2880, pp. 252–254.

1951. Polarized light navigation by arthropods. Trans. New York Acad. Sci., vol. 14, no. 1, pp. 11–14.

1954. Polarization patterns in submarine illumination. Science, vol. 120, no. 3127, pp. 927–932.

1955. Polarization of scattered sunlight in deep water. Deep-sea Res., vol. 3, suppl., pp. 426–434.

WATERMAN, T. H., AND W. E. WESTOLL

1956. Quantitative effect of the sun's position on submarine light polarization. Jour. Marine Res., vol. 15, no. 2, pp. 149–169.

WELTY, J. C.

1934. Experiments in group behavior of fishes; a study of the influences of the group on individual behavior. Physiol. Zool., vol. 7, pp. 85–128.

WESTENBERG, L.

1953. Acoustical aspects of some Indonesian fisheries. Jour. du Conseil, vol. 18, no. 3, pp. 311–325.

WEYL, H.

1952. Symmetry. Princeton, Princeton University Press, 168 pp.

WHEELER, W. M.

1928. The social insects. New York, Harcourt Brace and Co., xviii+378 pp.

WIENER, N.

1948. Cybernetics. New York, John Wiley and Sons, 194 pp.

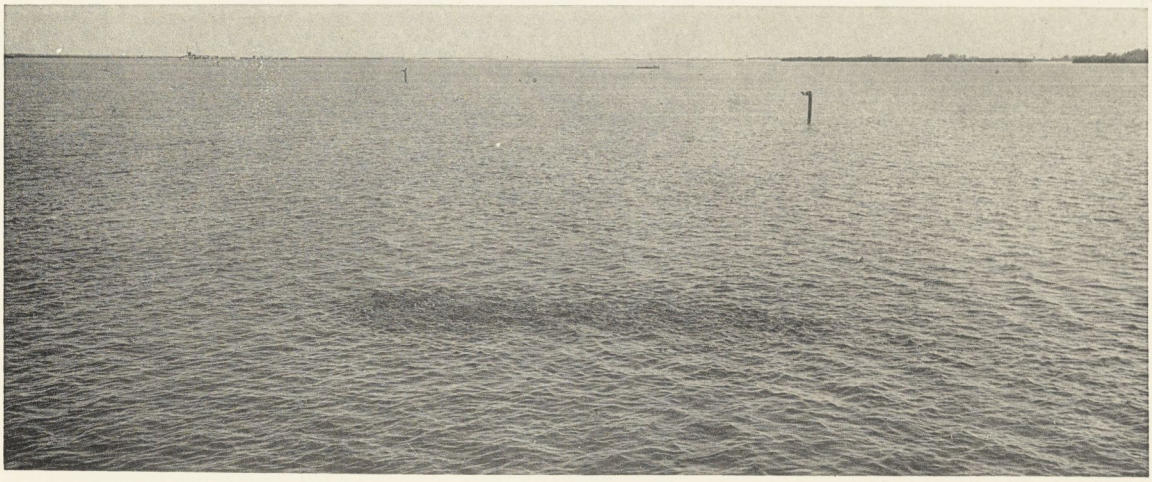
WOODHEAD, P. M. J.

1956. The behaviour of minnows (*Phoxinus phoxinus* L.) in a light gradient. Jour. Exp. Biol., vol. 33, no. 2, pp. 257–270.

YABE, H., AND T. MORI

1950. An observation on the schooling habits of bonito, *Katsuwonus vagrans*, and yellow fin, *Neothunnus macropterus*, under drifting timber on the surface of the ocean. Bull. Japanese Soc. Sci. Fish., vol. 16, no. 2, pp. 35–39.

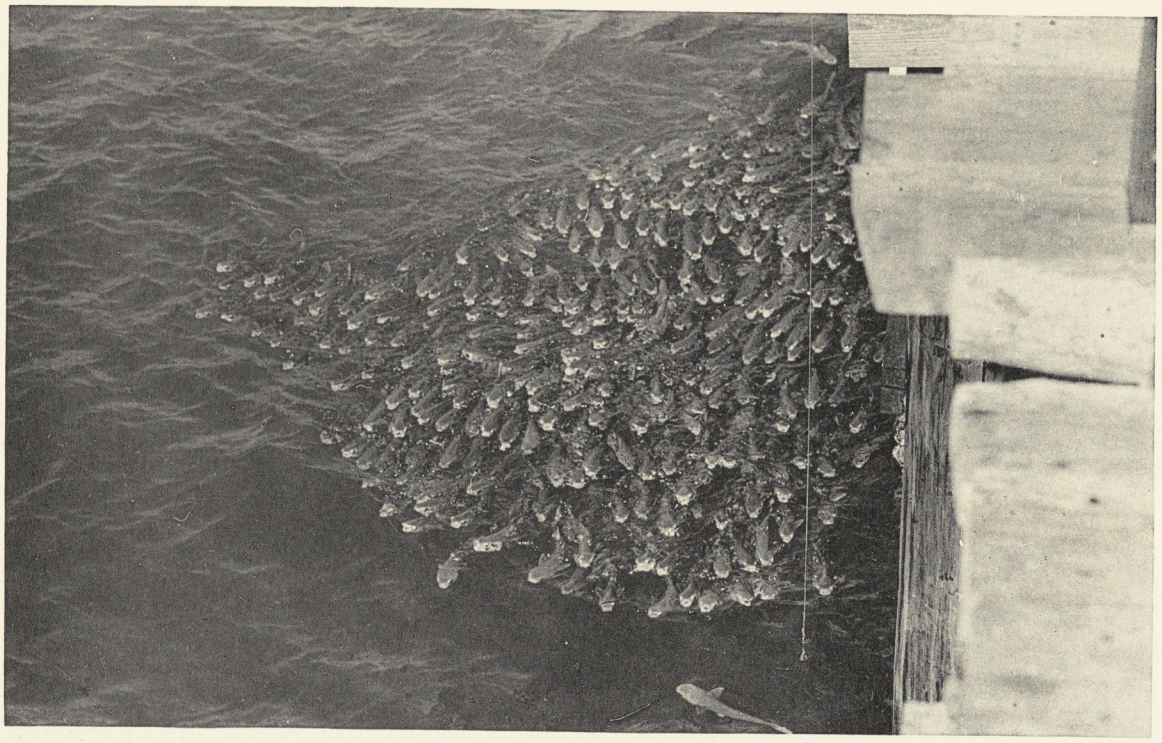
1



2

3

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



1

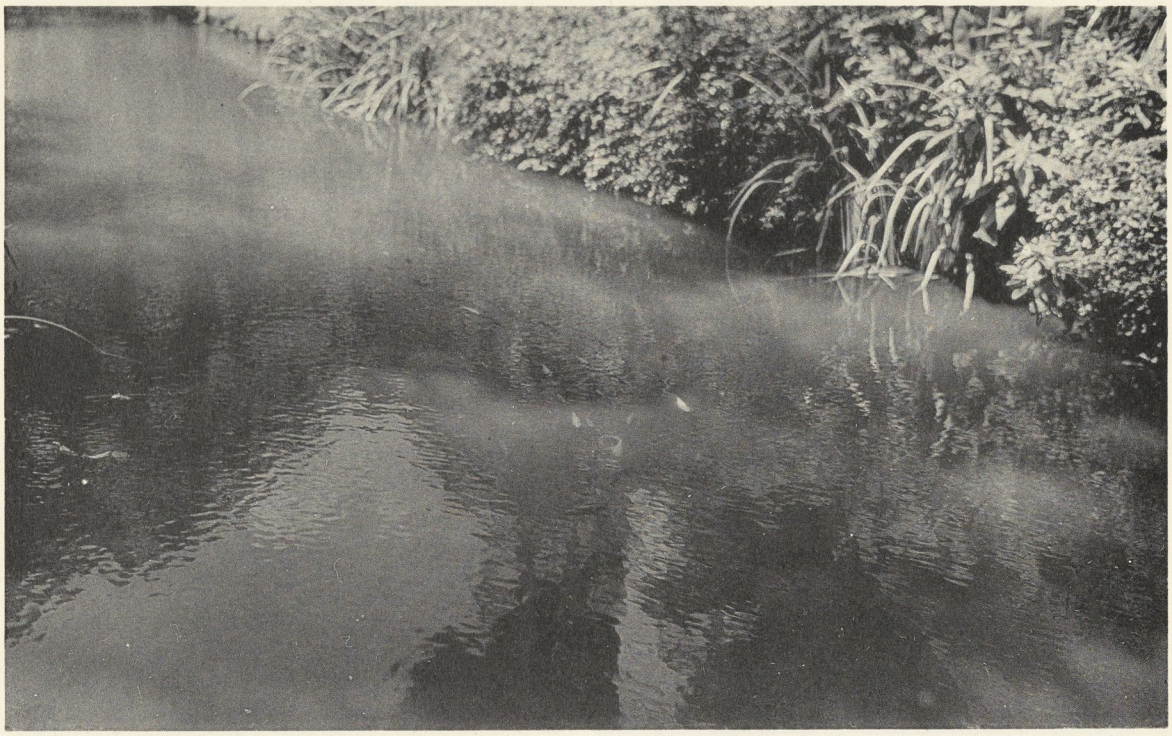
2

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

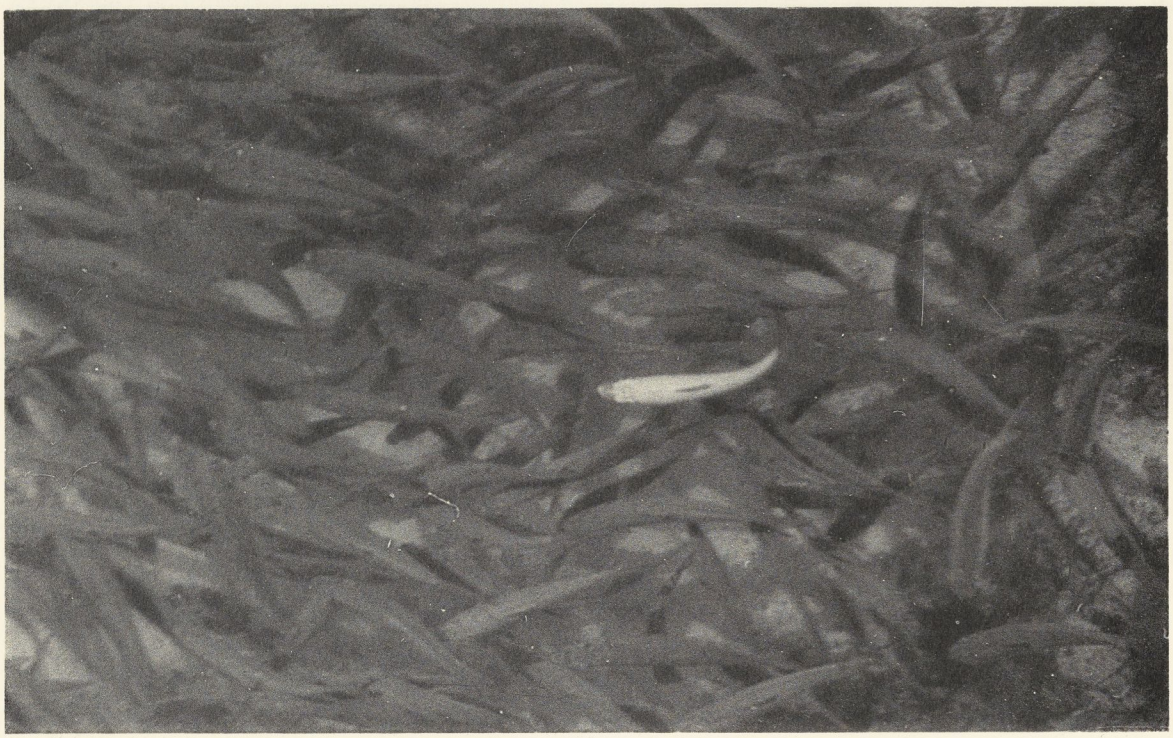
1

2

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



1



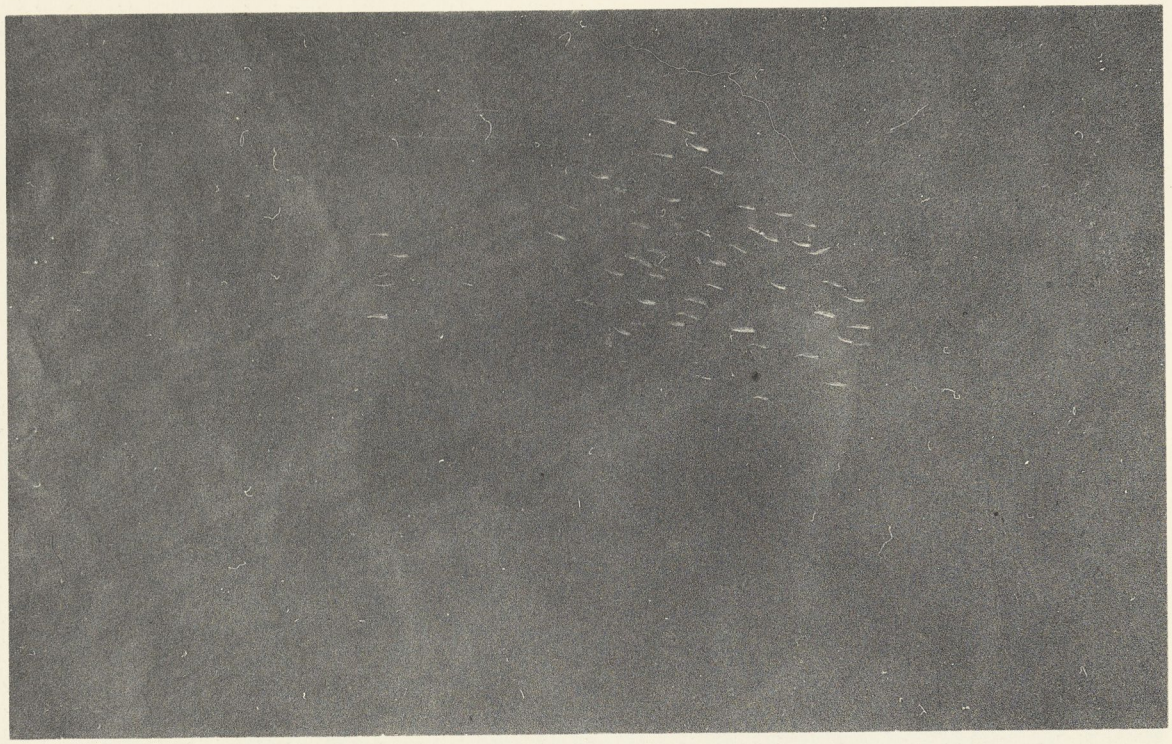
2

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

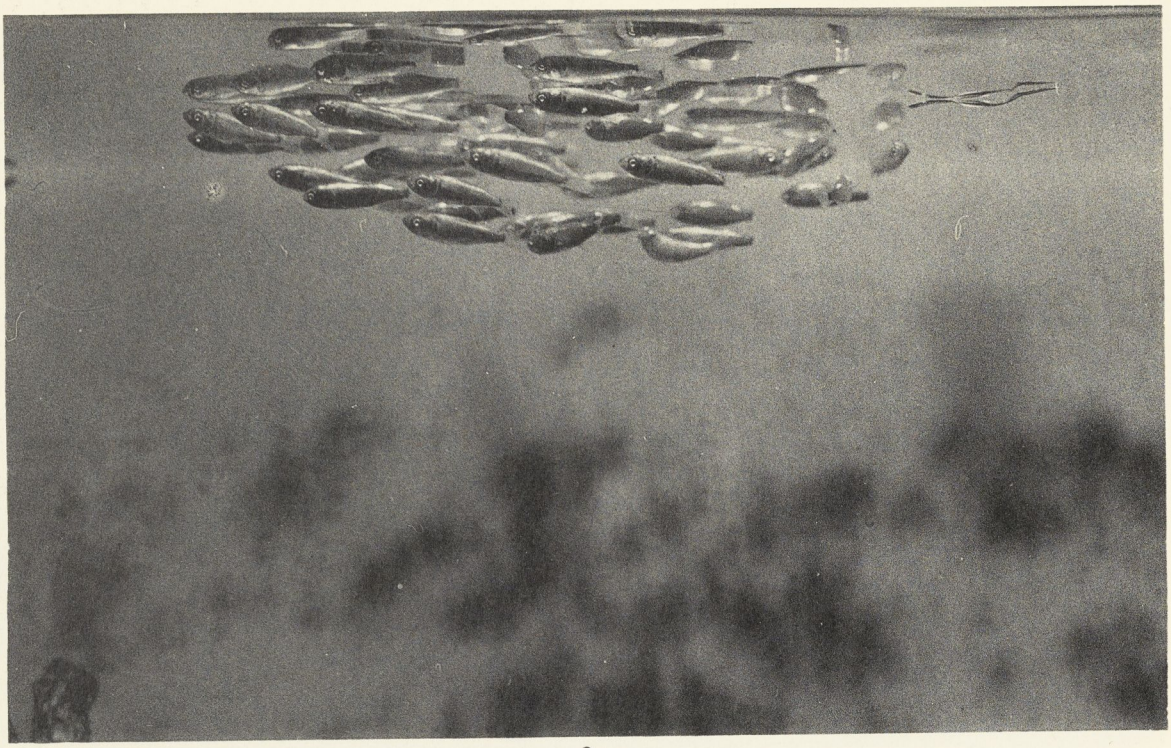
1

2

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



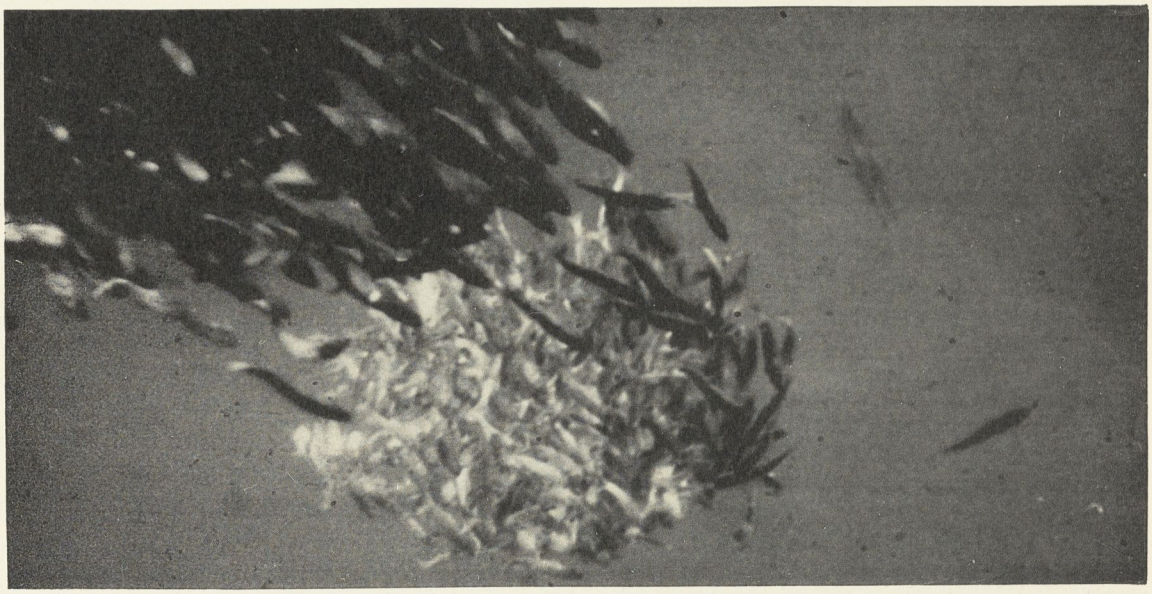
1



2

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

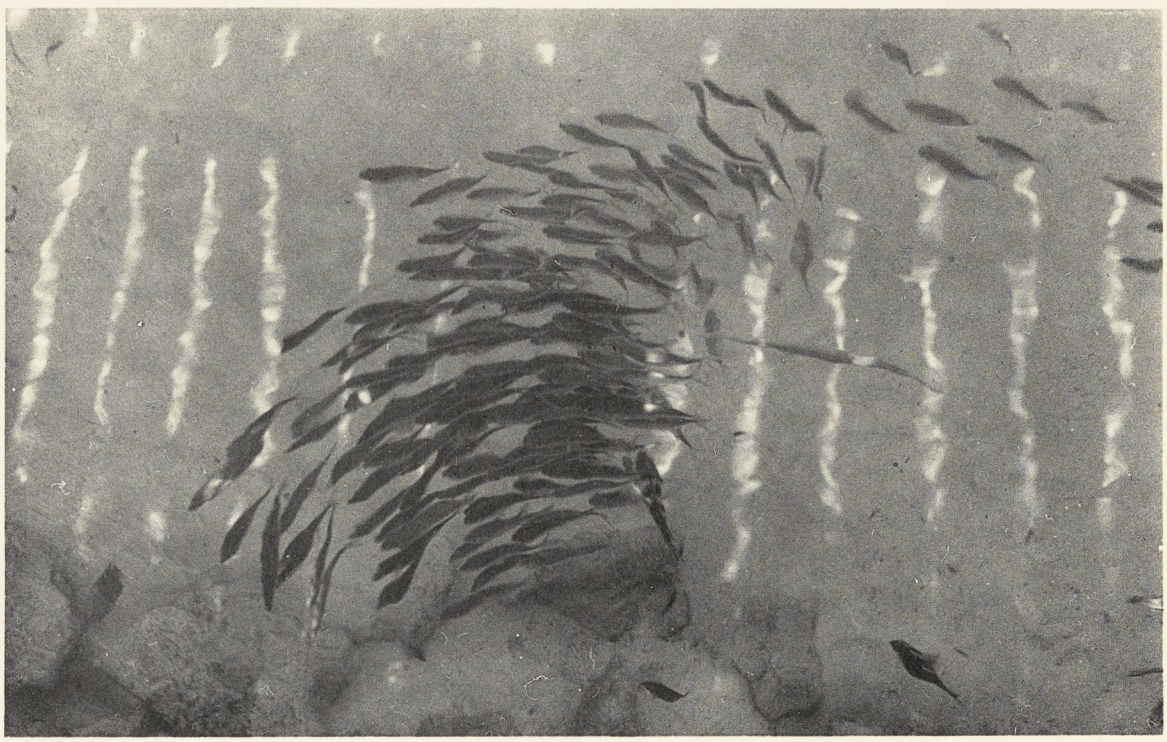
1



2

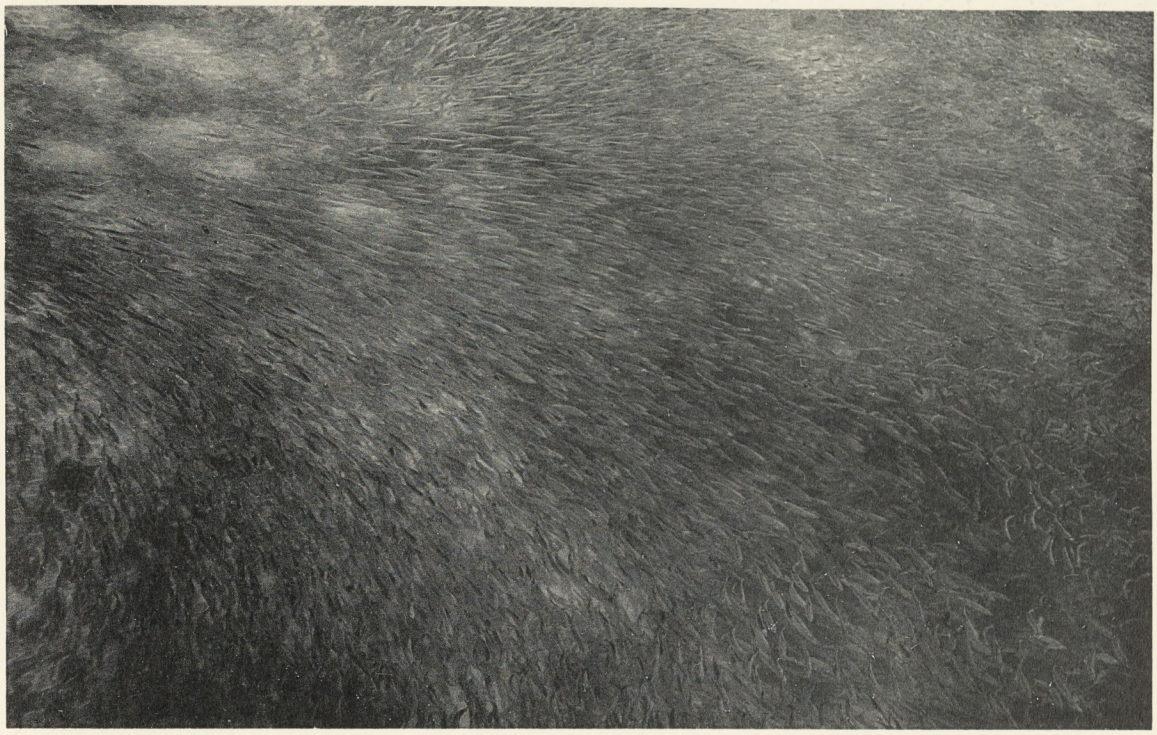
Group activity of young *Sebastodes paucispinis*. 1. A fully formed ball under the stern of a small boat. 2. The beginning of the formation of a ball. Photographs taken by Mr. Logan O. Smith near Catalina Island, California

1

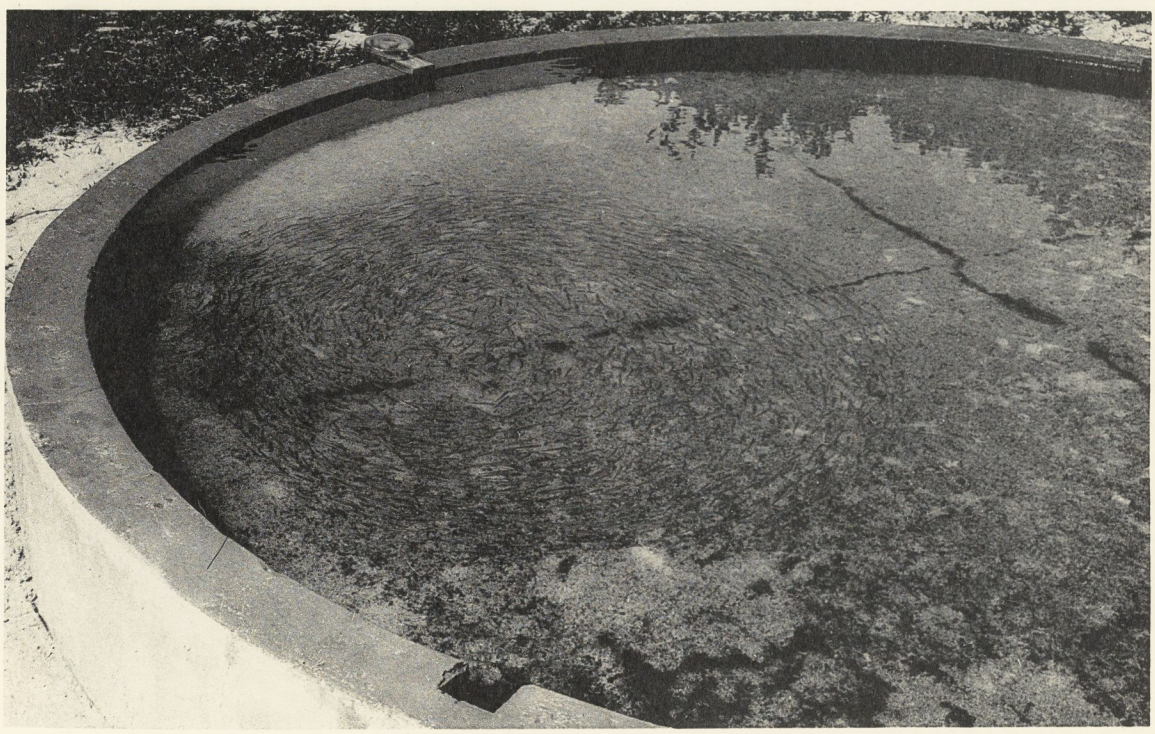


2

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

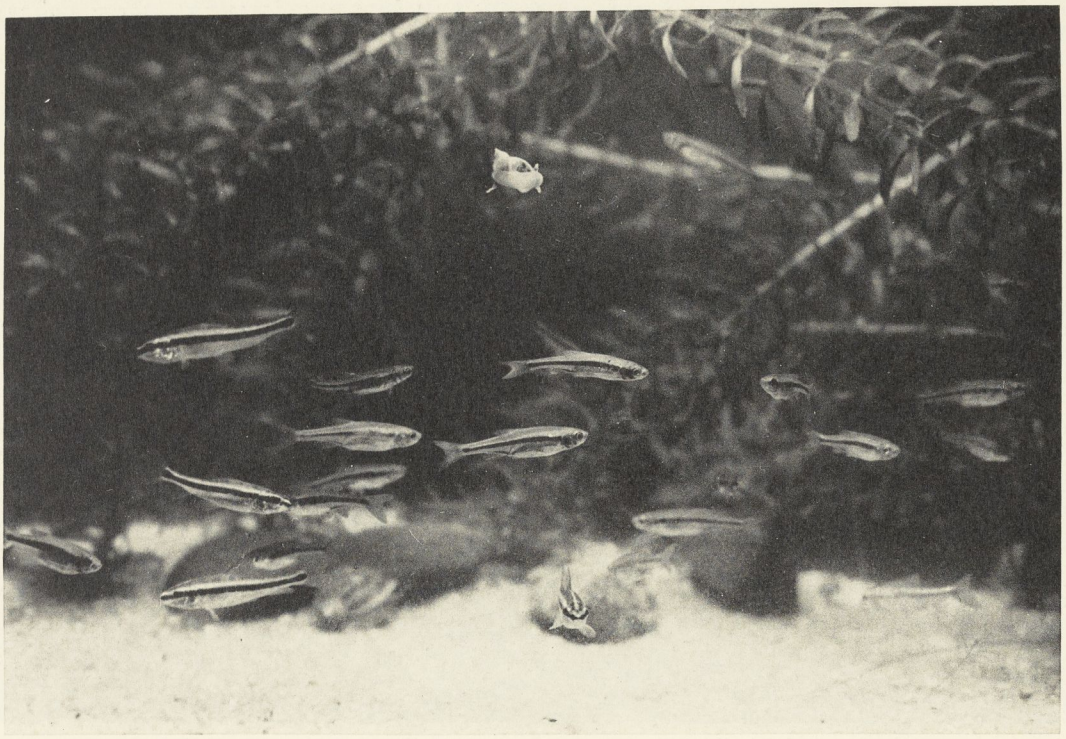


1

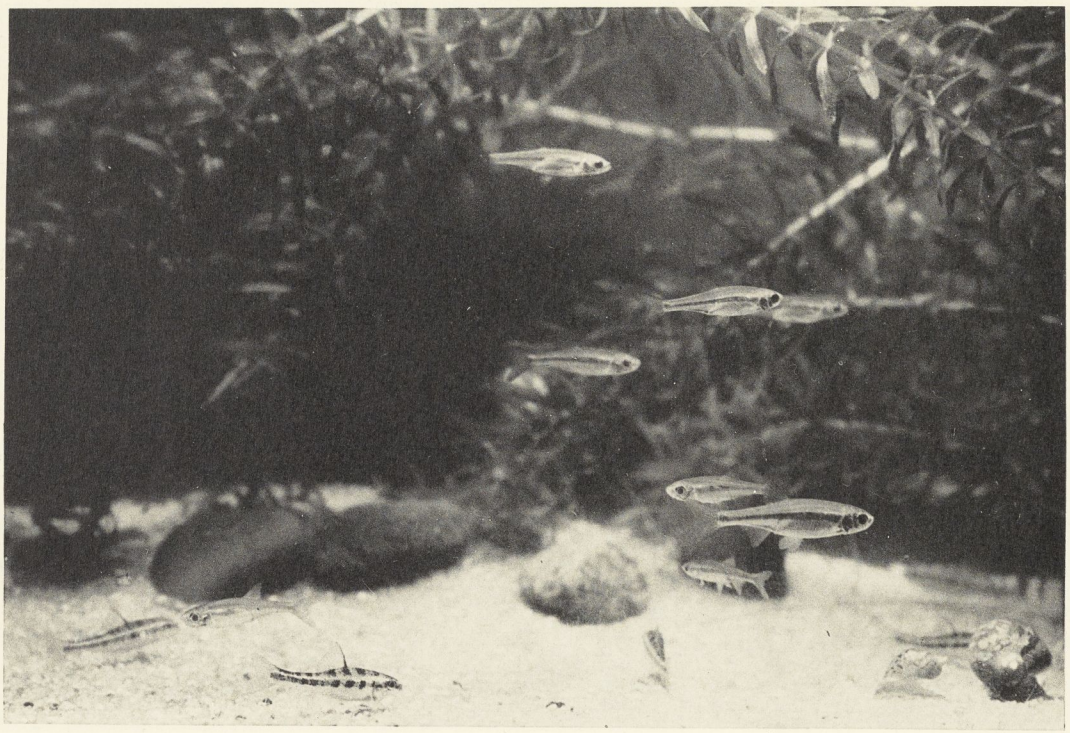


2

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

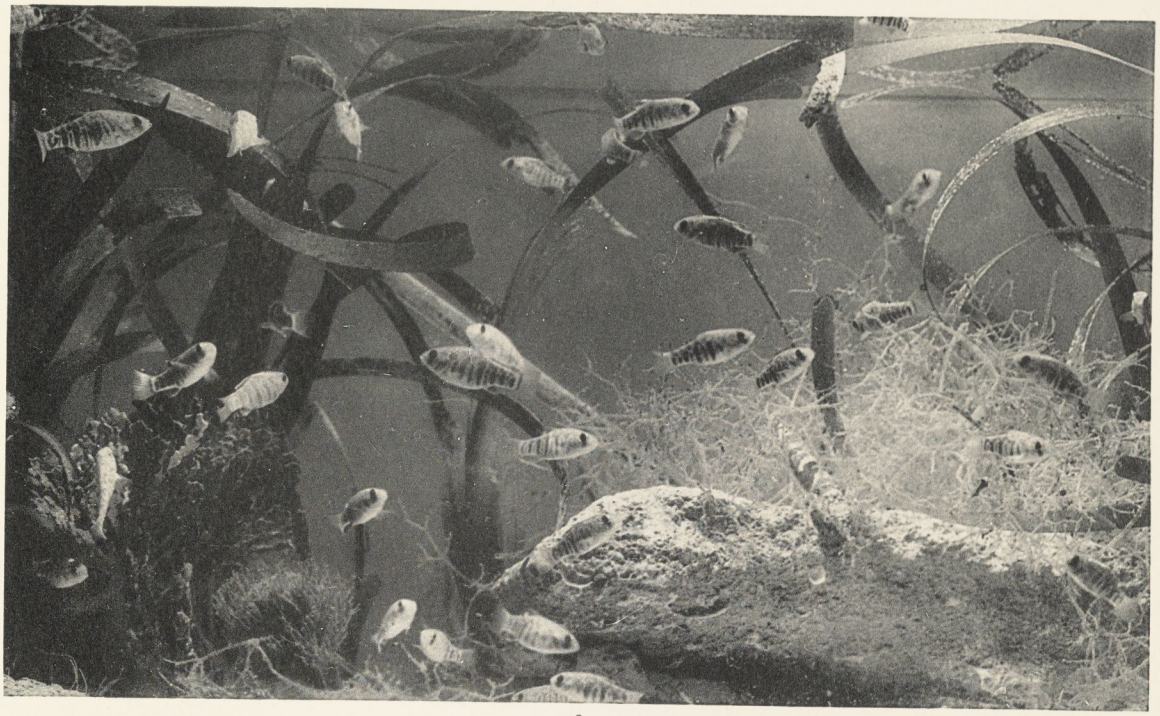


1

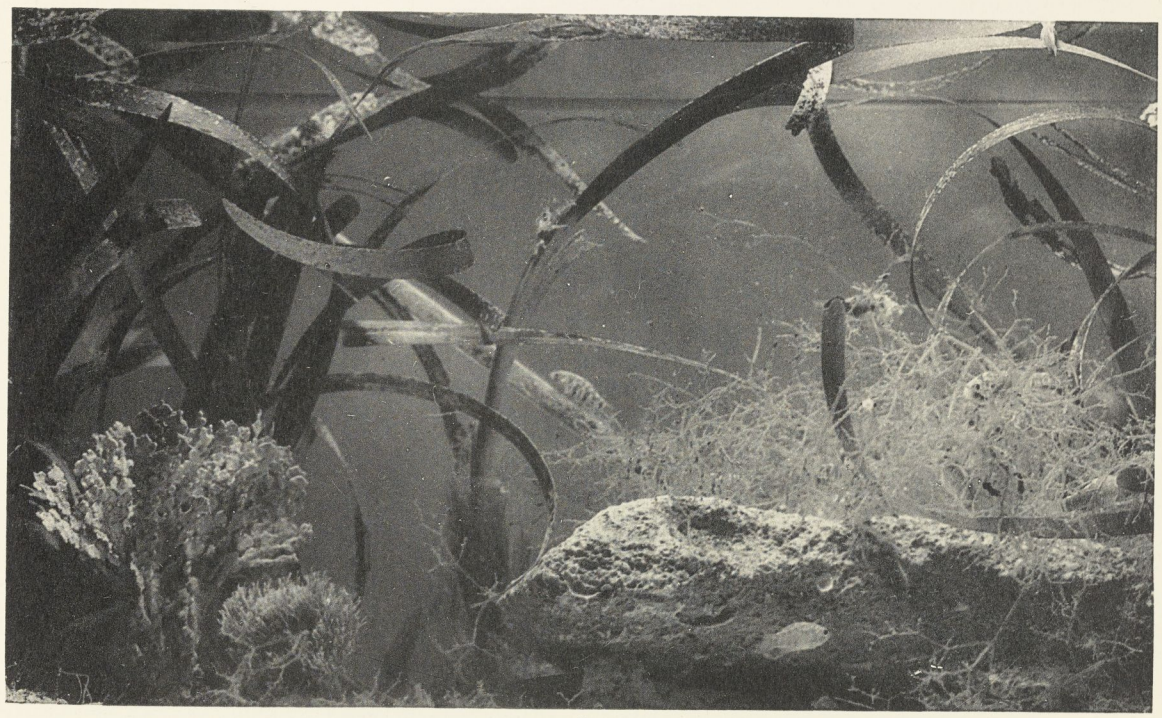


2

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



1



2

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

REPRINT No. 291 from *Animal Behaviour* 11, 1, January, 1963

P.R.N.

THE SIGNIFICANCE OF SOUND PRODUCTION DURING THE REPRODUCTIVE BEHAVIOUR OF *Notropis analostanus* (Family Cyprinidae)

BY JOHN F. STOUT

*Department of Zoology, University of Maryland, College Park, Maryland**

Introduction

The increased investigation of underwater sound production by marine organisms following the Second World War has demonstrated that sound production by fish is a common occurrence. Much of this information has come about as the result of attempts to catalogue these sounds by Fish (1952, 1954) and others. Fish (1954) found in a study of 60 species of Western North Atlantic fish that 54 species produced sounds. Sound production by several species of fresh-water minnows has been reported by Stout & Winn (1958), Stout (1959), Winn & Stout (1960), Stout (1960) and Delco (1960).

It has often been possible to correlate the fishes' sounds with definite behaviour patterns performed by the fish. Many of these sounds have been thought to be associated with some form of territorial or reproductive behaviour. Tavolga (1956, 1958) provided definite evidence that the "grunt" of the goby *Bathygobius soporator*, was connected with the reproductive behaviour of the species.

This association of a particular sound with a behaviour pattern has led to many hypotheses concerning the significance of the sound to the species of fish. For the most part these hypotheses were not supported by experimental data. A notable exception to this is the work of Tavolga (1958) which demonstrated that the "grunts" produced by a courting male, *Bathygobius soporator*, attracted females to a confined mature male as a visual stimulus and stimulated males to approach the sound source. Moulton (1956) gave evidence which indicated that the "staccato call" produced by a sea robin, *Prionotus* when played back to other sea robins resulted in more calls produced immediately after the playback was made than occurred in the interval between playbacks. Delco (1960) demonstrated that sounds produced by *Notropis lutrensis* were attractive to both males and females of this species, while sounds produced by *N. venustus* attracted only the male of this species.

*Present address: Department of Biological Sciences, Walla Walla College, College Place, Washington.

WALLA WALLA COLLEGE
CONTRIBUTIONS IN BIOLOGY
NUMBER 1

In previous publications (Stout & Winn, 1958; Stout, 1959; Winn & Stout, 1960; Stout, 1960) the sound production of *Notropis analostanus* and a brief description of the accompanying behaviour have been reported. Three sound patterns which are associated with reproductive behaviour have been described for this species. These sounds have been characterized as single "knocks", a "rapid series of knocks", and "purring". Analysis of the sounds suggested that they were basically the same sounds produced at differing rates and intensities. The male produces all 3 of these sounds as all of them have been heard when no females were present in the aquarium. Observations to date do not indicate that the female produces sounds.

This paper is a study of sound production during reproductive behaviour in the satinfin shiner, *Notropis analostanus*, and is a report on the first of a series of experiments designed to study the significance of sound production in this species. The experiments conducted on *Notropis analostanus* were concerned with investigating the significance of a "rapid series of knocks" produced during fighting behaviour between males, and "purring" sounds produced by a male during courtship of the female.

Sound as a cue in sex discrimination cannot be considered apart from other possible cues. For this reason a brief description of the sexual dimorphism and reproductive behaviour is given below.

Reproductive Behaviour of *Notropis analostanus*

A mature male and a gravid female, captured during the breeding season, are easily distinguished. The male is usually larger than the female. The colouration of the male is very different from the female and consists of a silver-blue body with fins bordered with a milky white. The female is a dull olive colour which is indistinguishable from the colouration of both males and females outside of the breeding season. A gravid female is distinguished by the distended abdomen, and a urogenital papilla which develops only during the breeding season.

At the beginning of the breeding season the males of this species establish territories beside a suitable egg-site, which is usually a crack in a rock or submerged log. Defence of the territory usually begins when one male chases another. The chasing may then develop into fighting behaviour characterized by the lateral threat display, during which the males extend their fins and swim parellel with each other, beating their tails towards each other. If the fighting becomes more vigorous, the males will often beat with their tails, nip, and bump one another. During the chasing behaviour the single "knocks" are produced by the males. These single "knocks" have also been heard during movement in a group of 2 or more fish outside of the breeding season, and thus are not always associated with definable reproductive behaviour. During the fight display the "rapid series of knocks" is produced.

When a female enters a territory, the male swims rapidly towards the female, and occasionally produces single "knocks". If the female does not swim away, the male will then rapidly circle the female several times. The male next swims quickly back to the potential egg-site, where it will vibrate its body in a manner similar to the vibration which occurs during spawning. (Further reference to this behaviour will be termed "solo-spawning"). If the female is ready to spawn she will follow the male to the egg-site and proceed to spawn. The "purring" sound is produced by the male during the circling and "solo-spawning" behaviour, and is occasionally produced during approaches to the female. The "purring" sound has not been heard during spawning.

Materials and Methods

The fish used in the experiments were collected from Paint Branch Creek and North West Branch Creek, in Prince Georges County, Maryland, between July 8th and July 27th, 1960. They were brought into the laboratory and placed in 15 gallons aquaria (24 inches long $\times$ 12½ inches wide $\times$ 12 inches high) containing approximately 50 per cent. stream and 50 per cent. conditioned tap water for a minimum of 1 day (usually 2 or 3 days), before being placed in 100 per cent. conditioned tap water. All trials were conducted in 50 gallon aquaria (36½ inches long $\times$ 18¾ inches wide $\times$ 18½ inches high), maintained ⅔-¾ full. The bottoms of the 50 gallon aquaria were covered with gravel, and on the left hand side 3 rocks were set up, 1 on top of the 2 others, to provide cracks which would be suitable for egg-sites. The water temperature ranged from 22°C. to 25°C. during the course of the experiments. All aquaria were aerated except during the experiments.

The "purring" sounds produced by courting males were recorded on Scotch magnetic tape with a Chesapeake Bay Instrument Corporation hydrophone (model No. LF-310 with N-140 internal preamplifier), a Magnecorder Tape Recorder Mechanism (model No. PT 63-A) and Recording and Playback Amplifier (model No. PJ 63-J). The "rapid series of knocks" was recorded on Magneribbon magnetic tape using a Magnemite portable tape recorder (model No. 610-EV) and the above mentioned hydrophone. A University Submergence Proof Speaker (model No. MM2L) was attached to the amplifier of the Magnecorder tape recorder for playbacks.

The duration and number of occurrences of the behaviour patterns under study were recorded on an Esterline-Angus model AW 20 Pen Operation Recorder. Other than a conscious attempt by the experimenter to avoid biasing the measurements taken, no special procedures were carried out to check on the presence of experimental bias in the recorded measurements.

The specified sounds, previously recorded on magnetic tape, were played back to the fish under various experimental conditions. Each trial consisted of a 5 minute experiment with playback of the recorded sounds, and a 5 minute control, during which a portion of the same tape used for the playback of the sounds was used, but which contained only background noise. The order of the experimental and control periods was determined by flipping a coin. Both experimental and control tapes were spliced into continuous loops so that the sounds played back during the trials were repetitions of the same sounds. In all trials the playback speaker was placed in the back right hand corner (determined when facing the aquarium) of the aquarium. Preliminary experiments suggested that if the males were fighting or courting continuously, no effect of the playback of the fighting or courting sounds could be shown. The same was true if the males were not fighting or courting. Therefore, trials were made only when the males were not fighting or courting continuously.

No measurements of the intensity of the sounds produced by the fish were made. Playbacks were made at the approximate intensity of

production by the fish, by recording a 1,000 c.p.s. sine wave, which produced a known deflection on an oscilloscope, using the same record volume as used for the original recording of fish sounds on the same tape recorder. This recorded sine wave was then played back through the same speaker used during the trials, and the playback volume which produced the same degree of deflection on the oscilloscope as the original 1,000 c.p.s. signal was determined. Thus, the tape recorder's playback volume was calibrated with its record volume so that sounds could by played back at the same intensity level at which they were recorded.

The following statistics were computed for each series of trials: (*a*) The average number of occurrences of the behaviour for both control and experimental periods, (*b*) per cent. increase or decrease of the series mean of the number of occurrences of the behaviour during the experimental periods from the control periods (the series mean of the occurrence during the control period was taken as 100 per cent.), (*c*) average duration per behavioural reaction in seconds for both experimental and control periods and (*d*) the per cent. increase or decrease of the experimental series mean of the average duration of each behavioural reaction above or below the control series mean (the control series mean of the average duration per behavioural reaction was taken as 100 per cent.).

Each series of trials was independently tested statistically. Rather than use a non-parametric procedure, a paired comparisons t-test at a 5 per cent. significance level was used to compare (1) the average number of occurrences and (2) average duration in seconds of the behavioural reactions for the control and the experimental periods. It is assumed that the differences are normally and independently distributed. Analysis of covariance tests were also run on trial series 3 and 4 in order to compare the number of occurrences of stages 1 and 2 (defined below) of the male's courtship behaviour. Since duplicate trials were conducted, the assumption of independence is open to question.

The following series of trials were performed:

1. Eleven different sets of 2 reproductively mature males were tested with the "rapid series of knocks", produced when males fight after 1 of the males had become dominant (Table I). Dominance in this study was defined as the condition where the great majority of the aggressive activity was performed by 1 of the males. The length of time which elapsed between the entrance of the 2 males into the aquarium until one of the males was dominant, varied from several minutes to an undetermined number of hours. In no case were trials carried out on fish that had been in the aquaria less than 2 hours. Trials were performed twice on 7 of the sets and once on 4 of the sets, giving a total of 18 trials. Aggressive behaviour was measured, as manifested by chasing and fighting, by lumping together these 2 types of aggressive behaviour.

2. Ten different sets of 2 reproductively mature males were tested as in series 1, except that the "purring" sound was used for the playbacks (Table II). Trials were performed twice on each of the groups, giving a total of 20 trials.

3. Eleven sets of 2 reproductively mature males and 2 females with immature eggs, were placed in the aquaria and when 1 of the males became dominant, the other male was removed (Table III). The "purring" sounds were played

Table I. The Number of Occurrences and Average Duration per Reaction of Aggressive Activity Between 2 Males During Playbacks of the Fighting Sounds. (The average duration was measured in seconds).

		Trial Number																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Mean
Number of occurrences	Exp.	32	18	17	15	26	29	27	43	25	23	36	39	17	18	21	22	9	19	24·2
	Cont.	18	9	16	4	11	7	12	13	30	20	17	35	12	9	20	10	14	6	14·6
	Increase of exp. over cont.	65·8%																		
Average duration	Exp.	1·9	1·5	1·1	4·4	2·2	2·3	2·6	1·6	3·9	2·0	2·3	4·3	1·3	1·7	2·5	1·8	2·2	1·2	2·3
	Cont.	2·0	3·1	1·0	3·4	1·9	1·8	1·6	1·1	1·7	1·3	1·7	2·5	1·2	1·4	1·9	1·8	2·4	1·2	1·8
	Increase of exp. over cont.	24·2%																		

Table II. The Number of Occurrences and Average Duration per Reaction of Aggressive Activity Between 2 Males During Playbacks of the Courtship Sounds. (The average duration was measured in seconds).

		Trial Number																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Mean
Number of occurrences	Exp.	23	26	21	22	5	10	51	10	18	43	20	18	35	36	30	53	67	7	9	12	25·8
	Cont.	8	8	14	7	3	14	26	17	9	22	15	8	29	24	13	38	54	5	7	16	16·9
	Increase of exp. over cont.	53·1%																				
Average duration	Exp.	1·9	3·7	5·4	1·6	1·2	3·5	2·7	1·8	2·2	1·5	1·7	1·2	1·6	2·4	2·4	3·3	2·4	2·9	1·1	1·3	2·3
	Cont.	1·6	2·9	3·2	1·3	1·0	2·1	2·1	2·3	2·4	1·4	1·9	0·7	2·1	2·1	2·8	4·3	2·0	2·6	1·1	1·2	2·1
	Increase of exp. over cont.	9·5%																				

back and the male's courtship of the females was measured in 2 stages. The first stage included approach and circling behaviour. The number and duration of "solo-spawning" motions made by the male comprised the second stage. Trials were repeated twice on each set of fish, giving a total of 22 trials.

4. Five sets of fish were set up as in series 3, with the exception that the sound used was the "rapid series of knocks" produced when males fight (Table IV). Trials were performed twice on each set of fish, giving a total of 10 trials.

Results

1. Playback of Fighting Sounds to 2 Males

Preliminary trials suggested that when the fighting sounds were played back to 2 males (1 being dominant) that were chasing and fighting, but not continuously, the number of occurrences and average duration per reaction of this aggressive behaviour increased. In the 18 trials carried out with this design there was a statistically significant increase (Tables I and V) for both of these measurements. Of the 18 trials 16 showed an increase in occurrence and 15 in average duration per reaction of the aggressive behaviour during the playback of the fighting sound over the control. Only 2 trials showed a decrease in occurrence, and only 3 in average duration.

2. Playback of Courtship Sounds to 2 Males

When the courtship sound was played back to 2 males, the occurrence of aggressive activity increased during the playback of the "purring" sounds to a statistically significant degree (Tables II and V). Of the 20 trials performed with this design 17 showed an increase during the playback of the courtship sounds and 3 showed a decreased occurrence. The average duration per behavioural reaction increased 13 times and decreased 7 times during the playback of the "purring" sounds (not statistically significant, Table V). During 9 of the trials "solo-spawning" was shown by the males. Eight out of these 9 showed an increased number of occurrences during the playback of the "purring" sounds, while 1 out of the 9 showed a decrease. In the other 11 trials no "solo-spawning" occurred.

3. Playback of Courtship Sounds to 1 Male and 2 Females

During playbacks of the courtship sounds to 1 male and 2 females the number of occurrences and average duration of both stages of the males' courtship increased to a statistically significant degree (Tables III, V and VI). Of these, 20 trials showed an increased number of occurrences and average duration of approach and circling behaviour (stage 1) during the playback of the courtship sounds while 2 decreased. "Solo-spawning" (stage 2) increased in occurrence during the playback of the courtship sounds during 15 of the trials, and decreased once. The average duration of "solo-spawning" increased during the experimental period 10 times, was equal with the control once, and decreased 5 times. "Solo-spawning" did not occur during 6 of the trials.

Table III. The Number of Occurrences and Average Duration per Reaction of a Male's Courtship of 2 Females with Playbacks of the Courtship Sounds. (Courtship was measured in 2 sequential stages. The first stage consisted of approach and circling behaviour and the second stage consisted of "solo-spawning" behaviour. The average duration was measured in seconds.)

			Trial number											
			1	2	3	4	5	6	7	8	9	10	11	12
Number of occurrences	Stage 1	Exp.	69	32	46	50	48	62	19	27	26	38	8	29
		Cont.	50	2	37	47	11	52	6	7	15	24	13	12
		Increase of exp. over cont.												
	Stage 2	Exp.	10	13	24	40	1	11	3	0	14	3	3	0
		Cont.	5	1	18	7	1	0	0	0	5	1	0	0
		Increase of exp. over cont.												
Average duration	Stage 1	Exp.	2·1	1·5	1·6	2·0	1·2	2·1	1·3	1·4	1·8	1·2	1·1	0·9
		Cont.	1·7	1·4	1·5	1·8	0·7	1·3	0·8	0·7	1·6	0·9	0·8	0·6
		Increase of exp. over cont.												
	Stage 2	Exp.	1·4	1·1	1·1	0·9	0·6	0·8	0·6	0	0·8	0·6	0·7	0
		Cont.	1·1	0·9	0·8	1·3	0·6	0	0	0	1·1	0·9	0	0
		Increase of exp. over cont.												

			Trial number										
			13	14	15	16	17	18	19	20	21	22	Mean
Number of occurrences	Stage 1	Exp.	32	14	11	32	48	35	24	43	52	2	34·0
		Cont.	17	6	10	15	27	29	18	26	37	4	21·1
		Increase of exp. over cont.											60·6%
	Stage 2	Exp.	0	11	0	3	16	12	34	0	16	0	9·7
		Cont.	0	6	0	0	2	15	0	0	9	0	3·2
		Increase of exp. over cont.											206·0%
Average duration	Stage 1	Exp.	1·1	2·0	1·1	1·2	1·5	1·4	1·5	1·4	1·4	2·7	1·5
		Cont.	1·2	1·0	0·9	1·1	1·2	1·5	1·2	1·2	1·1	0·4	1·1
		Increase of exp. over cont.											36·4%
	Stage 2	Exp.	0	0·6	0	0·8	1·0	0·7	0·9	0	0·8	0	0·6
		Cont.	0	0·7	0	0	0·8	0·8	0	0	0·7	0	0·5
		Increase of exp. over cont.											35·6%

Table IV. The Number of Occurrences and Average Duration per Reaction of a Male's Courtship of 2 Females with Playbacks of the Fighting Sounds. (Courtship was measured in 2 sequential stages. The first stage consisted of approach and circling behaviour and the second stage consisted of "solo-spawning" behaviour. The average duration was measured in seconds.)

			Trial Number										
			1	2	3	4	5	6	7	8	9	10	Mean
Number of occurrences	Stage 1	Exp.	53	23	10	21	67	8	21	11	9	33	25·6
		Cont.	52	27	8	18	52	9	48	26	15	41	29·6
		Decrease of exp. below cont.	—13·5%										
	Stage 2	Exp.	5	0	0	4	9	0	4	6	4	9	4·1
		Cont.	4	0	1	6	12	0	17	11	5	9	6·5
		Decrease of exp. below cont.	—36·9%										
Average duration	Stage 1	Exp.	1·0	1·1	1·5	1·1	1·1	1·2	1·7	1·0	1·3	1·6	1·3
		Cont.	1·6	1·3	1·6	1·5	1·3	1·1	1·5	0·9	1·5	1·6	1·4
		Decrease of exp. below cont.	—10·0%										
	Stage 2	Exp.	0·6	0	0	0·9	0·8	0	0·>	0·8	0·8	0·7	0·5
		Cont.	0·6	0	1·3	0·8	1·0	0	1·0	0·6	0·8	0·6	0·7
		Decrease of exp. below cont.	—20·9%										

Table V. The Results of Paired Comparisons t-tests which Compared the Number of Occurrences and Average Duration per Reaction of the Behaviour during the Control and the Experimental Periods for Each Series of Trials Given in Tables I, II, III and IV. (The 5 per cent. significance level was used for all trials).

Fish	Sound	Degrees of Freedom	Occurrence			Average duration		
			Variance	t	Confidence limits	Variance	t	Confidence limits
2 males	Fighting	17	2·16	4·45**	9·61 ± 4·56	·19	2·26*	·43 ± ·40
2 males	Courtship	19	1·95	4·58**	8·95 ± 4·09	·14	1·62	·22 ± ·29
1 male 2 females†	Courtship	21	2·09	6·14**	12·82 ± 4·35	·10	3·83**	·40 ± ·22
1 male 2 females†	Fighting	9	3·58	—1·12	—4·00 ± 8·09	·08	—1·73	—·14 ± ·19

*Significant at 5 per cent. significance level. **Significant at 1 per cent. significance level.
†The t-test was run on only stage 1 (approach and circling behaviour) of the male's courtship behaviour

4. Playback of Fighting Sounds to 1 Male and 2 Females

Playbacks of the fighting sounds to 1 male and 2 females resulted in an overall decrease of courtship which was not statistically significant (Tables IV, V, and VI). Of the 10 trials performed with this design 4 showed an increase in the number of occurrences of stage 1 during the experimental period and 6 showed a decrease. The average duration of the first stage of courtship increased during the experimental period 3 times, was equal to the control period

Table VI. The Results of Analysis of Covariance Tests which Compared the Increase or Decrease in the Number of Occurrences of Stage 1 and Stage 2 during the Male's Courtship Behaviour of the Female. (The 5 per cent. significance level was used for all trials).

Fish	Sound	Degrees of freedom	Variance	t	Confidence limits
1 male and 2 females	Fighting	14	1·13	—·45	·50±2·42
1 male and 2 females	Courtship	34	·06	2·30*	·54±·12

*Significant at 5 per cent. significance level.

once, and decreased 6 times. The occurrence of the second stage of courtship increased during the playback of the fighting sounds during 1 trial, and decreased during 6 trials. The average duration of "solo-spawning" increased during the experimental period in 4 trials and decreased in 3 trials. "Solo-spawning" did not occur during 3 trials.

Discussions and Conclusions

In the present study only males have been demonstrated to make sounds. Delco (1960) stated that the sounds produced by females of *Notropis lutrensis* and *N. venustus* caused the males to approach only the sounds of their own species. Although, no similar experiments were run with *N. analostanus*, no particular reaction to the speaker was noted in any experiments. All of these species are members of the subgenus *Cyprinella* (Gibbs, 1957), and are thus closely related. The conditions under which sounds were heard from only the females in the study by Delco did not cover all of the conditions under which sound produced by male *N. analostanus* in the present study. Observations in this study do not rule out sound production by the female, although it has not been demonstrated. The method, as described by Delco, used to demonstrate that only the female of the 2 species produces the sounds is not completely convincing, because his observations were made with both sexes in visual contact and separated by only aquarium glass. In observations on *N. analostanus* it was found that sounds produced by a male confined in a gallon jar could be heard very readily with a hydrophone placed at a distance of approximately 500 to 1,000 mm. from the jar, with the record volume set at the same level used for recording sounds from unconfined males. In the paper by Delco, the maximum distance the microphone could be placed from the fish confined in the smaller aquarium was about 150 mm. Thus, sounds could have been picked up very readily from either fish. Delco presented no evidence on how he decided which sex made the sound when they were in visual contact and separated by a glass partition which readily transmits sound from one water medium to the next.

Tables I and V demonstrate that both measurements of the intensity of aggressive behaviour between 2 males showed a statistically significant increase during the experimental period, when the fighting sound was played back. Therefore, it is concluded that the occurrence of the fighting sounds during aggressive behaviour between males stimulates the dominant male to more intense aggressive activity, and that a male which entered another male's territory while producing these sounds would be attacked more vigorously than a male which was not producing these sounds. At the present time nothing can be stated about the effect of the fighting sounds on the recessive male, or on aggressive males where a dominance relationship had not yet been established.

Two hypotheses about the function of the fighting sounds played back to the males could be made. It could be that the background noise which occurred during the control period resulted in an inhibition of aggressive behaviour, and that the playback of the fighting sounds released this inhibition. The other hypothesis is that the fighting sounds directly stimulated the male's aggressive responses. However, the hypothesis that the sounds directly affected the behaviour of the males is better substantiated when the fact is considered that the fighting sounds would always be quite similar when they occurred, while the background noise would vary to a much greater degree, especially between laboratory and field conditions.

In the series of trials during which the courtship sounds produced by a male were played

back to 2 males, there was a statistically significant increase in the occurrence of aggressive behaviour (Tables II and V) during the experimental period. Therefore, it is concluded that the courtship sounds stimulate aggressive behaviour between 2 males. Tavolga found that playbacks of the courtship sounds to males caused them to approach the sound source. No such behaviour was observed for *Notropis analostanus*. Observations (unpublished data) have suggested that a male *N. analostanus* that is courting a female is more aggressive towards other intruding males in the aquarium than is a male that is not courting. It is not surprising, therefore, that the sound which normally accompanies courtship should increase the amount of aggressive behaviour between males when played back to them. The increase of "solo-spawning" motions during the playback of the "purring" sounds even though no females were present suggests that this sound is significant in the stimulation of courtship.

In performing the experiments involving the playback of the courtship sound to 1 male and 2 females, females containing immature eggs were used. This was done because observations and preliminary experiments suggested that when a female which was ready to spawn was placed in an aquarium with a breeding male, spawning always occurred. During this courtship and spawning the male's behaviour was so continuous that it could not be increased by playbacks of the courtship sounds. On the other hand, mature males courted females with immature eggs in the normal manner, but not continuously. Tables III and V demonstrate that the approach and circling behaviour (stage 1) of the male increased significantly during playbacks of the courtship sounds. The "solo-spawning" (stage 2) behaviour also showed an increase. In the brief description of the male's courtship behaviour it was stated that "solo-spawning" immediately preceded spawning. The "solo-spawning" data were treated statistically using analysis of covariance techniques in order to test whether or not the increased occurrence of "solo-spawning" behaviour during the playbacks of the courtship sounds was greater to a significant degree than was the increased occurrence of the preceding approach and circling behaviour of the male's courtship behaviour. Table VI demonstrates that there was a significantly greater increase in the occurrence of "solo-spawning" behaviour than there was during the male's approach and circling behaviour during the playbacks of the courtship sounds. Therefore, it is concluded that the courtship sounds stimulated the male's courtship behaviour so that it occurred and proceeded to an advanced stage more often than in the absence of such sounds.

Tavolga (1958) in a similar series of experiments with the goby, *Bathygobius soporator*, was unable to demonstrate an increase in the courtship of this species during playback of the "grunts" produced by the courting male. This seems unusual, as he was able to demonstrate that females reacted much more readily to a breeding male confined in an Erlenmeyer flask, when the "grunts" were played back, than they did without the playback of the "grunts". In his study Tavolga makes no mention of a quantitative measure of the occurrence or duration of the behaviour he was studying. Thus, if the playbacks of the sound affected courtship by the male in such a way that the behaviour did not change in character, but simply increased in occurrence and duration, it would be difficult to detect without a quantitative measure of the time spent in this behaviour, unless the increase were very easily recognizable.

The playback of fighting sounds to 1 male and 2 female *Notropis analostanus* did not stimulate a statistically significant increase or decrease in the number of occurrences or the average duration of either stage of courtship by the male, as shown in Tables IV, V and VI. Therefore, it is concluded that the fighting sound does not stimulate courtship. These results when compared with those described above again demonstrate the ability of the male to discriminate between the fighting and courtship sounds.

Data have been offered above which demonstrate that the fighting and courtship sounds produced by male *Notropis analostanus* are discriminated between and reacted to differentially by males of this species. Delco (1960) and Tavolga (1958) worked with sound produced by more than one species. Delco (1960) studied 2 sounds, 1 characteristic for *Notropis venustus* and the second characteristic for *N. lutrensis*. These 2 sounds were presented simultaneously at either end of a large tank. It was found that a fish of either specieswould react to the sound normally produced by its own species by remaining in the end of the tank from which it was emanating for a longer period of time. It was concluded that the species of fish could discriminate between the sound produced by its own species and the sound produced by

the other species, and that this discrimination might act as an isolating mechanism between the 2 species. Tavolga (1958) played back the sound of a species of blenny to *Bathygobius soporator* that was very similar to the sound produced by this species, and obtained results similar to the playback of the sounds of *B. soporator*. These results may indicate a rather poor discriminative ability for *B. soporator*. This may be a reflection of the absence of a well developed auditory system such as that found in ostariophysid fishes. The ability of fish to discriminate between artificially produced sounds has been demonstrated for a number of species, especially ostariophysid fishes. Much of this work has been done by German workers studying the European minnow *Phoxinus laevis*. Kleerekoper & Chagnon (1955) demonstrated pitch discrimination in the American minnow *Semotilus atromaculatus*. To date, however, no report of discrimination between different sounds produced by the same fish, and reacted to differentially without previous laboratory conditioning has been made. Studies of this nature have been carried out. with birds. Frings, *et al.* (1958) were able to demonstrate a differential reaction of crows (*Corvus brachyrhynchos brachyrhynchos*) to playbacks of recorded "assembly" and "alarm" calls produced by the species and Frings *et al.* (1955) were able to demonstrate discrimination between "feeding" and "alarm" calls of the herring gull *Larus argentatus*.

The exact function of the fighting sounds in the establishment and maintenance of the territory, which involves aggressive behaviour, by the males of *N. analostanus*, cannot as yet be determined. It has been demonstrated that the fighting sound is stimulatory to the male possessing the territory in that he will be more aggressive towards another male which enters his territory when the fighting sound is played back. The fighting sound would allow for one male to discriminate the sex of another male as would the differential colouration and behaviour of the 2 sexes during the reproductive season. However, it has not been demonstrated that production of the fighting sound by the protecting male would hasten the retreat of a male intruder. Although there is little other than observational evidence, it is thought that sounds produced by territorial male birds tend to discourage the invasion of the bird's territory by another male of its own species.

The "purring" sounds produced by males during courtship have been demonstrated to be stimulatory to courtship behaviour. Since both sexes were present during the playbacks of the courtship sound, it cannot be stated whether the courtship sounds effected primarily the male, the female, or both sexes.

The data reported above demonstrate the utilization of one of the available cues in the sex discrimination and synchronization of the reproductive behaviour of *Notropis analostanus*. The differential nuptial colouration and behaviour must also be considered.

Summary

1. A brief description of the reproductive behaviour of *Notropis analostanus* was given,

2. The sounds produced by fighting males increased the occurrence and average duration of the aggressive behaviour of reproductively mature males.

3. The sounds produced when males court females increased the occurrence of aggressive behaviour between males, but did not increase the average duration of aggressive behaviour. "Solo-spawning" increased when the courtship sounds were played back, even though no females were present.

4. The courtship sounds when played back to 1 male and 2 females increased the occurrence and average duration, of courtship behaviour.

5. The fighting sounds when played back to 1 male and 2 females did not increase the occurrence and average duration of courtship behaviour.

6. Males are able to discriminate between the 2 sounds.

7. No orientation to the sound source was encountered.

Acknowledgments

This research is supported by grants from the National Institute of Neurological Diseases and Blindness, U.S. Public Health Service (B-3241), and the Office of Naval Research (N. R. 104-489) made to Dr. Howard Winn as principle investigator, the Sigma-Xi RESA Research Fund, by a National Science Foundation Summer Fellowship for Graduate Teaching Assistants, and by a Public Health Service Predoctoral Fellowship. Special thanks are due to Dr. Howard Winn for guidance and criticism during the investigations and for criticising the manuscript.

REFERENCES

Delco, E. (1960). Sound discrimination by males of two cyprinid fishes. *Texas J. Sci.*, **12,** 48-54.

Fish, M. P. (1954). The character and significance of sound production among fishes of the Western North Atlantic. *Bull Bingham Oceanog.. Coll.*, **14,** 1-109.

Fish, M. P., Kelsey, A. S., Jr. & Mowbray, W. H. (1952). Studies on the production of underwater sound by North Atlantic coastal fishes. *J. Marine Res.*, **11,** 180-193.

Frings, H., Frings, M., Cox, B. & Peissner, L. (1955). Auditory and visual mechanisms in food-finding behavior of the herring gull. *Wilson Bull.*, **67,** 155-170.

Frings, H., Frings, M., Jumber, J., Busnel, R., Giban, J. & Gramet, P. (1958). Reactions of American and French species of *Corvus* and *Larus* to recorded communication signals tested reciprocally. *Ecology* **39,** 126-131.

Gibbs, R. H., Jr. (1957). Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. I. Systematic status of the subgenus *Cyprinella*, with a key to the species exclusive of the *lutrensis-ornatus* complex. *Copeia*, **1957,** 185-195.

Kleerekoper, H. & Chagnon, E. C. (1954). Hearing in fish, with special reference to *Semotilus atromaculatus atromaculatus* (Mitchell). *J. Fisheries Res. Board Canada*, **11,** 130-152.

Moulton, J. M. (1956). Influencing the calling of sea robins (*Prionotus spp.*) with sound. *Biol. Bull.*, **111,** 180-193.

Stout, J. (1959). The reproductive behavior and sound production of the satinfin shiner. *Anat. Rec.*, **134,** 643-644 (abst.).

Stout, J. (1960). The significance of sound production during the reproductive behavior of *Notropis analostanus*. *Anat. Rec.*, **138,** 384-385 (abst.).

Stout, J. & Winn, H. (1958). The reproductive behavior and sound production of the satinfin shiner. *Anat. Rec.*, **132,** 511 (abst.).

Tavolga, W. N. (1956). Visual, chemical, and sound stimuli as cues in the sex discriminatory behavior of the gobiid fish, *Bathygobius soporator*. *Zoologica* **41,** 49-64.

Tavolga, W. N. (1958). The significance of underwater sounds produced by males of the gobiid fish, *Bathygobius soporator*. *Physiol. Zool.*, **31,** 259-271.

Winn, H. & Stout, J. (1960). Sound production by the satinfin shiner, *Notropis analostanus* and related fishes. *Science*, **132,** 222-223.

(*Accepted for publication* 12*th June*, 1962
Ms. number: 278).

UNIVERSITY OF CALIFORNIA UNIVERSITY EXTENSION

BERKELEY, CALIFORNIA

The Galápagos Islands Symposium

THE SYMBIOSIS BETWEEN SEA ANEMONES AND FISHES

by

Richard N. Mariscal
Department of Zoology
University of California
Berkeley 4, California

GALÁPAGOS INTERNATIONAL SCIENTIFIC PROJECT

January - March, 1964

RICHARD N. MARISCAL

PREVIOUS POSITIONS:

Teaching Assistant, Zoology, University of California, Berkeley
Teaching Assistant, Hopkins Marine Station, Stanford University
Research Assistant, Entomology, University of California, Berkeley
U.S. Naval Officer, First Lieutenant and Gunnery Officer, U.S.S. Manatee (AO-58)

SUMMARY OF PREVIOUS AND CURRENT RESEARCH ACTIVITIES:

Recently completed study on the entoproct, Barentsia gracilis, from San Francisco Bay - morphology and general life history.

Currently engaged in study of form and function of nematocysts of coelenterates - the ultrastructure as revealed by electron microscopy, as well as physiology.

Also working on relationship between sea anemones and anemone fishes from the tropical Pacific as part of nematocyst studies above.

SIGNIFICANT PUBLICATIONS:

A.M. thesis now being prepared for publication: 'The morphology and natural history of the entoproct, Barentsia gracilis."

Study on 'The nematocysts of the corallimorph anemone Corynactis californica', being prepared for publication.

RESEARCH PROPOSAL

of

Richard N. Mariscal

Based on a cursory review of the literature, one might be led to the conclusion that there are no Anthozoa, other than corals, and only a few Hydrozoa in the Galápagos Archipelago. This is no doubt a direct function of the amount of intertidal and subtidal collecting which has been conducted in these islands. Therefore, there are two major research routes which I plan to follow while in the Galápagos. One will be to make as complete a collection as possible of the coelenterate fauna (excluding the corals) from many different intertidal localities, with special attempts being made to study the fauna at those islands having unusual hydrographic conditions or differing markedly in this regard from others in the Archipelago. Secondly, and of equal importance, will be an attempt to discover and study all possible cases of symbiosis between coelenterates and other invertebrates and vertebrates. I will be especially looking for examples of the giant anemones and their pomacentrid fish symbionts which are so characteristic of the Indo-Pacific regions.

The coelenterates will be brought back to the continental United States for subsequent taxonomic study as well as electron microscopy. The electron microscopy will be part of a study in progress concerning the form and function of coelenterate nematocysts.

Ranking not far behind the above activities will be several other research endeavors. I am also currently engaged in a long-term taxonomic and morphologic study of the phylum Entoprocta. I plan to collect as many examples as possible of this group for subsequent study. Finally, in order to make full use of this opportunity to work in the Galápagos, I hope to undertake a study of general reef and shore ecology, in conjunction with a study of intertidal zonation. This kind of study would prove extremely valuable by way of comparison with other parts of the world, and is something which is completely unknown for the Galápagos region. This may turn out to be an extremely ambitious endeavor, and indeed, it is something which could be best done by several investigators working together. I hope to examine this possibility after meeting with other G.I.S.P. marine biologists.

Much of the above work will be done during periods of low tides, however, the availability of these will in no way hamper my progress, since I plan to use every opportunity to collect and make my studies with skin diving equipment. I also plan a good deal of underwater photography which will be invaluable for not only the general ecological study but also for specific coelenterate studies.

THE SYMBIOSIS BETWEEN SEA ANEMONES AND FISHES

by

Richard N. Mariscal
Department of Zoology
University of California
Berkeley 4, California

Abstract

The tropical symbiosis between primarily anemones of the family Stoichactidae and fish of the family Pomacentridae (genus Amphiprion) appears to be a mutualistic one wherein both partners benefit from the association. The fish benefit in finding protection from predators among the tentacles of the anemone, eating food wastes cast out by the anemone and possibly by being cleaned of parasites as an incidental result of bathing among the tentacles.

Although not all workers agree, the fish are thought to benefit the anemones by a kind of tactile stimulation or 'massaging' behavior, by removing inorganic and organic debris from upon and around the anemone, by circulating fresh oxygenated and food-rich water over the anemones, parasite removal, protection from disturbances, and finally by feeding large food particles to the anemone.

Although some Amphiprion species can interchange anemone hosts with impunity, others are restricted not only behaviorally but also physiologically due to a lack of immunity to certain anemone's nematocysts. The fishes are thought to recognize their anemones by a combination of visual and chemical stimuli. Territoriality is very well developed among the various species of Amphiprion. Many never venture more than a few centimeters from their hosts, while other fish are slightly more far-ranging. Many of the fish are very aggressive toward any other fish in the immediate vicinity of their home anemone. A number of differences have been noted in the behavior of the various Amphiprion species not only in regard to territoriality but also to flight and feeding behavior, aggressivity, and anemone preferences. In some cases, nearly a complete range of behavior is displayed by the various species of Amphiprion between two extremes.

A process of 'acclimation' to a new anemone is undergone by some, and possibly all, species of Amphiprion. This involves increasing the degree of contact with the anemone's tentacles while making a series of rapid rushes through them until nematocyst discharge is no longer provoked. This latter phenomenon is thought to occur due to either physiological changes on the part of the fish or the anemone. Some workers believe that the fishes may be recognized individually by their behavior, and that some kind of habituation towards the fish on the part of the anemone is involved. A second theory holds that the mucus or skin of the fish contains some kind of protective substance and that this material may be increased or altered somehow during the acclimation process.

However, based on all the evidence to date, a third possibility, somewhat inbetween the above two seems to provide the best answer. It is here suggested that the fish's exterior contains some sort of fairly specific chemical substance to which the anemone becomes habituated during the acclimation process. This habituation involves a raising of the threshold or inhibition of nematocyst discharge. This latter phenomenon could take place by either of two methods, neither of which must invoke any wild theorizing with no basis in the literature.

One involves a direct inhibition of the nematocyst-cnidoblast complex *in situ* in the tentacles by the chemical substances of the fish. These substances may act on the operculum or the cnidoblast surface directly during the acclimation process. The second idea postulates that anemones may be able to control their nematocyst discharge and that these organelles may not be independent effectors after all. This would involve a change in the receptor-effector system of the anemone so that the anemone itself would become habituated to the substances present on the fish and would no longer discharge its nematocysts in response to the fish. One additional bit of behavior, that of nibbling or mouthing of the anemone's tentacles by the fish, may also be important in developing and maintaining this inhibition.

No anemones whatsoever, let alone stoichactids, are known from the Galápagos nor have any species of *Amphiprion* ever been found there. However, both the fishes and anemones are found in other neighboring areas.

THE SYMBIOSIS BETWEEN SEA ANEMONES AND FISHES

INTRODUCTION

Although the attention of zoologists has been attracted for many years now to the extremely intimate relationship which exists between certain members of the fish family Pomacentridae and the anemone families Stoichactidae and Actinidae the underlying behavioral and physiological mechanisms are still quite poorly known. It will be the purpose of this paper to review all the current literature regarding this phenomenon and attempt to arrive at some conclusion regarding these mechanisms.

Valentyn (1726) was apparently the first to describe an Amphiprion, but it remained for the English naturalist, Collingwood, while on a trip to the south China sea in 1868, to make the first observations of the small, brightly colored fish living in association with a giant anemone.

It must be noted here that not only these initial ones but also the majority of subsequent accounts are the result of field or aquarium observations with a noticeable lack of controlled experimentation. However, in spite of these obvious shortcomings the most interesting papers to date are those of Verway (1930), Gohar (1948), Davenport and Norris (1958), Abel (1960b), Koenig (1960) , Eibl-Eibesfeldt (1960), Blösch (1961), and Davenport (1962b). Gudger has reviewed the published record up to 1947 while Mansuetti (1963) has similarly reviewed the reports of the relationship between fishes and jellyfishes.

Since De Bary (1879) first coined the word,"symbiosis", it has been used and misused and its original definition is commonly not associated with it. 'Symbiosis' is here used in De Bary's sense to indicate the 'living together', for better or for worse, of two phylogenetically unrelated organisms. The several major subdivisions within this general term will be here used as they are recognized by present-day parasitologists (e.g., Noble and Noble, 1961) to indicate the specific nature of the relationship. For example, commensalism is a symbiotic association which benefits one partner but not the other, while mutualism occurs when both symbionts are benefited. While a number of workers have termed the association reviewed here a commensal one, it seems more likely that it approaches mutualism, as will be seen below. Davenport (1955) and Dales (1957) have recently reviewed the wide array of animal symbioses in general.

Although the taxonomic mysteries of the genus Amphiprion are now well worked out thanks to Schultz and his co-workers (Schultz 1953, Schultz, et al 1960), the anemones are in a hopeless jumble for the non-specialist. While Schultz recognizes 15 good species of Amphiprion, most of which apparently associate with anemones, Carlgren (1949) lists roughly 25 species belonging to the family Stoichactidae with a number of these probably synonomous (Cadet Hand, personal communication). To these can be added, among others, the actinid, Physobrachia (Hand, in Ms).

BEHAVIOR OF THE ANEMONES

The anemones of the family Stoichactidae are the real giants of the anemone world, frequently attaining diameters of over two feet (Collingwood 1868, Saville-Kent 1893, Mariscal 1963) Fig. 5). They often show a preference for relatively shallow, protected areas either on the landward side of barrier reefs

or on the shallow bottoms of lagoons or embayments which may be strewn with dead coral. The stoichactid anemones usually occur singly with their complement of fish (Fig. 1), while a form such as Physobrachia is often found in large aggregations with one or two fish frequenting a number of anemones (Fig. 2).

These anemones show an amazing range of coloration from yellow to bright blue with a wide spectral display in between (Collingwood 1868, Saville-Kent 1893, 1897, Yonge 1930, Stephenson 1946).

It seems ridiculous to even seriously consider the question of whether or not stoichactid type anemones have nematocysts, since a sea anemone with no nematocysts is no anemone. However, Caspers (1939), in the only general histological study of Stoichactis in the literature reported that only spirocysts were present. He obviously misidentified the extremely common basitrichs, as Gudger (1947) points out, because a number of taxonomic studies since that time (e.g., Carlgren 1940, 1950) plus this author's personal observations leave no doubt as to their presence.

Other authors have doubted that the nematocysts were capable of capturing fish or other prey (Buhk, 1939). However, Gudger (1941) finds that some anemones are fully capable of capturing fish in the wild, while Eibl-Eibesfeldt (1960) reports the same for stoichactid anemones. Gohar (1934, 1948) reports fish-capture by stoichactids in aquaria as does Koenig (1960). On the other hand Kroll (1963) indicates that after a good deal of time under water neither he nor his colleagues have ever observed one of the giant anemones capturing fish in the wild. That the anemones are generally capable of such fish-capturing behavior seems no longer open to question; whether or not this is a part of their normal feeding behavior remains to be seen.

BEHAVIOR OF THE FISHES

Preference for specific anemones

A number of authors, beginning with Saville-Kent in 1893, have described the various degrees of specificity and strength of attachment of anemone fishes to their hosts. This ranges from Premnas biaculeatus, apparently inhabiting only one anemone species, to Amphiprion percula, which has been found in a number of different anemones the world over. (Verwey 1930, Gohar 1948, Eibl-Eibesfeldt 1960, Oesman 1960, Mariscal 1963). In many cases, fish brought into the aquarium can also be persuaded to accept other anemones. Verwey (1930), Hackinger (1959) and Oesman (1961) also find that the young of certain species of Amphiprion may be found in species of anemones never inhabited by the adults. The restriction of a fish species to a given anemone is very real in some instances with this fish being stung and killed in attempting to enter other anemones, while other fish species can enter the same anemones with impunity (Verwey 1930, Gohar 1948, Eibl-Eibesfeldt 1960, Oesman 1960).

Regarding the physical factors which might influence this preference, Verwey (1930) and Koenig (1960) both believe ecological factors, such as amount of silt, light, food, water movement, etc. may be important in the case of a relatively non-specific fish-anemone association. That this is certainly not the whole answer is indicated by Premnas biaculeatus, which will accept only one

species of anemone, whether in the wild or an aquarium. Sluiter (1888) and Verwey (1930) have looked for a relation between tentacle length and size of the fish; in general, larger fish prefer anemones with longer tentacles. However, Verwey observed that this relationship does not always hold (as has the author), especially for a ubiquitous form such as Amphiprion percula. Therefore he decided that not only ecological factors, but also the ratio of tentacle length to anemone diameter must also be considered, and that a shortcoming in the former might be offset by an increase in the latter. However, he presents no quantitative data to support this view.

Recognition of anemones by fishes

Gohar (1948) reports that upon releasing a fish back into an aquarium it will find its anemone immediately, even if the latter is badly contracted. In the absence of controls, observations of this sort mean little. Gohar implies that visual stimuli are involved here, since, in the absence of its own host, the fish prefer anemones of a similar color. Verwey (1930) similarly reports that, although the preferred anemone looked more like a different species due to its contracted state, a Premenas immediately recognized it and swam up to it. From several experiments of this nature, Verwey concluded that "optical stimuli gave the first reaction, after which chemical stimuli settled the question". Koenig (1960) states that reef fish normally living near anemones respond negatively to the image of numerous tentacles, while pelagic fishes show no recognition or fear of anemones and soon become their prey. Herre (1936) states that the fish can recognize their own anemones even when contracted, but gives no clue regarding how this is done. Davenport and Norris (1958) have experimentally demonstrated also the importance of visual versus chemical clues to the fish in anemone recognition.

Territoriality

Horst (1903) is probably the first to record the extreme aggressiveness of some members of the Amphiprion complex (enough to distract several people from their collecting duties). Gohar (1934) records how A. bicinctus would attack anything placed in its aquarium (including fish twice its own size), and Verwey (1930) describes how Premnas and A. ehippium "may swim at the intruder and bite at his legs and shoes".

Following the usual definition of territory as merely a defended area (see Thorpe 1956), there then seems to be little question that the above behavior represents territoriality and, in fact, has been so interpreted by numerous other observers including Moser (1931), Herre (1936), Ladiges (1939), Gohar (1948), Koenig (1960), Eibl-Eibesfeldt (1960), Oesman (1961), and Mariscal (1963). Usually a mated pair occupies any one anemone or group of anemones with the young being either driven off or eaten upon the completion of their planktonic larval life. The notable exception to this is Amphiprion percula, seven or more of which may be found inhabiting a single anemone. Here too, however, territories are maintained in the single anemone with a kind of equilibrium set up between fish that are trying to drive others off and those that persist in remaining (Verwey, 1930).

The author observed an interesting case of territoriality off Bougainville Island in Arawa Bay which consisted of three Amphiprion xanthurus and four Dascyllus trimaculatus all inhabiting the same anemone, although in separate

halves (Fig. 3). An uneasy truce was apparently in effect since an attempt by one of the Dascyllus to encroach on the opposite half of the anemone would elicit displays and aggressive behavior on the part of the Amphiprion (Fig. 4), while, on the other hand, the Dascyllus did not yield easily.

Adult fish not only drive off members of the same species, regardless of sex, but also members of other species. Verwey (1930) reports that these battles may go to the death between two adult Premnas of the same sex if brought together in the same aquarium, even without an anemone. On the other hand, Eibl-Eibesfeldt (1960) states that A. percula of the same sex remain quite friendly and school together until an anemone is introduced, and then the battle begins, occasionally lasting up to 24 hours. During these encounters or under conditions of extreme stress, several species produce loud grating sounds (Verwey 1930, Koenig 1960, Eibl-Eibesfeldt 1960).

Species-specific behavior

Although basically similar in habits and life history, several species of Amphiprion show marked differences in their behavior. For example, Sluiter (1888) and Ladiges (1939) have both commented that A. percula will always be found within a few inches of its anemone while forms like A. xanthurus or Premnas biaculeatus are much more far-ranging. Ladiges (1939), Verwey (1930), Oesman (1961), and Mariscal (1963) have all noted species-specific differences in flight behavior also. For example, A. percula, A. akallopisus, and A. perideraion (all fairly small, retiring, weak swimmers) in case of danger generally dive into the anemones tentacles, while P. biaculeatus, A. ehippium, A. melanopus, A. xanthurus, and A. polymnus (all larger and stronger swimmers) flee from their anemones when frightened. Verwey (1930) also found that only two out of the five fish he studied produced audible sound.

Additional anemone symbionts

Not only do more than one species of Amphiprion occasionally inhabit a single anemone (Verwey 1930, Oesman 1961, Mariscal 1963), but other unrelated pomacentrids may also be found in and around anemones. The most ubiquitous of these are the young of Dascyllus trimaculatus, a common reef damsel fish (Gohar 1948, Muller 1957, Koenig 1958, 1960, Hackinger 1959, Eibl-Eibesfeldt 1960, Mariscal 1963). Luther (1958) and Abel (1960 a, b) also give other fish examples especially in the Red Sea. In the case of D. trimaculatus, at least, the association is a bit hazardous since upon contact with the anemone's tentacles, it may be fatally stung (Müller 1957, Eibl-Eibesfeldt 1960, Mariscal 1963).

Saville-Kent (1893, 1897), Yonge (1930), Whitley (1932), and Mariscal (1963) have all observed the crustacean symbionts occasionally found with the Pacific giant anemones. Yonge calls the shrimp Periclimenes brevicarpalis, but does not identify the crab. Interestingly enough the crab, and especially the shrimp, are not only roughly the same color but have the same sort of banding pattern on their bodies as do a number of the Amphiprion species (eg., A. percula). On an isolated coral boulder off New Britain Island the author discovered a small Stoichactis, which besides having two different species of Amphiprion (perideraion and two young percula), also contained a crab, apparently the same as Saville-Kent's Barrier Reef form, and a number of small shrimp (over ten), also similar to Saville-Kent's. Absolutely nothing is known regarding the behavioral interactions of the above fishes, crustaceans, and anemones, although Davenport (1962b) has studied experimentally the relationship of the crab, Hyas araneus

and the anemone, Tealia felina.

NATURE OF THE SYMBIOSIS

Benefit to the fish

Protection: The major benefit provided by the anemone appears to be protection against predators, and indeed, evidence is available indicating this to be the case. Sluiter (1888) found that A. percula were unharmed in aquaria containing large predatory fish so long as the anemones were present. However, should the anemones be removed, the Amphiprion were pursued and eaten. Verwey (1930) and Eibl-Eibesfeldt (1960) both give similar observations, the latter in the natural reef environment. Koenig (1960) believes that the negative stimulus of a crown of tentacles causes reef fish to give anemones a wide berth, thereby protecting the fish. However, Montilla (personal communication to Davenport and Norris, 1958) and Kroll (1963) have observed free-living anemone-fish in the wild, while Moser (1931) believes that the fish never seek protection in the anemone, but that they only try to protect the anemone from its enemies. Gohar (1948), among others, has refuted the latter view, and most of the evidence favors the idea that anemone-fish do generally find protection in the vicinity of their anemones. Furthermore, the fish are known to return to the anemone's tentacles at night where they sleep until daybreak, implying again a protective function for the anemone. Koenig (1960) adds that the fish become much lighter in color at night when in the anemone, with any black coloration almost disappearing, while fish without anemones do not show this change. Townsend (1929) has also commented on this in other fishes, although the function is not clear.

The eggs of A. percula, at least, are 'immune' to Stoichactis nematocysts. De Crespigny's (1869) and Moser's (1931) idea that the eggs gain protection by being laid on the anemone's disc has never been substantiated, with all observations indicating they are laid on hard substrate in the vicinity of the anemone (Verwey 1930, Gohar 1948, Garnaud 1951, Davenport and Norris 1958, Oesman 1961).

It is interesting that Saville-Kent (1893), Weber (1913), and Herre (1936) have stated that the anemone fish actually seek shelter in the coelenteron of their hosts, but subsequent investigators, specifically looking for this behavior, have never observed it (Whitley 1927, 1932, Verwey 1930, Gohar 1934, 1948). The earlier authors merely may have collected anemones which contained anemone fish among their folds as has been commonly observed, and thought they had been hiding in the coelenteron.

Food: Many observers have noted Amphiprion species eating waste material and left-overs from its host's meals(Sluiter 1888, Yonge 1930, Verwey 1930, Moser 1931, Gohar 1934, Koenig 1960). Gohar (1948) even describes a fish cleaning out the coelenteron after the anemone has digested a large meal, while devouring choice tidbits in the process. Verwey also believed that the fish obtained nutrition from eating tentacles and/or mucus. This will be discussed later.

Other possibilities: Rieger (1962) found that an isolated A. perula, in the absence of an anemone, adopted a small stand of algae, behaving in and toward this as if it were an anemone, not only retiring there for the night, but also spending a good deal of its daylight hours there. The extremely remote possibility exists that the anemone may provide some sort of tactile stimulation for its fish, but this single observation is hardly enough from which to draw any conclusions. De Crespigny (1869) suggested that the constant nestling in among the tentacles may be effective in removing fish parasites.

Benefit to the anemone

Lures: Saville-Kent (1893) suggested that the Amphiprion acted as lures to draw prey fish into the anemone's tentacles. However, Gohar (1948) and Abel (1960 a) both disagree with this. Not only has such behavior never been observed but Abel makes the pertinent point that there are many other reef fish which are even more brightly colored and presumably conspicuous (at least to human eyes). A further possibility exists that the striking bands and colors of some anemone-fish may be a kind of warning coloration for potential predators, however no evidence is available.

Tactile stimulation: A number of workers have made the interesting observation that anemones 'pine away' and even die when separated from their resident fish. This is supposedly due to the lack of 'massaging' or "treating' of the anemones by the fish (De Crespigny 1869, Verwey 1930, Herre 1936, Gohar 1948, Koenig 1960). Gohar and Verwey and Herre mention how badly contracted anemones will expand almost immediately upon being touched by their fish. Interestingly enough, anemones which form the closest bonds with their fish seem to 'suffer' the most without them (e.g., Verwey: A. ehippium and P. braculeatus). The reverse may be partially true also in that P. biaculeatus, if deprived of its anemone will accept no other, as well as taking the longest time to adapt to a free-swimming existence in the aquarium.

Cleaning: Although Gohar (1948) contradicts the findings of Verwey (1930), Moser (1931), and Eibl-Eibesfeldt (1960) when he comes to the conclusion that the fish do not remove inorganic debris from on and around the anemone, the above authors as well as Koenig (1960) all agree that the fish do remove organic wastes from the anemone. De Crespigny (1869) and Verwey (1930) also have postulated that the fish remove necrotic tissue as well as anemone parasites

Verwey (1930) notes also that Premnas dug out and enlarged a hole in the coral rubble for its crevice dwelling anemone.

Water circulation: De Crespigny (1869), Sluiter (1888), Verwey (1930), and Herre (1936) all believe that the fish may be influential in circulating oxygenated water as well as food particles over their anemones.

Feeding: The remarkable feeding of the anemone host by the associated fish has been observed in the aquarium by too many authors to doubt that it occurs (Sluiter 1888, Verwey 1930, Herre 1936, Ladiges 1939, and Koenig 1960). The author has also observed this behavior in the aquarium at Green Island on the Great Barier Reef, Australia. However, the most striking feeding behavior has been recorded by Gohar (1934, 1948) who observed that when live sardines (Atherina), which were twice as long as the Amphiprion, were placed in the aquarium they were immediately siezed by the anemone-fish and forcibly dragged

against the tentacles of the anemone, being held there amidst great struggling until they were subdued. The anemone-fish then picked the bones of the Atherina after they were egested by the anemone.

On the other hand, Moser (1931) and Eibl-Eibesfeldt (1960) believe that anemones are only fed by their fish accidentally in the course of other activiti. Abel (1960 a) does not believe that the fish feed anemones in the wild, since in his underwater studies, he has never observed it. Furthermore, he states that large food particles such as those observed being carried to anemones in aquaria, are rarely available in the natural environment. However, Abel has studied only one species of anemone-fish (Amphiprion bicinctus) underwater, and not all anemone-fish are known to feed their anemones, even in aquaria. For example Ladiges (1939) reports that A. polymnus feeds the anemone large food chunks while eating the small ones itself. Premnas feeds its anemone very littl A. ehippium even less, and A. percula and A. akallopisus not at all. Kroll (1963) has confirmed this for A. percula in the Green Island Aquarium, although other species there do show the feeding behavior. In any case, the fact that some anemone-fish are never known to feed their anemones argues in favor of the idea that this type of behavior could not play a very substantial role in the latter's nutrition.

Not to be forgotten here is the fact that many of the giant anemones also maintain a symbiotic relationship with unicellular algae. The role of the zooxanthellae in the nutrition of these anemones has never been investigated, but Muscatine and Hand (1958) have found a transfer of material from the contained algae to the tissues of a California anemone (Anthopleura), while Muscatine and Lenhoff (1963) find a similar situation in a hydra. For the hydra (Chlorohydra viridissima), Muscatine (1963) finds the transferred material to be largely carbohydrates, especially glucose. It is interesting to note in passing that some of the largest invertebrates in the tropics, corals, the stoichactid anemones, and Tridacna clams, all contain symbiotic algae (see Yonge, 1957, for discussion of latter). It may turn out that the zooxanthellae are intimately involved in the nutrition of the giant anemones also, and that feeding by the fish is indeed insignificant.

Finally, the existence of so much surface area exposed to the surrounding medium in the form of the enlarged oral disc-column complex leads one to suspect that filter feeding may also be important in the nutrition of these forms.

NATURE OF THE PROTECTION ENJOYED BY THE FISH

Acclimation of fish to new anemones

Although probably not aware of it at the time, Whitley (1932), in his rough acclimatization experiments performed in the field on the Great Barrier Reef was apparently the first to observe this phenomenon. Gohar (1948) however, was the first to recognize that anemone-fish "may develop partnership with such anemones as Stoichactis (Discosoma) giganteum by cautiously approaching it", and that "the association is complete in one to a few days". Since then Davenport and Norris (1958) have furnished us with the most detailed study of this phenomenon, while Koenig (1960) and Oesman (1961) have also observed it.

Acclimation involves a number of cautious approaches to the strange anemone while at the same time gently touching some part of the body to the tentacles, as well as mouthing or nibbling the latter. Gradually the amount of clinging by the tentacles diminishes while the degree of penetration by the fish increases. Finally with a series of violent rushes the process is complete and the fish takes up residence in the anemone. The whole process is complete after one hour, on the average.

Protection through changes on the part of the fish

Mucus itself is a well-known protective mechanism among fishes. Jakowska (1963) states that "fish, covered by a mucus-secreting integument respond to a variety of environmental and pathogenic agents by altering the nature as well as the quantity of their mucus secretions". Luther (1958) has suggested that the association between Blennius and the fire coral, Millepora, in the Red Sea is made possible by the fish's mucus. Blennius is known locally as "Schleimfisch". Along the same lines, Davenport and Norris (1958) have made the rather cautious suggestion that "there is a possibility, though we cannot offer conclusive proof, that acclimation may be related to changes in the mucus coat of the fish". For example, some of their experiments have demonstrated that skinless Amphiprion flesh is devoured by Stoichactis, while flesh with skin attached is rejected. Furthermore, when pieces of Amphiprion and Fundulus (control fish) flesh, both with skin, are placed side by side on the anemone's disc, the Fundulus portion is ingested while the Amphiprion piece is worked slowly off the disc and discarded. These experiments indicate the presence of some sort of specific chemical factor in either the skin or mucus of the anemone-fish.

Based on his underwater field studies, Eibl-Eibesfeldt (1960) also believes that the Amphiprion species he studied are protected through a special substance on their bodies. Abel (1960 b), although studying a different fish-anemone relationship, finds that the mucus is the decisive factor in protecting his fish, (Gobius), but finds no evidence of acclimation behavior.

Protection on the part of the anemone

A storm of controversy has swirled around this subject since Gohar (1948) made the suggestion that the anemones recognize their fish partners by their "mode of movement". Gohar was led to this conclusion by the fact that anemones seemed to recognize only their own immediate symbionts and that other individuals of even the same species might be stung and eaten. Hackinger (1959) and Koenig (1960) agree with Gohar on the importance of individual recognition of the fish through its behavior.

De Crespigny (1869), Verwey (1930), Moser (1931), Herre (1936), Eibl-Eibesfeldt (1960) and Abel (1960 a) have all indicated that chemical recognition of the fish by the anemone may be taking place. Koenig (1960) gives further evidence of some sort of recognition in his confirmation of Verwey (193 Herre (1936), and Gohar (1948) regarding the almost unbelievable positive response of an anemone to a freshly introduced anemone fish: 'Man muss gesehen haben, wie intensiv sich Fische, die lange alleine waren, in die Aktinie kuscheln, und wie aktiv eine bisher isoliert gehaltene Aktinie die Fische 'umschlingt'". Sick or weakened anemones which do not respond actively enough are given up by the fish just as are weak or sick fish eaten by the

anemone (see also Gohar 1948, Oesman 1961). Davenport and Norris (1958) and Eibl-Eibesfeldt (1960) similarly report how injured fish provoke nematocyst discharge and are eaten by their anemones.

Koenig (1960) and Blösch (1961) have both made the extremely interesting observation that anemones which have been separated from any contact with anemone-fish for long periods of time will always sting these fish upon first contact. Koenig further states that because of this no fish will swim into a foreign anemone without first going through an acclimation procedure, and that all anemones in the vicinity of the fish's 'home' anemone are so treated. On the other hand, Blösch finds that if the anemone had been living with any anemone-fish just prior to the experiments, or if only the fish had been separated from the anemone for long periods of time, they were not stung. (Fig. 6). This is especially interesting in view of the fact that neither Davenport and Norris nor Eibl-Eibesfeldt took the added control precaution of previously isolating their anemones as well as the fish they studied.

Immunity to toxins of nematocysts

Although no chemical studies on Amphiprion have been conducted to date to study this, a number of observers, including Verwey (1930), Gohar (1934), Herre (1936), and Eibl-Eibesfeldt (1960), Koenig (1960) and Oesman (1961) have observed the nibbling of tentacles by Amphiprion. Verwey has suggested that this behavior may be involved in providing immunity to its host's nematocyst toxin. However, the observations of Koenig (1960) and Blösch (1961) that fish already living in anemones will still be stung by other previously isolated anemones, suggest that no immunity is present, or if present that it is not an effective protection in all cases.

On the other hand, Lane (1960), contrary to previous reports (see Mansueti 1963), finds that Nomeus, the fish commensal of Physalia, can indeed survive doses of toxin up to 10 times that required to kill other similar-sized fish. He believes that this immunity is acquired by Nomeus feeding on Physalia tentacles. Obviously experiments are needed with Amphiprion.

DISCUSSION OF PROTECTIVE MECHANISMS

Thus, we have two general hypotheses regarding the protective mechanisms of anemone fish: one centers on the fish (e.g., Davenport and Norris 1958, Eibl-Eibesfeldt 1960, Abel 1960 b); the other places the responsibility on the anemone (Gohar 1948, Koenig 1960, Blösch 1961). In the absence of specific information regarding the past history of his anemones, Abel's work demonstrates that the mucus is or contains the protective substance which somehow inhibits nematocyst discharge. Since Davenport and Norris and Eibl-Eibesfeldt did not use previously isolated anemones, their experiments still do not conclusively rule out the idea that some sort of change may be occurring on the part of the anemone during the acclimation process. It is also pertinent to note here that although Davenport (1962b) is correct in stating that Abel (1960b) found the mucus covering in the fish Gobius to be effective in its protection, Abel does not believe that his work necessarily substantiates Davenport and Norris' findings with Amphiprion because of the lack of an acclimation reaction in the case of Gobius.

Now, the above seems clear enough even after taking into consideration the criticisms of both sides by the other (i.e., Davenport 1962b, Blösch 1961). However, one further difficulty is encountered if one takes Blösch to be correct in his findings that the fish are not stung if the anemone had been living with other anemone fish prior to the experiments. We see that the single anemone used by Davenport and Norris had in fact been kept with two Amphiprion for several weeks prior to the experiments, yet all the fish they tested were still found to require a varying period of acclimation to the anemone. Gohar (1948) reports a similar situation. This, once again, speaks for some sort of individual change taking place on the part of the fish as it becomes acclimated.

Therefore, based on a careful study of the literature plus the author's personal observations and taking into consideration the range of species and individual variation reported, the following possibilities have emerged regarding the symbiotic relationship between the species of Amphiprion and their anemones:

1. Some sort of chemical factor is present in the skin or mucus of anemonefish. This factor is probably specific for only one to several species of anemones. It is here suggested that the acclimation process involves to a large degree a habituation (defined here after Thorpe, 1956; the relatively permanent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement) on the part of the anemone to the chemical factor present on the skin of the fish due to the repeated contact between the fish and the tentacles. This habituation might involve a change in the anemone's receptor-effector system in such a way that the anemone no longer discharged its nematocysts. A second possibility might be the direct inhibition of the nematocysts in situ on the tentacles by the fish skin substance. That this might be a very specific inhibition is borne out by Blösch's (1961) and Davenport's (1962b) observations that an anemone containing a symbiont (fish or crab) may still sting these inhabitants, if stimulated by another non-acclimated organism. Furthermore, as Koenig (1960) has indicated an important part of not only initiating but also maintaining this symbiosis is the nibbling and mouthing of the host's tentacles. Interestingly enough, Davenport (1962b) also observed this behavior on the part of the crab Hyas in the anemone Tealia.

Other possibilities are:

2. As suggested by Davenport and Norris, some sort of additional change may be taking place on the surface of the fish as well.

3. Nibbling of the tentacles may be a means of ingesting some sort of "anemone factor" which either alters the chemical nature of the fish's secretion or masks it with something resembling the anemone's "scent". In this regard, something in the urine or excretory products of the fish may be involved in habituating the anemone also, although this seems rather unlikely.

4. The fish may, during its acclimation passes, pick up more and more of the anemone's mucus on its own body surface, thereby camouflaging its own body secretions. However, observations by Blösch and Koenig in the case of anemones which had been isolated, but will still sting "acclimated" fish from other anemones does not bear this out. If one argues that the fish must individually acclimate to these new anemones, then how can one fish remain acclimated

to two or three anemones at the same time when it presumably is covered only by the mucus of the last anemone it inhabited? Furthermore, a crude experiment by the author which involved scrubbing the mucus by means of absorbent tissue (not a scalpel or other hard instrument which might break the skin) from a Amphiprion percula and then returning the fish to its anemone immediately produced no clinging of the tentacles. This was done two times with the same fish, and although hard on the fish, it did not alter the anemone's response towards it. It is possible that the fish could secrete a coating of its own mucus almost immediately upon return to the water, but it is doubtful if it could coat itself with a fresh layer of the anemone's mucus that rapidly.

Let it also be stated here that there is no evidence the anemones are continuously discharging their nematocysts in the presence of the fish and that the mucus merely acts as a sort of armor to prevent nematocyst penetration.

MECHANISM OF NEMATOCYST INHIBITION

Two possibilities are apparent if one hypothesizes that something on the fish's surface is responsible for inhibiting nematocyst discharge: one involves an inhibition of the cnidoblast-nematocyst complex directly in situ on the tentacles; the second postulates this substance affecting the anemone's receptor-effector system, thus implying a connection between the nematocysts and the anemone's nervous system. A site of action for the first possibility is suggested by the following. Glaser and Sparrow (1909), Parker and Van Alstyne (1932), Pantin (1942), and Jones (1947) consider the cnidocil (in coelenterates possessing this) or the free surface of the cnidoblasts themselves to be involved in chemoreception during nematocyst discharge. On the other hand, Yanagita (1949c, 1960a) and Yanagita and Wada (1959) found no definitive cnidoblast surrounding the nematocysts in the acontia of Haliplanella (Diadumene) luciae. Therefore, these authors, based on earlier work also, (Yanagita 1943, 1951, 1959a, b, c, 1960 b, c, Yanagita and Wada 1953, 1954) present evidence for the direct effect of various substances on the operculum of the nematocyst capsule and believe that this structure acts as a sort of chemoreceptor. Therefore, there is ample evidence that nematocyst cnidoblasts are capable of the direct reception of chemical information in initiating (or possibly inhibiting) nematocyst discharge. Whether this occurs in stoichactid type anemones is an entirely different question for which no evidence exists.

Until a few years ago the second idea above, that of some sort of nervous control over nematocyst discharge, would have been thought ridiculous due to the widespread current notion that nematocysts are independent effectors (Parker and Van Alstyne 1932, Pantin 1942, Jones 1947, Burnett, Lentz, and Warren 1960). In addition, Davenport (1962a, b) has found no evidence of any chemical factors from the symbiont affecting the neuromuscular physiology of the anemones he studies (however, he does not believe that this necessarily eliminates the possibility either). In the face of the above data, Baerends (1950, 1957) on the basis of very scanty evidence states that "there are several indications that Stoichactis (Discosoma) can put its cnidoblasts out of action". He further makes the suggestion that the nibbling and mouthing of the tentacles by Amphiprion may be a sign stimulus which "releases the inactivation of the cnidoblasts in the anemone". Koenig (1960) has suggested

essentially the same thing.

Recently, experimental evidence has come to light which indicates that Baerends may not be far wrong. Ross (1960), Ross and Sutton (1961a,b), and Davenport, Ross and Sutton (1961) found that the threshold for discharge of the nematocysts of the anemone, Calliactis was low in animals not on gastropod shells inhabited by hermit crabs (its normal habitat), while animals on their shells showed little tendency to discharge their nematocysts, apparently due to some sort of feedback from the shell through the pedal disc. This report represents the first substantial recent evidence that nematocysts (at least some nematocysts) may not be independent effectors. Shortly after this report, Lentz and Barrnett (1961) provided biochemical evidence for the possibility of at least partial nervous control of the nematocysts in hydra. It is also interesting to note here that some of the results in Burnett, Lentz, and Warren's recent (1960) paper pointed to this also although these authors concluded that the nematocysts involved were indeed independent effectors. Therefore, the additional possibility cannot be ruled out completely that a stoichactid type anemone may be able to control its nematocysts in response to a chemical substance from the fish. Once again the site of reception of this stimulus may be the cnidoblasts themselves although this remains to be elucidated.

ZOOGEOGRAPHY OF THE ANEMONES AND ANEMONE-FISHES

Although at least three species of Amphiprion (ehippium, percula, polymnus) (and presumably their anemones) are found as far east as the Society Islands, there is no indication of this genus or its associated anemones being present in the Galápagos Archipelago (Snodgrass and Heller 1905, Fowler 1938, Rosenblatt and Walker 1963). The author's collection of Physobrachia ramsayi and Amphiprion melanopus from Pago Pago, American Samoa may be the easternmost insular record for both members of the symbiosis. However, McMurrich (1904) and Carlgren (1951) indicate that Physobrachia (Gyrostoma) is found on the Juan Fernandez Islands (cold water environment) as well as several places on the Chilean mainland. However, this genus of anemones may be found with or without fish symbionts (Saville-Kent, 1893, 1897) and there is no evidence one way or the other that Amphiprion and its anemone hosts are present in the Galapagos. I hope not only to find out, but to find them.

Acknowledgment is gratefully made to Hopkins Marine Station of Stanford University and the National Science Foundation for the opportunity to conduct observations on the above relationship while participating in the TE VEGA Expeditions to the South Pacific during the summer of 1963. I would also like to thank Dr. Cadet Hand, Department of Zoology, University of California, Berkeley, for reading the manuscript and for assistance provided to me through his NSF Grant (GB-1237).

LITERATURE CITED

Abel, E.F. 1960a. Zur kenntnis des Verhaltens und der Ökologie von Fischen an Korallenriffen bei Ghardaqa (Rotes Meer). Zeit. Morph. Oekol. Tiere, 49: 430-503.

_____. 1960b. Liason faculatative d'un poisson (Gobius bucchicii Steindachner)et d'une anémone (Anemonia sulcata Penn.) en Méditerranée. Vie et Milieu, 11: 517-531.

Baerends, G.P. 1950. Specializations in organs and movements with a releasing function. Symp. Soc. Exp. Biol., 4: 337-359.

_____. 1957. The ethological analysis of fish behavior. In: Brown (ed.) The physiology of fishes, Vol. 2., New York: Academic Press

Bary, A. de. 1879. Die Erscheinung der Symbiose. Strassbourg: Tubner. (Not seen)

Blösch, M. 1961. Was ist die Grundlage der Korallenfischsymbiose: Schutzstoff oder Schutzverhalten? Naturwiss., 48: 387

Buhk, F. 1939. Lebensgemeinschaft zwischen Riesenseerosen und Korallenfischen. Wochenschrift Aquar. -und Terrarienkunde, 36: 672-674

Burnett, A.L.,Lentz, T., and Warren, M. 1960. The nematocysts of hydra (Part I) Ann. Soc. Roy. Zool. Belg., 90(1): 247-267.

Carlgren, O. 1940. A contribution to the knowledge of the structure and distribution of the cnidae in the Anthozoa. Kungl. Fysiografiska Sällskapets Handlingar, N.F., 51(3): 1-62

_____. 1949. A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. Kungl. Svenska Vetenskapsakedemiens Handlingar, 1(1): 1-121.

_____. 1950. Actiniaria and Corallimorpharia. Brit. Mus. (Nat. Hist.), Great Barrier Reef Expedition (1928-29) Sci. Repts., 5(7): 427-457.

_____. 1951. The actinian fauna of the Gulf of California. Proc. U.S. Nat. Mus., 101: 415-449.

Caspers, H. 1939. Histologische Untersuchungen über die Symbiose zwischen Aktinien und Korallenfischen. Zool. Anz., 126: 245-253.

Collingwood, C. 1868a. Note on the existence of gigantic sea-anemones in the China Sea, containing within them quasi-parasitic fish. Ann. and Mag. Nat. Hist., Ser. 4(1): 31-32

_____. 1868b. Rambles of a naturalist on the shores and waters of the China Sea. London: John Murray.

Crespigny, C. C. de. 1869. Notes on the friendship existing between the malacopterygian fish Premnas biaculeatus and the Actinia crassicornis. Proc. Zool. Soc. London, 1869: 248.

Dales, R.P. 1957. Interrelations of organisms . A. Commensalism. In: Hedgpeth. (ed.), Treatise on marine ecology and paleoecology, Vol. 1. Ecology. Mem. Geol. Soc. Amer., 67: 391-412

Davenport, D. 1955. Specificity and behavior in symbioses. Quart. Rev. Biol., 30(1): 29-46

_____. 1962a. The responses of actinians to electrical stimulation. Bull. Institut Océanographique Monaco, 1236: 1-24

_____. 1962b. Physiological note on actinians and their associated commensals. Bull. Institut Océanographique Monaco, 1237: 1-15.

_____, and Norris, K.S. 1958. Observations on the symbiosis of the sea anemone Stoichactis and the pomacentrid fish Amphiprion percula. Biol. Bull., 115(3): 397-410.

_____, Ross, D.M., and Sutton, L. 1961. The remote control of nematocyst discharge in the attachment of Calliactis parasitica to shells of hermit crabs. Vie et Milieu, 12(2) : 197-209.

Eibl-Eibesfeldt, I. 1960. Beobachtungen und Versuche an Anemonenfischen (Amphiprion) der Malediven und der Nicobaren. Z. Tierpsychol., 17(1):1-10.

Fowler, H.W. 1938. The fishes of the George Vanderbilt South Pacific Expedition. 1937. Acad. Nat. Sci. Phil., Monograph #2.

Garnaud, J. 1951. Nouvelles donnees sur l'Ethologie d'un Pomacentridé: Amphiprion percula Lacépède. Bull. Institut Océanographique Monaco, 998:1-1?

Glaser, O.C. and Sparrow, C.M. 1909. The physiology of nematocysts. J. Exp. Zool., 6(3): 361-382.

Gohar, A.F. 1934. Partnership between fish and anemone. Nature, 134: 291.

_____. 1948. Commensalism between fish and anemone (with a description of the eggs of Amphiprion bicinctus). Fouad I Univ. Publ. Mar. Biol. Sta. Ghardaqa (Red Sea), 6: 35-44.

Gudger, E.W. 1941. Coelenterates as enemies of fishes IV. Sea anemones as fish eaters. New England Naturalist, 10:1-8.

_____. 1947. Pomacentrid fishes symbiotic with giant sea anemones in Indo-Pacific waters. J. Royal Asiatic Soc. Bengal, 12(2): 53-76.

Hackinger, A. 1959. Freilandbeobachtungen an Aktinien und Korallenfischen. Mitteil. Biol. Sta. Wilhelminenberg, Wien, 2:72-74.(Not seen).

Hand, Cadet. in Ms. Anemones of Australia.

Herre, A.W. 1936. Some habits of Amphiprion in relation to sea anemones. Copeia, 1936(3): 167-168.

Horst, R. 1903. On a case of commensalism of a fish (Amphiprion intermedius) and a large sea anemone (Discosoma sp.). Notes Leyden Mus., 23:180-182.

Jakowska, S. 1963. Mucus secretions in fish - a note. Ann. N.Y. Acad. Sci., 106(2): 458-462.

Jones, C.S. 1947. The control and discharge of nematocysts in hydra. J. Exp. Zool. 105(1): 25-60.

Koenig, O. 1958. Ein Beitrag zur Fortpflanzungsbiologie von Dascyllus trimaculatus. Die Aquar. und Terr. Zeit., 11(3): 107-111.

_____. 1960. Verhaltensuntersuchungen an Anemonenfischen. Die Pyramide,8(2):52-5(

Kroll, I. 1963. Personal communication.

Ladiges, W. 1939. Das Ratsel der Symbiose zwischen den Riesenseerosen der Gattung Stoichactis und den Fischen der Gattungen Premnas and Amphiprion. Wochenschrift F. Aquar. Und Terrarienkunde, 46:669-676.

Lane, C.E. 1960. The Portuguese Man-of-War. Sci. Am. 202(3): 158-168.

Lentz, T.L. and Barrnett, R.J. Enzyme histochemistry of hydra. J. Exp. Zool., 142(2): 125-149.

Luther, W. 1958. Symbiose von Fischen mit Korallentieren und Krebsen im Roten Meer. Natur und Volk, 88(5): 141-146.

McMurrich, J.P. 1904. The Actiniae of the Plate Collection: Fauna Chilensis. Abhandlungen zur Kenntnis der Zoologie Chile. Zool. Jahrb. suppl. 6, 3(2): 215-306.

Mansuetti, R. 1963. Symbiotic behavior between small fishes and jellyfishes, with new data on that between the Stromateid, Peprilus alepidotus and the Scyphomedusa, Chrysaora quinquecirrha. Copeia, 1963 (1): 40-80.

Mariscal, R.N. 1963. Observations made in Pago Pago, American Samoa; Great Astrolabe reef, Fiji Islands; Vanikoro Island, Santa Cruz Islands; Guadalcanal, Bougainville, Solomon Islands; New Britain Island, Territory of New Guinea; Green Island, Great Barrier Reef, Queensland, Australia, all while participating as a member of Hopkins Marine Station's (Stanford University) TE VEGA Expeditions with the support of the National Science Foundation.

Moser, J. 1931. Beobachtungen über die Symbiose von Amphiprion percula mit Aktinien. Sitzungsberichte der Gesellschaft naturforschender Freunde Berlin, 1931(2): 160-167.

Müller W. 1957. Dascyllusarten. Die Aquar. und Terr. Zeit., 10(2):12-14.

Muscatine, L. 1963. Extracellular products of algae symbiotic with hydra. 44th Annual Meeting, Western Society of Naturalists, University of the Pacific, Stockton, California. 27 December, 1963

Muscatine, L. and Hand, C. 1958. Direct evidence for the transfer of materials from symbiotic algae to the tissues of a coelenterate. Proc. Nat. Acad. Sci., 44(12): 1259-1263.

Muscatine L. and Lenhoff, H.M. 1963. Symbiosis: on the role of algae symbiotic with hydra. Science, 142: 956-958.

Noble, E.R. and G.A. 1961. Parasitology. The biology of animal parasites. Philadelphia: Lea and Febriger.

Oesman, H. 1961. Erlebnisse mit Anemonenfischen. Die Aquar. und Terr. Zeit., 14(1): 49-52.

Pantin, C.F.A. 1942. The excitation of nematocysts. J.Exp. Biol. 19(3): 294-310.

Parker, G.H. and Van Alstyne, M.A. 1932. The control and discharge of nematocysts, especially in Metridium and Physalia. J. Exp. Zool., 63(2):329-344.

Rieger, W. 1962. Beobachtung an Amphiprion percula. Die Aquar. und Terr. Zeit., 15: 221-222

Rosenblatt, R.H. and Walker, B.W. 1963. The marine shore-fishes of the Galápagos Islands, Occ. Pap. Calif. Acad. Sci., 44: 97-106.

Ross, D.M. 1960. The association between the hermit crab Eupagurus bernhardus L. and the sea anemone Calliactis parasitica (Couch). Proc. Zool. Soc., B, London, 134: 43-57

_____,and Sutton, L. 1961a. The response of the sea anemone Calliactis parasitica to shells of the hermit crab Pagurus bernhardus. Proc. Roy. Soc., B, London, 155: 266-281

_____, and Sutton, L. 1961b. The association between the hermit crab Dardanus arrosor (Herbst) and the sea anemone Calliactis parasitica (Couch). Proc. Roy. Soc. B, London, 155: 282-291

Saville-Kent, W. 1893. The Great Barrier Reef of Australia. London: W.H. Allen and Co., Ltd.

_____. 1897. The naturalist in Australia. London: Chapman and Hall, Ltd.

Schultz, L.P. 1953. Review of the Indo-Pacific anemone fishes, genus Amphiprion, with descriptions of two new species. Proc. U.S. Nat. Mus., 103: 187-201.

_____, Chapman, W.M., Lachner, E.A., and Woods, L.P. 1960. Fishes of the Marshall and Marianas Islands. Bull., U.S. Nat. Mus., 202: 1-438.

Sluiter, C.P. 1888. Ein merkwürdiger Fall von Mutualismus. Zool. Anz., 11:240-2

Snodgrass, R.E. and Heller, E. 1905. Shore fishes of the Revillagigedo, Clipperton, Cocos, and Galápagos Islands. Proc. Washington Acad. Sci., 6:333-427.

Stephenson, T.A. 1946. Coral Reefs. Endeavour, 5:96-106

Thorpe, W.H. 1956. Learning and instinct in animals. London: Methuen.

Townsend, C.H. 1929. Records of changes in color among Fishes. Zoologica, 9:321-341

Valentyn, F. 1726. Oud en nieuw Oost-Indiën, etc. Vol.3. Omftandig Verhaal van de Geschiedenissen en Zaaken het Kerkelyke ofte den Godsdienst Betreffende, zoo in Amboina, etc. Dodrecht: Joannes Van Braam.

Verwey, J. 1930. Coral reef studies. I. The symbiosis between damselfishes and sea anemones in Batavia Bay. Treubia, 12(3-4): 305-366

Weber, M. 1913. Die Fische der Siboga Expedition. Siboga Expeditie, 57:334-335.

Whitley, G.P. 1927. The fishes of Michelmas Cay, North Queensland. Records Aust. Mus., 16: 1-32.

____. 1929. Some fishes of the order Amphiprioniformes. Mem. Queensland Mus., 9(3): 207-246.

____. 1932. Fishes. Brit. Mus. (Nat. Hist.) Great Barrier Reef Expedition (1928-29) Sci. Repts., 9: 267-316.

Yanagita, T.M. 1943. Discharge of nematocysts. J. Fac. Sci., Tokyo Imperial University, Sec. IV, 6(1): 97-108.

____. 1951. The influences of immersion media on the "longevity" of isolated nematocysts of sea-anemone. Nat. Sci. Report, Ochanomizu Univ., 2:117-123.

____. 1959a. Physiological mechanism of nematocyst responses in sea-anemone. I. Effects of trypsin and thioglycolate upon the isolated nematocysts. Jap. J. Zool., 12(3): 361-375.

____. 1959b. Physiological mechanism of nematocyst responses in sea-anemone. II. Effects of electrolyte ions upon the isolated cnidae. J. Fac. Sci. Univ. Tokyo, Sec. IV, 8(3): 381-400.

_____. 1959c. Physiological mechanism of nematocyst responses in sea-anemone. VII. Extrusion of resting cnidae - its nature and its possible bearing on the normal nettling response. J. Exp. Biol., 36(3): 478-494

____. 1960a. Physiological mechanism of nematocyst responses in sea-anemone. III. Excitation and anaesthetization of the nettling response mechanism. Compar. Biochem. Physiol., 1(2): 123-139

____. 1960b. Physiological mechanism of nematocyst responses in sea-anemone. IV. Effects of surface-active agents on the cnidae in situ and in isolation. Compar. Biochem. Physiol., 1(2): 140-154

____. 1960c. The physiological mechanism of nematocyst responses in sea-anemone. V. The effects of lipoid solvents on the cnidae in situ and in isolation. Annot. Zool. Japonensis, 33(4): 203-210.

____, and Wada, T. 1953. Discharge-inducing concentrations of acids and bases for the nematocysts of sea-anemone. Nat. Sci. Report, Ochanomizu Univ., 4(1): 112-118.

____, and Wada, T. 1954. Effects of trypsin and thioglycolate upon the nematocysts of the sea anemone. Nature, 173: 171

Yanagita, T.M. , and Wada, T. 1959. Physiological mechanism of nematocyst responses in sea-anemone. VI. A note on the microscopical structure of acontium, with special reference to the situation of cnidae within its surface. Cytologia, 24(1): 81-97.

Yonge, C.M. 1930. A year on the Great Barrier Reef. London: Putnam.

_____. 1957. C. Symbioses. In : Hedgpeth (ed.) , Treatise on marine ecology and paleoecology, Vol. 1. Ecology.Mem. Geol. Soc. Amer., 67 (1): 429-442.

Fig. 1. Amphiprion percula in a large Radianthus sp. Note one small fish near center of anemone and second in fold at far right. Vanikoro Island, Santa Cruz Islands. 3 September 1963.

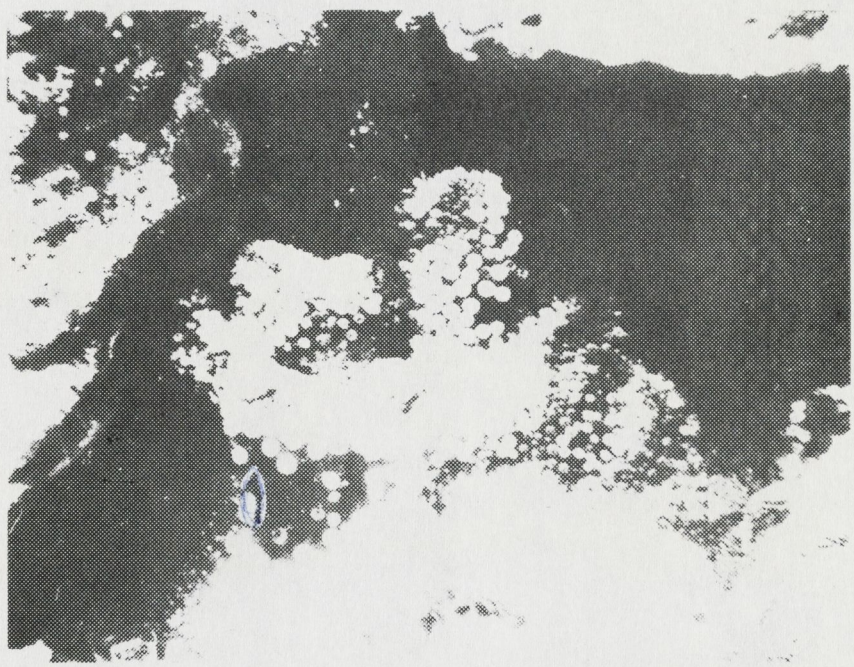


Fig. 2. Amphiprion with an aggregation of the crevice-dwelling anemone, Physobrachia ramsayi. Fish is to lower left. Vanikoro Island, Santa Cruz Islands. 3 September 1963.

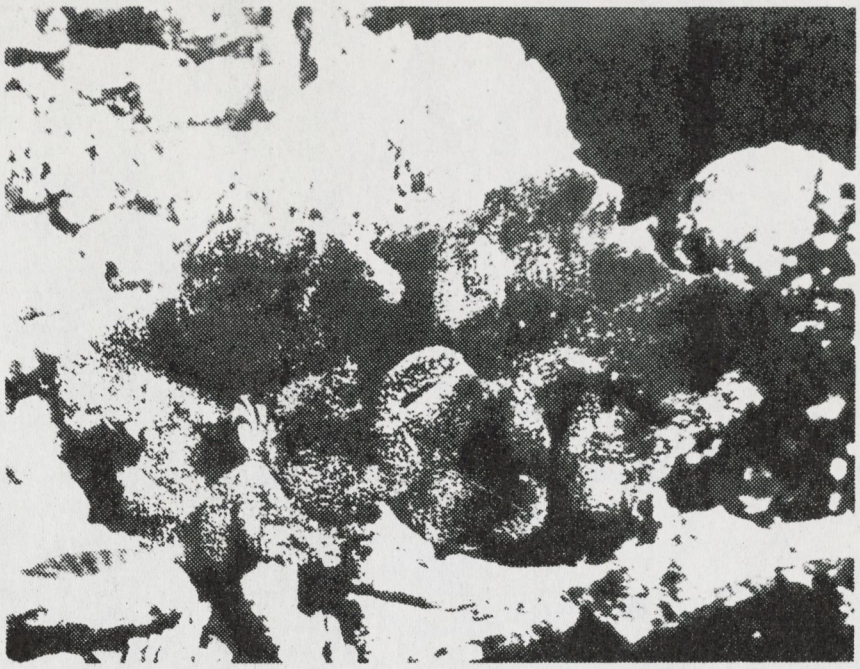


Fig. 3. Amphiprion xanthurus (left) and Dascyllus trimaculatus showing the segregation to different halves of Stoichactis sp. Takanupe Island, Arawa Bay off Bougainville Island, Solomons. 10 September 1963.

Fig. 4. Territorial encounter between Amphiprion xanthurus (left) and Dascyllus trimaculatus in Stoichactis sp. Takanupe Island, Arawa Bay off Bougainville Island, Solomons. 10 September 1963.

Fig. 5. Radianthus sp. to left with two Amphiprion perideraion (the two light-bodied fish above and to left of anemone). Two Amphiprion xanthurus (banded fish) to right in a Stoichactis sp. Fish at upper left is about 5 inches long for scale. Pongama Point, Arawa Bay, Bougainville Island. 10 September 1963.

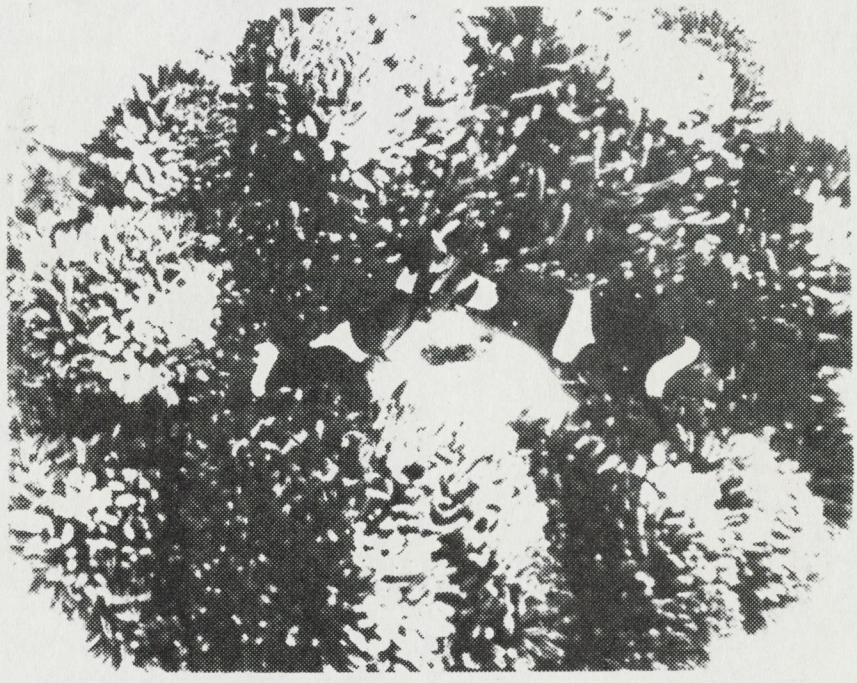


Fig. 6. Two Amphiprion percula which have just been released into a foreign Radianthus sp. with no apparent effect. Three other A. percula and one crab were inhabiting this anemone just prior to the new replacements. Pongama Point, Arawa Bay, Bougainville Island. 10 September 1963.

Dup.

PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

FOURTH SERIES

Vol. XXXI, No. 24, pp. 631–692, 11 figs. January 15, 1965

BEHAVIOR AND NATURAL REACTIONS OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX* GIRARD, UNDER THE INFLUENCE OF LIGHT OF DIFFERENT WAVE LENGTHS AND INTENSITIES AND TOTAL DARKNESS

By

Anatole S. Loukashkin and Norman Grant

California Academy of Sciences
San Francisco

I. INTRODUCTION

It has been known from times immemorial that certain fishes respond positively to artificial light and aggregate within illuminated zones. This peculiar behavior of fish has long been extensively exploited by fishermen. Torches and bonfires (still in use in some areas) were the first sources of artificial light for attracting the schools of fishes into nets and fish traps. With advancing technology, these light sources gave way to petrol and acetylene lamps and electricity, especially to the latter because of its applicability for underwater illumination (Verheijen, 1958). With underwater illumination possible, a new trend in commercial fishing has been developing since the end of World War II (Ellson, 1953), particularly in the Soviet Union

(Borisov, 1950; Borisov and Protasov, 1959; Leskutkin, Nikonorov and Patëev, 1955; Nikonorov, 1955, 1956, 1958, 1959a, 1959b; Terentiev, 1957). Instead of using conventional gear such as nets or traps, new, so-called "netless" fishing equipment has been introduced in certain fisheries. It consists of submerged electric lamps and the "fish pump." The fish attracted by the light at night are sucked into the pump funnel and pumped directly into the vessel's hold. In this technique, experiments have been made also to apply an electrical field within the illuminated zone so that the aggregated fish would be forced to swim toward the pump funnel, which is made the positive pole (Nikonorov and Patëev, 1959; Smith, 1955).

More and more species of fishes and other aquatic organisms have been reported in the literature as reacting positively to sources of artificial light under laboratory conditions or in the natural environments. Considerable research has been done on the structure and function of the fish eye (Baburina, 1955, 1958; Brett, 1959; Tamura, 1959; Vilter, 1950), on the ability of the fish to discriminate colors, and on innate preferential selectivity of monochromatic lights (Arora and Sperry, 1958; Breder, 1959; Bull, 1957; Kawamoto, 1959; Loukashkin and Grant, 1959), on the ability of fish to respond differently to different intensities of artificial light (Breder, 1959; Privolnev, 1956, 1958), and on many other specific problems related to fish behavior as it is affected by natural and artificial lights.

Out of the voluminous literature on the subject published in recent years and of special interest to the writers, only a few papers are selected and mentioned below. Borisov (1950) recorded 42 species and subspecies of fishes which responded positively to electric light. His list includes marine, anadromous and freshwater fishes found in the USSR; in 1955, he listed more than 60 forms. In 1954, Radovich and Gibbs reported 44 species of marine fishes from the waters of California and western Mexico which responded positively to electric light under natural conditions.[1] Baranov (1955) listed 17 species for the northwestern Pacific, and Parin (1958) mentioned 54 marine fishes collected at night light stations during oceanic exploration of the Pacific in 1954–55.[2]

Among pelagic fishes of commercial importance, the clupeids, or herring-like fishes, have been found the most responsive to artificial light, and

[1] Since the date of Radovich and Gibbs' report (1954), many more species of the fishes from the same area have been found to respond positively to electric light in the open sea (a continuously expanding unpublished list has been maintained by the California State Fisheries Laboratory at Terminal Island). While on research cruises of the California Fish and Game M/V *Alaska* in Mexican territorial waters in 1958 and 1961, the senior author recorded 20 species as supplementary to Radovich and Gibbs' list of 1954. These fishes are as follows: *Astroscopus zephyreus, Auxis* sp., *Carcharhinus lamiella, Cetengraulis mysticetus, Chloroscombrus orqueta, Cynoscion parvipinnis, Harengula thrissina, Menidia starksi, Mugil cephalus, Mugil* sp., *Nectarges nepenthe, Oligoplites* sp., *Polynemus* sp., *Pseudophallus starksii, Raja* sp., *Sphyraena* sp., *Sphyrna zygaena, Synodus lucioceps, Trachurops crumenophthalmus,* and *Upeneus* sp.

[2] A complete list of the fishes collected at night light stations by Parin in the Pacific Ocean during the 1954–1960 oceanological expeditions aboard the research vessel *Vitiaz* will be published by him and is in press.

most of the references herein cited refer to this family. Species displaying a strong positive taxis to artificial light, readily aggregating in masses within illuminated zones, are as follows: sardines—*Sardinops caerulea* (Radovich and Gibbs, 1954; Rasalon, 1959), *Sardinops sagax melanosticta* (Borisov, 1955; Yudovich and Kolegov, 1956), *Sardina pilchardus sardina* (Verheijen, 1957, 1958; Nikonorov, 1959), *Sardinella macrophthalma* (Breder, 1959), *Sardinella aurita* (Verheijen, 1958); herrings—*Clupea pallasii* (Gristchenko, 1951; Radovich and Gibbs, 1954; Baranov, 1955; Borisov, 1955; Nikolaev, 1957), *Clupea harengus harengus* (Craig and Baxter, 1952; Borisov, 1955; Blaxter and Parrish, 1958; Radakov and Soloviev, 1959; Tihonov, 1959; Zaitsev and Azhazha, 1959), *Clupea harengus membras* (Borisov, 1950, 1955); Caspian shads—*Alosa brashnikovi brashnikovi, Alosa brashnikovi agrachanica, Alosa caspia caspia, Alosa kessleri kessleri,* and *Alosa kessleri volgensis* (Borisov, 1955; Chugunova, 1955); Caspian sprats "kil'ka"—*Clupeonella delicatula caspia, Clupeonella engrauliformis,* and *Clupeonella grimmi* (Eremtstov and Nikonova, 1949; Tokarev, 1949; Borisov, 1950, 1955; Bondarenko, 1951; Prihodko, 1951, 1957a, b; Leskutkin and Prihodko, 1951; Safronov, 1952; Evtëev, 1953; Leskutkin, Nikonorov and Patëev, 1955; Lovetskaya, 1955, 1958; Nikonorov, 1955, 1956a, b, 1958, 1959a, b; Chugunova, 1955; Terentiev, 1957; Borisov and Protasov, 1959); sprats—*Sprattus sprattus sprattus* (Blaxter and Parrish, 1958), *Sprattus sprattus balticus,* and *Sprattus sprattus phalericus* (Borisov, 1950, 1955); Pacific round herring—*Etrumeus acuminatus* (Radovich and Gibbs, 1954); Pacific thread herring—*Opisthonema libertate* (Radovich and Gibbs, 1954); Atlantic dwarf herring—*Jenkinsia lamprotaenia* (Breder, 1959); and zunasi herring—*Harengula zunasi* (Sasaki, 1959).

Among other commercially important pelagic fishes which are known to respond strongly to artificial light are the following: anchovies—*Engraulis mordax, Anchoa delicatissima,* and *Anchoa compressa* (Radovich and Gibbs, 1954), *Engraulis japonica* (Borisov, 1950, 1955; Baranov, 1955; Parin, 1958), *Engraulis encrasicholus* (Verheijen, 1958), *Engraulis encrasicholus pontica* and *Engraulis encrasicholus maeotica* (Borisov, 1950, 1955; Safianova, 1952, 1958; Kirillov, 1955; Radakov, 1956); mackerels—*Scomber scombrus* (Blaxter and Parrish, 1958), *Pneumatophorus diego* (Radovich and Gibbs, 1954), and *Pneumatophorus japonicus* (Borisov, 1950, 1955; Baranov, 1955; Parin, 1958) jack-mackerels or horse-mackerels—*Trachurus symmetricus* (Radovich and Gibbs, 1954), *Trachurus japonicus* (Parin, 1958, Sasaki, 1959), and *Trachurus trachurus* (Borisov, 1950, 1955; Safianova, 1952, 1958; Radakov, 1956; Protasov, 1957; Blaxter and Parrish, 1958; Borisov and Protasov, 1959); saury—*Cololabis saira* (Pochekaev, 1949; Radovich and Gibbs, 1954; Baranov, 1955; Borisov, 1955; Yudovich, 1956; Parin, 1956, 1958; Gristchenko, 1957; Pokrovsky, 1957; Fukuhara, 1959); tunas—

Neothunnus macropterus and *Euthynnus yaito* (Hsiao, 1952; Tester, 1959); cod-like fishes—*Gadus morhua morhua* (Borisov, 1950, 1955; Lagunov, 1955), *Gadus morhua macrocephalus* (Baranov, 1955), *Melanogrammus aeglefinus, Odontogadus merlangus euxinus,* and *Boreogadus saida* (Borisov, 1955).[3] The behavioral studies conducted at the California Academy of Sciences have been confined to four species of marine pelagic fishes: Pacific sardine, *Sardinops caerulea* (Girard); northern anchovy, *Engraulis mordax* Girard; Pacific mackerel, *Pneumatophorus diego* (Ayres); and Pacific jack mackerel, *Trachurus symmetricus* (Ayres). The behavior and reactions of the sardine under the influence of white and colored lights and darkness have already been explored (Loukashkin and Grant, 1959). The present paper sums up the results of the study of the behavior and reactions of the northern anchovy stimulated by artificial light of different wave lengths and intensities and by darkness. In essence, it is a continuation of the earlier experimental work on sardines. The equipment, facilities, and methods (fig. 1) used in the laboratory experiments for the larger part of the study were exactly the same as described earlier for the sardine; therefore, to avoid unnecessary repetition the reader is referred to that report. However,

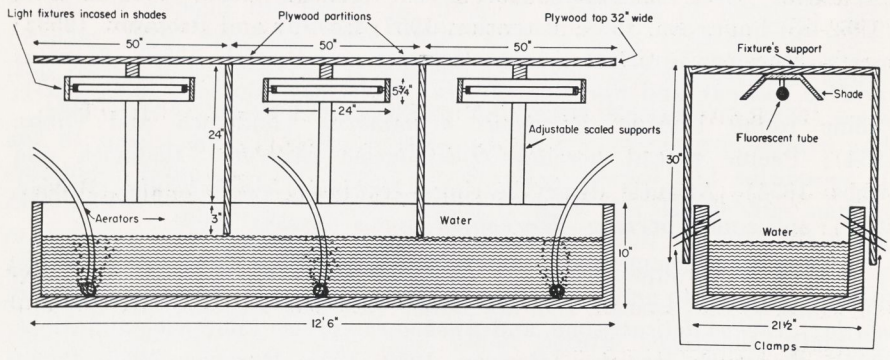


FIGURE 1. Sketch drawing of the experimental tank divided into three light zones for testing the anchovy's ability to discriminate colors of the light and intensities of white light. (After Loukashkin and Grant, 1959.)

changes in technique or equipment are noted and full information is presented in appropriate sections below.

For measuring light intensities, a Weston Illumination Meter, model 756, was used. This model is visual and cosine corrected, with direct dial read-

[3] The size of the present report excludes the possibility of listing all the other marine and freshwater fishes whose phototactic responses to artificial light have been tested in recent years. Readers interested in this subject will find more information in the accounts by Baranov (1955), Blaxter and Parrish (1958), Borisov (1950, 1955), Parin (1958), Pochekaev (1949), Privolnev (1958), Protasov (1957, 1958), Radovich and Gibbs (1954), Sasaki (1959), and especially in the Verheijen report (1958) in which a review of the literature on fish responses to light is included.

ings on the scales ranging from 0 to 500 foot-candles. The illumination meter was manufactured by the Weston Electrical Instrument Corporation of Newark, New Jersey.

This account is based on the experiments carried out on two large schools of adult anchovies kept in the display tanks of the Steinhart Aquarium, California Academy of Sciences, at different times (approximately two years apart). The majority of the experiments were devoted to the investigation of the ability of the anchovy to discriminate the same monochromatic lights, white light and darkness, which had been successfully applied in the experiments with the Pacific sardine (fig. 2). The second portion of the study involved the use of ultraviolet and infrared wave lengths and observations on the reactions of the anchovy to different intensities of the white light. As with the stock of the Pacific sardine used in earlier experiments, the northern anchovy schools were kept in a 1,000-gallon display tank illuminated with an ordinary 300-watt incandescent lamp which was suspended two feet above the water surface. Therefore, the fish used in the study can be considered "light-adapted" animals.

The scientific names of most of the fishes mentioned in the text are based on Roedel (1953) for the California and Mexican species, and on Berg (1932–33, 1949), Borisov and Ovsiannikov (1951), and Svetovidov (1952) for the fishes of the USSR.

II. REACTIONS OF NORTHERN ANCHOVY TO LIGHT WAVE LENGTHS AND INTENSITIES

(1) Preferential reactions to monochromatic lights, white light, and darkness.

The ability of the anchovy to react differently to different light wave lengths was tested in a tank which could be divided into two, three, or four

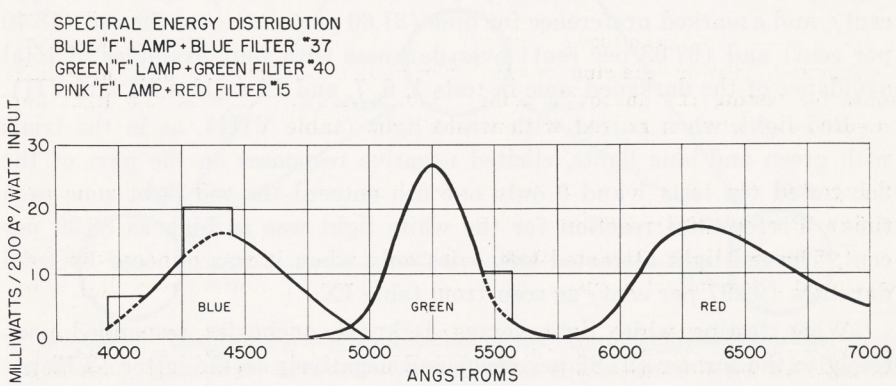


FIGURE 2. Spectral energy distribution of the monochromatic light sources used in the present study. (After E. A. Lindsay, 1948.)

zones and equipped with electric light sources of contrasting illumination. Results of the experiments of two-zone tests are presented in tables I–XI, those of the three-zone tests in tables XII and XIV, and of the four-zone tests in table XIII. In the two-zone tests different groups of six fish were subjected to the effect of a given pair of lights or of light and darkness. Each combination was used in two experiments consisting of six tests with 100 recorded observations, totalling 7,200 fish. Altogether, 79,200 fish are grouped in eleven tables for comparison of natural preference reactions to one type of illumination, or another. In testing the ability of the anchovy to distinguish green light from other colors, it was found that when this light was paired with white light, 5,424 fish out of 7,200 moved to or remained in the green-light zone, displaying definite preference for this light (74.34 per cent) over the white light (24.66 per cent), as seen from table I. When green and red lights were paired, this preference for green light rose to 97.86 per cent. The highest degree of negative reactions to red light in tests 2, 6, and 12 was manifested by total avoidance of the red light zone, as shown in table II. When green light was presented along with blue light, anchovies were able to differentiate these two lights in contrast to the Pacific sardine, which was unable to do so (Loukashkin and Grant, 1959). As seen from table III, anchovies reacted preferentially to green light; 73.18 per cent of the individuals which were tested selected the "green zone," compared to 26.82 per cent which showed preference for the "blue zone." When paired with a darkened zone, the green-light zone was frequented by 6,918 fish (96.08 per cent), while only 282 (3.92 per cent) made occasional movements of short duration into the darkened zone. In tests 1 and 5, avoidance of the darkened zone was total (table IV).

When testing the blue light paired with white light or red light or darkness, fish responded favorably to the blue light. Table V shows a slight preference for blue (52.15 per cent) over the white light (47.85 per cent), and a marked preference for blue (81.60 per cent) over the red (18.40 per cent) and (97.03 per cent) over darkness with four examples of total avoidance of the darkened zone in tests 1, 6, 7, and 12 (tables VI and VII).

Red light, when paired with white light (table VIII), as in the trials with green and blue lights, elicited negative responses on the part of the fish tested (in tests 1 and 9 only one fish entered the red light zone each time). Preferential reaction for the white light was as high as 88.39 per cent. The red light attracted anchovies only when it was opposed by total darkness (92.97 per cent) as seen from table IX.

When testing white light versus darkness, anchovies responded positively to the former (97.88 per cent) and negatively to the latter (2.12 per cent) with total avoidance of that zone in tests, 4, 5, 6, 8, 10, 11, and 12 (table X). This is in full accord with other experiments in which an illumi-

nated zone was presented with the darkened one (tables IV, VII, and IX).

Diagrammatic interpretation of the relationship in the effects of different lights on the anchovy's discriminating ability tested in pairs is shown in figure 3.

To evaluate the significance of the apparent preference responses of the fish to monochromatic lights, the same groups of anchovies, either before or after experiment, were kept in a two-zone tank under a white light of the same intensity. The results obtained are presented in table XI, and they clearly display a normal distribution of 7,200 fish very close to a 50:50 ratio; however, the relationship varied from test to test. The average distribution of anchovies for 12 tests was found to be 50.06 per cent for one zone, and 49.94 per cent for the other. These tests were considered as controls.

After completing the series of experiments in a two-zone tank, anchovies were subjected to experiments in three-zone and four-zone tanks. In these experiments light intensities were maintained at a uniform level for all lights as in the two-zone experiments, or they were presented in different values. The latter modification was intended to see if the increment in light intensity would elicit a change in response because of brightness of illumination regardless of the color of light. The results of these experiments are presented in tables XII and XIII. The first four experiments in a three-

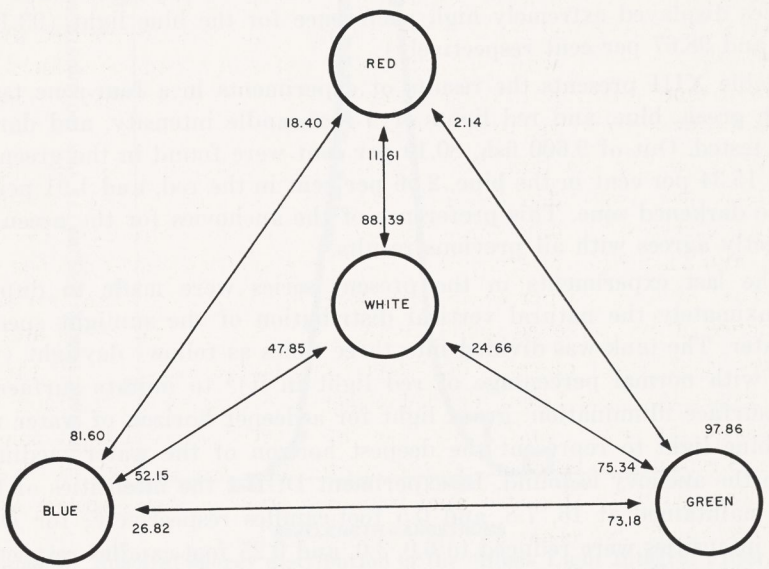


FIGURE 3. Diagrammatic interpretation of the relationships between the effects of different lights on the anchovy's discriminating ability tested in pairs in the two-zone tank. Positive and negative reactions are expressed in per cent. All sources of light were maintained at 9 foot-candle intensity.

zone tank illuminated with white, green, and red lights, regardless of variation in intensities, demonstrated overwhelming preference of the anchovies for the green light. The positive preference responses in these experiments for the green light averaged as high as 66.33 per cent (14,400 fish), though in separate cases this preference varied from 56.0 per cent to 72.0 per cent. Negative responses to the other two lights were as follow: 19.63 per cent for white light and 14.04 per cent for red light. These results are in full agreement with those obtained for the green light when tested in pairs with the others in a two-zone tank. In experiment WGD (table XII) the intensity of the green light was reduced to 6 foot-candles, while the white-light intensity was increased up to 30 foot-candles. The third zone was darkened. Again, anchovies responded in favor of the green light (69.33 per cent). In another experiment RDW (table XII) red and white lights were presented in intensities of 30 foot-candles with the middle zone darkened. As anticipated, the white-light zone was frequented most of all (50.34 per cent), and red-light zone least of all (19.33 per cent). The reason why more fish were found in the darkened zone than in the red-light zone may have been that the white light penetrated the darkened zone. In other experiments, DBR-1 and DBR-2 (table XIII), the blue and red lights were applied, the third zone having been darkened. In both experiments with uniform intensities of 9 foot-candles and with contrasting intensities (4 foot-candles for the blue light, and 30 foot-candles for the red light) anchovies displayed extremely high preference for the blue light (93.16 per cent and 98.67 per cent respectively).

Table XIII presents the results of experiments in a four-zone tank in which green, blue, and red lights of 9 foot-candle intensity, and darkness were tested. Out of 9,600 fish, 80.19 per cent were found in the green-light zone, 15.34 per cent in the blue, 2.56 per cent in the red, and 1.91 per cent in the darkened zone. This preference of the anchovies for the green light perfectly agrees with all previous results.

The last experiments in the present series were made to duplicate approximately the natural vertical distribution of the sunlight spectrum in water. The tank was divided into three zones as follow: daylight (white light with normal percentage of red light in it)[4] to imitate surface and near-surface illumination; green light for a deeper horizon of water mass; and blue light to represent the deepest horizon of the water medium in which the anchovy is found. In experiment DGB-1 the intensities of lights were maintained at 16, 7.8, and 0.5 foot-candles respectively; for DGB-2 these intensities were reduced to 6.0, 3.0, and 0.25 foot-candles respectively (table XIV). The results of 12 tests with a group of nine anchovies in each of the two experiments show the same preferential tendency of the fish

[4] General Electric 20-watt "Daylight" fluorescent tube 24 inches long, ordering symbol F20T12/D.

toward the green light as in all other experiments in which various combinations of monochromatic and white lights were applied. This preference for the green light was found to be 48.57 per cent, in the experiment DGB-1, and 44.79 per cent in DGB-2 compared to 30.01 per cent and 30.24 per cent respectively for the daylight and 21.42 per cent and 25.40 per cent for the blue light.

(2) Responses to ultraviolet wave length.

In this series of experiments, low and high intensity sources of ultraviolet radiation were used. In the first set of experiments a "black light" 20-watt fluorescent tube (24 inches long) manufactured by the General Electric Company (trade symbol F20T12/BLB) was used. Its spectrographic characteristics are shown by the curve in figure 4, from which it is seen that this lamp emits a certain amount of visible light, too. This source

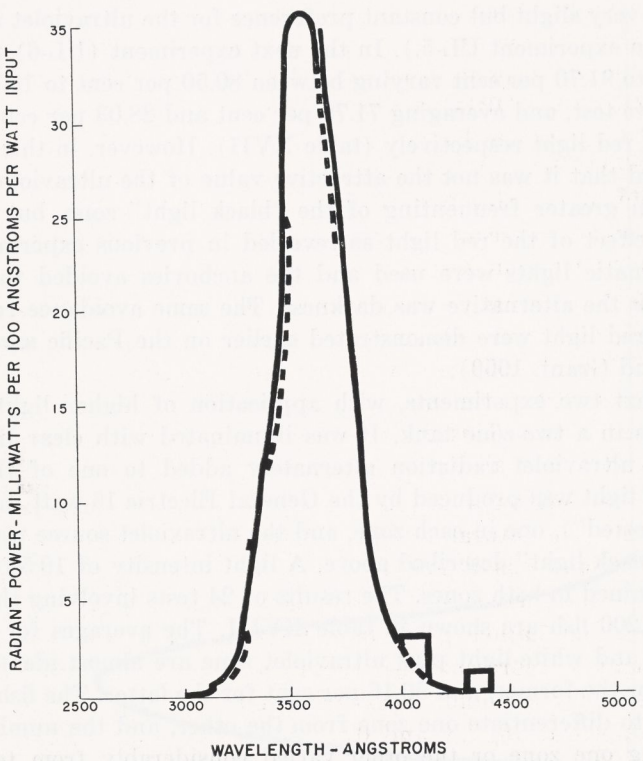


FIGURE 4. Spectral energy distribution of the "Black Light Integral Filter Fluorescent Lamp" manufactured by the General Electric Company. Official drawing on file with the Company based on 40-watt lamp is reproduced here with written permission of the manufacturer. The curve is also typical for the 20-watt lamp (F20T12/BLB) used in the present study.

of ultraviolet radiation was first tested paired with monochromatic lights, using the same colored fluorescent tubes and filters as in the preceding series. Because of the extremely low intensity of the "black light," the other lamps were masked to reduce the intensity of colored lights to the level of the former, which was as low as 0.2 foot-candle. The results of six experiments covering the distribution of 57,600 fish are tabulated in tables XV–XVII.

Paired with blue light, the ultraviolet wave length had no specific effect upon behavior of the anchovies. The average figures show a 50:50 distribution ratio (table XV). The ultraviolet-green combination revealed slight preferential reactions toward the green light (54.79 per cent). This tendency was observed in all of the 24 tests (table XVI), while in ultraviolet-blue combination fish responses varied considerably from test to test, especially in experiment UL-1.

In experiments using ultraviolet light and red light, anchovies at first displayed very slight but constant preference for the ultraviolet zone (52.25 per cent in experiment UL-5.). In the next experiment (UL-6) this preference rose to 91.70 per cent varying between 80.50 per cent to 100.0 per cent from test to test, and averaging 71.79 per cent and 28.03 per cent for ultraviolet and red light respectively (table XVII). However, in this case it can be assumed that it was not the attractive value of the ultraviolet rays that resulted in greater frequenting of the "black light" zone, but rather the repelling effect of the red light as revealed in previous experiments when monochromatic lights were used and the anchovies avoided the red-light zone unless the alternative was darkness. The same avoidance reactions toward the red light were demonstrated earlier on the Pacific sardine (Loukashkin and Grant, 1959).

The next two experiments, with application of higher light intensity, were made in a two-zone tank. It was illuminated with clear light, and a source of ultraviolet radiation alternately added to one of these zones. The white light was produced by the General Electric 15-watt incandescent lamp ("frosted"), one in each zone, and the ultraviolet source was the same 20-watt "black light" described above. A light intensity of 10.5 foot-candles was maintained in both zones. The results of 24 tests involving the distribution of 19,200 fish are shown in table XVIII. The averages for the white-light zone and white-light plus ultraviolet zone are almost identical: 49.84 per cent for the former, and 50.16 per cent for the latter. The fish seemed to be unable to differentiate one zone from the other, and the numbers of fish frequenting one zone or the other varied considerably from test to test, especially in experiment UL-7.

Following this, an ultraviolet source of very high intensity was tested. For this purpose a "New Black-Ray Model B-100 (3660Å)" equipped with 100-watt mercury spotlight bulb, ballast, and ultraviolet-transmitting Kopp

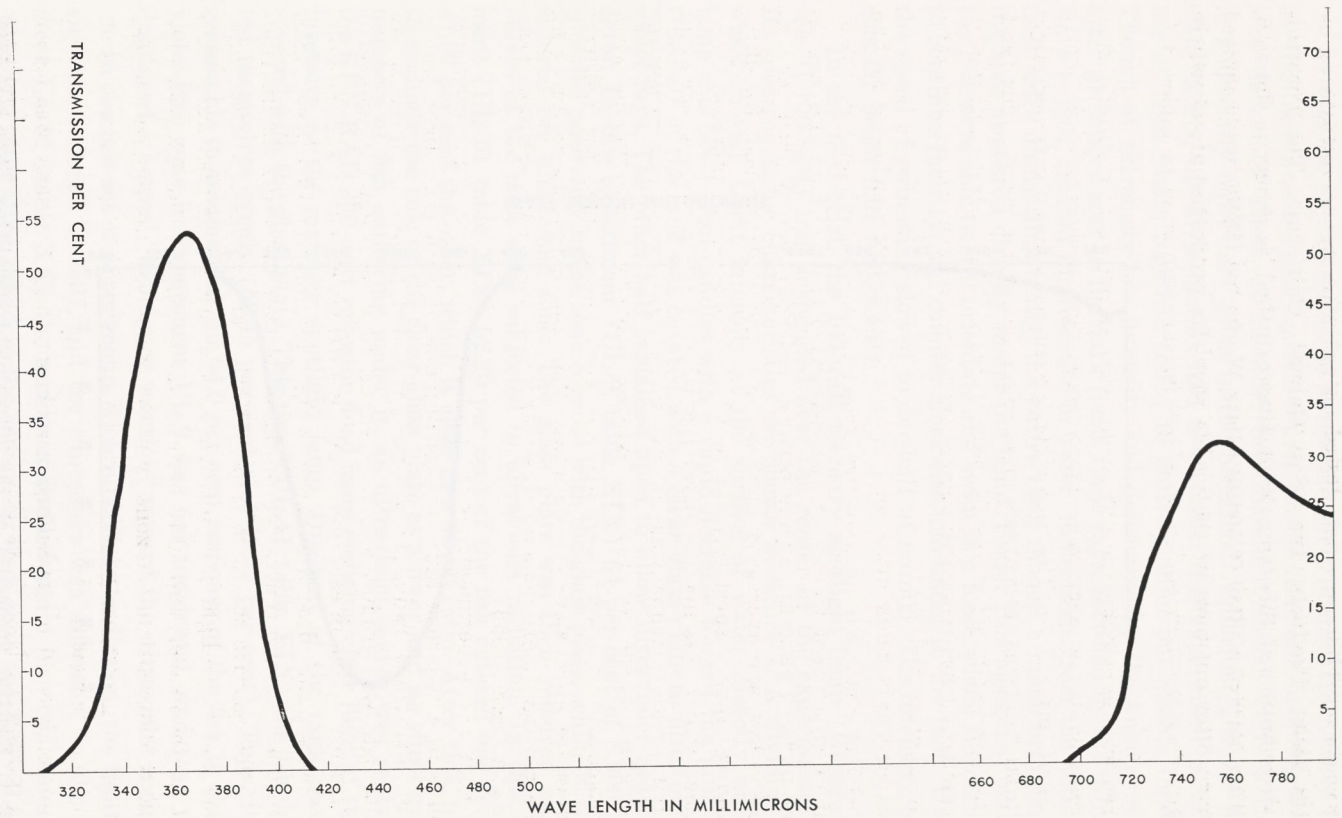


FIGURE 5. Spectral properties of the ultraviolet transmitting filter "Kopp no. 41" as used on the "New Black-Ray Model B-100 (3660Å)" lamp manufactured by the Ultra-Violet Products, Inc., San Gabriel, California. Courtesy of the manufacturer.

41 filter was used. This source of ultraviolet radiation was manufactured by the Ultra-Violet Products, Inc., San Gabriel, California. The spectral-energy distribution of this lamp, with filter attached, is shown in figure 5. In addition, an extra filter (Corning Glass Works, no. 5840) was acquired in order to filter out most of the visible rays. Its properties are shown in figure 6.

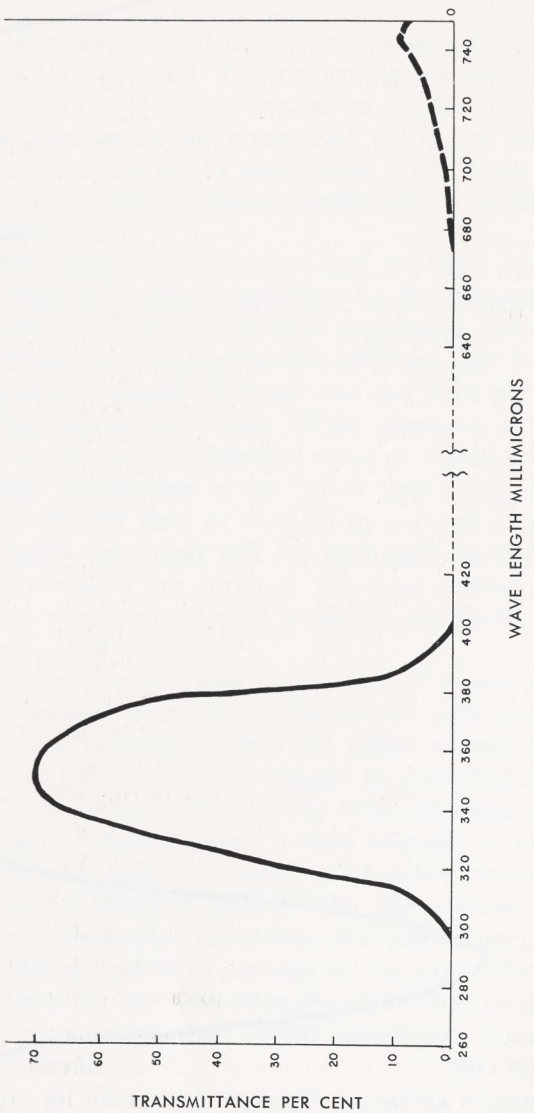


FIGURE 6. Spectral properties of the ultraviolet-transmitting filter no. 5840 (7–60) of the Corning Glass Works. Courtesy of the manufacturer.

At first, attempts were made to test the effect of ultraviolet wave lengths in total darkness by placing this source in one zone and keeping the other zone darkened. These, as all other tests herein reported, were carried out in a specially built dark room in the Steinhart Aquarium. Despite all possible efforts, the investigators had to abandon this experiment because the use of both filters together failed to entirely filter out visible light rays. Though of extremely low intensity and detectable by the human eye only after prolonged stay in the dark room, these rays, fortified by the ultraviolet wave length, created fluorescence in water. Reflections from the bottom and tank sides dimly illuminated the entire tank though a much brighter glowing spot appeared directly under the lamp. Under this meager illumination the fish were able to still orientate and swim in a loose school formation and to continue their typical counter-clockwise movement in the tank. However, the speed of swimming slowed to one-half of normal. The intensity of light was far below 0.01 foot-candle.

In the next trial, the 100-watt mercury spotlight lamp (General Electric H-100-SP4) was suspended over the center of the experimental tank. Its spectrographic characteristics are shown in figure 7. A dividing shield was removed. Light intensity at the surface of water directly under the lamp was 500+ foot-candles with a rapid decrease toward the tank's ends. One-half of the tank was covered with a clear glass plate to filter out ultraviolet rays. The other half remained open to allow ultraviolet radiation to enter. In this experiment (UL-9, table XIX) 64 per cent of 8,000 fish responded positively to the zone covered with the glass plate, while 36 per cent entered the ultraviolet zone. The glass plate was then removed and both halves of the tank were subjected to ultraviolet radiation. In this experiment (UL-10, table XIX) 52.20 per cent of the fish entered one zone, and 47.80 per cent the other, which is close to a 50:50 ratio. After this, in order to evaluate the role of the clear-glass plate as a filter and its effect upon the numbers of fish gathering under it, an ultraviolet source was replaced by the KEN-RAD 300-watt reflector flood lamp emitting clear light of the same intensity as the mercury spotlight lamp. One-half of the tank was again covered with the glass plate. This time (UL-11, table XIX) the fish distributed themselves evenly (50.45 per cent and 49.55 per cent). Thus, it seems reasonable to assume that the 64.0 per cent response of the fish to the ultraviolet-free zone in experiment UL-9 was not incidental, and that the fish displayed a normal "avoidance reaction" toward the ultraviolet zone.

In the last set of experiments with ultraviolet radiation, the light intensity was reduced by half, and the procedure was different. In the experiment UL-12 (table XX) the tank was divided again into two zones by installing a separating shield in the center. In each zone one KEN-RAD 300-watt reflector flood lamp emitting white light of 225 foot-candle intensity

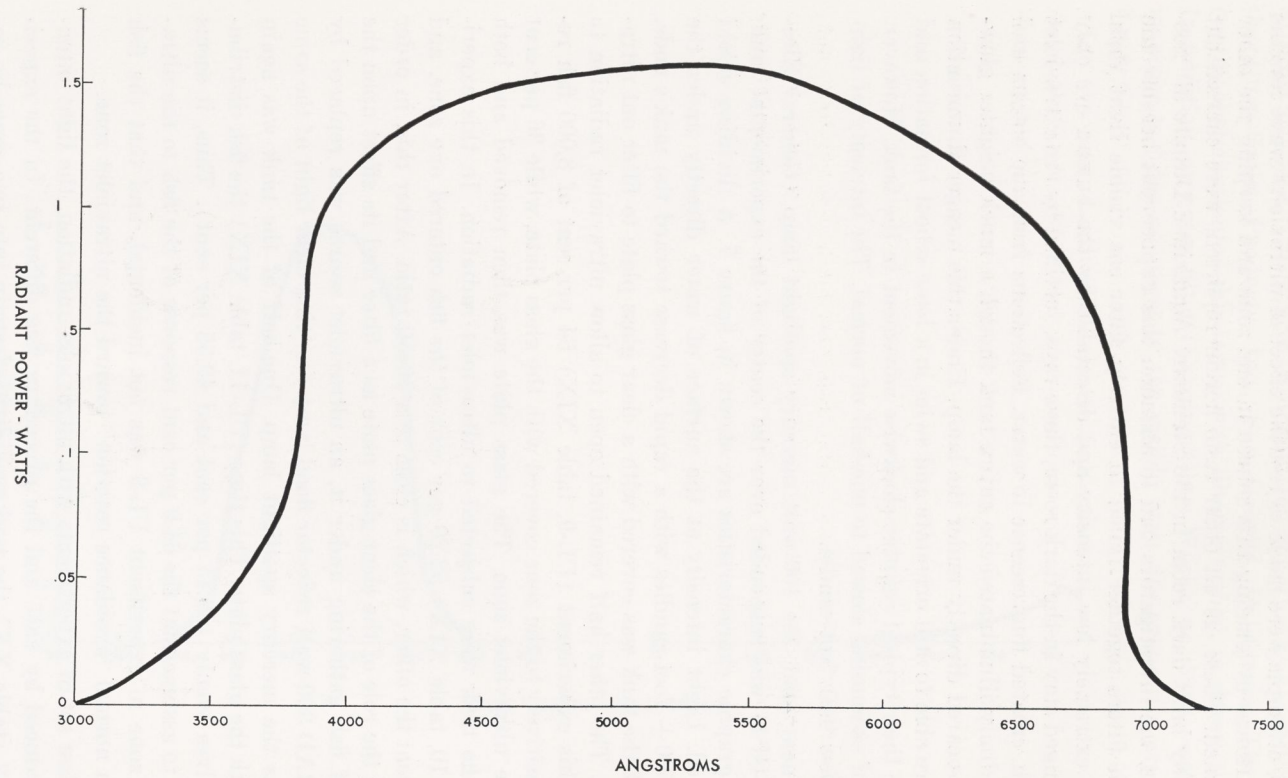


FIGURE 7. Spectral energy distribution of the General Electric 100-watt mercury reflector spotlight lamp (near-ultraviolet region of the spectrum) No. H–100–SP4 (Black Light) based on the data published by the manufacturer. [The pamphlet "Mercury Lamps and Transformers," LS–103, second printing, dated January 1958.] Courtesy of the General Electric Company.

was installed. In ten tests involving 6,000 fish, as anticipated, there resulted a more or less even distribution of fish (48.47 per cent and 51.53 per cent). In experiment UL-13 (table XX), one of the white lights was replaced with 100-watt mercury spotlight lamp (ultraviolet), and the positions of these two sources were alternated during the experiment. The intensity of light in both zones remained the same as in the previous experiment. Throughout all ten tests, the anchovies consistently preferred the white-light zone. Their responses for the white-light zone varied between 60.0 per cent to 100.0 per cent from test to test, averaging 72.1 per cent and displaying negative or avoidance reaction toward the ultraviolet zone (27.9 per cent) once again. Diagrammatic interpretation of the anchovy reactions toward the ultraviolet wave length is shown in figure 8.

(3) Responses to infrared wave length.

In this series of experiments the first tests were made in a two-zone tank; one zone was exposed to infrared radiation, the other remained in total darkness. Instead of being six inches deep, as in all other experiments, the

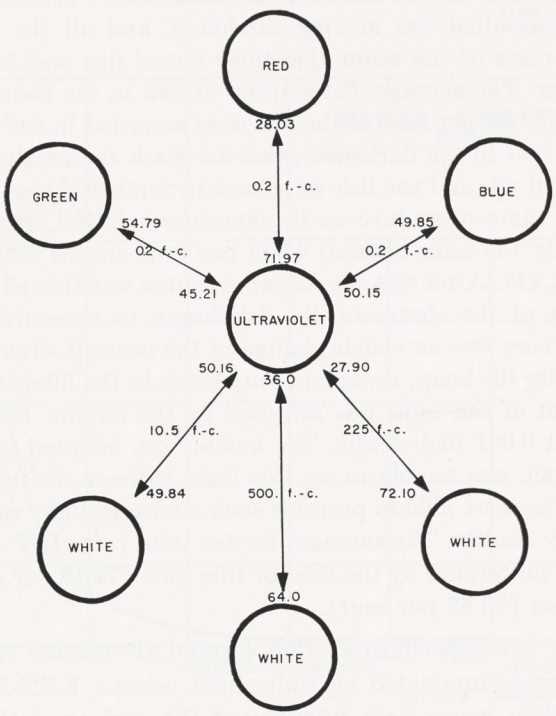
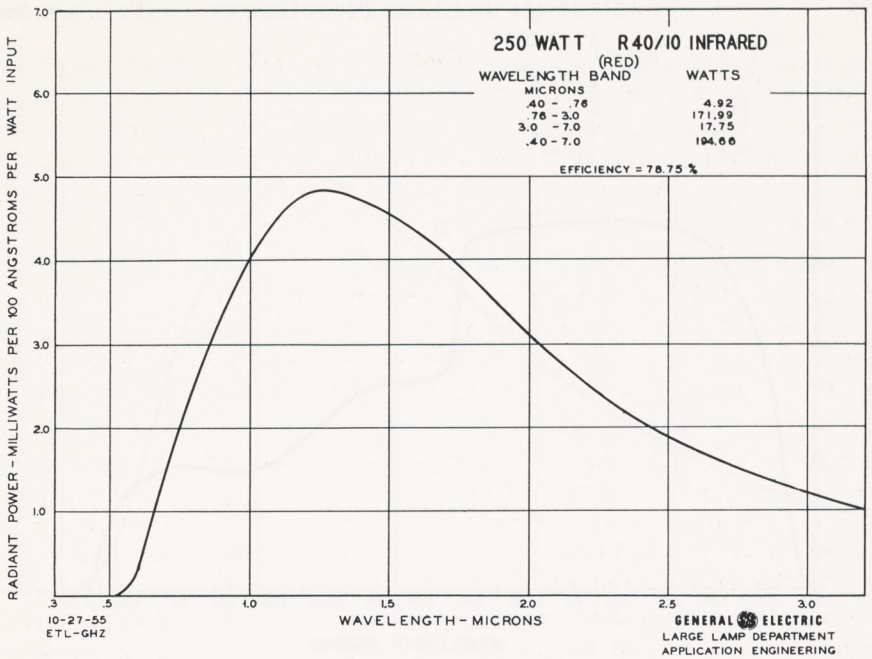


FIGURE 8. Diagrammatic interpretation of the anchovy's reactions toward the ultraviolet wave length in relation to opposing monochromatic and white lights. Positive and negative reactions are expressed in per cent.

water level was lowered to three inches and the lamp was suspended six inches above its surface. A G.E. 250-watt reflector heat lamp with red coating provided the source of the infrared radiation (its spectrographic features are shown in figure 9). A Corning filter no. 2540 was used to absorb all visible rays, transmitting infrared rays alone. Figure 10 shows the spectrographic properties of this filter.

Eight anchovies were placed in an experimental tank two hours prior to testing and were kept there in total darkness. A recording of fish distribution was made every ten minutes with the aid of dimmed ruby-red flashlight; this operation required not more than two or three seconds and only the fish in one zone were counted at a time. Altogether ten tests each of 30 recorded observations were made covering the distribution of 2,400 fish. The results of experiment INF-1 are shown in table XXI. From the very start, it was clearly evident that the fish did not respond to infrared radiation. In both darkened and infrared zones, they behaved in exactly the same manner as did the Pacific sardine in total darkness (Loukashkin and Grant, 1959). The school was broken up; fish were scattered throughout the tank; swimming speed was slowed almost to a "stand still"; orientation was completely lost, individual fish moving randomly, and all the fish moved so close to the surface of the water that their dorsal fins and backs projected above the water. The average distribution of fish in ten tests was found to be about even: 51.33 per cent of the fish were recorded in the infrared zone, and 48.67 per cent in the darkened zone. To check the results, the infrared lamp was turned off, and the fish were kept in total darkness in both zones. Following the same procedure as in experiment INF-1, the investigators obtained exactly the same results: 48.58 per cent and 51.42 per cent (exp. INF-2, table XXI). After this, an infrared source was turned on again, and to the surprise of the observers, the fish began to concentrate under the lamp, though there was no visible change in the over-all situation. The mirror, placed under the lamp, revealed a tiny crack in the filter, through which just a pin point of red light was reflected by the mirror. Intensity of this light was about 0.001 foot-candle. The human eye, adapted to the darkness of the dark room, was unable to see this light without the use of a mirror, but the anchovies were able to perceive such a meager light value and to respond to it very readily. The averages for ten tests (exp. INF-3, table XXI) show a definite preference by the fish for this zone (74.17 per cent) over the zone of darkness (25.83 per cent).

In the next two experiments (INF-4 and INF-5, table XXII), one of the two zones was illuminated by white light using a KEN-RAD 300-watt reflector floodlight lamp; light intensity at the surface of the water measured 500 foot-candles. The other zone was illuminated with a G.E. 250-watt reflector heat lamp without red coating, which emitted both white light and



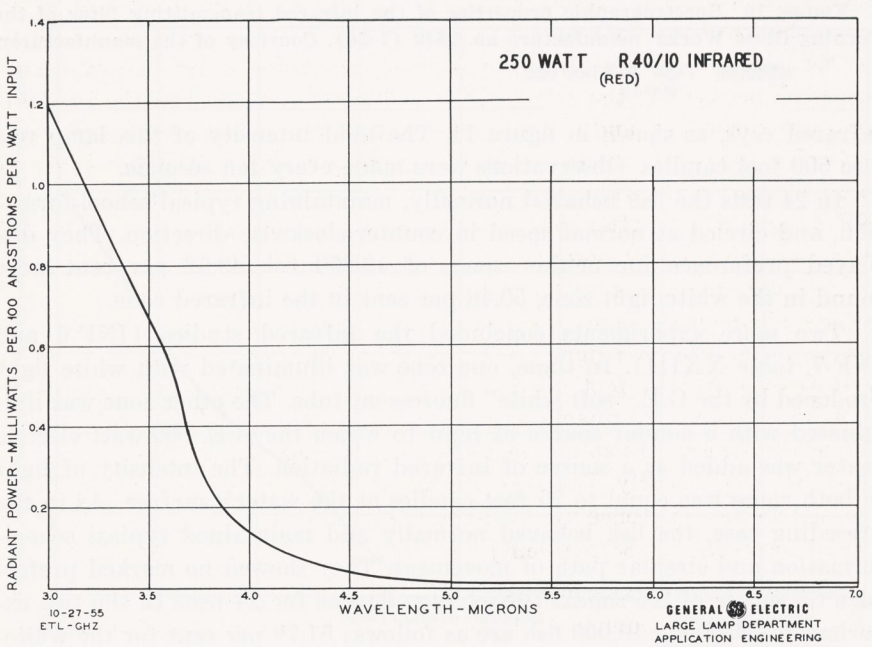


FIGURE 9. Spectral energy distribution of the 250-watt reflector heat lamp with red coating (infrared) manufactured by the General Electric Company. These graphs are official manufacturer's copies reproduced here with the Company's written permission.

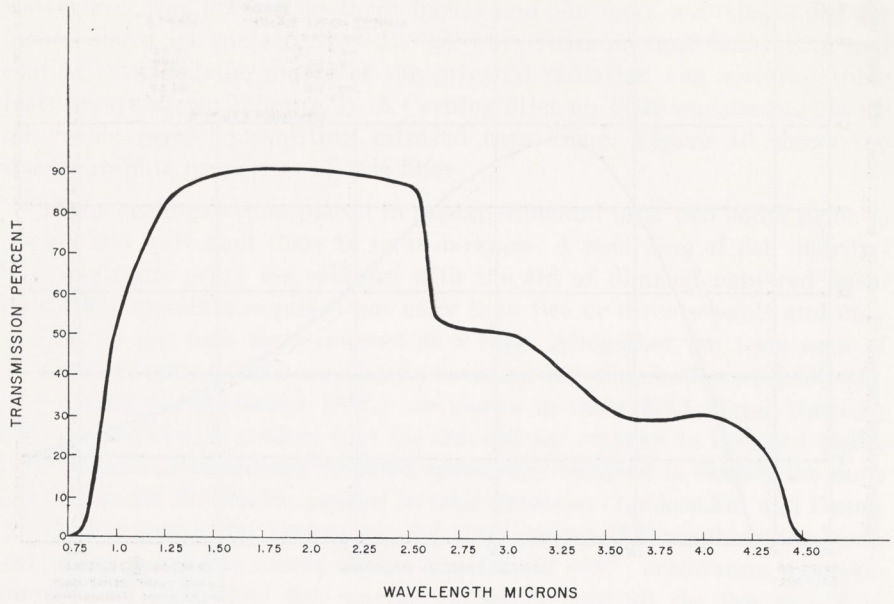
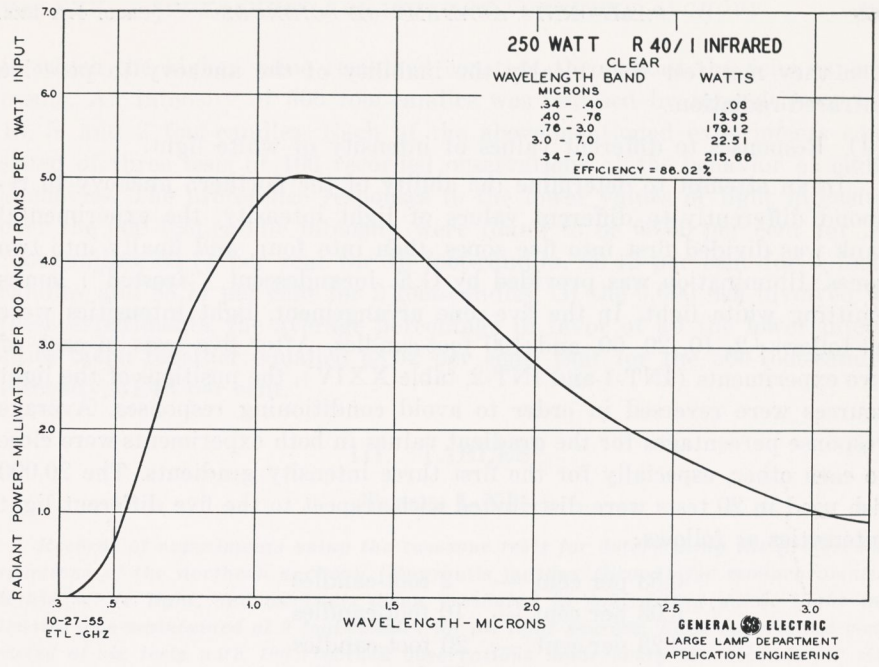


FIGURE 10. Spectrographic properties of the infrared transmitting filter of the Corning Glass Works' manufacture no. 2540 (7–56). Courtesy of the manufacturer.

infrared rays, as shown in figure 11. The light intensity of this lamp was also 500 foot-candles. Observations were made every ten seconds.

In 24 tests the fish behaved normally, maintaining typical school-formation, and circled at normal speed in counter-clockwise direction. They displayed preference for neither zone; of 19,200 fish 49.52 per cent were found in the white light zone, 50.48 per cent in the infrared zone.

Two more experiments concluded the infrared studies (INF-6 and INF-7, table XXIII). In these, one zone was illuminated with white light produced by the G.E. "soft white" fluorescent tube. The other zone was illuminated with a similar source of light to which the G.E. 600-watt electric heater was added as a source of infrared radiation. The intensity of light in both zones was equal to 25 foot-candles at the water's surface. As in the preceding case, the fish behaved normally and maintained typical school-formation and circular path of movement. They showed no marked preference for either of the zones. The average figures for 24 tests in the two experiments involving 19,000 fish are as follows: 51.79 per cent for the white-light zone and 48.21 per cent for the white-light-plus-infrared-wave-length zone. For all practical purposes these figures show an even distribution of the fish, and as in all other experiments with application of infrared radia-



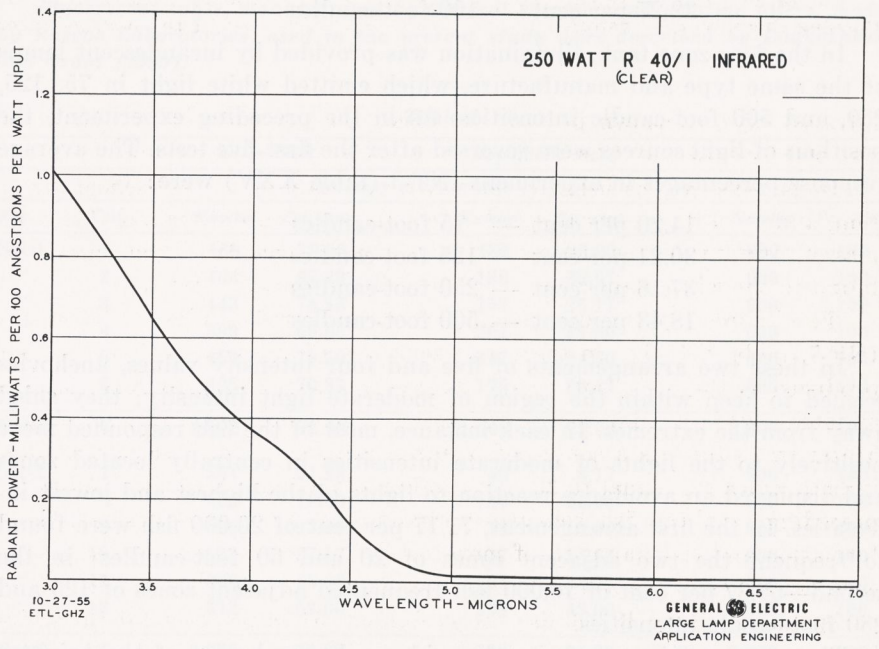


FIGURE 11. Spectral energy distribution of the 250-watt reflector clear heat lamp (infrared) manufactured by the General Electric Company. These graphs are official copies of the manufacturer. Courtesy of the General Electric Company.

tion they manifest very clearly the inability of the anchovy to perceive infrared radiation.

(4) Responses to different values of intensity of white light.

In an attempt to determine the ability of the northern anchovy to respond differently to different values of light intensity, the experimental tank was divided first into five zones, then into four, and finally into two zones. Illumination was provided by G.E. incandescent ("frosted") lamps emitting white light. In the five-zone arrangement, light intensities were as follows: 2, 10, 20, 50, and 100 foot-candles. After five tests in each of two experiments (INT-1 and INT-2, table XXIV), the positions of the light sources were reversed in order to avoid conditioning responses. Average response percentages for the gradient values in both experiments were close to each other, especially for the first three intensity gradients. The 20,000 fish used in 20 tests were distributed with respect to the five different light intensities as follows:

0.53 per cent — 2 foot-candles
6.03 per cent — 10 foot-candles
29.23 per cent — 20 foot-candles
41.94 per cent — 50 foot-candles
22.27 per cent — 100 foot-candles

In the four-zone tank, illumination was provided by incandescent lamps of the same type and manufacture, which emitted white light in 75, 125, 250, and 500 foot-candle intensities. As in the preceding experiment, the positions of light sources were reversed after the first five tests. The average response percentages in experiment INT-3 (table XXV) were:

14.20 per cent — 75 foot-candles
30.21 per cent — 125 foot-candles
37.16 per cent — 250 foot-candles
18.43 per cent — 500 foot-candles

In these two arrangements of five and four intensity values, anchovies seemed to keep within the region of moderate light intensity; they shied away from the extremes. In each instance, most of the fish responded more positively to the lights of moderate intensities in centrally located zones and displayed an avoidance reaction to lights of the highest and lowest intensities. In the first arrangement, 71.17 per cent of 20,000 fish were found to frequent the two adjacent zones of 20 and 50 foot-candles; in the second—67.37 per cent of 10,000 fish frequented adjacent zones of 125 and 250 foot-candle intensities.

The most striking example of avoidance by anchovies of the brighter zone was demonstrated in experiments INT-4, INT-5, INT-6, and INT-7, when intensities of white light were presented in sharply contrasting pairs,

in which the higher value remained constant throughout the four experiments. An intensity of 500 foot-candles was opposed by intensities of 20, 10, 5, and 2 foot-candles. Each of the above-mentioned experiments consisted of three tests of 100 recorded observations of the behavior of eight anchovies. The preference responses to the lower values of light intensity over the 500 foot-candle intensity were found to be 65.50 per cent for 20 foot-candles, 64.71 per cent for 10 foot-candles, 60.42 per cent for 5 foot-candles, and 83.71 per cent for 2 foot-candles. Of the 9,600 fish involved in these experiments, the average percentage in favor of all the lower intensities taken together equalled 68.52 per cent; that for the 500-foot-candle intensity, 31.48 per cent.

III. TABLES

TABLES I–XI

Records of experiments using the two-zone tests for determining the preference reactions of the northern anchovy (Engraulis mordax *Girard) for monochromatic lights, white light, and darkness when presented in contrasting pairs. Light intensity was maintained at 9 foot-candles for all light sources. Each experiment consisted of six tests with 100 recorded observations made every ten seconds for six anchovies subjected to the effect of the light.*

Fluorescent tubes, manufactured by General Electric, and gelatine filters, made by Rascoe Laboratories, used in the present study were described by Loukashkin and Grant (1959).

Table I

		Green Light		*Soft White Light*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
GR-1	1	468	78.00	132	22.00	600	100
"	2	404	67.33	196	32.67	600	100
"	3	443	78.83	157	26.17	600	100
"	4	399	66.50	201	33.50	600	100
"	5	453	75.50	147	24.50	600	100
"	6	425	70.83	175	29.17	600	100
Total	6	2,592	72.00	1,008	28.00	3,600	100
GR-2	7	551	91.83	49	8.17	600	100
"	8	468	78.00	132	22.00	600	100
"	9	582	97.00	18	3.00	600	100
"	10	523	87.17	77	12.83	600	100
"	11	396	66.00	204	34.00	600	100
"	12	312	52.00	288	48.00	600	100
Total	6	2,832	78.67	768	21.33	3,600	100
Grand Total	12	5,424	75.34	1,776	24.66	7,200	100

Table II

		Green Light		*Red Light*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
GR-3	1	597	99.50	3	0.50	600	100
"	2	600	100.00	0	0.00	600	100
"	3	561	93.50	39	6.50	600	100
"	4	593	98.83	7	1.17	600	100
"	5	597	99.50	3	0.50	600	100
"	6	600	100.00	0	0.00	600	100
Total	6	3,548	98.56	52	1.44	3,600	100
GR-4	7	598	99.67	2	0.33	600	100
"	8	599	99.83	1	0.17	600	100
"	9	591	98.50	9	1.50	600	100
"	10	514	85.67	86	14.33	600	100
"	11	596	99.33	4	0.67	600	100
"	12	600	100.00	0	0.00	600	100
Total	6	3,498	97.17	102	2.83	3,600	100
Grand Total	12	7,046	97.86	154	2.14	7,200	100

Table III

		Green Light		*Blue Light*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
GR-5	1	433	72.17	167	27.83	600	100
"	2	429	71.50	171	28.50	600	100
"	3	383	63.83	217	36.17	600	100
"	4	381	63.50	219	36.50	600	100
"	5	480	80.00	120	20.00	600	100
"	6	465	77.50	135	22.50	600	100
Total	6	2,571	71.42	1,029	28.58	3,600	100
GR-6	7	563	93.82	37	6.17	600	100
"	8	419	68.33	181	31.67	600	100
"	9	280	46.67	320	53.33	600	100
"	10	505	84.17	95	15.83	600	100
"	11	441	73.50	159	26.50	600	100
"	12	490	81.67	110	18.33	600	100
Total	6	2,698	74.94	902	25.06	3,600	100
Grand Total	12	5,269	73.18	1,931	26.82	7,200	100

Table IV

		Green Light		*Darkness*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
GR-7	1	600	100.00	0	0.00	600	100
"	2	454	75.67	146	24.33	600	100
"	3	557	92.83	43	7.17	600	100
"	4	597	99.50	3	0.50	600	100
"	5	600	100.00	0	0.00	600	100
"	6	594	99.00	6	1.00	600	100
Total	6	3,402	94.50	198	5.50	3,600	100
GR-8	7	594	99.00	6	1.00	600	100
"	8	559	93.17	41	6.83	600	100
"	9	592	98.67	8	1.33	600	100
"	10	583	97.17	17	2.83	600	100
"	11	594	99.00	6	1.00	600	100
"	12	594	99.00	6	1.00	600	100
Total	6	3,516	97.67	84	2.33	3,600	100
Grand Total	12	6,918	96.08	282	3.92	7,200	100

Table V

		Blue Light		*Soft White Light*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
BL-1	1	180	30.00	420	70.00	600	100
"	2	464	77.33	136	22.67	600	100
"	3	373	62.17	227	37.83	600	100
"	4	333	55.50	267	44.50	600	100
"	5	367	61.17	233	38.83	600	100
"	6	318	53.00	282	47.00	600	100
Total	6	2,035	56.53	1,565	43.47	3,600	100
BL-2	7	379	63.17	221	36.83	600	100
"	8	289	48.17	311	51.83	600	100
"	9	237	39.50	363	60.50	600	100
"	10	280	46.67	320	53.33	600	100
"	11	234	39.00	366	61.00	600	100
"	12	303	50.50	297	49.50	600	100
Total	6	1,722	47.83	1,878	52.17	3,600	100
Grand Total	12	3,757	52.15	3,443	47.85	7,200	100

Table VI

		Blue Light		Red Light		Total	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
BL-3	1	474	79.00	126	21.00	600	100
"	2	591	98.50	9	1.50	600	100
"	3	353	58.83	247	41.17	600	100
"	4	390	65.00	210	35.00	600	100
"	5	438	73.00	162	27.00	600	100
"	6	523	88.83	77	11.17	600	100
Total	6	2,769	76.95	831	23.05	3,600	100
BL-4	7	597	99.50	3	0.50	600	100
"	8	576	96.00	24	4.00	600	100
"	9	403	67.17	197	32.83	600	100
"	10	526	87.67	74	12.33	600	100
"	11	499	83.17	101	16.87	600	100
"	12	505	84.17	95	15.83	600	100
Total	6	3,106	86.28	494	13.72	3,600	100
Grand Total	12	5,875	81.60	1,325	18.40	7,200	100

Table VII

		Blue Light		Darkness		Total	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
BL-5	1	600	100.00	0	0.00	600	100
"	2	538	89.67	62	10.33	600	100
"	3	578	96.33	22	3.67	600	100
"	4	565	94.17	35	5.83	600	100
"	5	578	96.33	22	3.67	600	100
"	6	600	100.00	0	0.00	600	100
Total	6	3,459	96.08	141	3.92	600	100
BL-6	7	600	100.00	0	0.00	600	100
"	8	594	99.00	6	1.00	600	100
"	9	592	98.67	8	1.33	600	100
"	10	560	93.33	40	6.67	600	100
"	11	581	96.83	19	3.17	600	100
"	12	600	100.00	0	0.00	600	100
Total	6	3,527	97.97	73	2.03	3,600	100
Grand Total	12	6,986	97.03	214	2.97	7,200	100

Table VIII

		Red Light		*Soft White Light*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
RD-1	1	1	0.17	599	99.83	600	100
"	2	40	6.67	560	93.33	600	100
"	3	8	1.33	592	98.67	600	100
"	4	48	8.00	552	92.00	600	100
"	5	89	14.83	511	85.17	600	100
"	6	81	13.50	519	86.50	600	100
Total	6	267	7.42	3,333	92.58	3,600	100
RD-2	7	13	2.16	587	97.84	600	100
"	8	104	17.33	496	82.67	600	100
"	9	1	0.17	599	99.83	600	100
"	10	209	34.83	391	65.17	600	100
"	11	233	38.83	367	61.17	600	100
"	12	9	1.50	591	98.50	600	100
Total	6	569	15.80	3,031	84.20	3,600	100
Grand Total	12	836	11.61	6,364	88.39	7,200	100

Table IX

		Red Light		*Darkness*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
RD-3	1	570	95.00	30	5.00	600	100
"	2	594	99.00	6	1.00	600	100
"	3	454	75.67	146	24.33	600	100
"	4	583	97.17	17	2.83	600	100
"	5	600	100.00	0	0.00	600	100
"	6	581	96.83	19	3.17	600	100
Total	6	3,382	93.94	218	6.06	3,600	100
RD-4	7	569	94.83	31	5.17	600	100
"	8	520	86.67	80	13.13	600	100
"	9	593	98.83	7	1.17	600	100
"	10	537	89.50	63	10.50	600	100
"	11	588	98.00	12	2.00	600	100
"	12	505	84.17	95	15.83	600	100
Total	6	3,312	92.00	288	8.00	3,600	100
Grand Total	12	6,694	92.97	506	7.03	7,200	100

Table X

		Soft White Light		*Darkness*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
WH-1	1	594	99.00	6	1.00	600	100
"	2	566	94.33	34	5.67	600	100
"	3	589	98.17	11	1.83	600	100
"	4	600	100.00	0	0.00	600	100
"	5	600	100.00	0	0.00	600	100
"	6	600	100.00	0	0.00	600	100
Total	6	3,549	98.58	51	1.42	3,600	100
WH-2	7	543	90.50	57	9.50	600	100
"	8	600	100.00	0	0.00	600	100
"	9	554	92.33	46	7.67	600	100
"	10	600	100.00	0	0.00	600	100
"	11	600	100.00	0	0.00	600	100
"	12	600	100.00	0	0.00	600	100
Total	6	3,497	97.14	103	2.86	3,600	100
Grand Total	12	7,046	97.88	154	2.12	7,200	100

Table XI

		Soft White Light		*Soft White Light*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
CON-1	1	263	48.83	337	56.17	600	100
"	2	286	47.67	314	52.33	600	100
"	3	349	58.27	251	41.73	600	100
"	4	350	58.33	250	41.67	600	100
"	5	228	38.00	372	62.00	600	100
"	6	371	61.83	229	38.17	600	100
Total	6	1,847	51.31	1,753	48.65	3,600	100
CON-2	7	384	64.00	216	36.00	600	100
"	8	238	39.67	362	60.33	600	100
"	9	302	50.33	298	49.67	600	100
"	10	224	37.33	376	62.67	600	100
"	11	318	53.00	282	47.00	600	100
"	12	291	48.50	309	51.50	600	100
Total	6	1,759	48.86	1,841	51.14	3,600	100
Grand Total	12	3,604	50.06	3,596	49.94	7,200	100

TABLE XII

Records of experiments using the three-zone tests for determining the preference reactions of the northern anchovy in monochromatic and white lights of equal and different intensities. Each experiment is based on six tests of 100 recorded observations, with six anchovies used in each test.

Exp.	*Soft White Light*		*Green Light*		*Red Light*		*Total*	
	Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
	Light Intensity 9 f.-c.		*Light Intensity 9 f.-c.*		*Light Intensity 9 f.-c.*			
WGR-1	1,158	32.17	2,016	56.00	426	11.83	3,600	100
	Light Intensity 30 f.-c.		*Light Intensity 9 f.-c.*		*Light Intensity 9 f.-c.*			
WGR-2	516	14.33	2,496	69.33	588	16.34	3,600	100
	Light Intensity 30 f.-c.		*Light Intensity 6 f.-c.*		*Light Intensity 30 f.-c.*			
WGR-3	432	12.00	2,448	68.00	720	20.00	3,600	100
	Light Intensity 30 f.-c.		*Light Intensity 30 f.-c.*		*Light Intensity 30 f.-c.*			
WGR-4	720	20.00	2,592	72.00	288	8.00	3,600	100
Total	2,826	19.63	9,552	66.33	2,022	14.04	14,400	100
	Other combinations in three-zone tests							
	Soft White Light Intensity 30 f.-c.		*Green Light Intensity 6 f.-c.*		*Darkness Intensity 0 f.-c.*			
WGD	804	22.33	2,496	69.33	300	8.34	3,600	100
	Red Light Intensity 30 f.-c.		*Darkness Intensity 0 f.-c.*		*Soft White Light Intensity 30 f.-c.*			
RDW	696	19.33	1,092	30.33	1,812	50.34	3,600	100
	Darkness Intensity 0 f.-c.		*Blue Light Intensity 9 f.-c.*		*Red Light Intensity 9 f.-c.*			
DBR-1	186	5.17	3,354	93.16	60	1.67	3,600	100
	Darkness Intensity 0 f.-c.		*Blue Light Intensity 4 f.-c.*		*Red Light Intensity 30 f.-c.*			
DBR-2	48	1.33	3,552	98.67	0	0.00	3,600	100

TABLE XIII

Records of experiments using the four-zone tests for determining the preference reactions of the northern anchovy for monochromatic lights and darkness. Each of the two experiments is based on six tests of 100 recorded observations, with eight anchovies used in each test.

Exp.	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
	(Darkness — 0 f.-c.; Lights — 9 f.-c. intensity)									
	Darkness		*Red Light*		*Blue Light*		*Green Light*		*Total*	
DRBG-1	123	2.56	204	4.25	849	17.69	3,624	75.50	4,800	100

TABLE XIII — CONT.

Exp.	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
	(Darkness: 0 f.-c.; Lights — 9 f.-c. intensity)									
	Darkness		*Green Light*		*Blue Light*		*Red Light*		*Total*	
DRBG-2	60	1.25	4,074	84.88	624	13.00	42	0.87	4,800	100
	Darkness		*Green Light*		*Blue Light*		*Red Light*		*Total*	
Total	183	1.91	7,698	80.19	1,473	15.34	246	2.56	9,600	100

TABLE XIV

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to white and monochromatic lights arranged so as to approximately duplicate vertical distribution of sunlight spectrum in water mass. Nine fish were used in each test.*

		Blue Light		*Green Light*		*Daylight*		*Total*	
		Intensity — 0.5 f.-c.		*Intensity — 7.8 f.-c.*		*Intensity — 16 f.-c.*			
		Frequency of Occurrence							
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
DLGB-1	1	245	27.22	422	46.87	233	25.89	900	100
"	2	216	24.00	448	49.78	236	26.22	900	100
"	3	207	23.00	435	48.73	258	28.67	900	100
"	4	216	24.00	411	45.67	273	30.33	900	100
"	5	175	19.44	432	48.00	293	32.56	900	100
"	6	186	20.67	434	48.22	280	31.11	900	100
"	7	201	22.33	416	46.22	283	31.45	900	100
"	8	188	20.89	407	45.22	305	33.89	900	100
"	9	151	16.78	435	48.33	314	34.89	900	100
"	10	162	18.00	469	52.11	269	29.89	900	100
"	11	156	17.33	472	55.45	272	30.22	900	100
"	12	210	23.33	455	50.56	235	26.11	900	100
Total	12	2,313	21.42	5,246	48.57	3,241	30.01	10,800	100
		Reduced intensities:							
		Blue — 0.25		*Green — 3.00*		*Daylight — 6.00*			
DLGB-2	1	275	30.56	400	44.44	225	25.00	900	100
"	2	281	31.22	402	44.67	217	24.11	900	100
"	3	246	27.33	396	44.00	258	28.67	900	100
"	4	275	30.56	336	37.33	289	32.11	900	100
"	5	231	25.67	379	42.11	290	32.22	900	100
"	6	226	25.11	416	46.22	258	28.67	900	100
"	7	199	22.11	428	47.56	273	30.33	900	100
"	8	203	22.56	406	45.11	291	32.33	900	100
"	9	210	23.33	425	47.22	265	29.45	900	100
"	10	221	24.55	421	46.78	258	28.67	900	100
"	11	157	17.44	386	42.89	357	39.67	900	100
"	12	219	24.33	396	44.00	285	31.67	900	100
Total		2,743	25.40	4,791	44.36	3,266	30.24	10,800	100

TABLES XV–XVII

Records of experiments using the two-zone tests for determining the preference reactions of the northern anchovy (Engraulis mordax *Girard) to monochromatic lights (blue, green, and red) and black light (ultraviolet radiation) presented in contrasting pairs. A light intensity of 0.2 foot-candle was maintained for all light sources applied. Two experiments were run using each contrasting pair of lights; each experiment consisted of twelve tests of 100 recorded observations of distribution of eight anchovies subjected to testing. Fluorescent tubes of General Electric manufacture 24" long and gelatine filters of Rascoe laboratories as sources for the blue, green, and red lights used in the present study were the same as described by Loukashkin and Grant (1959) in their experiments with the Pacific Sardine.*

For ultraviolet radiation a fluorescent "black light" tube of the same length as the monochromatic light tubes was used (General Electric, F20T12/BLB).

Table XV

	Blue Light			*Ultraviolet Radiation*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
UL-1	1	507	63.37	293	36.63	800	100
"	2	554	69.25	246	30.75	800	100
"	3	509	63.63	291	36.37	800	100
"	4	584	73.00	216	27.00	800	100
"	5	507	63.37	293	36.63	800	100
"	6	420	52.50	380	47.50	800	100
"	7	394	49.25	406	50.75	800	100
"	8	285	35.63	515	64.37	800	100
"	9	400	50.00	400	50.00	800	100
"	10	264	33.00	536	67.00	800	100
"	11	321	40.13	479	59.87	800	100
"	12	308	38.50	492	61.50	800	100
Total	12	5,053	52.62	4,547	47.37	9,600	100
UL-2	13	423	52.87	377	47.13	800	100
"	14	415	51.87	385	48.13	800	100
"	15	417	52.12	383	47.88	800	100
"	16	388	48.50	412	51.50	800	100
"	17	397	49.63	403	50.37	800	100
"	18	383	47.88	417	52.12	800	100
"	19	363	45.38	437	54.62	800	100
"	20	389	48.63	411	51.37	800	100
"	21	359	44.88	441	55.12	800	100
"	22	331	41.38	469	58.62	800	100
"	23	322	40.25	478	59.75	800	100
"	24	332	41.50	468	59.50	800	100
Total	12	4,519	47.07	5,081	52.93	9,600	100
Grand Total	24	9,572	49.85	9,628	50.15	19,200	100

Table XVI

		Blue Light		*Ultraviolet Radiation*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
UL-3	1	432	54.00	368	46.00	800	100
"	2	441	55.12	359	44.88	800	100
"	3	422	52.75	378	47.25	800	100
"	4	432	54.00	368	46.00	800	100
"	5	468	58.50	332	41.50	800	100
"	6	427	53.37	373	46.63	800	100
"	7	470	58.75	330	41.25	800	100
"	8	426	53.25	374	46.75	800	100
"	9	419	52.37	381	47.63	800	100
"	10	470	58.75	330	41.25	800	100
"	11	432	54.00	368	46.00	800	100
"	12	426	53.25	374	46.75	800	100
Total	12	5,265	54.84	4,335	45.16	9,600	100
UL-4	13	462	57.75	338	42.25	800	100
"	14	449	56.12	351	43.88	800	100
"	15	467	58.37	333	41.63	800	100
"	16	386	48.50	414	51.50	800	100
"	17	428	53.50	372	46.50	800	100
"	18	436	54.50	364	45.50	800	100
"	19	462	57.75	338	42.25	800	100
"	20	449	56.12	351	43.88	800	100
"	21	467	58.37	333	41.63	800	100
"	22	386	48.50	414	51.50	800	100
"	23	428	53.50	372	46.50	800	100
"	24	436	54.50	364	45.50	800	100
Total	12	5,256	54.75	4,344	45.25	9,600	100
Grand Total	24	10,521	54.79	8,679	45.21	19,200	100

Table XVII

		Red Light		*Ultraviolet Radiation*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
UL-5	1	387	43.38	413	51.62	800	100
"	2	365	45.63	435	54.37	800	100
"	3	327	40.88	473	59.12	800	100
"	4	360	45.00	440	55.00	800	100
"	5	386	48.25	414	51.75	800	100
"	6	337	42.13	463	57.87	800	100
"	7	375	46.88	425	53.12	800	100
"	8	351	43.88	449	56.12	800	100
"	9	358	44.75	442	55.25	800	100
"	10	471	58.87	329	41.13	800	100

Table XVII — Cont.

		Red Light		*Ultraviolet Radiation*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
"	11	444	56.50	356	44.50	800	100
"	12	423	52.87	377	47.13	800	100
Total	12	4,584	47.75	5,016	52.25	9,600	100
UL-6	13	89	11.13	711	88.87	800	100
"	14	93	11.62	707	88.38	800	100
"	15	136	17.00	664	83.00	800	100
"	16	117	14.62	683	85.38	800	100
"	17	156	19.50	644	80.50	800	100
"	18	109	13.62	691	86.38	800	100
"	19	35	4.38	765	95.62	800	100
"	20	25	3.12	775	96.88	800	100
"	21	6	0.75	794	99.25	800	100
"	22	10	1.25	790	98.75	800	100
"	23	0	0.00	800	100.00	800	100
"	24	21	2.62	779	97.38	800	100
Total	12	797	8.30	8,803	91.70	9,600	100
Grand Total	24	5,381	28.03	13,819	71.97	19,200	100

TABLE XVIII

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to white light and ultraviolet rays presented simultaneously in a two-zone tank. Eight fish were used in each test.*

		White light zone		*Ultraviolet zone*		*Total*	
		Two G.E. 15-watt incandescent lamps. Intensity 10.5 foot-candles		*Two G.E. 15-watt incandescent lamps and 1 fluorescent G.E. "Black light" tube. Intensity 10.5 f.-c.*			
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
UL-7	1	282	35.25	518	64.75	800	100
"	2	240	30.00	560	70.00	800	100
"	3	316	39.50	484	60.50	800	100
"	4	325	40.63	475	59.39	800	100
"	5	328	41.00	472	59.00	800	100
"	6	302	37.75	498	62.25	800	100
"	7	482	60.25	318	39.75	800	100
"	8	520	65.00	280	35.00	800	100
"	9	546	68.25	254	31.75	800	100

TABLE XVIII — CONT.

		White light zone: Two G.E. 15-watt incandescent lamps. Intensity 10.5 foot-candles		Ultraviolet zone: Two G.E. 15-watt incandescent lamps and 1 fluorescent G.E. "Black light" tube. Intensity 10.5			
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
"	10	480	60.00	320	40.00	800	100
"	11	484	60.50	316	39.50	800	100
"	12	434	54.25	366	45.75	800	100
Total	12	4,739	49.37	4,861	50.63	9,600	100
UL-8	13	463	57.87	337	42.13	800	100
"	14	427	53.37	373	46.63	800	100
"	15	416	52.00	384	48.00	800	100
"	16	474	59.25	326	40.75	800	100
"	17	459	57.37	341	42.63	800	100
"	18	436	54.50	364	45.50	800	100
"	19	366	45.75	434	54.25	800	100
"	20	373	46.63	427	53.37	800	100
"	21	371	46.38	429	53.62	800	100
"	22	358	44.75	442	55.25	800	100
"	23	331	41.38	469	58.62	800	100
"	24	378	47.25	422	52.75	800	100
Total	12	4,852	50.54	4,748	49.46	9,600	100
Grand Total	24	9,591	49.84	9,609	50.16	19,200	100

TABLE XIX

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to white light and ultraviolet rays presented in pairs in a two-zone tank. Eight fish were used in each test.*

		General Electric 100-watt mercury spot-light lamp suspended over the middle of the tank. Intensity 500+ foot-candles					
		Zone "A" covered with clear glass to filter out ultraviolet rays		Zone "B" free for ultraviolet radiation		Total	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
UL-9	1	663	82.87	137	17.13	800	100
"	2	704	88.00	96	12.00	800	100
"	3	639	79.85	161	20.15	800	100
"	4	569	71.12	231	28.88	800	100
"	5	347	43.38	453	56.62	800	100

TABLE XIX — CONT.

		General Electric 100-watt mercury spotlight lamp suspended over the middle of the tank. Intensity 500+ foot-candles					
		Zone "A" covered with clear glass to filter out ultraviolet rays		*Zone "B" free for ultraviolet radiation*		*Total*	
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
"	6	421	52.62	379	47.38	800	100
"	7	418	52.25	382	47.75	800	100
"	8	402	50.25	398	49.75	800	100
"	9	388	48.50	412	51.50	800	100
"	10	569	71.12	231	28.88	800	100
Total	10	5,120	64.00	2,880	36.00	8,000	100
		Clear glass filter removed, both zones under effect of ultraviolet radiation					
UL-10	1	361	45.13	439	54.87	800	100
"	2	375	46.88	425	53.12	800	100
"	3	361	45.13	439	54.87	800	100
"	4	448	56.00	352	44.00	800	100
"	5	428	53.37	372	46.63	800	100
"	6	440	55.00	360	45.00	800	100
"	7	441	55.12	359	44.88	800	100
"	8	450	56.25	350	43.75	800	100
"	9	416	52.00	384	48.00	800	100
"	10	456	57.00	344	43.00	800	100
Total	10	4,176	52.20	3,824	47.80	8,000	100

To check the role of the glass filter in experiment UL-9, it was introduced again, but instead of 100-watt mercury spotlight (ultraviolet) KEN-Rad 300-watt reflector flood light (white) lamps were installed in each zone. Light intensity was 500+ foot-candles. The results are shown below.

		Zone "A" covered with glass		*Zone "B" open free*		*Total*	
UL-11	1	432	54.00	368	46.00	800	100
"	2	431	53.87	369	46.13	800	100
"	3	398	49.75	402	50.25	800	100
"	4	393	49.12	407	50.88	800	100
"	5	408	51.00	392	49.00	800	100
"	6	404	50.50	396	49.50	800	100
"	7	371	46.38	429	53.62	800	100
"	8	420	50.25	380	49.75	800	100
"	9	371	46.38	429	53.62	800	100
"	10	408	51.00	392	49.00	800	100
Total	10	4,036	50.45	3,964	49.55	8,000	100

TABLE XX

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to white light and ultraviolet rays presented in pairs in a two-zone tank. Six fish were used in each test. Experiment UL–12 shows typical distribution of the fish when white light alone was applied, and experiment UL–13 shows change in distribution after replacing the white-light lamp in one of the zones with a lamp producing ultraviolet radiation.*

Exp.	*Test*	*Zone "A"*		*Zone "B"*		*Total*	
		Frequency of Occurrence					
		Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
		KEN-RAD 300-watt reflector flood light lamp (white) Intensity 225 f.-c.		*KEN-RAD 300-watt reflector flood light lamp (white) Intensity 225 f.-c.*			
UL-12	1	240	40.00	360	60.00	600	100
"	2	263	43.84	337	56.16	600	100
"	3	270	45.00	330	55.00	600	100
"	4	280	46.67	320	53.37	600	100
"	5	300	50.00	300	50.00	600	100
"	6	240	40.00	360	60.00	600	100
"	7	280	46.67	320	53.37	600	100
"	8	340	56.67	260	43.33	600	100
"	9	335	55.83	265	44.17	600	100
"	10	360	60.00	240	40.00	600	100
Total	10	2,908	48.47	3,092	51.53	6,000	100
		KEN-RAD 300-watt reflector flood light lamp (white) Intensity 225 f.-c.		*G.E. 100-watt mercury spotlight lamp (ultraviolet). Intensity 225 f.-c.*			
UL-13	1	600	100.00	0	0.00	600	100
"	2	477	79.50	123	20.50	600	100
"	3	387	64.50	213	35.20	600	100
"	4	404	67.33	196	32.67	600	100
"	5	372	62.00	228	38.00	600	100
"	6	380	63.33	220	36.67	600	100
"	7	400	66.67	200	33.33	600	100
"	8	420	70.00	180	30.00	600	100
"	9	480	80.00	120	20.00	600	100
"	10	406	67.67	194	32.37	600	100
Total	10	4,326	72.10	1,674	27.90	6,000	100

TABLE XXI

Records of preference responses of the northern anchovy (Engraulis mordax *Girard) to infrared radiation and total darkness in a two-zone tank. Eight fish were used in each test.*

Exp.	*Test*	*Infrared Radiation*		*Total Darkness*		*Total*	
		G.E. 250-watt reflector heat lamp with red coating and Corning infrared transmitting filter.		*Absolute Darkness*			
		Frequency of Occurrence					
		Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
INF-1	1	167	69.58	73	30.42	240	100
"	2	135	56.25	105	43.75	240	100
"	3	135	56.25	105	43.75	240	100
"	4	106	44.17	134	55.85	240	100
"	5	162	67.50	78	32.50	240	100
"	6	96	40.00	144	60.00	240	100
"	7	98	40.83	142	59.17	240	100
"	8	74	30.84	166	69.16	240	100
"	9	153	63.75	87	36.25	240	100
"	10	106	44.17	134	55.83	240	100
Total	10	1,232	51.33	1,168	48.67	2,400	100
		Total Darkness		*Total Darkness*			
INF-2	1	170	70.83	70	29.19	240	100
"	2	124	51.67	116	48.33	240	100
"	3	105	43.75	135	56.25	240	100
"	4	116	48.33	124	51.67	240	100
"	5	120	50.00	120	50.00	240	100
"	6	95	39.58	145	60.42	240	100
"	7	96	40.00	144	60.00	240	100
"	8	86	35.83	154	64.17	240	100
"	9	150	62.50	90	37.50	240	100
"	10	104	43.33	136	56.67	240	100
Total	10	1,166	48.58	1,234	51.42	2,400	100
		Infrared: Visible Red. Corning filter cracked and began to transmit visible red in the intensity about 0.001 f.-c.		*Total Darkness*			
INF-3	1	124	51.67	116	48.33	240	110
"	2	183	76.25	57	24.75	240	110
"	3	170	70.83	70	29.17	240	100
"	4	166	69.17	74	30.83	240	100
"	5	166	69.17	74	30.83	240	100
"	6	192	80.00	48	20.00	240	100
"	7	196	81.67	44	18.33	240	100
"	8	201	83.75	39	16.25	240	100
"	9	192	80.00	48	20.00	240	100
"	10	190	79.17	50	20.83	240	100
Total	10	1,780	74.17	620	25.83	2,400	100

TABLE XXII

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to white light and infrared radiation in a two-zone tank. Eight fish were used in each test.*

Exp.	*Test*	*Clear Light*		*Infrared Radiation*		*Total*	
		KEN-RAD 300-watt reflector flood light lamp. Light intensity - 500 f.-c.		*G.E 250-watt reflector infrared (heat) industrial lamp (white bulb). Light intensity - 500 f.-c.*			
		Frequency of Occurrence					
		Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
INF-4	1	377	47.13	423	52.87	800	100
"	2	352	44.00	448	56.00	800	100
"	3	370	46.25	430	53.75	800	100
"	4	363	45.38	437	54.62	800	100
"	5	365	45.63	435	54.37	800	100
"	6	352	44.00	448	56.00	800	100
"	7	406	50.75	394	49.25	800	100
"	8	399	49.88	401	50.12	800	100
"	9	393	49.13	407	50.97	800	100
"	10	480	60.00	320	40.00	800	100
"	11	441	55.12	359	44.88	800	100
"	12	413	51.62	387	48.38	800	100
Total	12	4,711	49.07	4,889	50.93	9,600	100
INF-5	13	415	51.87	385	48.13	800	100
"	14	405	50.62	395	49.38	800	100
"	15	413	51.62	387	48.38	800	100
"	16	471	58.87	329	41.13	800	100
"	17	401	50.12	399	49.88	800	100
"	18	442	55.25	358	44.75	800	100
"	19	388	48.50	412	51.50	800	100
"	20	379	47.38	421	52.62	800	100
"	21	344	43.00	456	57.00	800	100
"	22	385	48.13	415	51.87	800	100
"	23	364	45.50	436	54.50	800	100
"	24	389	48.63	411	51.37	800	100
Total	12	4,796	49.96	4,804	50.04	9,600	100
Grand Total	24	9,507	49.52	9,693	50.48	19,200	100

TABLE XXIII

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to white light and infrared radiation plus visible light in a two-zone tank. Eight fish were used in each test.*

Exp.	*Test*	*White Light*		*Infrared Radiation*		*Total*	
		Fluorescent tube "Soft White" light; Intensity 25 f.-c.		*Fluorescent tube "Soft White" light, and G.E. 600-watt electric heater. Intensity 25 f.-c.*			
		Frequency of Occurrence					
		Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
INF-6	1	374	46.75	426	53.25	800	100
"	2	390	48.75	410	51.25	800	100
"	3	373	46.63	427	53.37	800	100
"	4	406	50.75	394	49.25	800	100
"	5	389	48.63	411	51.37	800	100
"	6	404	50.50	396	49.50	800	100
"	7	438	54.75	362	45.25	800	100
"	8	459	57.37	341	42.63	800	100
"	9	410	51.50	390	48.50	800	100
"	10	434	54.25	366	45.75	800	100
"	11	429	53.62	371	46.38	800	100
"	12	425	53.12	375	46.88	800	100
Total	12	4,931	51.36	4,669	48.64	9,600	100
INF-7	13	419	52.37	381	47.63	800	100
"	14	458	57.25	342	42.75	800	100
"	15	420	52.50	380	47.50	800	100
"	16	387	48.38	413	51.62	800	100
"	17	415	51.87	385	48.13	800	100
"	18	388	48.50	412	51.50	800	100
"	19	394	49.25	406	50.75	800	100
"	20	449	56.12	351	43.88	800	100
"	21	402	50.25	398	49.75	800	100
"	22	435	54.37	365	45.63	800	100
"	23	416	52.00	384	48.00	800	100
"	24	429	53.62	371	46.38	800	100
Total	12	5,012	52.21	4,588	47.79	9,600	100
Grand Total	24	9,943	51.79	9,257	48.21	19,200	100

TABLE XXIV

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to light gradient tests using five-zone tank and white light (G.E. incandescent lamps) ranging in its intensity from 2 to 100 foot-candles. Ten fish were used in each test.*

		Zone "A"		*Zone "B"*		*Zone "C"*		*Zone "D"*		*Zone "E"*			
		2 f.-c.		*10 f.-c.*		*20 f.-c.*		*50 f.-c.*		*100 f.-c.*		*Total*	
		Frequency of Occurrence											
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
INT-1	1	4	0.40	143	14.30	390	39.00	312	31.20	151	15.10	1,000	100
"	2	3	0.30	83	8.30	247	24.70	390	39.00	277	27.70	1,000	100
"	3	1	0.10	95	9.50	261	26.10	337	33.70	306	30.60	1,000	100
"	4	15	1.50	62	6.20	271	27.10	370	37.00	282	28.20	1,000	100
"	5	2	0.20	43	4.30	332	33.20	374	37.40	249	24.90	1,000	100
"	6	2	0.20	54	5.40	250	25.00	385	38.50	309	30.90	1,000	100
"	7	0	0.00	9	0.90	315	31.50	424	42.40	252	25.20	1,000	100
"	8	1	0.10	26	2.60	253	25.30	406	40.60	314	31.40	1,000	100
"	9	19	1.90	52	5.20	242	24.20	394	39.40	293	29.30	1,000	100
"	10	2	0.20	50	5.00	315	31.50	367	36.70	266	26.60	1,000	100
Total	10	49	0.49	617	6.17	2,876	28.76	3,759	37.59	2,699	26.99	10,000	100
INT-2	11	3	0.30	23	2.30	258	25.80	532	53.20	184	18.40	1,000	100
"	12	1	0.10	28	2.80	265	26.50	486	48.60	220	22.00	1,000	100
"	13	7	0.70	75	7.50	264	26.40	511	51.10	143	14.30	1,000	100
"	14	2	0.20	37	3.70	346	34.60	436	43.60	179	17.90	1,000	100
"	15	1	0.10	93	9.30	297	29.70	486	48.60	123	12.30	1,000	100
"	16	26	2.60	78	7.80	339	33.90	447	44.70	110	11.00	1,000	100
"	17	2	0.20	61	6.10	306	30.60	418	41.80	213	21.30	1,000	100
"	18	9	0.90	68	6.80	242	24.20	425	42.50	256	25.60	1,000	100
"	19	3	0.30	65	6.50	359	35.90	418	41.80	155	15.50	1,000	100
"	20	4	0.40	62	6.20	293	29.30	470	47.00	171	17.10	1,000	100
Total	10	58	0.58	590	5.90	2,969	29.69	4,629	46.29	1,754	17.54	10,000	100
Grand Total	20	107	0.53	1,207	6.03	5,845	29.23	8,388	41.94	4,453	22.27	20,000	100

TABLE XXV

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to light gradient tests using four-zone tank and white light (incandescent lamps) ranging in its intensity from 75 to 500 foot-candles. Ten fish were used in each test.*

		Zone "A"		*Zone "B"*		*Zone "C"*		*Zone "D"*		*Total*	
		75 f.-c.		*125 f.-c.*		*250 f.-c.*		*500 f.-c.*			
		Frequency of Occurrence									
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
INT-3	1	144	14.40	280	28.00	396	39.60	180	18.00	1,000	100
"	2	167	16.70	275	27.50	360	36.00	198	19.80	1,000	100
"	3	175	17.50	218	21.80	362	36.20	245	24.50	1,000	100
"	4	137	13.70	291	29.10	365	36.50	207	20.70	1,000	100
"	5	170	17.00	356	35.60	377	37.70	97	9.70	1,000	100
"	6	178	17.80	289	28.90	377	37.70	156	15.60	1,000	100
"	7	116	11.60	308	30.80	380	38.00	196	19.60	1,000	100
"	8	111	11.10	301	30.10	326	32.60	262	26.20	1,000	100
"	9	133	13.30	356	35.60	363	36.30	148	14.80	1,000	100
"	10	89	8.90	347	34.70	410	41.00	154	15.40	1,000	100
Total	10	1,420	14.20	3,021	30.21	3,716	37.16	1,843	18.43	10,000	100

TABLE XXVI

Records of preference reactions of the northern anchovy (Engraulis mordax *Girard) to different intensities of white light presented in sharply contrasting pairs in a two-zone tank. Eight fish were used in each test.*

		Zone "A"		*Zone "B"*			
		Frequency of Occurrence					
Exp.	*Test*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
		(A)	*500 f.-c.*		*20 f.-c.*		
INT-4	1	256	32.00	544	68.00	800	100
"	2	297	37.11	503	62.89	800	100
"	3	275	34.38	525	65.62	800	100
Total	3	828	34.50	1,572	65.50	2,400	100
		(B)	*500 f.-c.*		*10 f.-c.*		
INT-5	1	319	39.88	481	60.12	800	100
"	2	302	37.75	498	62.25	800	100
"	3	226	28.25	574	71.75	800	100
Total	3	847	35.29	1,553	64.71	2,400	100
		(C)	*500 f.-c.*		*5 f.-c.*		
INT-6	1	335	41.88	465	58.12	800	100
"	2	334	41.75	466	58.25	800	100
"	3	285	35.63	515	64.37	800	100
Total	3	954	39.58	1,446	60.42	2,400	100
		(D)	*500 f.-c.*		*2 f.-c.*		
INT-7	1	210	26.25	590	73.75	800	100
"	2	127	15.88	673	84.12	800	100
"	3	54	6.75	746	93.25	800	100
Total	3	391	16.29	2,009	83.71	2,400	100
Grand Total	12	3,020	31.48	6,580	68.52	9,600	100

IV. DISCUSSION

(1) On responses of the northern anchovy to monochromatic lights in relation to reactions of other species.

As stated in the introduction, the experiments described in the preceding pages were carried out as a part of the general study on color vision in certain species of the marine pelagic fishes of the Pacific Ocean. The first stage of this study was published in 1959 by the present investigators. At that time they studied the Pacific sardine to determine the influence of monochromatic and white lights and darkness as environmental stimuli for elucidation of behavioral changes in schooling patterns and conversely to

determine the ability of the sardine to discriminate colored and white lights qualitatively. Those experiments demonstrated clearly that different lights and darkness do affect school behavior and schooling patterns; also shown was the ability of the sardine to discriminate between lights on the basis of wave length. The sardines were attracted most of all by green light; they were repelled by both red light and total darkness (Loukashkin and Grant, 1959).[5]

The results of recent experiments with the northern anchovy, to determine their ability to discriminate among differently colored lights and darkness, are strikingly similar to those obtained in the experiments with the Pacific sardine. The anchovy, however, was able to differentiate green light from the blue, while the sardine failed to do so. In choice experiments in which the blue and white lights were presented responses of the anchovy in favor of the blue light (52.15 per cent) were lower than those of the sardine (73.05 per cent). Comparative data on the responses of these two species are assembled in the table XXVII.

TABLE XXVII

Comparison of preference reactions of the northern anchovy and Pacific sardine to monochromatic and white lights in a two-zone tank.

Description	*Responses in per cent*	
	Light source	*Light Source*
	Green	*White*
Anchovy	75.34	24.66
Sardine	78.63	21.37
	Green	*Red*
Anchovy	97.86	2.14
Sardine	95.25	4.17
	Green	*Blue*
Anchovy	73.18	26.82
Sardine	49.17	50.83
	Blue	*White*
Anchovy	52.15	47.85
Sardine	73.05	26.95
	Blue	*Red*
Anchovy	81.60	18.40
Sardine	97.26	2.74
	Red	*White*
Anchovy	11.61	88.39
Sardine	12.43	87.57

[5] Verheijen (1956, 1958, 1959), speaking of the mass gathering phenomena of certain clupeids under the light at night at sea, disqualifies the interpretation of these phenomena in terms of "positive phototaxis," "being attracted," "intensity preferendum," or "light optimum." He considers all of them unsatisfactory and he attributes the above phenomena merely to a "mass photic disorientation" of the fish.

In the series of experiments comparing the effects of green, blue, red, and white lights in a two-zone tank (tables I, II, III, V, VI, VIII) only 2,315 fish or 10.72 per cent out of 21,600 fish responded positively to red light, and 19,285 fish or 89.28 per cent responded positively to the other lights. The negative reaction of the sardine toward red light was stronger: of 36,000 fish, 2.300 or 6.67 per cent were found in the red-light zone, and 33,610 fish or 93.33 per cent in the other light zones. Comparative data are shown below to better illustrate the preferential responses of the anchovy and sardine to colored and white lights.

TABLE XXVIII

	Description	Responses in per cent	
		Anchovy	Sardine
(A)	Green	82.13	74.35
	Blue, Red, White together	17.87	25.65
(B)	Blue	53.52	73.71
	Green, Red, White together	46.48	26.29
(C)	Red	10.72	6.67
	Green, Blue, White together	89.28	93.33
(D)	White	53.63	45.30
	Green, Blue, Red together	46.37	54.70

In the three- and four-zone tank (tables XII, XIII, and XIV) green light was found to have the same effect as in the two-zone tank. The anchovies consistently responded in favor of the green light regardless of the intensities of the opposing lights. As was true for sardines (Loukashkin and Grant, 1959), anchovies were attracted mostly by the blue-green region of the spectrum. They showed a preference for green light over blue, for green over red, and for green over white. A preference for blue, in the absence of green, over red and white was also evident. Similar results were obtained by Breder (1959) in his experiments using monochromatic lights of low intensities (2 foot-candles) on *Sardinella macrophthalma, Jenkinsia lamprotaenia,* and some other fishes. He observes that, when contrasting colored lights are presented in pairs, "a general tendency is evident for fishes to respond more definitely toward the shorter wave lengths (the blue and greens) and much less toward the longer wave lengths (reds)."

The attractive value of the blue-green region of the spectrum was demonstrated in experimental studies by several Japanese behaviorists on young marine fishes, such as *Oplegnathus fasciatus, Stephanolepis cirrhifer, Scomberomorus niphonius, Fugu niphobles, Fugu rubripes, Mugil cephalus, Girella punctata, Pempheris japonica, Trachurus japonicus,* and the fresh-

water *Oryzias latipes* (Kawamoto, 1959; Kawamoto and Konishi, 1952; Kawamoto and Takeda, 1950, 1951; Ozaki, 1951).

Protasov (1957) investigated the responses of several species of the Black Sea fishes to monochromatic and white lights in the seaquaria of the Sebastopol Biological Station. He found that the ombre, *Corvina umbra,* responded positively to violet, blue, light blue, green and white lights, and even to ultraviolet rays. The juvenile sturgeon "sevriuga," *Acipenser stellatus,* was found to be phototatic to all types of lights applied but the responses were rather quantitative in character. The fish reacted positively only to higher intensities of the light, regardless of color. The horsemackerel "stavrida," *Trachurus trachurus,* displayed indifference to the blue-green region of the spectrum, but when the intensity of the light was increased ($\times 5$) the fish reacted negatively. This fish responded less positively to white light than to red, especially when water temperature was lowered.[6]

A year later, Protasov (1958) published the results of his studies on the sensitivity of the fish eye to different wave lengths of light, establishing boundaries of the visible spectrum for certain marine and freshwater fishes, as shown in the following table:

Species	*Limits in millimicrons*
Trygon pastinaca	≈ 420 — ≈ 620
Acipenser stellatus	≈ 420 — ≈ 700
Mugil auratus	≈ 430 — ≈ 700
Scorpaena porcus	≈ 400 — ≈ 600
Silurus glanis	≈ 500 — ≈ 700
Cyprinus carpio	≈ 480 — ≈ 700
Squalus acanthias	≈ 400 — ≈ 620

He also tested the ability of the fish to discriminate monochromatic lights regardless of their intensities, applying the electrophysiological method suggested by Bongard (1955) and Bongard and Smirnova (1959). This study revealed that *Mugil auratus* could distinguish blue, green, red, and orange lights from one another, but failed to distinguish blue from the violet and "extreme red" from red. *Scorpaena porcus* could discriminate red, yellow, orange, green, blue, and light-blue lights, but was unable to discriminate violet from the blue and "extreme red" from the red. The Black Sea turbot, *Rhombus maeoticus,* could distinguish blue, light blue, green, yellow, orange, and red lights, but could not differentiate violet from the blue.[7]

[6] The rather unusual reaction of the Black Sea horsemackerel (in view of the Kawamoto experiments with the Japanese horsemackerel) had been reported earlier by Safianova (1952), who demonstrated preferential reactions of this fish to the orange-red illumination.

[7] Protasov's studies would have been more complete had he determined the ability of his fishes to react preferentially to certain wave lengths as well.

As to the responses of marine fishes to monochromatic lights in experiments under natural conditions in the open sea, there are several reports of interest to be mentioned in connection with the present study. Pochekaev (1949), testing the effects of overhead and submerged electric lights in the inshore waters of Sakhalin Island as possible attractants in local fisheries, obtained positive phototactic reactions as follows: (1) of the pond smelt, *Hypomesus olidus;* saury, *Cololabis saira;* and Eastern dace *Leuciscus brandti* (all three in juvenile stage) to white, yellow, and violet lights; (2) adult dace, to white and yellow (violet light was not used); and (3) trout "kundzha," *Salvelinus leucomaenis,* pond smelt and saury (all adult), to white light (the other two sources were not used).[8]

In addition to Pochekaev's data on pond smelt, Baranov (1955) found this fish also responded readily to and aggregated in quantities around submerged electric lamps emitting blue, red, and white light, the latter appearing to be the more effective attractant. As to the saury, Yudovich (1956) and Gristchenko *et al.* (1957) described the effectiveness of the blue and red lights in experimental saury catches in the northwestern Pacific. The blue light was used to attract the fish to the vessel (up to forty 500-watt incandescent lamps were installed along one side of the vessel); the red light (not more than four 500-watt incandescent lamps on the opposite side of the vessel) was used for operational purposes. When an aggregation would form in the blue light zone, the light would be extinguished and the red lamps would be turned on. The fish aggregation then would move from the darkened zone into the new dimly illuminated red zone where conical lift nets or blanket nets were installed. Upon lifting the nets, the red lights would be turned off and the blue lights turned on. This procedure would be repeated several times at one night light station.[9]

Experiments carried out by Japanese fishery biologists in the open sea revealed the effectiveness of other monochromatic lights in attracting saury. Light of 4,000 angstroms (violet) wave length was found to be most effective, and that of 6,000 angstroms (red) the least effective (Takayama, 1956).

[8] Pochekaev indicated that violet light attracted the squid, *Ommastrepes sloani pacificus,* in great masses. A marked preference for violet light over both yellow and white lights was displayed by an instant phototaxis following switching on of the violet lamp and in a short time by the mass aggregation of the squid schools within the illuminated zone. The other two lights were found to be good attractants too, but to a much lesser degree. Positive phototaxis toward white light was recorded for the California squid, *Loligo opalescens,* by Radovich and Gibbs (1954) and for the Mediterranean squid, *Loligo vulgaris,* by Verheijen (1958).

[9] The use of a two-light arrangement as described by Yudovich (1956) and Gristchenko (1957) was introduced in the saury fisheries industry of Japan in the years following the end of World War II; it has been highly appreciated by the fishermen whose catches have rapidly increased (Parin, 1956; Pokrovsky, 1957). The total annual landings of saury in prewar years (1936-1939) in Japan, before the use of artificial lights, amounted to less than 10,000 metric tons. With introduction of light attractants, the catch in 1947 reached 22,900 metric tons; in 1950, 126,400 metric tons; and in 1954, 292,700 metric tons (Rass, 1956). By 1957 the number of fishing vessels with electric-light equipment employed in saury fisheries exceeded 2,000; the annual catch for the same year reached 375,000 metric tons (Fukuhara, 1959).

In experimental studies of natural visual responses of the yellowfin tuna, *Neothunnus macropterus,* and little tunny, *Euthynnus yaito,* in the Hawaii Marine Laboratory of the University of Hawaii, electric lights of white, blue, green, orange, red, and yellow colors were applied. The fish responded to colored and white lights, but "green light appeared to attract tuna" (Hsiao, 1952; Tester, 1959).

According to Nikonorov (1956a), the Caspian anchovy-like sprat "kilka," *Clupeonella engrauliformis,* in its natural environment "prefers" white light emitted by the submerged electric lamp when this light was presented paired with green or red lights. When green and red lights were presented together, the fish concentrated near the green lamp. In studying another Caspian sprat, *Clupeonella delicatula caspia,* under identical environmental conditions and using monochromatic and white lights, Borisov (1955) found out that the most effective attractant was ordinary white light. The results of his trials, expressed in per cent, are shown below:

Catches made with application of:	
white light	57.2
yellow light	27.6
orange light	5.9
blue light	5.0
green light	3.8
red light	0.5
no light	0.0
Total	100.0

In evaluating the results of his exploration, Borisov observed, "Here, apparently, is reaction to the intensity of light but not to the color of light." From this remark it could be assumed that light intensities of the lamps used by Borisov and his associates were not uniform, and therefore the results he obtained were not conclusive.[10]

During the present investigation, two other species of schooling marine fishes, occasionally available for comparative study, were subjected to the influence of lights. One of them, the topsmelt, *Atherinops affinis* (Ayres), was kept in captivity for quite a long time; the second, the Pacific herring, *Clupeaa pallasii* Valenciennes, had been captured at the end of the spawning season and was used in tests following the fish's initial adaptation to an artificial environment in the 1000-gallon display tanks of the Steinhart Aquarium. The results obtained with these fishes are shown in tables below:

[10] Borisov never mentioned either light intensity figures or spectrographic values of his monochromatic lights in his report. This is also true for most of the Russian works cited in the present paper.

TABLE XXIX

Records of responses of the topsmelt to monochromatic and white lights and darkness. Each experiment consisted of five tests of 100 recorded observations on a group of eight fish. Light intensity was maintained at the 5 foot-candle level.

Experiment number	Pair of contrasting light zones					
	Zone "A"		Zone "B"		Total	
	Frequency of distribution					
	Number	Per cent	Number	Per cent	Number	Per cent
Top-1	Green light		Red light			
	3,970	99.25	30	0.75	4,000	100
Top-2	Blue light		Red light			
	3,610	90.25	390	9.75	4,000	100
Top-3	Blue light		White light			
	3,400	85.25	590	14.75	4,000	100
Top-4	Red light		Darkness			
	2,536	63.40	1,464	36.60	4,000	100

As seen from this table, the preference responses of the topsmelt were toward the green and blue lights. As in the case of the Pacific sardine and northern anchovy, the red light had no attractive value, except when it was opposed by darkness.

TABLE XXX

Records of responses of the Pacific herring to monochromatic and white lights. Each experiment consisted of five tests of 100 recorded observations on a group of six fish. Light intensity was maintained at the 10 foot-candle level.

Experiment number	Pair of Contrasting light zones					
	Zone "A"		Zone "B"		Total	
	Frequency of distribution					
	Number	Per cent	Number	Per cent	Number	Per cent
Hrg-1	Blue light		Red light			
	2,115	70.50	885	29.50	3,000	100
Hrg-2	Green light		Red light			
	1,591	53.10	1,409	46.90	3,000	100
Hrg-3	White light		Red light			
	1,524	50.80	1,476	49.20	3,000	100

Possibly, because of the physical and physiological condition of the herring captured during spawning season (in fact, a few females spawned on the tank's walls soon after delivery of the captured fish), their responses to monochromatic and white lights are quite different from those of the an-

chovy and topsmelt. Only in one of the three experiments did the herring display strongly negative reactions to red light and preferentially positive reaction to the contrasting light (blue). Gristchenko (1951) and Nikolaev (1957), speaking of the Pacific herring, and Tihonov (1959)—of the Atlantic herring, state that in experiments conducted in the open sea they found seasonal changes in phototactical behavior of this fish to the artificial lights. During the fattening period, both herrings reacted positively to light, and readily aggregated in masses in the illuminated zone. During the spawning season they became phototactically negative.[11] This may well explain the confusing results shown in the table XXX.

In closing this discussion on color vision in fishes, a few words should be said about the results of certain experiments in which "training" techniques have been successfully applied (*e.g.*, feeding responses associated with a stimulus of restricted wave length). In the classical work of Reeves (1919) the sunfish, *Lepomis gibbosus,* and horned dace, *Semotilus atromaculatus,* were trained to discriminate light of longer wave lengths from light of shorter wave lengths and from clear light. *Blennius pholis,* used in experiments reported by Bull (1957) in which he applied differential conditioning, displayed unusual ability to qualitatively discriminate monochromatic lights. One of the most interesting studies on color vision in fishes recently published is that of Arora and Sperry (1958). These investigators applied training techniques too. *Astronotus ocellatus* was used as an experimental animal. They found that this fish was able to distinguish red, blue, yellow, and green lights, and painted objects from each other and from various shades of grey. After training, the optic nerve was sectioned; the fish became blind. Regeneration of the sectioned optic nerve and restoration of vision took from 36 to 40 days; upon recovery of vision the fish displayed an ability to discriminate among the colors without further training. A fish which had not been trained prior to the blinding, by sectioning of the optic nerve, learned color discrimination as fast as normal fish. In the opinion of Arora and Sperry, the fish were able to discriminate between colors qualitatively rather than merely because of variation in intensity. In the much earlier work of Brown (1937), who worked with large-mouth black bass, it was concluded that, "in general, and excepting the violet, the degree of difference of different colors to bass is a function of difference in wave length." Puchkov (1954) states, "the ability of the fish to distinguish colors undoubtedly exists." Discussing the results of von Frisch's (1933) experiments, Puchhov observed, "if the fish were color blind, it would per-

[11] Similar seasonal peculiarities in the behavior of certain marine fishes were recently reported by several Russian investigators: Parin (1956) in regard to saury; Safianova (1952, 1958) and Radakov (1956) concerning the Black Sea anchovy, *Engraulis encrasicholus pontica,* and horsemackerel, *Trachurus trachurus;* and Lovetskaya (1958) about the Caspian sprat, *Clupeonella delicatula caspia.*

Of the freshwater fishes, adult bream, *Alburnus alburnus,* in experimental studies in the laboratory carried out by Privolnev (1956) displayed phototactical periodicity with a change four times a year.

ceive the red color as grey, and thus it would mistake red cups for the grey ones of corresponding brightness. However the fish always distinguished red cups from the grey ones of different degrees of brightness." Walls (1942) flatly concluded that "no reasonable student of the problem [of the color vision in fishes] any longer doubts that fishes—all duplex teleosts at least—can experience hue as a sensation-quality apart from brightness." Fifteen years later, Brett (1957) recognized Walls' statement as the best formulated conclusion to the problem.

As to the present study of the innate ability of the northern anchovy to react differently to light of different wave lengths, the authors are inclined to consider the anchovy's perception of the applied lights strictly as a function of wave length apart from the intensity of the light, in accordance with their earlier report on color vision in the Pacific sardine (Loukashkin and Grant, 1959).

(2) On responses of the northern anchovy to ultraviolet wave length in relation to reactions of other species.

Illumination of the aquatic media differs from that of the aerial environments both quantitatively and qualitatively. Clark (1954) said that the sunlight upon entering water undergoes many changes. First of all, about 10 per cent or more of the light is lost because of reflection at the surface or beneath it. Traveling downward, the light is further modified not only in its intensity but also in its spectral and other properties.[12]

Baburina (1955) states that infrared rays are absorbed in the first meter layer of water. Ninety per cent of the red rays disappear within a depth of five meters; and ninety per cent of the green region of sunlight spectrum is absorbed before reaching thirteen meters of depth. Only violet and ultraviolet rays reach a depth of five hundred meters. The ultraviolet rays were detected 1,000 and more meters below the ocean surface. In conformity with this she maintains that "the eye of the fish is less sensitive to the red and more sensitive to the yellow, green, blue, and violet rays than the human eye, but in contrast with the human eye it is also sensitive to the ultraviolet region of the spectrum." Craig and Baxter (1952), speaking of the physiological importance of the ultraviolet component of natural light in aquatic environments, observed that "in the sea water there is differential absorption so that the centre of maximum intensity is displaced somewhere towards shorter wave lengths, the precise effect depending upon depth and the nature of the sea water. We should not, therefore, be surprised to find marine creatures sensitive to a range including a portion of ultraviolet spectrum." These theoretical reasonings concerning the ability of the fish

[12] For instance, Boden *et al.* (1960) found that in the Bay of Biscay sunlight passing through water "becomes steadily bluer with depth until at 400 meters the spectrum peaks sharply between 475 and 480 millimicrons."

eye to perceive ultraviolet wave lengths appear to be well founded and correct as has been demonstrated by recent experiments in both the open sea and in the laboratory.

Protasov (1957), who applied an electrophysiological method in the investigation of vision in a number of marine fishes, obtained definite proof that the Black Sea ombre, *Corvina umbra,* could respond to ultraviolet rays as positively as to the rays of the visible spectrum.[13]

With facilities, sources of radiation, and techniques used in the present study, natural responses of the anchovy to ultraviolet rays seemed to be misleading because the fish responded inconsistently to ultraviolet light in various combinations with opposing wave lengths of light. These responses were found to vary from indifferent and negative to highly positive. Because of this seemingly individualistic and confusing behavior of the anchovy in response to the ultraviolet radiation, further experimentation is necessary, especially in total darkness with the application of better filters totally isolating the wave lengths of the visible region of the spectrum. Breder (1959), who experienced the same difficulties with his experimental fishes, in his very carefully worded conclusion states "there is some evidence to support the view that some fishes show a positive reaction toward ultraviolet wave length, but this requires extended analysis . . ." He found out that males of *Gambusia* sp. were ultraviolet positive, the females negative. In his experiments *Anoptichthys hubbsi* reacted positively, and *Anoptichthys jordani* negatively in one case; both species were slightly negative in another case. *Jenkinsia lamprotaenia* was found to be "ultraviolet positive to a very marked extent," and *Atherina stipes* showed an individualistic behavior toward the ultraviolet, being either attracted, or repelled, or indifferent. *Brachydanio rerio* displayed a strong positive reaction to the ultraviolet radiation.

As to the use of sources of ultraviolet radiation in tests in the open sea, only a few attempts have been made. A Netherlands research vessel carried out experiments along the Belgian coast but without success (de Boer, 1950). Craig and Baxter (1952), however, obtained immediate reactions of several species of marine fishes and other marine organisms to a submerged source of ultraviolet radiation (125-watt "black" ultraviolet lamp). They list the following fishes as influenced by ultraviolet rays: herring, mackerel, horsemackerel, dogfish, and whiting. Blaxter and Parrish (1958) also obtained positive aggregation of fish around the same source of radiation as used by Craig and Baxter, but they assumed that the reactions to the ultraviolet light might have been "due to the fluorescence from microorganisms in the water" rather than to the "black light" itself.

The inconclusive results of the experiments herein discussed prompt

[13] Of freshwater fishes, the trout and pike have been known to perceive ultraviolet wave lengths of light ("Reflector," 1949).

the authors to consider the data obtained as a preliminary step toward further experimentation using improved sources of radiation and applying perfected techniques in the study of behavioral responses of the marine fishes toward ultraviolet radiation.

(3) On responses of the northern anchovy to infrared radiation with reference to experiments of other behaviorists.

There was no evidence that they were attracted, repelled, or frightened by the radiation, which suggests that they did not perceive the infrared wave length. This conforms with work of Duncan (1956) who found that fingerling silver salmon, *Oncorhynchus kisutch,* failed to respond in any manner to infrared radiation. Breder (1959) has found no indicative evidence that fishes would respond differently to radiant heat (infrared radiation) and ambient temperature.

(4) On responses of the northern anchovy to different values of intensity of white light.

The experiments using white light of varying intensities in two separate arrangements (in one these intensities ranged from 2 to 100 foot-candles, in the other from 75 to 500 foot-candles) revealed a natural ability of the anchovy to respond positively to intensities of moderate values regardless of the order of light arrangement, and to react negatively to both the highest and the lowest intensities in the arrangement. On the other hand, in a series of experiments utilizing sharply contrasting light intensities presented in pairs, the anchovies always responded positively to the lower values and displayed a marked avoidance reaction toward the brighter illumination. The results obtained in the present preliminary study suggest other tests, to be made in near future, might disclose the degree of sensitivity of the fish eye to the changes in the intensity of illumination, as well as the specific adaptation of the eye to certain intensity values as earlier demonstrated by Privolnev (1958) on samples of young carp, *Cyprinus carpio,* and young tench, *Tinca tinca.* He had found both were able to differentiate intensities of white light when these intensities were 75 per cent to 85 per cent greater than those to which the experimental fish were originally adapted.

As with other species found suitable for training, the northern anchovy and Pacific sardine should not present any difficulty in training studies. Usually, the newly delivered wild anchovies and sardines began to take food after 5 to 7 days of acclimation to the artificial environment of the Steinhart Aquarium. Following this, the fish were trained to break up the school, to ascend to the surface, and to swim close to the position occupied by the feeding person. The training consisted of propelling a tablespoon in the

water for 10–15 seconds prior to dropping live food (brine shrimp) into water. Both the sardines and anchovies became conditioned to the sound of propelling the spoon, developing a feeding reaction within three to five trials (once a day), and they retained this response permanently. This conditioned response was of great help to the investigators at times when they had to pick up a few live specimens from the 1,000-gallon tank.

V. SUMMARY

1. The present investigation was conducted in order to study experimentally the effects of various types of illumination on the northern anchovy, *Engraulis mordax* Girard, from the point of view of its ability to discriminate between different wave lengths of the light spectrum and different intensity values of the white light.

2. The discriminating ability of the anchovy in regard to different types of visible and non-visible light radiation was explored in the specially constructed dark room and an experimental wooden tank which was divisible into a number of light zones [in accordance with the nature of the experiment to be carried out].

3. In the two-zone experiments the following paired lights were tested: green-blue, green-red, green-white, green-darkness, blue-red, blue-white, blue-darkness, red-white, red-darkness, and white-darkness. Ultraviolet was tested in pairs with green, blue, red, white, and darkness; infrared with darkness or with white light.

4. In the three-zone experiments the following combinations of lights were tested: green-red-white, green-white-darkness, red-white-darkness, blue-red-darkness, and blue-green-white ("daylight").

5. In the four-zone experiments the green-blue-red-darkness combination was tried.

6. In the two-zone experiments with monochromatic and white lights, the intensity was maintained uniformly at the 9 foot-candle level; in experiments with monochromatic lights and ultraviolet rays the intensity was adjusted to the maximum intensity of the "black lamp" which was equivalent to 0.2 foot-candle. In other experiments using ultraviolet or infrared wave lengths and white light or darkness, the intensities varied from almost zero to 500+ foot-candles.

7. In the three- and four-zone experiments, the intensities of monochromatic and white lights tested were either uniform or of different values.

8. In all combinations of monochromatic and white lights, the effect of red light on the anchovy remained invariably negative in contrast to the sharply positive reaction of these fish toward other lights tested.

9. In two-zone choice experiments the positive reaction of the anchovy for green light was found to be 97.86 per cent over the red (2.14 per cent);

75.34 per cent over white (24.66 per cent); 73.18 per cent over blue (26.82 per cent). The preference for other lights, tested in pairs, was as follows: 81.60 per cent for blue light over red (18.40 per cent), and 52.15 per cent over white (47.85 per cent); and 88.39 per cent for white light over red (11.61 per cent).

10. In the three- and four-zone experiments, the anchovies consistently demonstrated positive responses toward the green light as they did in the two-zone experiments. Even a considerable increase in the intensities of the opposing lights could not alter the positive reaction to green light.

11. In the two-zone experiments using ultraviolet light paired alternately with green, blue, or red light, the anchovies displayed three conflicting responses. These responses were "indifference" in ultraviolet versus blue light (50.15 per cent – 49.85 per cent), "slightly negative" (45.21 per cent) when ultraviolet was contrasted with green light (54.79 per cent), and "highly positive" (71.97 per cent) when it was paired with red (28.03 per cent).

12. In the other two-zone experiments, when ultraviolet and white lights of much higher intensities were tested, the results were confusing as described above. With respect to the ultraviolet light, the responses of the anchovies varied from negative or avoidance (36:64), through indifference (50:50), to positive (72:28).

13. In experiments utilizing infrared radiation, the anchovies seemed totally unable to perceive it.

14. In experiments intended to test the ability of anchovies to differentiate among different white light intensity values they seemed able to do so as evidenced in the tests with four and five intensity zones, and even more markedly in the two-zone experiments.

15. In the five-zone test arrangement in which intensities of light ranged from 2 to 100 foot-candles, the fish responded preferentially to the moderate intensities of the central zones (29.23 per cent for the 20 foot-candle zone, and 41.94 per cent for the 50 foot-candle zone, or 71.17 per cent for both).

16. In the four-zone test arrangement of white light used in intensities of 75, 125, 250 and 500 foot-candles, the anchovies reacted toward the moderate intensities of 125 foot-candles (30.21 per cent) and 250 foot-candles (37.16 per cent).

17. In the two-zone test experiments involving sharply contrasting intensities of 500 foot-candles, as a constant value, paired with much lower values ranging from 2 to 20 foot-candles, the reaction of the anchovies was always in favor (60.42 per cent to 83.71 per cent, averaging 68.52 per cent) of the lower intensity values.

18. The experiments herein described and discussed reveal a few important factors in the reactions of the anchovy to light and darkness: (1) the an-

chovy is a phototactic animal; (2) it is capable of discriminating qualitatively between monochromatic (green, blue, red) and white lights; (3) it is able to distinguish green light from blue (the Pacific sardine failed to do so); (4) it shows a preference for green and blue lights over white; (5) it proved to react strongly negatively to red light. However, the fish tolerated this type of illumination when it was tested as an alternative to total darkness, and showed a highly positive response in such a case to the red light; (6) in its reaction toward the ultraviolet wave lengths it displayed a rather individualistic pattern of behavior; (7) it is unable to perceive infrared radiation; (8) it is capable of reacting differently to different intensities of white light ranging from 2 foot-candles to 500 foot-candles.

VI. 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, Senior Scientist 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; to Dr. Earl S. Herald, Curator of Aquatic Biology, California Academy of Sciences, for his willing cooperation and valuable counsel; and to Dr. Alan E. Leviton, Curator of the Department of Amphibians and Reptiles, and Mrs. Lilian Dempster, Associate Curator of Fishes, California Academy of Sciences, for their extremely helpful assistance in preparing the manuscript. Acknowledgment is made also to Mr. Garth I. Murphy, Coordinator of the California Cooperative Oceanic Fisheries Investigations, and to Miss Carol Bumgardner for helpful and constructive criticism of the manuscript; and to the management of the General Electric Company, the Ultra-Violet Products, and the Corning Glass Works for providing important data and for their permission to reproduce official charts in the present study.

LITERATURE CITED

ARORA, H. L., and R. W. SPERRY

1958. Studies on color discrimination following optic nerve regeneration in the cichlid fish, *Astronotus ocellatus*. Anatomical Record, vol. 131, no. 3, p. 529.

BABURINA, E. A.

1955. Structural and functional properties of the fish eye. Trudy Sovestchania po voprosam povedenia i razvedki ryb 1953 g. (Transactions of the Conference on the problems of fish behavior and reconnaissance of the fish, 1953.) Edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 5, pp. 90–103, 12 text figs., Moscow, Academy of Sciences Press, in Russian.

BABURINA, E. A. — Cont.

1958. Characteristic properties of development of the eyes and their functions in fishes. Trudy Sovestchania po fiziologii ryb 1956 g. (Transactions of the Conference on physiology of the fishes, 1956.) Edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 8, pp. 101–110, 10 text figs., Moscow, Academy of Sciences Press, in Russian.

BARANOV, J. B.

1955. Experimental catch of fish with the aid of electric light in waters of Primorie. Izvestia (Bulletin) of the Pacific Research Institute of Fisheries and Oceanography, vol. 43, pp. 139–166, 7 text figs., Vladivostok, in Russian.

BERG, L. S.

1932–33. Les poissons des eaux de l'U.R.S.S. et des pays limitrophes, 3–e edition, revue et augmentée, 899 pp., 762 text figs., 1 map on separate sheet (in color). Published by the All-Union Research Institute of Lake and River Fisheries, Leningrad, in Russian.

BERG, L. S., *et al.*, editors

1949. Commercial fishes of the U.S.S.R. (see under Ministry of Fisheries Industry).

BLAXTER, H. H. S., and B. B. PARRISH

1958. The effect of artificial lights on fish and other marine organisms at sea. Marine Research, no. 2, 24 pp., 3 text figs., 7 tables, 1 plate, Scottish Home Department, Edinburgh.

BODEN, B. P., E. M. KAMPA, and J. M. SNODGRASS

1960. Underwater daylight measurements in the Bay of Biscay. Journal of the Marine Biological Association of the United Kingdom, vol. 39, no. 2, pp. 227–238, 8 text figs., 2 tables and 1 plate, Cambridge, University Press.

BOER, P. A. DE

1950. Ervaringen met het echolood tijdens de ijle haringteelt op de Belgische kust. Visserij-Nieuws, 2(11)127 (Summarized in the World Fisheries Abstracts, vol. 1, no. 4, July–August, 1950).

BONDARENKO, A. F.

1951. The mass catch of the sprat "kil'ka" with electric light. Rybnoie Hoziaistvo, no. 12, pp. 8–10 (Fisheries Economy), Moscow, in Russian.

BONGARD, M. M.

1955. Colorimetry on animals. Doklady Akademii Nauk S.S.S.R. (Compte Rendus of the Academy of Sciences of the U.S.S.R.), vol. 103, no. 2. [After V. P. Protasov, Electrophysiological study of vision in fishes, 1958, as listed below], in Russian.

BONGARD, M. M., and M. S. SMIRNOVA

1959. Color vision in man and animals. Priroda (Nature), no. 5. [After I. V. Nikonorov, 1959, Application of light blocks in sprat fishing with fish pump, Rybnoie Hoziaistvo, no. 12, pp. 42–47, 5 text figs., in Russian.]

BORISOV, P. G.

1950. Fishing with the aid of electric light, 24 pp., 10 text figs., Moscow, in Russian.

1955. The behavior of fishes under the influence of artificial light. Trudy Sovestchania po voprosam povedenia i razvedki ryb 1953 g. (Transactions of the Conference on the problems of fish behavior and reconnaissance of fish, 1953.) Edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 5, pp. 121–143, 5 text figs., Moscow, Academy of Sciences Press, in Russian.

BORISOV, P. G., and N. S. OVSIANNIKOV

1951. A key to the commercial fishes of the U.S.S.R., 178 pp., 267 text figs., Moscow, in Russian.

BORISOV, P. G., and V. P. PROTASOV

1959. The employment of incandescent lamps and selective sources of light for catching the fish. Rybnoie Hoziaistvo (Fisheries Economy), no. 12, pp. 48–49, Moscow, in Russian.

BREDER, C. M., JR.

1959. Studies on social groupings in fishes. Bulletin of the American Museum of Natural History, vol. 117, no. 6, pp. 397–481, 28 text figs., 20 tables, and plates Nos. 70–81 with 23 photos., New York.

BRETT, J. R.

1957. The sense organs: the eye. Chapter II, part 1, in *The Physiology of Fishes*, vol. II, Behavior, Edited by Margaret E. Brown. Pp. 121–154, 10 text figs., and 1 table, New York.

BROWN, F. A., JR.

1937. Responses of the large-mouth black bass to colors. Illinois Natural History Survey Bulletin, vol. 21, no. 2, pp. 33–55, 10 text figs., 11 tables and 1 color plate.

BULL, H. O.

1957. Behavior: Conditioned responses. Chapter III, part 1, in *The Physiology of Fishes*, vol. II, Behavior, Edited by Margaret E. Brown. Pp. 211–228, 1 text fig., 1 table, New York.

CHUGUNOVA, N. I.

1955. Discussion (on responses of the Caspian sprat and shads to the underwater electric light). Trudy Sovestchania po voprosam povedenia i razvedki ryb 1953 g. (Transactions of the Conference on the problems of fish behavior and reconnaissance of fish, 1953.) Edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 5, pp. 206–212, 6 text figs., Moscow, in Russian.

CLARKE, G. L.

1954. Elements of ecology. Contribution no. 704 from the Woods Hole Oceanographic Institution, 534 pp., many text figs., New York – London,

CRAIG, R. E., and I. G. BAXTER

1952. Observations in the sea on the reaction to ultraviolet light of certain sound scatterers. Journal of the Marine Biological Association of the United Kingdom, vol. 31, no. 2, pp. 223–227, 1 plate with 2 photos., Cambridge University Press.

DUNCAN, R. 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., 9 text figs.

ELLSON, J. G.

1953. Experiments with a "fish pump." Commercial Fisheries Review, vol. 15, no. 2, pp. 27–29, 4 text figs., Washington, D.C.

EREMTSTOV, F. Z., and M. G. NIKONOVA

1949. Catching the sprat "kil'ka" with electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 3, pp. 19–20, Moscow, in Russian.

EVTËEV, I. A.

1953. The influence of the moonlight on catching the sprat "kil'ka" with the aid of electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 4, pp. 16, Moscow, in Russian.

FRISCH, K.

1933. Sind der Fische farbenblind? Zoologische Jahrbücher, Abteilung für Allgemeine Zoologie, Bd, 33. [After Prof. N. V. Puchkov, 1954, listed below.]

FUKUHARA, A.

1959. Some improvements in the stick-held dipnet for saury fishing. An article in *Modern Fishing Gear of the World*, edited by Hilmar Kristjonsson, pp. 422–425, 11 text figs., London, England.

GRISTCHENKO, G. I.

1951. Experimental herring fishing with application of the electric light. Izvestia (Bulletin) of the Pacific Research Institute of Fisheries and Oceanography, no. 34, Vladivostok. [After T. I. Privolnev, 1956, as listed below], in Russian.

GRISTCHENKO, G. I., V. V. LANDYSHEVSKY, and A. J. YUGANSON

1957. The results of the saury fishing in the Pacific Ocean using electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 3, pp. 15–17, 1 text fig., Moscow, in Russian.

HSIAO, S. C.

1952. Observations on the reaction of tuna to artificial light. (Contribution no. 24 of the Hawaii Marine Laboratory, University of Hawaii, Honolulu, Hawaii.) Special Scientific Report – Fisheries, no. 91, U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., pp. 36–58, 3 text figs. and 8 tables.

HURST, P. M., JR.

1952. Can fish see color? Pennsylvania Angler, vol. 21, no. 12, p. 5.

KAWAMOTO, N. Y.

1959. The significance of the quality of light for the attraction of fish. An article in *Modern Fishing Gear of the World*, edited by Hilmar Kristjonsson, pp. 553–555, 1 table, London, England.

KAWAMOTO, N. Y., and J. KONISHI

1952. The correlation between wavelength and radiant energy affecting phototaxis. Report, Faculty of Fisheries, Prefectural University of Mie, vol. 1, no. 2, pp. 197-208.

KAWAMOTO, N. Y., and M. TAKEDA

1950. Studies on the phototaxis of fish. Japanese Journal of Ichthyology, vol. 1, no. 2, pp. 101–115.

1951. The influence of wavelengths of light on the behavior of young marine fish. Report, Faculty of Fisheries, Prefectural University of Mie, vol. 1, no. 1, pp. 41–53, 8 text figs. and 13 tables.

KIRILLOV, V. M.

1955. On the possibilities of increasing landings of the anchovy in the Black Sea. Rybnoie Hoziaistvo (Fisheries Economy), no. 8, pp. 11–14, Moscow, in Russian.

LAGUNOV, I. I.

1955. From the experience of underwater observations from the bathysphere. Rybnoie Hoziaistvo (Fisheries Economy), no. 8, pp. 54–57, Moscow, in Russian.

LESKUTKIN, A. F., I. V. NIKONOROV, and A. H. PATËEV

1955. The catching the sprat "kil'ka" with fish pump and with using electric light. Trudy Vsesoiuznogo Nauchno-issledovatelskogo Instituta Morskogo Rybnogo Hoziaistva i Okeanografii (VNIRO) (Transactions of the All-Union Research Institute of the Marine Fisheries and Oceanography), vol. 30, pp. 4–30, Moscow, in Russian.

LESKUTKIN, A. F., and B. I. PRIHODKO

1951. Behavior of the sprat "kil'ka" in the illuminated zone at the fishing with electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 12, pp. 11–12, Moscow, in Russian.

LINDSAY, E. A.

1948. The use of fluorescent lamps for examining color proofs. Reprint from Photo-engravers 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.

LOUKASHKIN, A. S., and N. GRANT

1959. Behavior and reactions of the Pacific sardine, *Sardinops caerulea* (Girard), under the influence of white and colored lights and darkness. Proceedings of the California Academy of Sciences, Fourth Series, vol. 29, no. 15, pp. 509–548, 23 text figs., 9 tables, San Francisco.

LOVETSKAYA, A. A.

1955. Discussion (on responses of the three species of the Caspian sprats to the underwater electric light). Trudy Sovestchania po voprosam povedenia i razvedki ryb 1953 g. (Transactions of the Conference on the problems of fish behavior and reconnaissance of the fish, 1953), edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 5, pp. 182–186, 6 text figs., Moscow, in Russian.

1958. On the reaction of the sprat "kil'ka" to the light. Trudy Sovestchania po fiziologii ryb 1956 g. (Transactions of the Conference on the physiology of the fishes, 1956), edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 8, pp. 121–123, Moscow, in Russian.

MINISTRY OF FISHERIES INDUSTRY OF THE U.S.S.R.

1949. Commercial fishes of the U.S.S.R. Description of fishes (text to the atlas of colored plates of fishes), 787 pp., 10 color plates and many text figs., edited by Leo S. Berg in association with A. S. Bogdanov, N. I. Kozhin, and T. S. Rass; All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO), Moscow, in Russian.

NIKOLAEV, A. P.

1957. On the fishing of fattening herring in the inshore waters of Sakhalin island with employment of electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 3, pp. 12–14, 3 text figs., Moscow, in Russian.

NIKONOROV, I. V.

1955. Catching the Caspian sprat "kil'ka" with the aid of underwater electric illumination and the fish pump. 32 pp., Moscow, in Russian.

1956a. The observations on the behavior of the Caspian sprats. 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, pp. 21–36, 10 text figs., Moscow, in Russian.

1956b. The theoretical foundation and experimental investigation of the fishing of the Caspian sprat with fish pump and underwater illumination. Rybnoie Hoziaistvo (Fisheries Economy), no. 1, pp. 73–77, 8 text figs., Moscow, in Russian.

1958. The catching Caspian sprat "kil'ka" with the fish pump and underwater illumination. 96 pp., Moscow, in Russian.

1959a. Application of the light blocks in sprat fishing with the fish pump. Rybnoie Hoziaistvo (Fisheries Economy), no. 12, pp. 42–47, 5 text figs., Moscow, in Russian.

1959b. The basic principles of fishing for the Caspian "kil'ka" by underwater light. An article in *Modern Fishing Gear of the World*, edited by Hilmar Kristjonsson, pp. 559–566, 15 text figs., London, England.

NIKONOROV, I. V., and A. H. PATËEV

1959. Sprat fishing with pump and underwater illumination with application of pulsating electrical current. Rybnoie Hoziaistvo (Fisheries Economy), no. 7, pp. 53–58, 4 text figs., Moscow, in Russian.

OZAKI, HSAO

1951. On the relation between the phototaxis and the aggregation of young marine fishes. Report, Faculty of Fisheries, Prefectural University of Mie, vol. 1, no. 1, pp. 55–66, 10 text figs., 5 tables.

PARIN, N. V.

1956. Distribution of concentrations of saury and modern methods of saury fishing in the north-western part of the Pacific Ocean. Rybnoie Hoziaistvo (Fisheries Economy), no. 7, pp. 57–61, 3 text figs., Moscow, in Russian.

1958. The ichthyofauna of the pelagial of the north-western part of the Pacific Ocean. Priroda (Nature), no. 5, pp. 60–66, 7 text figs., Moscow, in Russian.

PARRISH, B. B., and R. E. CRAIG

1951. Sonic layers in the sea. Nature, no. 168, p. 472, London.

POCHEKAEV, V. M.

1949. Reactions of certain aquatic organisms to the electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 3, pp. 36–39, 3 text figs., Moscow, in Russian.

POKROVSKY, A. N.

1957. On the Japanese saury fishing with the blanket net and light. Rybnoie Hoziaistvo (Fisheries Economy), no. 3, pp. 75–78, 2 text figs., Moscow, in Russian.

PRIHODKO, B. I.

1951. On sprat Caspian "kil'ka" fishing with electric light in winter. Rybnoie Hoziaistvo (Fisheries Economy), no. 8, pp. 43–46, Moscow, in Russian.

1957. Some new data on the behavior of the Caspian sprat "kil'ka" within electric light zone. Rybnoie Hoziaistvo (Fisheries Economy), no. 10, pp. 47–52, 5 text figs., 3 tables, Moscow, in Russian.

PRIVOLNEV, T. I.

1956. The reaction of fish to the 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, pp. 3–20, 5 text figs., Moscow, in Russian.

1958. The reactions of fish to different intensities of the light. Trudy Sovestchania po fiziologii ryb 1956 g. (Transactions of the Conference on physiology of the fishes, 1956.) Edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 8, pp. 93–96, 1 text fig., Academy of Sciences Press, Moscow, in Russian.

PROTASOV, V. R.

1957. Reactions of certain Black-Sea fishes to the 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 9, pp. 144–146, 2 tables, Moscow, in Russian.

PROTASOV, V. R. — Cont.

1958. Electrophysiological study of vision in fishes. Trudy Sovestchania po fiziologii ryb 1956 g. (Transactions of the Conference on physiology of the fishes, 1956), edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 8, pp. 111–114, 2 text figs., 2 tables, Academy of Sciences Press, Moscow, in Russian.

PUCHKOV, N. V.

1954. The physiology of fishes, 369 pp., 108 text figs., Moscow, in Russian.

RADAKOV, D. V.

1956. On studying behavior of the fishes during the fishing operations. 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, pp. 37–46, Moscow, in Russian.

RADAKOV, D. V., and B. S. SOLOVIEV

1959. The first experimental employment of the submarine for observation of the herring's behavior. Rybnoie Hoziaistvo (Fisheries Economy), no. 7, pp. 16–21, 4 text figs., Moscow, in Russian.

RADOVICH, J., and E. D. GIBBS

1954. The use of a blanket net in sampling fish populations. California Fish and Game, vol. 40, no. 4, pp. 353–365, 7 text figs., 4 tables, Sacramento, California.

RASALON, S. B.

1959. The development of the Philippine Bagnet (Basnig) for increased efficiency. An article in *Modern Fishing Gear of the World*, edited by Hilmar Kristjonsson, pp. 418–421, 7 text figs., London, England.

RASS, T. S.

1956. On the fisheries of Japan. Rybnoie Hoziaistvo (Fisheries Economy) no. 1, pp. 61–62, Moscow, in Russian.

REEVES, C. D.

1919. Discrimination of light of different wave lengths by fish. Behavior Monographs, London, vol. 4, no. 3, serial number 19, pp. I–IV + 1–106, 17 text figs.

"REFLECTOR"

1949. Views on the news. Electrical Review, no. 145, p. 787.

ROEDEL, P. M.

1953. Common Ocean Fishes of the California Coast. Fish Bulletin, no. 91: 184 pp., 175 text figs., 1 color plate. State of California, Department of Fish and Game, Marine Fisheries Branch.

SAFIANOVA, T. E.

1952a. On the anchovy fishing with electric light in the Black Sea in winter. Rybnoie Hoziaistvo (Fisheries Economy), no 3, pp. 21–22, Moscow, in Russian.

1952b. Reactions of the Black-Sea fishes to the electric light. Materials of the Conference held at the Ministry of Fisheries Industry of the U.S.S.R. [After V. R. Protasov, 1957, as listed below.] Moscow, in Russian.

SAFIANOVA, T. E. — Cont.

1958. On certain correlations in the changes of reaction to the light in the anchovy "hamsa" and horsemackerel "stavrida" throughout the year. Trudy Sovestchania po fiziologii ryb 1956 g. (Transactions of the Conference on physiology of the fishes, 1956.) Edited by E. N. Pavlovsky, Academy of Sciences of the U.S.S.R., Ichthyological Commission, issue 8, pp. 97–100, Moscow, Academy of Sciences Press, in Russian.

SAFRONOV, P. A.

1952. My experimental catch of the sprat "kil'ka" with electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 4, pp. 53–54, Moscow, in Russian.

SASAKI, T.

1959. The use of light attraction for traps and setnets. An article in *Modern Fishing Gear of the World*, edited by Hilmar Kristjonsson, pp. 556–558, 5 text figs., 2 tables, London, England.

SMITH, K. A.

1955. Use of an electric attraction and guiding device in experiments with a "fishpump." Commercial Fisheries Review, vol. 17, no. 2, pp. 1–7, 4 text figs., Washington, D.C.

SVETOVIDOV, A. N.

1952. Herring-like fishes (Clupeidae). Fauna S.S.S.R. (The Fauna of the U.S.S.R.), new series no. 48, vol. 2, no. 1, Fishes, 331 pp., 54 text figs., 53 plates on separate pages; Zoological Institute of the Academy of Sciences of the U.S.S.R., Academy Press, Moscow - Leningrad, in Russian.

TAKAYAMA, S.

1956(?) Saury lift net fishing with light. Fisheries Statistics and Technological Development (in Pokrovsky, 1957, On the Japanese saury fishing with the blanket net and light, in Russian).

TAMURA, T.

1959. Fundamental studies on the visual sense in fish. An article in *Modern Fishing Gear of the World*, edited by Hilmar Kristjonsson, pp. 543–547, 1 text fig., 3 tables, London, England.

TERENTIEV, A. V.

1957. Technical development in the fisheries industry of the U.S.S.R., in the past forty years. Rybnoie Hoziaistvo (Fisheries Economy), no. 11, pp. 31–39, 3 text figs., Moscow, in Russian.

TESTER, A. L.

1959. Summing of experiments on the response of tuna to stimuli. An article in *Modern Fishing Gear of the World*, edited by Hilmar Kristjonsson, pp. 538–542, London, England.

TIHONOV, D. P

1959. Some supplementary data on the reaction of herring to the electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 4, pp. 13–14, Moscow, in Russian.

TOKAREV, A. K.

1949. The anchovyform sprat "kil'ka" and catching it with the aid of light. Rybnoie Hoziaistvo (Fisheries Economy), no. 6, pp. 33–36, Moscow, in Russian.

VERHEIJEN, F. I.

1956. On a method for collecting and keeping clupeids for experimental purposes, together with some remarks on fishery with light-sources and a short description of free cupulae of the lateral line organ on the trunk of the sardine, *Clupea pilchardus* Wabl. Reprint from Pubblicazioni della Stazione Zoologica di Napoli, vol. 28, pp. 225–240, 1 text fig., 1 table with 4 photos.

1958. The mechanisms of the trapping effect of artificial light sources upon animals. Reprint from the Archives Néerlandaises de Zoologie, vol. 13, no. 1, pp. 1–107, 6 text figs., 1 plate.

1959. Attraction of fish by the use of light. An article in *Modern Fishing Gear of the World*, edited by Hilmar Kristjonsson, pp. 548–549, 1 text fig., London, England.

VILTER, V.

1950. Adaptation biologique de l'appareil visuel et les structures rétiniennes de la sardine. Compte Rendus de Sceances de la Societe Biologique, vol. 144, nos. 3–4, pp. 200–203.

WALLS, G. L.

1942. The vertebrate eye and its adaptive radiation. Cranbrook Institute of Sciences Bulletin, no. 19, XIV + 785 pp., 195 text figs., 1 plate.

YUDOVICH, J. V.

1956. Experimental saury fishing with the aid of electric light. Rybnoie Hoziaistvo (Fisheries Economy), no. 4, pp. 8–11, 2 text figs., Moscow, in Russian.

YUDOVICH, J. V., and P. A. KOLEGOV

1956. Scouting of the sardine and experimental sardine fishing in the Sea of Japan. Rybnoie Hoziaistvo (Fisheries Economy), no. 2, pp. 17–19, 2 text figs., Moscow, in Russian.

ZAITSEV, V. P., and V. G. AZHAZHA

1959. Submarine scientific expeditions on the "Severianka." Rybnoie Hoziaistvo (Fisheries Economy), no. 7, pp. 7–16, 7 text figs., Moscow, in Russian.

THE EVOLUTION OF A PATTERN OF SOUND PRODUCTION ASSOCIATED WITH COURTSHIP IN THE CHARACID FISH, *GLANDULOCAUDA INEQUALIS*

KEITH NELSON

University of California, Berkeley

Reprinted from EVOLUTION, Vol. 18, No. 4, January 28, 1965
pp. 526–540
Made in United States of America

THE EVOLUTION OF A PATTERN OF SOUND PRODUCTION ASSOCIATED WITH COURTSHIP IN THE CHARACID FISH, *GLANDULOCAUDA INEQUALIS*

KEITH NELSON[1]
University of California, Berkeley

Accepted June 3, 1964

One of the most rewarding aspects of the study of animal behavior is the rare chance to trace back to its antecedents the emergence of an entirely new pattern of behavior, and to observe the changes in behavioral organization which have accompanied it. In *Glandulocauda*, a small, internally fertilizing South American characid fish, the production of a sound associated with rhythmic air-gulping has been incorporated into the male's courtship pattern; at least four of the remaining genera of the tribe to which *Glandulocauda* belongs are mute.

The aims of the present paper are four. First, a description and analysis of the relation of sound production to courtship will be given. This will be followed by a description of the physical characters of the sound. Third, because of the association of sound production in *Glandulocauda* with rhythmic air-gulping, it must be determined whether or not air-gulping is of respiratory significance; experiments which indicate that it is not will be presented. Finally, a description will be given of the patterning of the putative feeding act, Nipping Surface; this act appears to be the antecedent of rhythmic air-gulping in *Glandulocauda*.

MATERIALS AND METHODS

One male and several female *Glandulocauda inequalis* from a tributary of Guahyba Bay, Rio Grande do Sul, Brazil, and many specimens of the related species *Coelurichthys tenuis* and *C. microlepis* were obtained in June, 1962, from A. V. and Harald Schultz. Two young but mature male *G. inequalis* from a spawning of one of the original females were also observed, but they died in my absence before their sound production could be analyzed. In the summer of 1961 stocks of another glandulocaudine, *Corynopoma riisei*, were obtained in Trinidad.

Fish were kept, singly and in groups, in 5-, 7-, 15-, and 30-gallon aquaria, most of which were planted with *Sagittaria* and *Fontinalis*. *Corynopoma* was maintained at 24–25° C; tanks containing *Glandulocauda* were kept at 18–22° C. Natural lighting was supplemented by 25–75-watt bulbs. Water hardness and pH were not controlled.

Timed records of behavior were made using an Esterline-Angus 20-channel operations recorder coupled to a keyboard. For recording and monitoring sound production a hydrophone was constructed consisting of a Cal-Rad contact microphone designed for use with a harmonica, coated with vinyl plastic. This was used with Wollensak model T-1500 and Viking model 75 magnetic tape recorders run at 3¾ and 7½ inches per second. Simultaneous records were made on tape recorder and operations recorder; these were correlated and the sounds analyzed on a Kay Electric Company sonagraph, using the wide-band filter and both "high shape" and "FL-1" shaping circuits.

For the respiration experiments, the apparatus shown in fig. 1 was used. This was a 7-gallon aquarium which was divided into two compartments, A and B, by a plastic partition. The partition was perforated by two slots running nearly the full tank width; these slots were covered with

[1] Present address: Zoölogisch Laboratorium, Leiden. This work was conducted during tenure of a National Science Foundation graduate fellowship, with partial support from N.S.F. Grant G-13082. I wish to thank Drs. Peter Marler, Frank Beach, and Donald Wilson for their help and advice in the course of the work, Mr. George Hersh for his valuable assistance, and Drs. Howard Winn and Kees Groot for their constructive suggestions upon reading this paper.

The Body-Wag, an Innate Behavioral Characteristic of Bony Fishes

BY DR. GEORGE S. MYERS

Those who observe live fishes take it for granted that different types of fishes have different habits—different ways of swimming, spawning, eating, etc. Just as the ornithologist can often identify the taxonomic family to which a distant but visible bird belongs solely by the way it flies, so the ichthyologist can often recognize the family to which a fish belongs by its movements. Many behavioral patterns are quite as characteristic of certain types of fishes as are the points of anatomy that are used in classification.

During the past 30 years, the whole science of animal behavior has grown up, with a complex terminology used in the analysis of behavioral sequences and patterns. Most of the researchers in this field, however, even those who work primarily with fishes, are much too occupied with meticulous study of a few species to become acquainted with behavioral characteristics of fishes in general. For this reason, they have failed to notice that certain of these behavioral acts appear to be much more deep-seated than others. Some, indeed, seem to occur throughout all or nearly all the modern types of bony fishes (teleosts) and thus may be far more unchanging during evolution than most anatomical characters.

The one I wish to mention is one that I call the body-wag. When two male fighting-fishes (*Betta*) line up beside each other, spread their fins, and project the gill (branchiostegal) membranes below the throat, they then go into an apparently tense, stiff-bodied, jerky "body-wag"—before breaking off the display and attacking. Much the same maneuver is exhibited by the cichlid fishes, upon which so much behavioral research has been conducted.

Those behaviorists who have worked primarily with cichlids and anabantoids have apparently had no reason to assume that this stiff, jerky body-wag, given with expanded fins and lowered gill membranes, is more widespread among fishes than the taxonomic families with which they have worked. However, the body-wag is much more widely characteristic of teleost fishes than has ever been noticed.

I have seen what is obviously the same stiff body-wag (called *tail-wag* by Baerends) in many displaying or fighting Cichlidae, Centrarchidae, Belontiidae (=Anabantidae, in part), Pomacentridae, Serranidae, and other families of spiny-rayed percoid fishes. I have observed it in the long-jawed goby (*Gillichthys mirabilis*), in a gadid, and in both Poeciliidae and Cyprinodontidae.

BRAND NEW

The Most Sensational Fish Food You Can Buy . . . Guarantees Your Fish Better Growth, Vigor, and Coloration or Your Money Back!

Now you can be *sure* your fishes and turtles get all the vitamins, minerals, protein, and bulk they need. No more spitting out essential foods they don't like—foods that collect on the bottom to cloud and contaminate your aquarium.

New Oscar foods are in *pellet* form, and each formula is blended with natural foods your fishes and turtles can't resist—shrimp, tuna, crab, liver, and high-protein whale meat. Either this revolutionary food gives them better growth, vigor, and coloration in 30 days, or you get your money back . . . no questions asked (see below).

HERE'S HOW IT'S DONE: Shown are some Tropical Fish Food pellets, in "coarse" grade. Each of these tiny pellets contains a balanced diet. Each contains an exacting blend of the nutrients your fishes must have for healthy growth, vigor, and coloration. Note the absence of powdery waste, the uniform size. Only the finest materials were used, and only Oscar's unique triple-grind, mix, press, and grading process makes this possible . . . guarantees you the finest fish food your money can buy.

5 SPECIAL FORMULAS Each of five special formulas contains its own concentration of those nutrients ichthyologists state are the most beneficial to each variety of fish: a 54% protein formula for the tropical fish and guppy foods; a concentrated carbohydrate formula for goldfish; a concentrated vegetable base formula for mollies. The turtle formula is fortified with vitamins A and D to help prevent soft shell.

TRY THIS FREE OFFER. Ask your dealer for your free sample of Oscar Tropical Fish Food. If he has yet to stock Oscar foods, let us know. We'll see that free samples are sent to him immediately.

GUARANTEED: If your fishes or turtles don't actually look better and more vigorous in just 30 days of feeding with the specified formula, return the unused portion to your dealer and your money will be refunded. Buy a can of Oscar Fish or Turtle food today!

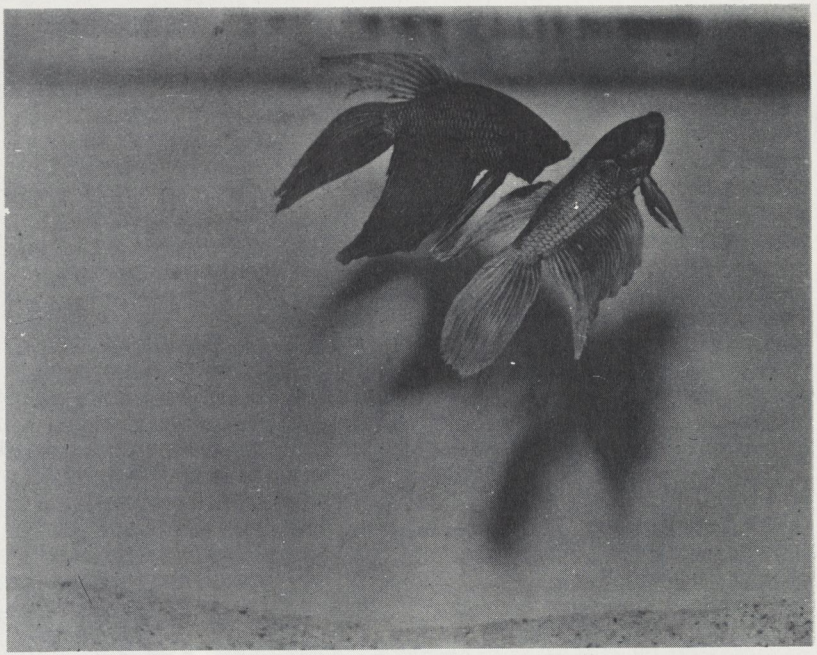
OSCAR ENTERPRISES, INC. / 1216 FIFTH ST. DEPT. C BERKELEY, CALIFORNIA

ALL IT TAKES . . .

Just one drop of Oscar Ban-Ich will rid your prized fishes of annoying *ich* better and faster than any other *ich* remedy on the market. It's safe to use, too, because Oscar's one-drop dispenser bottle leaves no room for error. Squeeze the plastic container, count out one drop for every gallon of water in your tank. That's all there is to it. And when you buy your one- or four-ounce plastic bottle of Ban-Ich, why not stock up on these other famous Oscar remedies to stay on the safe side: Ban-All remedy and tonic, Ban-Chlor water conditioner, Ban-N-Blue methylene blue, and Ban-N-Clear, a water clarifier. You'll find them all displayed in their unbreakable plastic containers colored in bright magenta at leading pet stores everywhere. Come in and stock up today.

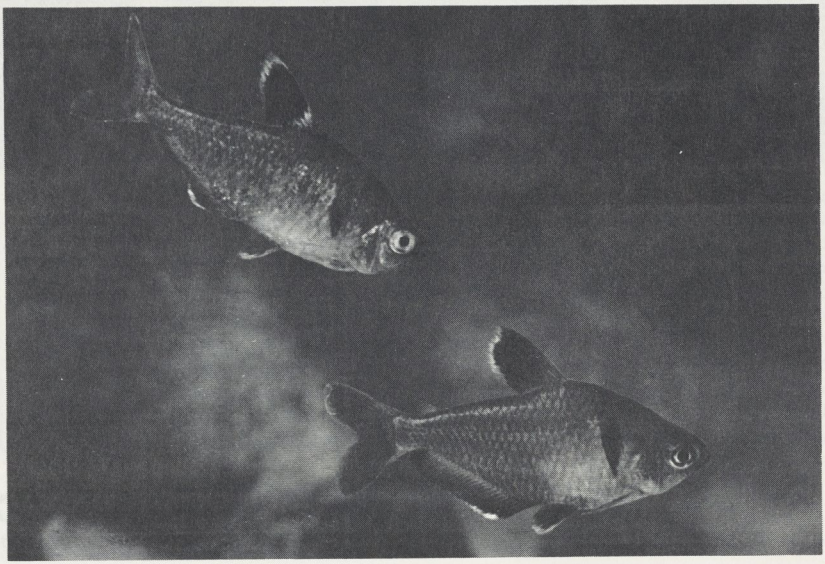
OSCAR ENTERPRISES, INC.

1216 FIFTH ST., DEPT. L2, BERKELEY, CALIF.



Just before two male fighting-fishes begin to fight, they display the tense, stiff-bodied, jerky body-wag. Photo by G. J. M. Timmerman.

Hyphessobrycon callistus, another species in which the author has observed the body-wag. Photo by Gunter Senfft.



The author was surprised to observe the body-wag in the glass-catfish, Kryptopterus bicirrhus. Photo by Milan Chvojka.

More surprisingly, I have observed it in a number of Cyprinidae, notably some *Notropis, Barbus partipentazona,* and *Brachydanio rerio.* It is common in the Characidae, notably in *Hyphessobrycon callistus.* Most surprising of all, I have observed it in the small glass-catfish, *Kryptopterus bicirrhus,* at dusk, when these fishes become much more active than in daylight.

This maneuver, which is much more than a mere tail-wag, would appear to be a common characteristic throughout the teleosts, although it often becomes part of a more complicated display or combat pattern which differs considerably from family to family and order to order. Undoubtedly there are certain groups of bony fishes which do not display the body-wag (possibly eels do not), but its general occurrence would lead one to suspect that teleosts which do not display the body-wag have probably lost the characteristic by the evolution of body forms or behavior not suitable for its expression.

ONLY EUREKA

VIBRATOR AQUARIUM PUMPS HAVE *STAINLESS STEEL* DIAPHRAGMS

NEVER NEEDS CHANGING

GUARANTEED FOR 2 YEARS

H·D

(HEAVY DUTY)

VIBRATOR PUMP

RUNS 5 FILTERS!
QUIET! LONG LIFE!
NEW DESIGN!

$7.95

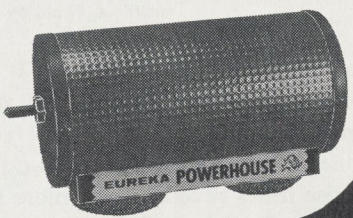
SUGGESTED RETAIL

POWERHOUSE VIBRATOR PUMP

RUNS 10 OUTLETS!
HIGH POWER!

$11.95

SUGGESTED RETAIL



EUREKA

PRODUCTS CO., HILLSIDE, N. J.

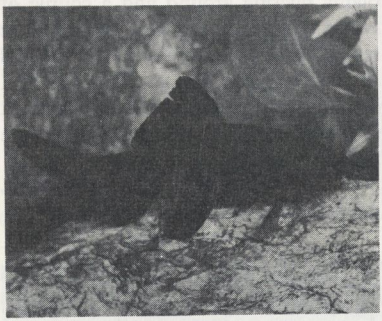
"WORLD'S FINEST AQUARIUM PRODUCTS"

If your local source is unable to supply, write us for information.

first came in and were identified (1956). The scientific name is Hyphessobrycon rubrostigma; *it is described in* Exotic Tropical Fishes *on page F-350.00.*

4. Let's get this business of "stripes" and "bars" cleared up first. On a fish, a stripe runs horizontally and a bar runs vertically. Your fish probably have bars and not stripes. These are very prominent in Cichlasoma severum, *especially when young.*

5. With the best of care, about 6 months. These fish are usually aggressive only toward their own kind. You might get two fish which are perfectly friendly and get along well, or two which would act like mortal enemies.



Labeo bicolor

Catfish change

Q. 1. Some time ago I purchased two *Corydoras*, which I took to be *C. aeneus*. Now it seems that one has a longer snout and higher back. Is it of the species *C. aeneus?* If not can the species be hybridized?

2. Is there any way to sex young catfish?

3. Do you know of a company that ships live tubifex or daphnia?

Don Bailey, Northport, Ala.

A. *1. I have seen it often:* Corydoras aeneus *and* Brochis coeruleus *look very much alike when young, but when they get a little older the* Brochis coeruleus *becomes higher in the body and its snout is longer. Don't waste your time trying to hybridize them: they are two separate genera, and it is highly unlikely that you will have any luck.*

2. I presume you mean the Corydoras *species. This will work only on fish that are at least three-quarters grown: look down at them, the males are slimmer.*

3. No, your dealer probably has some arrangements that will get them shipped to him in season.

AQUATOP

AQUARIUM COVER . . .

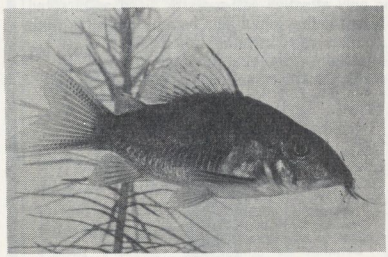
with small corner cutouts for heater and filter—fish stay in; dirt stays out.

Aqua Top reduces evaporation and helps maintain a constant water temperature. Made of transparent heat-resistant plastic. No rust or corrosion. Ideal for marine tanks too.

Available in standard sizes at all quality dealers.

GENERAL ENTERPRISES
56 Macomber Avenue, Springfield, Mass.

Please mention T.F.H.
when writing to advertisers

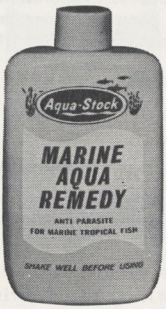


Brochis coeruleus

Find your salt water fish problem here...

Due to Parasites	☐ Itch ☐ Salt Water Itch ☐ Blotchy Skin ☐ Loss of Color or Appetite ☐ Rapid Breathing
Caused by Fungus	☐ Fungus Growth on Mouth or Body ☐ Fin or Tail Rot ☐ Open Wound or Sores

Solve it with...



Marine Aqua Remedy

The only effective anti-parasite. Used as directed, this fast acting liquid kills harmful parasites while it soothes raw, irritated skin tissue. Lab-tested for two years Marine Aqua Remedy has proved safe and effective. **4 fluid ozs. 98c**

Sea Cure

The fungus remover that works. Fungus on your fish is harmful and contagious. To stop fungus and to keep your fish healthy and active, use Sea Cure. It goes to work instantly—gives fast help. **4 grams 98c**

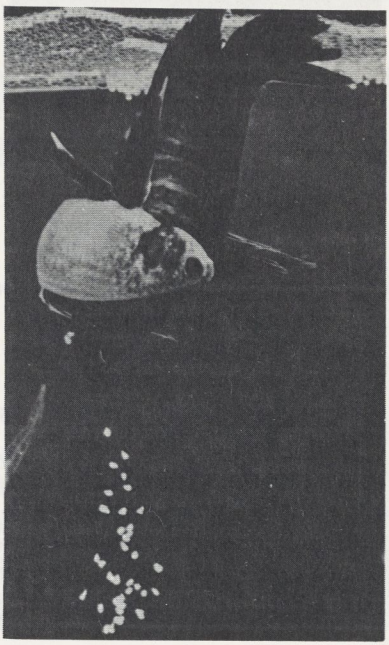
AQUARIUM STOCK COMPANY INC.
27 MURRAY ST., NEW YORK, N. Y.
8070 BEVERLY BLVD., LOS ANGELES, CALIF.

Betta dilemma

Q. I am having a bit of a dilemma with my bettas. I put a male and a female in a 10-gallon aquarium to breed and the female nearly killed my best male! I couldn't understand this because the female was bursting with eggs. I put in another male who really proved who was master and they bred. The male built a nest about 5 inches in diameter, including some plant leaves. Now when I try to catch the female I almost ruin the nest. The pair don't seem to fight now, but what's going to happen later? Will the male kill the female or will they work it out until the fry are free-swimming? I have plenty of bushy plants floating around and a couple of sword plants. I am told that if the temperature is lowered the bettas will become lazy and not tend to fight. If I did this would it harm the development of the babies? The present temperature is 81°F.

Mike Fox, Detroit, Mich.

Spawning bettas



EVERGLADES

Find out from . . .

WHAT FINE TROPICAL FISH AND AQUARIUM PLANTS ARE

PET SHOPS AND AQUARIUMS

Write for our *Special Lists issued regularly*. Your name will then be placed on our Mailing List.

WHOLESALE ONLY!

"Everglades"
Aquatic Nurseries, Inc.
P. O. Box 587, Tampa, Fla. 33601

A. *When you put out a pair of fish to spawn, both must be ready, the male with his sperm and the female with her eggs. In your first attempt the female was ready and the male was not. In such a fix a frustrated female can become almost as nasty as a male. The second male was ready and was therefore accepted. Catching a female after spawning is a bit of a test of patience and perseverance. If you feel that you cannot, remember that the bubble-nest is no longer required once the fry can swim and take both parents out then; trouble is, the male is very nervous when guarding a nest and can mistake his well-meaning mate for an intruder.*

Gold to silver

Q. Can you help me? My goldfish has gone silver. I've fed him a number of things: daphnia, aquarium plants, lettuce, etc. Is he too old to stay gold? He's 10 inches long and very fat. Does he need to go on a diet? Is this natural?

Kathleen Pool, Newton, N.J.

A. *I've heard of countries going off the gold standard, but* fish! *There are color changes that take place in young fish, but a 10-inch fish usually holds its color. Probably he has become fat not only because he has gotten plenty of food, but because he does not get much exercise in his aquarium. Keep his water clean and fresh and do not feed him more than he can clean up in 5 minutes. Maybe he'll go back on the gold standard in time.*

Success with blue gouramis

Q. I have a pair of blue gouramis. Both are about 4 inches in length. They are the last survivors from a spawning I had two years ago, and have never been separated. Recently I decided to try for another generation. The pair was conditioned and put into a 10-gallon tank with an undergravel filter and water sprite for plants. To my surprise the male was not aggressive and allowed the

AQUARIUM PLANTS THRIVE

and so do fish. . . when you use Plantabbs Aquarium Plant Foods.

Plantabbs Aquarium Plant Foods, liquid or tablets, feed your aquarium plants to thriving, full bloomed beauty. Healthful to fish, too. Use 1 tablet to 5 gallons of water every 10 days or 1 capfull of liquid to 10 gallons of water every 15 days. Guaranteed safe!

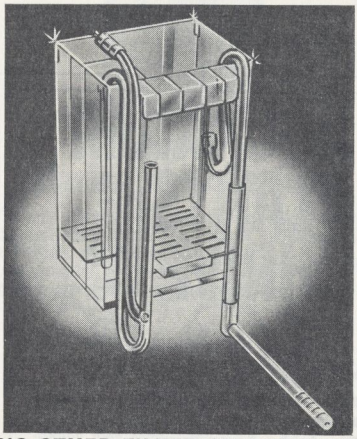
PLANTABBS®
AQUARIUM PLANT FOODS
Plantabbs Corp. • Baltimore 1, Maryland

Please Mention T. F. H. When Writing to Advertisers

Is Scattergood Too Good?

We are flattered to find that some apparently think so. They think our quality standards so high that few can afford us. Some believe our designs are so complex that few can understand them. One surprised us by referring to us as "the high and mighty." Some have darkly intimated that we might even be socialistic because we make filters that are enormously more efficient and don't wear out (you can always use an axe if you want to get rid of them) and activated carbon that lasts approximately a year instead of old-fashioned bone char and spun glass that require constant replacement.

We aren't really flattered by being so misinterpreted. We think our quality standards are just jim-dandy and that any changes should be upwards, not downwards. As for our design complexity — everything works . . . and so enormously more efficiently that hobbyists by the hundreds of thousands swear by us and not at us. And it makes us very moody to think of our being socialistic when our highest ambition is to be as capitalistic as possible, because we assure everyone that we—all just love that capital.



". . . the fifth complete filter I have ordered from you. I will use no other."
L.P.B., Livermore Falls, Me.

"Last July I purchased one of your (Filterkings) and I can honestly say it was the wisest purchase I have ever made. Nothing can even come close to comparing with it."
W.L., Cleveland, Ohio

"Your (Filterking) is the only one that really works."
R.L.G., M.D.
Falls Church, Va.

SCACO ACTIVATED CARBON
The wonder-working carbon that SCATTERGOOD filters are designed to use. Gives water so clear that the fish seem suspended in space. Enormously more effective than bone charcoal, as proved by laboratory tests.

NO OTHER FILTER OF ANY TYPE IS "JUST AS GOOD" AS A SCATTERGOOD DESIGNED AND MANUFACTURED ONLY BY SCATTERGOOD FILTERS CO.

• See our complete line at quality dealers everywhere

If there is no Scattergood dealer near you, write for free catalog and booklet "Getting the Most Out of Your Filter."

Scattergood Filters Co.

ESTABLISHED 1947 — MILLER 7, MISSOURI

female to help build the nest. Even after spawning, both fish cared for the eggs side by side. I thought this was unusual so for experimental purposes I left the pair in the tank for 48 hours after the fry had hatched. Neither parent made any attempt to eat their young. Two days after I removed the pair they regained their deep blue breeding color and began an act of "kissing" similar to that of the kissing gourami. I believe the actions of this pair is out of the ordinary. Do you have any comment on this? Can you explain their strange behavior?

Robert E. Steiner,
Jamaica, N.Y.

A. *The only comment I could make is that you did everything properly and used a pair of fish that were well acquainted with each other. Their behavior is not strange, merely a normal spawning by healthy fish under good conditions.*

Teo Way Yong & Sons

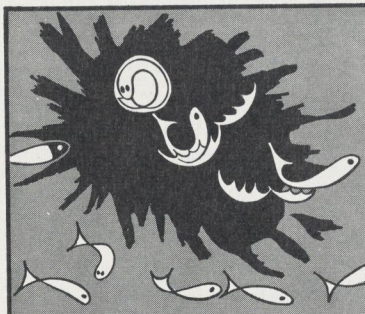
Importers & Exporters of Fancy Tropical Fishes, Wild Birds & Animals

Shipments to Any Part of the World

1063, Yio Chu Kang Road
Singapore 19

Cable Address:
"CATFISH" SINGAPORE

Please Mention T.F.H. When Writing to Advertisers



RECOMMENDED FOR ALL TYPES OF MARINE FISH

Wonder of the Sea **Marine Aquarium Mix**

SPECIAL OFFER
Marine Kit
Hydrometer, Ph Test Kit, 1.5 Oz. Buffer and 5# Wonder of the Sea Salt.
$9.95 (Prepaid)

- Developed, manufactured, and used by one of the largest importers of marine fish in the country.
- 5 lb. Bag $4.50 Prepaid anywhere in the United States. (Makes approx. 18 gal. Marine Water.)

Send cashier check or money order:

ADAMS TROPICAL FISH
2420 E. PACIFIC COAST HWY.
LONG BEACH, CALIF. 90813

Dealers and wholesalers inquire on your letterheads please.

Crossbreeding vs. inbreeding

I raise veiltail guppies and came up with something unusual. I took a male Hahnel guppy and crossbred it with a female blue delta guppy. The results were successful. In these broods there were about 35 babies. Some of the babies were white on the bottom and the rest of the body gray. I would appreciate it if you could answer these questions:

Q. 1. After each crossbreeding will the babies get smaller and not grow to a large size?

2. What should I feed them besides very fine dry food, frozen baby brine shrimp and frozen daphnia?

3. Do the baby guppies have to be sexed so the males will have large veiltails and lots of color?

Tim Verity, Palos Heights, Ill.

A. *Guppy babies are always white and gray and colors do not appear until later months.*

1. Crossbreeding will not make the fish smaller, but I think you mean inbreeding. Inbreeding for many generations will result in a smaller sized guppy.

2. Try not to feed extremely *fine food, as baby guppies will not eat it and the uneaten food will pollute the water. There is a great variety of frozen foods*

Please mention T.F.H.
when writing to advertisers

FANCY GUPPIES

Our Guppies are winning blue ribbons for their proud owners everywhere. Letters tell us that even the best of friends aren't telling where they bought their Guppies. All of our Guppies are tank raised indoors. Most colors available. $6.00 a pair; 2 pair for $11.00; $8.00 per trio, 2 trios for $15.00. Write for descriptive brochure. Special styrafoam insulated containers assure guaranteed live delivery by Air Mail. No C.O.D. please.

RAINBOW GUPPY AQUARIUM
P. O. Box 535 Leesburg, Florida

Please Mention T.F.H. When Writing to Advertisers

FIRST PRIZE WINNER AT THE INTERNATIONAL 1960 GUPPY SHOW, BERLIN, GERMANY

THE BRONZE DELIGHT

After more than 30 years of breeding exhibition guppies, Mr. Hartung now introduces his greatest achievement — the Bronze Delight with its large Veil-tail breeds true. They are a firm hybrid of golden and gray guppies. You may choose from Green, Leopard, Blue, Variegated or Blue-green tails. $14 per pair. ($5.00 extra for Trio).

HARTUNG GUPPY SPECIALIST

Other prize-winning varieties are: your choice of Red, Blue, Black, Dark Blue, Variegated — only $6.50 a pair. Albino Veils, $8 a pair. Beautiful Green Body and Veils $9 a pair. GUARANTEED Live Delivery — Postpaid. Send check or money order to WM. HARTUNG, 91-34 - 88th St., Woodhaven 21, N. Y. — VI 7-2538.

Behulve

Made in United States of America
Reprinted from COPEIA, 1965, No. 2, June 25
pp. 224–228

Reproductive Behavior of the Sacramento Perch, *Archoplites interruptus*

STEPHEN B. MATHEWS

Reproductive Behavior of the Sacramento Perch, *Archoplites interruptus*

STEPHEN B. MATHEWS

The reproductive behavior of *Archoplites interruptus* in natural situations and in captivity was observed during the spring of 1961 and 1962 to determine how it resembles that of other centrarchids. In most respects, *Archoplites* conforms to the normal centrarchid pattern of behavior. The male establishes a territory prior to spawning, the sexes are paired at spawning, sex recognition is accomplished largely by differential behavior, and the male alone guards the eggs. Unlike other centrarchids, the male does not make a nest. Rapid tail fanning of the sexually active male, which is a behavioral mechanism of other centrarchids normally associated with nest building or protection against egg siltation, was thought to serve mainly in sexual differentiation.

INTRODUCTION

THE reproductive behavior of the Sacramento perch, *Archoplites interruptus* (Girard), the only indigenous member of the Centrarchidae west of the Rocky Mountains, is of particular interest considering the very uniform pattern of reproductive behavior among most centrarchid species, as outlined by Breder (1936). The suggestion has been advanced that *Archoplites* is unique within the family in that the male does not guard the nest after spawning (Neale 1931, Murphy 1948). Lack of nest guarding, allowing predation on eggs by introduced species of fishes, was believed by these writers an important cause for the decline in numbers of this species in its native central California waters, which included the Sacramento–San Joaquin and the Salinas–Pajaro river systems, and Clear Lake, Lake County. Murphy (1948) reported aggregate spawning of *Archoplites* in Clear Lake, which is unlike the normal paired spawning of centrarchids.

The decline of *Archoplites* was noted by Jordan and Evermann (1896), and Rutter (1908) regarded it as rare. Very few *Archoplites* presently occupy the Sacramento–San Joaquin system, although Lockington (1879) wrote that they occurred there in "immense numbers." I know of only one recent occurrence, in 1963, in the Sacramento River (pers. comm. from Mr. Donald Stevens, California Department of Fish and Game). The present status of this species in the Salinas–Pajaro system is uncertain. Murphy (1948) found *Archoplites* uncommon in Clear Lake. Several ponds and man-made reservoirs within its native geographical range presently contain *Archoplites*, but these populations are apparently from artificial stocking.

I would like to thank my former fellow students at the University of California in Berkeley for their part in this study, Donald Seegrist, who introduced me to the Sacramento perch, and John Hopkirk, who took careful notes of spawning in the aquarium when I was not present. The late Dr. Paul R. Needham of the University of California reviewed the original manuscript.

METHODS

Field observations of reproductive behavior of *Archoplites* were made during the spring of 1961 and 1962 in Lake Anza, Tilden Regional Park, Contra Costa County, a 6- to 10-acre fluctuating reservoir, and in a 10-acre farmpond referred to herein as Kingfish Lake. This pond is 4.5 miles south of Manteca, San Joaquin County, and 200 yards west of the intersection of MacMillan and Hayes county roads.

Sacramento perch were introduced to Lake Anza in March 1953, after chemical treatment had removed unwanted fish populations. They are now abundant and reach a maximum total length of about 160 mm at a maximum age of about 6 years (Mathews 1962, unpublished master's thesis, University of California, Berkeley). Kingfish Lake, which had no fish, received a plant of 65 adult Sacramento perch from Lake Anza in May 1961. These fish spawned, and by the following spring all offspring were sexually mature and ranged in length from 95 to 125 mm.

In 1961 and 1962, adults were placed in a 20-gallon aquarium prior to spawning and observed. The tank was equipped with heater and aerator. Rocks, gravel, sand, and rooted vegetation covered the bottom. Daily

FRESHWATER FISHERIES
REPRINT No 99

THE RESPONSE OF TROUT TO TRANSLATION AND ROTATION OF THE VISUAL FIELD

Dr. D. H. A. Marr

Translation and rotation of the visual field were produced by displacement of linear vertically striped patterns formed of alternately arranged 1 inch wide black and white strips and by rotation of a similarly striped annulus around a vertical axis. In both cases the displacement speed was 12·6 cm./sec. The fish (trout parr 6·0 cm. long were used) was confined in a cradle so that pattern movement could be confined accurately to regions of the field of view. Translation and rotation of a pattern either in front of or on one side of the fish, both from head to tail and from tail to head, released a steering movement of the tail which if the fish had been free to move would have rotated the fish in the same sense as the angular direction of movement of the pattern as seen by the fish. However, translation and rotation of a pattern behind the fish released a steering movement of the tail which would have rotated the fish in the opposite sense to that of the angular direction of movement as observed by the fish. Movement in front of the fish always released a larger steering movement than did equivalent movement behind the fish.

Thus when a fish is exposed to rotation of a striped cylinder the stimuli produced by the movement in front of and behind the fish are antagonistic. It is suggested that trout are able to follow the moving cylinder because the stimulus produced by pattern movement in front of the fish is more effective in releasing a steering movement than is pattern movement behind the fish. However, when a fish is exposed to simultaneous translation of two linear patterns in the same direction the motor action released by the stimulus produced by movement in front of the fish supplements that released by the stimulus due to movement behind the fish since both stimuli release steering movements which turn the fish to face in the same direction as that of the movement of the patterns.

Reprinted from Rep. Challenger Society, 3, No. XVII, 1965

R. J. B.

Reprinted from

THE GALÁPAGOS

Proceedings of the Symposia of the

Galápagos International Scientific Project

Edited by **ROBERT I. BOWMAN**

UNIVERSITY OF CALIFORNIA PRESS

Berkeley and Los Angeles 1966

Richard N. Mariscal

20 The Symbiosis between Tropical Sea Anemones and Fishes: A Review

Abstract

The best-studied symbiosis involving sea anemones and fishes is that between anemones of the family Stoichactiidae and fishes of the family Pomacentridae (genus *Amphiprion*). This relation appears to be a mutualistic one wherein both partners may benefit from the association. The fish benefit in finding protection from predators among the tentacles of the anemone, eating food wastes cast out by the anemone and possibly by being cleaned of parasites as an incidental result of bathing among the tentacles.

Although not all workers agree, it has been suggested that the fish variously benefit the anemones by a kind of tactile stimulation or "massaging" behavior, by removing inorganic and organic debris from upon and around the anemone, by circulating fresh oxygenated and food-rich water over the anemones, parasite removal, protection from disturbances, and in some cases by carrying food particles to the anemone.

Although some *Amphiprion* species can interchange anemone hosts with impunity, others are apparently restricted to only one or a few species of anemones. The fishes are thought to recognize their anemones by a combination of visual and chemical stimuli. Territoriality is very well developed among the various species of *Amphiprion*. Many never venture more than a few inches from their hosts, while others are more far-ranging. Many of the fish are very aggressive toward any other fish (either of the same or different species) in the immediate vicinity of their home anemone. A number of differences have been noted in the behavior of the various *Amphiprion* species not only in regard to territoriality but also to flight and feeding behavior, aggressiveness, anemone preferences, and sound production.

A process of "acclimation" to a new anemone is undergone by some, and possibly all, species of *Amphiprion*, as well as at least one species of *Dascyllus*. This involves increasing the degree of contact with the anemone's tentacles while making a series of passes through them until nematocyst discharge is no longer provoked. This latter phenomenon is thought to occur due to physiological changes on the part of either the fish or the anemone. Some workers believe that during acclimation some kind of habituation toward the fish by the anemone is involved. A second theory holds that the mucus of the fish is or contains a protective substance and that this material may be increased or altered during the acclimation process. Once acclimation is complete, this substance presumably inhibits nematocyst discharge directly.

If a change on the part of the anemone is taking place, some sort of habituation to the chemical substance on the surface of the fish could be occurring during acclimation. This habituation might involve a raising of the threshold or inhibition of nematocyst discharge. This latter phenomenon could take place by either of two methods.

One involves a direct inhibition of the nematocyst-cnidoblast complex in situ in the tentacles by the chemical substances of the fish. These substances may act on the operculum or the cnidoblast surface directly during the acclimation process. The second idea postulates that anemones may be able to control their nematocyst discharge and that these organelles may not be independent effectors after all. This would involve a change in the receptor-effector system of the anemone so that the anemone itself would no longer discharge its nematocysts in response to the fish.

Introduction

Although the attention of zoologists has been attracted for many years to the extremely intimate relation which exists between certain members of the fish family Pomacentridae (genus *Amphiprion*) and the anemone families Stoichactiidae and Actiniidae, the underlying behavioral and physiological mechanisms are still quite poorly known. It will be the purpose of this paper to review the current literature concerning this phenomenon and to attempt some conclusions regarding these mechanisms.

Valentyn (1726) was apparently the first to describe an *Amphiprion*, but it remained for the English naturalist, Collingwood, while on a trip to the South China Sea in 1868, to make the first observations of the small, brightly colored fish living in association with a giant anemone.

It must be noted here that not only these initial accounts but also the majority of subsequent ones are the result of field or aquarium observations with a notable lack of controlled experimentation. The most interesting papers to date are those of Verwey (1930), Gohar (1948), Davenport and Norris

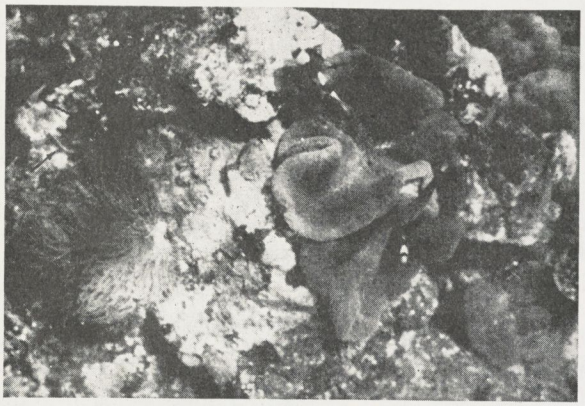


FIG. 1. *Radianthus* sp. (left) with two *Amphiprion perideraion* (above and left of anemone). Two *Amphiprion xanthurus* (right) in a *Stoichactis* sp. For scale, the *Amphiprion* at upper left of *Stoichactis* is about 5 in. long. Pongama Point, Arawa Bay, Bougainville Island, Sept. 10, 1963.

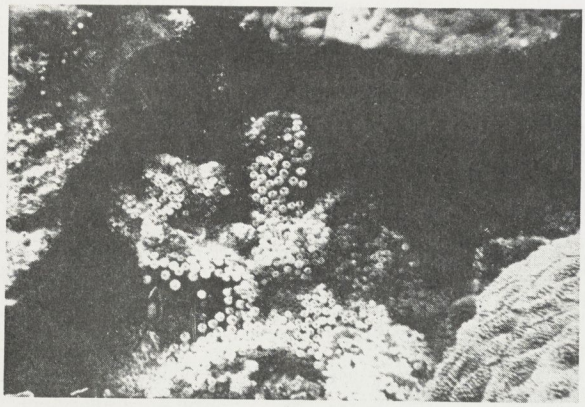


FIG. 2. *Amphiprion* with an aggregation of the crevice-dwelling anemone, *Physobrachia ramsayi*. Fish is at lower left of anemone. Astrolabe Reef, Vanikoro Island, Santa Cruz Islands (New Hebrides), Sept. 3, 1963.

(1958), Abel (1960*b*), Koenig (1960), Eibl-Eibesfeldt (1960), Blösch (1961), Davenport (1962*b*), Stevenson (1963), Graefe (1964), and Schneider (1964). Gudger has reviewed the published record up to 1947 while Mansuetti (1963) has similarly reviewed the reports of the relation between fishes and jellyfishes.

Since De Bary first introduced the term symbiosis in 1879, it has been used and misused repeatedly. "Symbiosis" is here used in De Bary's broad sense to indicate the living together, for better or for worse, of two phylogenetically unrelated organisms (see Allee, et al., 1949; Davenport, 1955; and Caullery, 1952). The several major subdivisions within this general term will be used here as they are recognized by present-day parasitologists (e.g., Noble and Noble, 1964) to indicate the specific nature of the relation. For example, commensalism is a symbiotic association which benefits one partner but not the other, while mutualism occurs when both symbionts are benefited. While a number of workers have termed the association reviewed here a commensal one, it seems more likely that it approaches mutualism, as will be seen below. Davenport (1955), Dales (1957), and Osche (1963) have recently reviewed the wide array of animal symbioses in general.

Although the taxonomic difficulties of the fish genus *Amphiprion* are now fairly well worked out thanks to Schultz and his co-workers (Schultz, 1953; Schultz et al., 1960), the anemones are a real problem even for the specialist. While Schultz recognizes 15 good species of *Amphiprion*, probably all of which associate with anemones, Carlgren (1949) lists roughly 25 species of anemones belonging to the family Stoichactiidae, with a number of these probably synonymous (Cadet Hand, Charles Cutress, personal communications). To these anemone-fish anemones can be added, among others, the actiniid, *Physobrachia* (Hand, in Ms).

THE ANEMONES

The anemones of the family Stoichactiidae are the real giants of the sea-anemone world, frequently attaining diameters of over 2 feet (Collingwood, 1868*a*, *b*; Saville-Kent, 1893; Mariscal, Ms) (fig. 1). They often show a preference for relatively shallow, protected reef areas either on the landward side of fringing and barrier reefs or on the shallow bottoms of lagoons or embayments, which may be strewn with dead coral. The stoichactiid anemones usually occur singly with their complement of fish, while a form such as *Physobrachia* is often found in large aggregations with one or two fish frequenting a number of anemones (fig. 2).

These anemones show an amazing range of coloration from yellow to bright blue with a wide spectral display in between (Collingwod, 1868*a*, *b*; Saville-Kent, 1893, 1897; Yonge, 1930; Stephenson, 1946).

It may seem unnecessary to consider seriously the question of whether or not stoichactiid-type anemones have nematocysts. However, Caspers (1939), in the only general histological study of *Stoichactis* in the literature reported that only spirocysts were present. He obviously misidentified the extremely common basitrichs, as Gudger (1947) points out, because a number of taxonomic studies since that time (e.g., Carlgren 1940, 1950) plus my personal observations leave no doubt as to their presence.

Other authors have doubted that the nematocysts were capable of capturing fish or other prey (Buhk, 1939). However, Mitchell-Hedges (1937) and Gudger (1941) find that some anemones are fully capable of capturing fish in the wild, while Eibl-Eibesfeldt (1960) reports the same for stoichactiid anemones. Gohar (1934, 1948) and Herre (1936) report fish capture by stoichactiids in aquaria, as does Koenig (1960). That the anemones are generally capable of such fish-capturing behavior seems no longer open to question; whether or not this represents a substantial part of their normal feeding behavior remains to be seen.

THE FISHES

Preference for Specific Anemones.—A number of authors, beginning with Saville-Kent in 1893, have described the various degrees of specificity and strength of attachment of anemone fishes to their hosts. This ranges from *Premnas biaculeatus*, apparently inhabiting only one anemone species, to *Amphiprion xanthurus*, which has been found in a number of different anemones the world over (Verwey, 1930; Eibl-Eibesfeldt, 1960; Mariscal, Ms). In many cases, fish brought into the aquarium can also be persuaded to accept other anemones (e.g., Verwey, 1930; Coates, 1964). Verwey, Hackinger (1959), Oesman (1961), and Graefe (1963, 1964) also find that the young of certain species of *Amphiprion* may be found in species of anemones never inhabited by the adults. The restriction of an *Amphiprion* species to a given anemone is very real in some instances, with one species being stung and killed if it enters other anemones, while other species can enter different anemones with impunity (Verwey, 1930; Gohar, 1948; Eibl-Eibesfeldt, 1960; Oesman, 1961). Furthermore, some fish make no attempt to enter some foreign stoichactiids which experiments show to be lethal (Eibl-Eibesfeldt, 1960).

Regarding the physical factors which might influence this preference, Verwey (1930), Herre (1936), and Koenig (1960) all believe that ecological factors, such as amount of silt, light, food, water movement, etc. may be important in the case of a relatively nonspecific fish–anemone association. That this is certainly not the whole answer is indicated by the behavior of *Premnas biaculeatus*, which apparently accepts only one species of anemone, whether in the wild or an aquarium. Sluiter (1888) and Verwey (1930) have looked for a relation between tentacle length and size of the fish; in general, larger fish prefer anemones with longer tentacles. However, Verwey observed, as has the author, that this relation does not always hold, especially for a form such as *Amphiprion xanthurus*. Therefore Verwey decided that not only ecological factors, but also the ratio of tentacle length to anemone diameter must be considered, and that shorter tentacles might be offset by a larger overall diameter of the anemone itself. However, he presents no quantitative data to support this view.

Recognition of Anemones by Fishes.—Gohar (1948) reports that upon releasing a fish back into an aquarium it will find its anemone immediately, even if the latter is badly contracted. In the absence of controls, observations of this sort mean little. Gohar implies, however, that visual stimuli are involved here, since, in the absence of its own host, the fish prefer anemones of a similar color. Verwey (1930) reports that, although the preferred anemone looked more like a different species due to its contracted state, a *Premnas* immediately recognized it and swam up to it. From several experiments of this nature, Verwey concluded that "optical stimuli gave the first reaction, after which chemical stimuli settled the question." Koenig (1960) states that reef fish normally living near anemones respond negatively to the image of numerous tentacles, while pelagic fishes show no recognition or fear of anemones and soon become their prey. Herre (1936) states that the fish can recognize their own anemones even when contracted, but gives no clue regarding how this is done. Davenport and Norris (1958) also have experimentally demonstrated the importance of visual versus chemical clues to the fish in anemone recognition.

Territoriality.—Horst (1903) was probably the first to record the extreme aggressiveness of some members of the *Amphiprion* complex (enough to distract several people from their collecting duties). Gohar (1934) records how *A. bicinctus* would attack anything placed in its aquarium (even fish half again its own size), and Verwey (1930) describes how *Premnas* and *A. ephippium* "may swim at the intruder and bite at his legs and shoes." Eibl-Eibesfeldt (1960) has described the fighting behavior of *A. percula* and *A. akallopisos*, while more recently Schneider (1964) has done the same for *A. xanthurus* and *A. polymnus*.

Following the usual definition of territory as merely a defended area (see Odum and Odum, 1959), there then seems to be little question that the above behavior represents territoriality and, in fact, has been so interpreted by numerous observers including Verwey (1930), Moser (1931), Herre (1936), Ladiges (1939), Gohar (1948), Koenig (1960), Eibl-Eibesfeldt (1960), Oesman (1961), Schneider (1964), and myself. Usually a mated pair occupies any one anemone or group of anemones with the young either being driven off or eaten upon the completion of their planktonic larval life. One notable exception to this is *Amphiprion percula*, seven or more of which may be found inhabiting a single anemone. Here too, however, territories are maintained in the single anemone with a kind of equilibrium set up between fish that are trying to drive others off and those that persist in remaining (Verwey, 1930).

I observed in Arawa Bay, Bougainville, an interesting case of territoriality consisting of three *Amphiprion xanthurus* and four young *Dascyllus trimaculatus* all inhabiting the same anemone, although in separate halves (fig. 3). An uneasy truce was apparently in effect since an attempt by one of the *Dascyllus* to encroach on the opposite half of the anemone would elicit displays and aggressive behavior on the part of the *Amphiprion* (fig. 4), while on the other hand, the *Dascyllus* did not yield easily. The *Dascyllus* occasionally contacted the tentacles with their fins and were apparently acclimated to the anemone in this case.

Adult fish not only drive off members of the same species, regardless of sex, but also members of other species. Verwey (1930) reports that these battles may go to the death between two adult *Premnas* of the same sex if brought together in the same aquarium, even without an anemone. On the other hand, Eibl-Eibesfeldt (1960) states that *A. percula* of the

FIG. 3. *Amphiprion xanthurus* (left) and *Dascyllus trimaculatus* (right) showing the segregation to different halves of a single *Stoichactis* sp. Takanupe Island in Arawa Bay off Bougainville Island, Sept. 10, 1963.

FIG. 4. Territorial encounter between *Amphiprion xanthurus* and *Dascyllus trimaculatus*, both inhabiting different halves of the same *Stoichactis* sp. *Amphiprion* at right pursuing lowermost *Dascyllus*. Takanupe Island in Arawa Bay off Bougainville Island, Sept. 10, 1963.

same sex remain quite friendly and school together until an anemone is introduced, and then the battle begins. During these encounters or under conditions of extreme stress, several species produce distinct sounds (Verwey, 1930; Koenig, 1960; Eibl-Eibesfeldt, 1960; Schneider, 1964). The last author has studied this in detail and finds that he can break the sounds down both electronically and behaviorally into three distinct types, all of which are probably important in the wild in maintaining territories. An incidental by-product of this territorial defense is that the anemone may be "protected" from predators and other disturbances in the field.

Species–Specific Behavior.—Although basically similar in habits and life history, several species of *Amphiprion* show marked differences in their behavior. For example, Sluiter (1888) and Ladiges (1939) have both commented that *A. percula* will always be found within a few inches of its anemone while forms like *A. xanthurus* or *Premnas biaculeatus* are much more far-ranging. Ladiges (1939), Verwey (1930), Oesman (1961) and I (Ms) have all noted species-specific differences in flight behavior also. For example, *A. percula*, *A. akallopisos*, and *A. perideraion* (all fairly small, retiring, weak swimmers) in case of danger generally dive into the anemone's tentacles, while *P. biaculeatus*, *A. ephippium*, *A. melanopus*, and *A. xanthurus* (all larger and stronger swimmers) flee from their anemones when frightened. Verwey (1930) also found that only two out of the five species of fish he studied produced audible sound. Eibl-Eibesfeldt (1960) and Schneider (1964) also describe differences in fighting behavior among the various species of *Amphiprion* they studied.

Additional Anemone Symbionts.—Not only do more than one species of *Amphiprion* occasionally inhabit a single anemone (Verwey, 1930; Oesman, 1961; Mariscal, Ms), but other pomacentrids may also be found in and around anemones. The most ubiquitous of these are the young of *Dascyllus trimaculatus* (see above), (Gohar, 1948; Harry, 1953; Müller, 1957; Koenig, 1958, 1960; Eibl-Eibesfeldt, 1960; Graefe, 1964; Mariscal, Ms). Luther (1958), Hackinger (1959), Abel (1960*a*, *b*), and Graefe (1963, 1964) also list other fish symbionts, especially from the Red Sea. Stevenson (1963) has found *Dascyllus albisella* closely associated with the actiniid anemone *Macranthea* (*Marcanthia*) *cookei* in Hawaii. In the case of some *D. trimaculatus*, at least, the association can be a bit hazardous since upon contact with the anemone's tentacles, it may be fatally stung (Müller, 1957; Eibl-Eibesfeldt, 1960).

Saville-Kent (1893, 1897), Yonge (1930), Whitley (1932) and I (unpublished manuscript) have all observed the crustacean symbionts occasionally found with the Pacific giant anemones. Yonge calls the shrimp *Periclimenes brevicarpalis*, but does not identify the crab. Interestingly enough the crab, and especially the shrimp, are not only roughly the same color but have the same sort of banding pattern on their bodies as do a number of the *Amphiprion* species (e.g., *A. percula*). On an isolated coral boulder off New Britain, I discovered a small *Stoichactis*, which besides having two different species of *Amphiprion* (*perideraion* and two young *percula*), also contained a crab, apparently the same as Saville-Kent's Barrier Reef form, and a number of small shrimp (over ten), also similar to Saville-Kent's. Nothing is known regarding the behavioral interactions of the above fishes, crustaceans, and anemones. However, Davenport (1962*b*) has studied experimentally the relation of the crab, *Hyas arancus* and the anemone, *Tealia felina*.

NATURE OF THE SYMBIOSIS

Benefit to the Fish.—The major benefit provided by the anemone would appear to be protection against predators, and indeed, evidence is available indicating this to be the case. Sluiter (1888) found that

specimens of *Amphiprion percula* were unharmed in aquaria containing large predatory fish so long as the anemones were present. Upon removal of the anemones, however, the anemone fish were pursued and eaten. Verwey (1930), Coates (1964) and Eibl-Eibesfeldt (1960) give similar observations, the latter in the natural reef environment. In this connection, Coates (1964) has made the remarkable observation in the New York Aquarium that shortly after the introduction of some voracious lion-fish, the anemone fish moved several of their anemones up onto a thin projecting gorgonian stalk as well as the sides of the aquarium, presumably to provide themselves with a wider range of refuges from the attacks of the lion-fish! When an anemone was to be moved, 5 or 6 *A. percula* would gently nudge the anemone's pedal disc until it released its grip (requiring up to 30 minutes). Then each fish would take a tentacle in its mouth and together carry the anemone to the new site, where it was held in place until it reattached. Aside from any purposive implications, this is an astonishing bit of concerted behavior and is more reminiscent of some marine mammals than fishes.

However, Montilla (personal communication to Davenport and Norris, 1958) has observed free-living anemone fish in the wild, while Moser (1931) believes that the fish never seek protection in the anemone, but rather that they "protect" the anemone from its enemies. Gohar (1948), among others, has refuted the latter view, and the evidence favors the idea that anemone fish do generally find protection in the vicinity of their anemones. Furthermore, the fish are known to return to the anemone's tentacles at night, where they sleep until daybreak, implying again a protective function for the anemone. Koenig (1960) adds that the fish become much lighter in color at night when in the anemone, with any black coloration almost disappearing; while fish without anemones do not show this change. Townsend (1929) has also commented on this color change in other fishes, although the function is not clear.

The eggs of *Amphiprion percula*, at least, are "immune" to *Stoichactis* nematocysts. De Crespigny's (1869) and Moser's (1931) idea that the eggs gain protection by being laid on the anemone's disc has never been substantiated, with all observations indicating they are laid on hard substrate in the vicinity of the anemone (Verwey, 1930; Gohar, 1948; Garnaud, 1951; Davenport and Norris, 1958; Oesman, 1961; Springmann, 1963).

It is interesting that Saville-Kent (1893), Weber (1913), and Herre (1936) have stated that the anemone fish actually seek shelter in the coelenteron of their hosts, but other investigators, specifically looking for this behavior, have not observed it (Whitley, 1927, 1929, 1932; Verwey, 1930; Gohar, 1934, 1948).

Many observers have noted *Amphiprion* species eating waste material and leftovers from the host's meals (Sluiter, 1888; Yonge, 1930; Verwey, 1930; Moser, 1931; Gohar, 1934; Koenig, 1960). Gohar (1948) even describes a fish cleaning out the coelenteron after the anemone has digested a large meal, while devouring choice tidbits in the process. Verwey also believed that the fish obtained nutrition from eating tentacles and/or mucus. This will be discussed later.

De Crespigny (1869) suggested that the fish's constant nestling in among the tentacles of its anemone might be effective in removing ectoparasites from the fish.

Benefit to the Anemone.—Saville-Kent (1893) suggested that the *Amphiprion* acted as lures to draw prey fish into the anemone's tentacles. However, Gohar (1948), Eibl-Eibesfeldt (1960), and Abel (1960*a*) disagree with this. Not only has such behavior never been observed but Abel makes the pertinent point that there are many other reef fish which are even more brightly colored and presumably conspicuous (at least to human eyes).

A further possibility exists that the striking bands and colors of some anemone fish may be a kind of warning coloration for potential predators. Here, however, the coloration presumably would be directed toward advertisement of the anemone's unpleasant qualities rather than any distastefulness of the fish, since, as mentioned earlier, the fish are often readily eaten in the absence of an anemone. Another possibility worth investigating is that of territory advertisement, both intra- and interspecifically among the various species of anemone fish which may inhabit the same general reef area. Thus, aggressiveness, sound production, and strong visual stimulation (i.e., color and/or banding) may all be involved in territory maintenance. Finally, in some cases, the bands may serve to break up the outline of the fish and help to conceal it, while the color of other *Amphiprion* species (e.g., *perideraion* and *akallopisos*) may be quite similar to the color of the anemone's tentacles, thereby making the fish inconspicuous.

A number of workers have made the interesting observation that anemones "pine away" and even die when separated from their resident fish. This is supposedly due to the lack of "massaging" or "treating" of the anemones by the fish (De Crespigny, 1869; Verwey, 1930; Herre, 1936; Gohar, 1948; Koenig, 1960). For example, Gohar, Verwey, and Herre mention how badly contracted anemones will expand almost immediately upon being touched by their fish. Interestingly enough, anemones which form the closest bonds with their fish seem to "suffer" the most without them (e.g., Verwey: *Amphiprion ephippium* and *Premnas biaculeatus*). The reverse may be partially true also in that *P. biaculeatus*, if deprived of its anemone will accept no other, as well as taking the longest time to adapt to a free-swimming existence in the aquarium.

However, the above seems questionable when one considers that not all anemones are affected adversely by the removal of their fish, and some species which are commonly found with fish symbionts have been reported to exist in the wild without fish (see Saville-Kent, 1893, 1897).

Finally, though some anemones are supposedly affected by loss of their fish, others reportedly are affected by having too many fish; Coates (1964) notes that if too many fish seek refuge in too few anemones, "the anemones seem to give up and die." However, there is no experimental evidence to indicate that the anemones are ever adversely affected, either with too many or too few fish.

Although Gohar (1948) contradicts the findings of Verwey (1930), Moser (1931), and Eibl-Eibesfeldt (1960) when he comes to the conclusion that the fish do not remove inorganic debris from on and around the anemone, the above authors, as well as Koenig (1960), all agree that the fish do remove organic wastes from the anemone. De Crespigny (1869) and Verwey also have postulated that the fish remove necrotic tissue as well as anemone parasites, the former behavior having been observed by Eibl-Eibesfeldt in the field.

Verwey (1930) notes also that *Premnas* dug out and enlarged a hole in the coral rubble around its crevice-dwelling anemone.

De Crespigny (1869), Sluiter (1888), Verwey (1930), and Herre (1936) all believe that the fish may be influential in circulating oxygenated water as well as food particles over the anemone. This, however, would seem to be of minor importance in the normal reef environment.

Although Moser (1931) and Eibl-Eibesfeldt (1960) believe that anemones are only "fed" by their fish accidentally in the course of other activities, the remarkable taking of food to the anemone host by the associated fish has been observed in the aquarium by too many authors to doubt that it occurs (Sluiter, 1888; Verwey, 1930; Herre, 1936; Ladiges, 1939; and Koenig, 1960). I have also observed this behavior in the aquarium at Green Island on the Great Barrier Reef, Australia, and Graefe (1964) has observed it in field experiments. The most striking behavior along these lines has been recorded by Gohar (1934, 1948), who observed that when live sardines (*Atherina*), which were larger than the resident *Amphiprion bicinctus*, were placed in the aquarium, they were immediately attacked by the anemone fish and forced into the tentacles of the anemone until subdued by the nematocysts, whereupon the anemone fish dragged the *Atherina* back to the anemone, which proceeded to ingest the prey. The anemone fish then picked the bones of the *Atherina* after they were egested by the anemone.

Although Abel (1960*a*) does not believe that *Amphiprion bicinctus* normally takes food to its anemone in the field, Graefe (1964) describes how small pieces of food fed to *A. bicinctus* in the field were eaten by the fish, and large chunks were taken to the anemone and pushed into the tentacles. However, Graefe, like Abel, does not believe that this is a common natural occurrence, since such large particles were never seen in the underwater environment. However, not all anemone fish are known to take food to their anemones, even in aquaria. For example, Verwey (1930) reports that *Premnas* "feeds" its anemone very little, *A. ephippium* even less, and *A. percula* and *A. akallopisos* not at all. Croll (personal communication) has confirmed this for *A. percula* in the Green Island Aquarium, although other species there do take food to their anemones. In any case, the above behavior probably would not play a very great role in the normal nutrition of the anemone. Graefe's interesting observations (1964) that specimens of *A. bicinctus* closely associated with an anemone took food to the anemone when fed, but that other *A. bicinctus*, which spent a good deal of time in a hole in the coral near their anemone, "fed" the hole when presented with food should put the whole idea of "feeding" behavior in the proper perspective; that is, it simply represents a return of food to the home territory of the fish.

It must be remembered that many, if not all, of the giant anemones also maintain a symbiotic relation with unicellular algae, in addition to the symbiotic association with their fish. The role of the zooxanthellae in the nutrition of these anemones has never been investigated, but Muscatine and Hand (1958) have found a transfer of material from the contained algae to the tissues of a California anemone (*Anthopleura*), while Muscatine and Lenhoff (1963) find a similar situation in a hydra. For the hydra (*Chlorohydra viridissima*), Muscatine (1963) finds the transferred material to be largely carbohydrates, especially glucose. It is interesting to note in passing that some of the largest invertebrates in the tropics—corals, the stoichactiid anemones, and tridacnid clams—all contain symbiotic algae (see Yonge, 1957, for discussion of latter). It may turn out that the zooxanthellae are intimately involved in the nutrition of the giant anemones also.

Finally, the existence of so much surface area exposed to the surrounding medium in the form of the enlarged oral disc-column complex leads one to suspect that filter feeding may also be involved in the nutrition of the anemones.

NATURE OF THE PROTECTION ENJOYED BY THE FISH

Acclimation of Fish to New Anemones.—Although probably not aware of it at the time, Whitley (1932), in his rough acclimatization experiments performed in the field on the Great Barrier Reef was apparently the first to observe this phenomenon. Gohar (1948), however, was the first to recognize that anemone fish "may develop partnership with such anemones as *Discosoma giganteum* by cautiously approaching it," and that "the association is complete in one to a few days." Since then Davenport and Norris (1958) have furnished us with the most detailed study of this phenomenon, while Koenig (1960), Oesman (1961), and Graefe (1963, 1964) have also observed it. Stevenson (1963) has recently described the first case of acclimation behavior between an anemone (*Macranthea*) and a fish other than an *Amphiprion*-type pomacentrid. In *Amphiprion*, acclimation involves a

number of cautious approaches to the strange anemone while at the same time gently touching some part of the body to the tentacles, as well as mouthing or nibbling the latter. Gradually the amount of clinging by the tentacles diminishes, while the degree of penetration by the fish increases. Finally, with a series of violent rushes the process is complete and the fish takes up residence in the anemone. The whole process is complete after 1 hour, on the average (Davenport and Norris, 1958).

Stevenson (1963), in his studies of *Dascyllus albisella*, finds that the initial acclimation behavior is similar to *Amphiprion*, but that the first contacts with the tentacles were due to the fish coming to a halt and then backing tailfirst into them, while *Amphiprion* first made contact during a series of distinctive passes just above the anemone's disc. The possibly significant nipping of tentacles (see section on Nematocyst Inhibition) was also performed by *Dascyllus*. Contrary to the frantic dashing about which characterized the end of the acclimation process for *Amphiprion*, Stevenson found that *Dascyllus* tended to cease all motor activity except respiration for periods up to 30 seconds, followed by "finning" in one spot among the tentacles. The time of acclimation was also much shorter for *Dascyllus*, ranging from 5 to 11 minutes. Stevenson also reports what appears to be a kind of acclimation to *Dascyllus*' more common coral-head host. This involved a rapid rushing about among the branches in addition to a "picking" or nibbling of the coral surface. The time of acclimation here was on the order of 4 to 7 minutes.

Protection Through Changes on the Part of the Fish.—Mucus itself is a well-known protective mechanism among fishes. Jakowska (1963) states that "Fish, covered by a mucus-secreting integument respond to a variety of environmental and pathogenic agents by altering the nature as well as the quantity of their mucous secretions." Luther (1958) suggests that the association between *Blennius* and the fire coral, *Millepora*, in the Red Sea is made possible by the fish's mucus. *Blennius* is known locally as *"Schleimfisch."* Along the same lines, Davenport and Norris (1958) have made the suggestion that for *Amphiprion percula*, "acclimation may be related to changes in the mucus coat of the fish." For example, some of their experiments have demonstrated that skinless *Amphiprion percula* flesh is devoured by *Stoichactis*, while flesh with skin attached is rejected. Furthermore, when pieces of *Amphiprion* and *Fundulus* (control fish) flesh are placed side by side on the anemone's disc with the skin side down, the *Fundulus* portion is ingested while the *Amphiprion* piece is worked slowly off the disc and discarded. These and other experiments demonstrate the presence of some sort of specific chemical factor on the surface of the anemone fish.

Based on his underwater field studies, Eibl-Eibesfeldt (1960) also believes that the *Amphiprion* species he studied are protected through a special substance on their bodies. Abel (1960*b*), although studying a different fish-anemone relation, finds that the mucus is the decisive factor in protecting his fish, (*Gobius*), but finds no evidence of acclimation behavior.

Protection on the Part of the Anemone.—A storm of controversy has swirled around this subject since Gohar (1948) made the suggestion that the anemones recognize their fish partners by their "mode of movement." Gohar was led to this conclusion by the fact that anemones seemed to recognize only their own immediate symbionts and that other individuals of even the same species might be stung and eaten. Hackinger (1959) and Koenig (1960) agree with Gohar on the importance of individual recognition of the fish through its behavior.

De Crespigny (1869), Verwey (1930), Moser (1931), Herre (1936), Eibl-Eibesfeldt (1960), Abel (1960*a*) and Stevenson (1963) have all indicated that chemical recognition of the fish by the anemone may be taking place. Koenig (1960) gives further evidence of some sort of recognition in his confirmation of Verwey (1930), Herre (1936), and Gohar (1948) regarding the almost unbelievable positive response of an anemone to a freshly introduced anemone fish: *Man muss gesehen haben, wie intensiv sich Fische, die lange alleine waren, in die Aktinie kuscheln, und wie aktiv eine bisher isoliert gehaltene Aktinie die Fische "umschlingt."* Stevenson (1963) likewise mentions both aquarium and field behavior of *Dascyllus* which corresponds quite closely to Koenig's observations:

> Fish that lay quietly among the tentacles were often rocked back and forth by the action of the tentacles which actively curled around them. At other times when fish were immobile or were finning in one spot, individual tentacles curled around and apparently touched the fish with their tips. The contact evoked an immediate response from the tentacles which withdrew by contracting and swinging away from the fish. This action strongly suggested the presence of an agent that definitely repelled them.

Koenig further mentions how sick or weakened anemones which do not respond actively enough are given up by the fish, just as are weak or sick fish (i.e., inactive) eaten by the anemone (see also Gohar, 1948; Oesman, 1961). However, the experiments of Davenport and Norris (1958) and Eibl-Eibesfeldt (1960) contradict these findings and negate the importance of behavior or "mode of movement" per se in protecting the fish. They found that not only whole dead *Amphiprion*, but even isolated pieces of intact *Amphiprion* skin caused no general nematocyst discharge when these objects were dragged across or placed on the anemone's disc.

Koenig (1960) and Blösch (1961) have both made the extremely interesting observation that anemones which have been separated from any contact with anemone fish for long periods of time will always sting

these fish upon first contact. Koenig further states that because of this no fish will swim into a foreign anemone without first going through an acclimation procedure, and that all anemones in the vicinity of the fish's "home" anemone are so treated. On the other hand, Blösch finds that if the anemone had been living with any anemone fish just prior to the experiments, or if only the fish had been separated from the anemone for long periods of time, they were not stung.

If one performs the simple experiment of adding new fish from one *Stoichactis* to another anemone of the same species from which the symbionts have just been removed, it is observed that the new fish settle into the tentacles of the new anemone without being stung (fig. 5). Although this might be explained by saying that the anemone still remained acclimated to its prior symbionts, one could just as easily say that the fish still retained some sort of protective substance on their surfaces. Thus, isolation experiments will be essential in future attempts to assess the respective roles of the anemones and fishes.

Graefe (1963, 1964) has also found a similar situation in his studies of young *Amphiprion bicinctus* living in the anemone *Radianthus* (=*Antheopsis*) *koseirensis*. Here, however, Graefe found that if the fish were isolated from their own anemone for 1 hr or more they were stung upon reintroduction and had to go through a brief acclimation period of several minutes. In addition, it was found that *Radianthus* which had contained only very small *A. bicinctus* until the time of the experiment, stung large fish of the same species which came from another *Radianthus* of the same size. However, anemone fish of the same or smaller size were not stung in a new anemone. There is also an upper limit to the size of fish tolerated in that adult *A. bicinctus* are never found in *Radianthus*. This has led Graefe to the idea that *A. bicinctus* is not protected from *Radianthus* by any chemical substance on the fish's surface, but that the anemone "recognizes" the resident fish by means of its size and consequent degree of tactile stimulation of the tentacles and oral disc. Thus, the nematocyst discharge which is provoked by a large *A. bicinctus* is due to the increased mechanical contact of the fish's body surface against the nematocysts in the enveloping tentacles of the contracted oral disc. However, *Stoichactis* will tolerate *A. bicinctus* of all sizes. Graefe felt that this was due to the seemingly reduced responsiveness of *Stoichactis* to mechanical stimulation as compared with *Radianthus*. Although the above results are quite interesting, they still do not completely eliminate the possibility that some chemical factor may be present on the surface of *A. bicinctus*, and more direct experiments such as the type performed by Davenport and Norris are needed in order to completely evaluate the *A. bicinctus* relation.

Immunity to Toxins of Nematocysts.—Although no physiological studies of possible immunity have been conducted to date on *Amphiprion* or other fish inhabiting anemones, a number of observers including

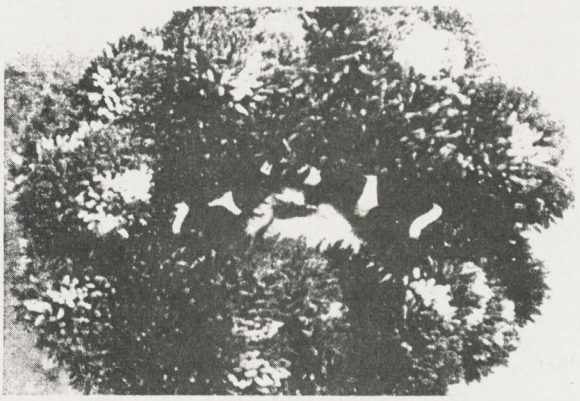


FIG. 5. Two *Amphiprion percula* from another anemone which have just been released into a new *Stoichactis* with no apparent adverse effect. Three other *A. percula* and one crab were inhabiting this anemone just before the new replacements. Pongama Point, Arawa Bay, Bougainville Island, Sept. 10, 1963.

Verwey (1930), Gohar (1934), Herre (1936), Eibl-Eibesfeldt (1960), Koenig (1960), Oesman (1960), and Stevenson (1963) have observed the nibbling of tentacles by the fish. Based largely on Cantacuzene's (1925) experiments with hermit crabs and anemones, Verwey suggested that the tentacle nibbling may be involved in providing immunity to the host's nematocyst toxins. However, Verwey's own isolation experiments, as well as the more recent observations of Koenig (1960), Blösch (1961), and Graefe (1963, 1964), that fish already living in anemones will still be stung by either the same (after a short period of separation) or different previously isolated anemones, suggests that either no immunity is present, or if present, it is not always adequate protection. Also, Blösch (1961) finds that an anemone may still kill its *Amphiprion* if nematocyst discharge is provoked by a non-acclimated organism.

In the well-known *Physalia-Nomeus* relation, Zahl (1952) likewise does not believe that the fish, *Nomeus*, is immune to the toxin of *Physalia* nematocysts since the fish were stung and killed when in contact with the *Physalia* tentacles as the two were netted. He also did not find any tentacle remains in the stomach of *Nomeus*. On the other hand, Lane (1960), has found *Physalia* nematocyst remains in the stomach of *Nomeus* and finds further that *Nomeus* can survive injected doses of toxin up to 10 times that required to kill other similar-sized fish. The general consensus, then, is that *Nomeus* (as well as other fish symbionts of jellyfish) (see Mansuetti, 1963), manages to maintain its rather precarious relation with *Physalia* by skillful avoidance of the host's tentacles. Since contacts are inevitable, the immunity acquired, presumably by eating the host's tentacles, is generally sufficient to overcome the effects of casual stingings. However, massive tentacle contact (while being netted, for example) will generally negate this immunity and cause death.

DISCUSSION OF PROTECTIVE MECHANISMS

Thus, we have two general hypotheses regarding the protective mechanisms of anemone fish: one centers on the fish's surface (mucous) coating (e.g., Davenport and Norris, 1958; Eibl-Eibesfeldt, 1960; Abel, 1960*b*); the other places the responsibility on the anemone (e.g., Gohar, 1948; Koenig, 1960; Blösch, 1961; Graefe, 1963, 1964).

If one postulates that the mucous on the surface of the fish is involved, two possibilities are apparent: (1) the mucus might contain very little or no surface-active agents or other factors which are known to provoke nematocyst discharge (e.g., see Pantin, 1942*b*, and Yanagita, 1960*b*), as Graefe (1963, 1964), has suggested, or (2) it might contain some substance which inhibited nematocyst discharge (Davenport and Norris, 1958; Eibl-Eibesfeldt, 1960; and Abel, 1960*b*). Considering the lack of an acclimation reaction between *Gobius* and *Anemonia*, Abel's work demonstrates that the mucus is or contains a protective substance which is responsible for inhibiting nematocyst discharge. Davenport and Norris, as well as Eibl-Eibesfeldt, do not consider the fish to lack adequate stimuli for nematocyst discharge, but rather find that the idea of an inhibitory substance is more in keeping with their experimental results. But since neither Davenport and Norris nor Eibl-Eibesfeldt used previously isolated anemones, their experiments still do not conclusively rule out the notion that some sort of change may also be occurring on the part of the anemone during the acclimation process. On the other hand, Blösch's and Koenig's anemone isolation experiments still do not explain satisfactorily such observations as Gohar's (1948) and Davenport and Norris' (1958) in which an anemone not previously isolated from anemone fish was still capable of stinging other fish of the same species which approached it. Perhaps Graefe's (1963, 1964) work concerning a size factor may be pertinent to the above.

Thus, we have the following possibilities concerning the symbiotic relation between the species of *Amphiprion* (and possibly *Dascyllus*) and their anemones:

1. Some sort of chemical factor is present in the mucus of anemone fish. This factor is probably specific for only one to several species of anemones because of either its chemical nature or relative concentration or both. One possibility is that the acclimation process may involve a habituation (defined here after Thorpe, 1963: the relatively permanent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement) on the part of the anemone to the chemical factor present on the skin of the fish because of the repeated contact between the fish and the tentacles. This habituation might involve a raising of the threshold or inhibition of nematocyst discharge. This could occur in either of two ways: (*a*) a direct inhibition of the nematocyst-cnidoblast (nematocyte?) complex in situ on the tentacles by the fish mucus substance or (*b*) a change in the anemone's receptor-effector system in such a way that the anemone no longer discharged its nematocysts in response to a stimulus from the anemone fish. That this inhibition is not complete and may be overcome by a sufficient stimulus is evidenced by Blösch's (1961) observations that contact of the anemone with the finger of the observer may cause a general nematocyst discharge which is capable of killing the resident *Amphiprion*. Furthermore, as Koenig (1960) has indicated, an important part of not only initiating but also maintaining this symbiosis may be the nibbling of the host's tentacles, as well as the general activity of the fish among them. Interestingly enough, various workers have noted this nibbling behavior by crabs which also associate with anemones (e.g., Davenport, 1962*b*, for the crab *Hyas* and the anemone *Tealia*).

2. Response to a size factor, as postulated by Graefe, may be involved.

3. As suggested by Davenport and Norris, a change may be taking place on the surface of the fish, presumably in the mucous secretion.

4. Nibbling of the tentacles may be a means of ingesting some sort of "anemone factor" which either alters the chemical nature of the fish's secretion or masks it with something resembling the anemone's "scent." In this regard, something in the urine or excretory products of the fish may be involved in habituating the anemone also. An additional possibility is that a slight immunity to the nematocyst toxins of the host anemone may be acquired in this manner, as has been reported for other coelenterate symbionts. This might serve to offset any "accidental" stingings by the anemone.

The suggestion has also been made that the fish may, during its acclimation passes, pick up more and more of the anemone's mucus on its own surface, thereby camouflaging its own body secretions. However, observations by Blösch, Koenig, and Graefe with anemones that had been isolated, but could still sting "acclimated" fish from other anemones do not bear this out. If one argues that the fish must individually acclimate to these new anemones, then it must be explained how a fish can remain acclimated to two or three anemones at the same time when presumably it is covered only by the mucus of the last anemone it inhabited.

Let it also be stated here that there is no evidence that the anemones continuously discharge their nematocysts in the presence of the fish and that the mucus merely acts as a sort of armor to prevent nematocyst penetration.

Finally, there is always the possibility that we may be faced with more than one way of arriving at the same goal; that is, a combination of the above methods may be involved in the protection of the fish from the anemone's nematocysts.

MECHANISM OF NEMATOCYST INHIBITION

Two possibilities are apparent if one hypothesizes that something on the fish's surface is responsible for inhibiting nematocyst discharge: one involves an in-

hibition of the cnidoblast-nematocyst complex in situ on the tentacles; the second postulates that this substance affects the anemone's receptor-effector system, and thus implies a connection between the nematocysts and the anemone's nervous system.

A number of workers, including Wagner (1905), Glaser and Sparrow (1909), Parker and Van Alstyne (1932), Pantin (1942*a*, *b*), and Jones (1947) consider the cnidocil (in coelenterates possessing this) or the free surface of the cnidoblast itself to be involved in the reception of stimuli for discharge. Yanagita (1943, 1959*a*, *b*, *c*, 1960*a*, *b*, *c*) and Yanagita and Wada (1953, 1954, 1959) have made the most thorough study of this process to date, using the acontia of *Haliplanella* (=*Diadumene*) *luciae*.

These authors find two distinct processes involved in the discharge of nematocysts: first, an extrusion of the nematocyst tip containing the operculum through the surface of the acontium, and secondly, the actual firing and eversion of the nematocyst thread itself. The nematocyst-extrusion response in sea water is caused by such diverse stimuli as various cations (K^+, NH_4^+), electric shock, certain surface-active substances, lipoid solvents, and the mechanical contact of various solid food materials, all of which act on the surface of the acontial epithelial cells containing the nematocysts. In this process, the above nematocyst-extrusion factors have had to overcome the extrusion-suppressing action of various anions (Cl^-, Br^-) and anesthetics (e.g., Mg^{++}) which may be present in the external medium. Finally, these same extrusion-suppressing substances (i.e., the anions) now function in tripping the exposed operculum and firing the nematocyst.

Thus, there seems to be ample evidence that nematocysts or their enclosing cells or both are capable of receiving chemical information directly from the environment in the initiation and inhibition of nematocyst discharge. Although Yanagita and Wada's work dealt only with acontial nematocysts, some of Pantin's earlier work (1942*a*, *b*) with *Anemonia* tentacles produced similar results. If there is a change in the mucous coat of the fish during acclimation, as Davenport and Norris (1958) suggest and if Yanagita is correct, it is possible that the concentration of certain nematocyst extrusion-suppressing substances (e.g., some anions), might be increased in the mucous coat during acclimation and that this may be sufficient to inhibit nematocyst discharge in the presence of the fish. However, only further experiments can determine the applicability of the above to stoichactiid anemones and anemone fish.

Although various microscopists about the turn of the century observed what they considered to be nerves running to cells containing nematocysts, later work (both morphological and physiological) tended to discredit these findings (see Weill, 1934, for review of early work) and provide further evidence for the idea that nematocysts are truly independent effectors, not subject to any control by the animal (e.g., Wagner, 1905; Parker and Van Alstyne, 1932; Pantin, 1942*a*, *b*; Ewer, 1947; Jones, 1947; and Burnett, Lentz, and Warren, 1960). In addition, Davenport (1962*a*, *b*) has found no experimental evidence of any chemical factors from various symbionts affecting the neuromuscular physiology of the anemone hosts, with the notable exception of the *Calliactis* hermit crab shell relation (Davenport, Ross, and Sutton, 1961; Ross and Sutton, 1961).

On the other hand, more recent light-microscopical work (Spangenberg and Ham, 1960; Semal-Van Gansen, 1952; see also Mackie et al., 1961) has reconfirmed the presence of nerves running to at least some nematocysts, in addition to finding a distinct nervous system in hydra. This latter fact has been seriously open to question (see Lenhoff and Loomis, 1961) because of the difficulty of the electron microscopists in even finding either nerve cell bodies or fibers in hydra, let alone any connection of the nervous system with nematocysts (Chapman and Tilney, 1959*a*, *b*; Slautterback and Fawcett, 1959; Slautterback, 1961; Hess, 1961). However, this problem has been clarified with Slautterback (1963) and Lentz's (1963) findings of distinct nervous elements in their more recent electron-microscopical material of hydra. Only improved electron-microscopical techniques will be able to provide us with further morphological information regarding the innervation of nematocysts. Lentz and Barrnett (1963*a*, *b*) also have physiological evidence for the presence of a nervous system and its effect on growth and differentiation in hydra, as well as histochemical and pharmacological evidence (Lentz and Barrnett, 1961*a*, *b*, 1962*a*, *b*) regarding the presence and action of the hydra nervous system. Finally, Passano (1961, 1963) and Passano and McCullough (1962, 1963) have recorded rhythmically occurring action potentials from hydra electrically, the origin of which these workers believe to be the hydra nervous system.

Based on his observations that a hungry stoichactiid would readily capture and kill sardines, while a well-fed individual would rarely seize any kind of food, Gohar (1948) suggested that anemones harboring anemone fish "seem to exert control over their adhesive and stinging powers, these functions being more than simple reflex to touch." Until a few years ago, then, the second idea above—that of a coelenterate exercising some sort of nervous or humoural control over its nematocyst discharge—would have been regarded with a good deal of skepticism. But in spite of the aforementioned conflicting data, Baerends (1950, 1957), made the statement that "there are several indications that *Discosoma* can put its cnidoblasts out of action." He further suggested that the nibbling and mouthing of the anemone's tentacles by *Amphiprion* may be a sign stimulus which "releases the inactivation of the cnidoblasts in the anemone" (Baerends, 1950: 345). Koenig (1960) has suggested essentially the same thing. If taken at face value, what these authors are suggesting (aside from Baerends' questionable implication of some sort of "internal release mechanism" on the part of the anemone) is that the anemone somehow is exercising direct control over the discharge of its nematocysts and that these

organelles are not independent effectors. Recently, experimental evidence has been provided from additional sources which lends support to this idea.

Davenport, Ross, and Sutton (1961) found that the threshold for nematocyst discharge of the anemone, *Calliactis*, was low in animals not on gastropod shells inhabited by hermit crabs (the anemone's normal habitat), while sea anemones on their shells showed little tendency to discharge their nematocysts, apparently due to some sort of feedback from the shell via the pedal disc—in other words, the anemone is somehow controlling the discharge of its nematocysts. Ross and Sutton (1964) have also found that the nematocysts of *Stomphia* do not follow the independent-effector hypothesis. Bouchet (1961), on the basis of her feeding experiments, likewise believes that hydra's nematocysts are not independent effectors, but also are under the control of the animal. Interestingly enough, although Burnett, Lentz, and Warren (1960) interpret their work on hydra feeding as supporting the independent-effector hypothesis, a number of their results just as easily can be taken to support the opposite view. Their concluding statement is pertinent in this regard: "Thus, it has been established that hydra is not able to prevent nematocyst discharge completely after rich feeding. The animal is merely capable of *reducing* the number of nematocysts discharged" (italics mine). Perhaps this statement was a bad choice of words, but the fact that the animal is capable of influencing its nematocyst discharge in any way at all should force a more critical examination of the idea that these nematocysts may *not* be acting as independent effectors.

In addition to the above behavioral work, Lentz and Barrnett (1961*a*, *b*, 1962*a*, *b*), and Wood and Lentz (1964) have recently provided biochemical evidence for the possibility of at least partial nervous control of the nematocysts in hydra. It is interesting to note in passing that a number of recent investigators beginning with Ewer (1947) and including Burnett, Lentz, and Warren (1960), Bouchet (1961), and Lentz and Barrnett (above) have all noticed some distinct differences in the responses of the several different types of hydra nematocysts. Although some of the results are conflicting, there are indications that some hydra nematocysts (e.g., desmonemes or holotrichs or both) may be independent effectors, while others (e.g., stenoteles) may be under the control of the animal. This speculation might be pertinent to some of the light-microscope findings (e.g., Mackie, et al., 1961) that nerves in hydra have not been found running up to all nematocyst-containing cells.

In any case, the above results suggest that the additional possibility of a stoichactiid-type anemone being able to control its nematocyst discharge in response to some kind of stimulus provided by an anemone fish cannot be ruled out completely. Once again, the site of reception of this stimulus may be the nematocyst-containing cells themselves, although this also remains to be elucidated.

Finally, it is hoped that this review will stimulate some thought as to what direction future research endeavors might take concerning the extremely fascinating symbiosis between fishes and sea anemones.

ZOOGEOGRAPHY OF SEA ANEMONES AND ANEMONE FISHES

Although at least four species of *Amphiprion* are found as far east as the Society Islands and the Tuamotu Archipelago, there is no record of this genus or its associated anemones being present in the Galápagos Archipelago (Snodgrass and Heller, 1905; Fowler, 1938; Harry, 1953; Rosenblatt and Walker, 1963). Regarding the anemones, McMurrich (1904) and Carlgren (1951) indicate that *Physobrachia* (=*Gyrostoma*) is found on the Juan Fernández Islands as well as several places on the Chilean mainland. However, this genus of anemones may be found with or without symbiotic fish (Saville-Kent, 1893, 1897).

While participating in the recent Galápagos International Scientific Project, I likewise found no species of *Amphiprion* present in the Galápagos, nor was there evidence of any fish associating with Galápagos anemones. In addition, none of the characteristic anemones of the tropical Pacific (e.g., *Stoichactis*, *Radianthus*) that are known to harbor symbiotic fish were found in the Galápagos. Indeed, one had the impression that the Galápagos anemone fauna decidedly resembled more temperate forms rather than tropical. This impression was further supported by Dr. Patricio Sanchez (personal communication), who pointed out that at least one of the Galápagos anemones in my collection (*Bunodosoma*) was identical to a common intertidal form found off the coast of Chile. Carlgren (1959) believes that the distribution of this form as well as that of *Phymactis* may be continuous from the lower South American coast all the way to the Gulf of California. Carlgren also records *Antholoba achates* as having a distribution including Tierra del Fuego, parts of the coast of South America, and the Galápagos, which further indicates the nontropical nature of at least some Galápagos anemones.

Acknowledgments

Acknowledgment is gratefully made to Hopkins Marine Station of Stanford University and the National Science Foundation for the opportunity to study various aspects of tropical biology while participating in the TE VEGA Expeditions to the South Pacific during the summer of 1963. A note of appreciation is also due Miss Isobel Bennett of the University of Sydney for first drawing my attention to the above symbiosis on the reefs of Samoa, and to Dr. Rolf L. Bolin, who served as Chief Scientist of the TE VEGA while I was aboard. I should like to thank Dr. Cadet Hand for assistance provided to me through his NSF Grant GB-1237, which enabled me to participate in the Galápagos Expedition. Dr. Hand and Dr. Ralph I. Smith of the University of California, Berkeley, and Dr. Demorest Davenport of the University of Cali-

fornia, Santa Barbara, read a preliminary draft of the manuscript and offered valuable suggestions.

Literature Cited

Abel, E. F.
1960*a*. Zur Kenntnis des Verhaltens und der Ökologie von Fischen an Korallenriffen bei Ghardaqa (Rotes Meer). Z. Morph. Ökol. Tiere, 49: 430-503.
1960*b*. Liason faculatative d'un poisson (*Gobius bucchichii* Steindachner) et d'une anémone (*Anemonia sulcata* Penn.) en Méditerranée. Vie et Milieu, 11: 517-531.

Allee, W. C., O. Park, A. E. Emerson, T. Park, and K. P. Schmidt
1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia.

Baerends, G. P.
1950. Specializations in organs and movements with a releasing function. Symp. Soc. Exp. Biol., 4: 337-359.
1957. The ethological analysis of fish behavior. *In*: M. E. Brown [Ed.] The physiology of fishes, vol. 2., Academic Press, New York.

Blösch, M.
1961. Was ist die Grundlage der Korallenfischsymbiose: Schutzstoff oder Schutzverhalten? Naturwissenschaften, 48: 387.

Bouchet, C.
1961. Le contrôle de la décharge nématocystique chez l'Hydre. C. R. Acad. Sci. Paris, 252: 327-328.

Buhk, F.
1939. Lebensgemeinschaft zwischen Riesenseerosen und Korallenfischen. Wochschr. Aquar.- und Terrarienkunde, 36: 672-674.

Burnett, A. L., T. Lentz, and M. Warren
1960. The nematocysts of hydra (Part I) Ann. Soc. Roy. Zool. Belg., 90(1): 247-267.

Cantacuzene, J.
1925. Immunité d'*Eupagurus prideauxii*, vis-a-vis des poisons de l'*Adamsia palliata*. C. R. Soc. Biol. Paris, 92: 1133-1136.

Carlgren, O.
1940. A contribution to the knowledge of the structure and distribution of the cnidae in the Anthozoa. Kungl. Fysiografiska Sällskapets Handlingar, N. F., 51(3): 1-62.
1949. A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. Kungl. Svenska Vetenskapsakad. Handlingar, 1(1): 1-121.
1950. Actiniaria and Corallimorpharia. Brit. Mus. (Nat. Hist.), Great Barrier Reef Expedition (1928-29) Sci. Repts., 5(7): 427-457.
1951. The actinian fauna of the Gulf of California. Proc. U.S. Nat. Mus., 101: 415-449.
1959. Corallimorpharia and Actiniaria with description of a new genus and species from Peru. Lunds Universitets Årsskrift., N. F., Avd. 2, 56(6): 1-38.

Caspers, H.
1939. Histologische Untersuchungen über die Symbiose zwischen Aktinien und Korallenfischen. Zool. Anz., 126: 245-253.

Caullery, M.
1952. Parasitism and symbiosis. Sidgwick and Jackson, Ltd., London.

Chapman, G. B., and L. G. Tilney
1959*a*. Cytological studies of the nematocysts of hydra. I. Desmonemes, isorhizas, cnidocils, and supporting structures. J. Biophys. and Biochem. Cytol., 5(1): 69-78.
1959*b*. Cytological studies of the nematocysts of hydra. II. The stenoteles. J. Biophys. and Biochem. Cytol., 5(1): 79-84.

Coates, C. W.
1964. Safe hiding places moved while you wait. Animal Kingdom, 67(3): 77-79.

Collingwood, C.
1868*a*. Note on the existence of gigantic sea-anemones in the China Sea, containing within them quasi-parasitic fish. Ann. and Mag. Nat. Hist., ser. 4(1): 31-32.
1868*b*. Rambles of a naturalist on the shores and waters of the China Sea. John Murray, London.

Crespigny, C. C. de
1869. Notes on the friendship existing between the malacopterygian fish *Premnas biaculeatus* and the *Actinia crassicornis*. Proc. Zool. Soc. London, 1869: 248,-249.

Dales, R. P.
1957. Interrelations of organisms. A. Commensalism. *In*: J. W. Hedgpeth [Ed.]. Treatise on marine ecology and paleoecology, Vol. 1. Ecology. Mem. Geol. Soc. Amer., 67: 391-412.

Davenport, D.
1955. Specificity and behavior in symbioses. Quart. Rev. Biol., 30(1): 29-46.
1962*a*. The responses of actinians to electrical stimulation. Bull. Institut Océanographique Monaco, 1236: 1-24.
1962*b*. Physiological notes on actinians and their associated commensals. Bull. Institut Océanographique Monaco, 1237: 1-15.

Davenport, D., and K. S. Norris
1958. Observations on the symbiosis of the sea anemone *Stoichactis* and the pomacentrid fish *Amphiprion percula*. Biol. Bull., 115(3): 397-410.

Davenport, D., D. M. Ross, and L. Sutton
1961. The remote control of nematocyst-discharge in the attachment of *Calliactis parasitica* to shells of hermit crabs. Vie et Milieu, 12(2): 197-209.

Eibl-Eibesfeldt, I.
1960. Beobachtungen und Versuche an Anemonenfischen (*Amphiprion*) der Malediven und der Nicobaren. Z. Tierpsychol., 17(1): 1-10.

Ewer, R. F.
1947. On the functions and mode of action of the nemotocysts of Hydra. Proc. Zool. Soc. London, 117: 365-376.

Fowler, H. W.
1938. The fishes of the George Vanderbilt South Pacific Expedition. 1937. Acad. Nat. Sci. Phil., Monograph # 2.

Garnaud, J.
1951. Nouvelles données sur l'Ethologie d'un Pomacentridé: *Amphiprion percula* Lacépède. Bull. Institut Océanographique Monaco, 998: 1-12.

Glaser, O. C., and C. M. Sparrow
1909. The physiology of nematocysts. J. Exp. Zool., 6(3): 361-382.

Gohar, A. F.
1934. Partnership between fish and anemone. Nature (London), 134: 291.
1948. Commensalism between fish and anemone (with a description of the eggs of *Amphiprion bicinctus*). Fouad I Univ. Publ. Mar. Biol. Sta. Ghardaqa (Red Sea), 6: 35-44.

Graefe, G.
1963. Die Anemonen-Fisch-Symbiose and ihre Grundlage—nach Freilanduntersuchungen bei Eilat/Rotes Meer. Naturwissenschaften, 50(11): 410.
1964. Zur Anemonen-Fisch-Symbiose, nach Freilanduntersuchungen bei Eilat/Rotes Meer. Z. Tierpsychol., 21(4): 468-485.

Gudger, E. W.
1941. Coelenterates as enemies of fishes IV. Sea anemones and corals as fish eaters. New England Nat., 10: 1-8.
1947. Pomacentrid fishes symbiotic with giant sea anemones in Indo-Pacific waters. J. Royal Asiatic Soc. Bengal, 12(2): 53-76.

Hackinger, A.
1959. Freilandbeobachtungen an Aktinien und Korallenfischen. Mitteil. Biol. Sta. Wilhelminenberg, Wien, 2: 72-74.

Harry (Rofen), R.
1953. Icthyological field data of Raroia Atoll, Tuamotu Archipelago. Atoll Res. Bull., 18: 1-190.

Herre, A. W.
1936. Some habits of *Amphiprion* in relation to sea anemones. Copeia, 1936(3): 167-168.

Hess, A.
1961. The fine structure of cells in *Hydra*. p. 1-49. *In*: H. M. Lenhoff and W. F. Loomis [Eds.]. The biology of hydra: 1961. Univ. Miami Press, Coral Gables.

Horst, R.
1903. On a case of commensalism of a fish (*Amphiprion intermedius*) and a large sea anemone (*Discosoma sp.*). Notes Leyden Mus., 23: 180-182.

Jakowska, S.
1963. Mucus secretions in fish—a note. Ann. N. Y. Acad. Sci., 106(2): 458-462.

Jones, C. S.
1947. The control and discharge of nematocysts in hydra. J. Exp. Zool., 105(1): 25-60.

Koenig, O.
1958. Ein Beitrag zur Fortpflanzungsbiologie von *Dascyllus trimaculatus*. Aquar. u. Terr. Z., 11(3): 107-111.
1960. Verhaltensuntersuchungen an Anemonenfischen. Pyramide, 8(2): 52-56.

Ladiges, W.
1939. Das Ratsel der Symbiose zwischen den Riesenseerosen der Gattung *Stoichactis* und den Fischen der Gattungen *Premnas* und *Amphiprion*. Wochschr. Aquar. u. Terrarienkunde, 46: 669-676.

Lane, C. E.
1960. The Portuguese man-of-war. Sci. Am., 202(3): 158-168.

Lenhoff, H. M., and W. F. Loomis [Eds.]
1961. The biology of hydra and of some other coelenterates: 1961. Univ. Miami Press, Coral Gables.

Lentz, T. L.
1963. Fine structure of the nervous system of hydra. Anat. Rec., 145: 334.

Lentz, T. L., and R. J. Barnett
1961*a*. Enzyme histochemistry of hydra nematocysts. Anat. Rec., 139: 312.
1961*b*. Enzyme histochemistry of hydra. J. Exp. Zool., 147(2): 125-149.
1962*a*. Relationship of enzyme activity to nematocyst discharge in hydra. Anat. Rec., 142: 315.
1962*b*. The effect of enzyme substrates and pharmacological agents on nematocyst discharge. J. Exp. Zool., 149(1): 33-38.
1963*a*. The effect of neuropharmacological agents on regeneration in hydra. Anat. Rec., 145: 334.
1963*b*. Role of the nervous system in regenerating hydra: the effect of neuropharmacological agents. J. Exp. Zool., 154: 307-327.

Luther, W.
1958. Symbiose von Fischen mit Korallentieren und Krebsen im Roten Meer. Natur und Volk, 88(5): 141-146.

Mackie, G. O., et al.
1961. Discussion on: Is there a nervous system in hydra? p. 69-76. *In*: H. M. Lenhoff and W. F. Loomis [Eds.]. The biology of hydra: 1961. Univ. Miami Press, Coral Gables.

Mansuetti, R.
1963. Symbiotic behavior between small fishes and jellyfishes, with new data on that between the stromateid, *Peprilus alepidotus* and the scyphomedusa, *Chrysaora quinquecirrha*. Copeia, 1963 (1): 40-80.

McMurrich, J. P.
1904. The Actiniae of the Plate Collection: Fauna Chilensis. Abhandlungen zur Kenntnis der Zoologie Chile. Zool. Jahrb. suppl. 6, 3(2): 215-306.

Mitchell-Hedges, F. A.
1937. Battles with monsters of the sea. D. Appleton-Century Co., New York.

Moser, J.
1931. Beobachtungen über die Symbiose von *Amphiprion percula* mit Aktinien. Sitzungsber. Gesell. Naturf. Freunde Berlin, 1931(2): 160-167.

Müller, W.
1957. Dascyllusarten. Aquar. u. Terr. Z., 10(2): 12-14.

Muscatine, L.
1963. Extracellular products of algae symbiotic with hydra. Amer. Zool., 3(4): 526.

Muscatine, L., and C. Hand
1958. Direct evidence for the transfer of materials from symbiotic algae to the tissues of a coelenterate. Proc. Nat. Acad. Sci., 44(12): 1259-1263.

Muscatine, L., and H. M. Lenhoff
1963. Symbiosis: on the role of algae symbiotic with hydra. Science, 142: 956-958.

Noble, E. R., and G. A. Noble
1964. Parasitology. The biology of animal parasites. 2d ed. Lea and Febiger, Philadelphia.

Odum, E. P., and H. T. Odum
1959. Fundamentals of ecology. 2d ed. W. B. Saunders Co., Philadelphia.

Oesman, H.
1961. Erlebnisse mit Anemonenfischen. Aquar. u. Terr. Z., 14(1): 49-52.

Osche, G.
1963. Ökologie des Parasitismus und der Symbiose (einschliesslich Phoresie, Epökie und Kommensalismus). Fortschr. Zool., 15: 125-164.

Pantin, C. F. A.
1942*a*. The excitation of nematocysts. Nature (London), 149: 109.
1942*b*. The excitation of nematocysts. J. Exp. Biol., 19(3): 294-310.

Parker, G. H., and M. A. Van Alstyne
1932. The control and discharge of nematocysts, especially in *Metridium* and *Physalia*. J. Exp. Zool., 63(2): 329-344.

Passano, L. M.
1961. Discussion on: Is there a nervous system in hydra? p. 69-76. *In*: H. M. Lenhoff and W. F. Loomis [Eds.]. The biology of hydra: 1961. Univ. Miami Press, Coral Gables.
1963. Primitive nervous systems. Proc. U.S. Natl. Acad. Sci., 50: 306-313.

Passano, L. M., and C. B. McCullough
1962. The light response and the rhythmic potentials of hydra. Proc. U.S. Natl. Acad. Sci., 48: 1376-1382.
1963. Pacemaker hierarchies controlling the behavior of hydras. Nature (London), 199: 1174-1175.

Rosenblatt, R. H., and B. W. Walker
1963. The marine shore-fishes of the Galápagos Islands. Occ. Pap. Calif. Acad. Sci., 44: 97-106.

Ross, D. M., and L. Sutton.
1961. The response of the sea anemone *Calliactis parasitica* to shells of the hermit crab *Pagurus bernhardus*. Proc. Roy. Soc., B, 155: 266-281.
1964. Inhibition of the swimming response by food and of nematocyst discharge during swimming in the sea anemone *Stomphia coccinea*. J. Exp. Biol., 41(4): 751-757.

Saville-Kent, W.
1893. The Great Barrier Reef of Australia. W. H. Allen and Co., Ltd., London.
1897. The naturalist in Australia. Chapman and Hall, Ltd., London.

Schneider, H.
1964. Bioakustische Untersuchungen an Anemonenfischen der Gattung *Amphiprion* (Pisces). Z. Morph. Ökol. Tiere, 53: 453-474.

Schultz, L. P.
1953. Review of the Indo-Pacific anemone fishes, genus *Amphiprion*, with descriptions of two new species. Proc. U. S. Natl. Mus., 103: 187-201.

Schultz, L. P., W. M. Chapman, E. A. Lachner, and L. P. Woods
1960. Fishes of the Marshall and Marianas Islands. Bull., U. S. Natl. Mus., 202: 1-438.

Semal-Van Gansen, P.
1952. Note sur le systeme nerveux de l'hydra. Acad. Roy. Belg. Bull. Cl. Sci., 38(7): 718-735.

Slautterback, D. B.
1961. *In* Discussion on: Is there a nervous system in hydra? p. 69-76. *In*: H. M. Lenhoff and W. F. Loomis [Eds.]. The biology of hydra: 1961. Univ. Miami Press, Coral Gables.
1963. Cytoplasmic microtubules. I. Hydra. J. Cell Biol., 18: 367-388.

Slautterback, D. B., and D. W. Fawcett
1959. The development of the cnidoblasts of Hydra. An electron microscope study of cell differentiation. J. Biophys. and Biochem. Cytol., 5: 441-452.

Sluiter, C. P.
1888. Ein merkwürdiger Fall von Mutualismus. Zool. Anz., 11: 240-243.

Snodgrass, R. E., and E. Heller
1905. Shore fishes of the Revillagigedo, Clipperton, Cocos and Galápagos Islands. Proc. Washington Acad. Sci., 6: 333-427.

Spangenberg, D. B., and R. G. Ham
1960. The epidermal nerve net of hydra. J. Exp. Zool., 143: 195-201.

Springmann, W.
1963. Misslungene Zucht von *Amphiprion percula*. Aquar. u. Terr. Z., 16(6): 174-176.

Stephenson, T. A.
1946. Coral reefs. Endeavour, 5: 96-106.

Stevenson, R. A.
1963. Behavior of the pomacentrid reef fish *Dascyllus albisella* Gill in relation to the anemone *Marcanthia* [*sic*] *cookei*. *Copeia*, 1963(4): 612-614.

Thorpe, W. H.
1963. Learning and instinct in animals. Methuen, London.

Townsend, C. H.
1929. Records of changes in color among fishes. Zoologica, 9: 321-341.

Valentyn, F.
1726. Oud en nieuw Oost-Indiën, etc. Vol. 3. Omftandig verhaal van de geschiedenissen en zaaken het kerkelyke ofte den Godsdienst betreffende, zoo in Amboina, etc. Joannes Van Braam, Dordrecht.

Verwey, J.
1930. Coral reef studies. I. The symbiosis between damselfishes and sea anemones in Batavia Bay. Treubia, 12(3-4): 305-366.

Wagner, G.
1905. On some movements and reactions of *Hydra*. Quart. J. Microscop. Sci., 48: 585-622.

Weber, M.
1913. Die Fische der Siboga Expedition. Siboga Expeditie, 57: 334-335.

Weill, R. F.
1934. Contribution à l'étude des cnidaires et de leurs nématocystes. Travaux de la Station Zool. Wimereux, 10, 11.

Whitley, G. P.
1927. The fishes of Michelmas Cay, North Queensland. Records Aust. Mus., 16: 1-32.
1929. Some fishes of the order Amphiprioniformes. Mem. Queensland Mus., 9(3): 207-246.
1932. Fishes. Brit. Mus. (Nat. Hist.) Great Barrier Reef Expedition (1928-29) Sci. Repts., 9: 267-316.

Wood, J. G., and T. L. Lentz
1964. Histochemical localization of amines in *Hydra* and in the sea anemone. Nature (London), 201: 88-90.

Yanagita, T. M.
1943. Discharge of nematocysts. J. Fac. Sci., Tokyo Imperial University, Sec. IV, 6(1): 97-108.
1959*a*. Physiological mechanism of nematocyst responses in sea-anemone. I. Effects of trypsin and thioglycolate upon the isolated nematocysts. Jap. J. Zool., 12(3): 361-375.
1959*b*. Physiological mechanism of nematocyst responses in sea-anemone. II. Effects of electrolyte ions upon the isolated cnidae. J. Fac. Sci. Univ. Tokyo, Sec. IV, 8(3): 381-400.
1959*c*. Physiological mechanism of nematocyst responses in sea-anemone. VII. Extrusion of resting cnidae—its nature and its possible bearing on the normal nettling response. J. Exp. Biol., 36(3): 478-494.
1960*a*. Physiological mechanism of nematocyst responses in sea-anemone. III. Excitation and anaesthetization of the nettling response mechanism. Compar. Biochem. Physiol., 1(2): 123-139.
1960*b*. Physiological mechanism of nematocyst responses in sea-anemone. IV. Effects of surface-active agents on the cnidae *in situ* and in isolation. Compar. Biochem. Physiol., 1(2): 140-154.

1960*c*. The physiological mechanism of nematocyst responses in sea-anemone. V. The effects of lipoid solvents on the cnidae *in situ* and in isolation. Annot. Zool. Japonensis, 33(4): 203-210.

Yanagita, T. M., and T. Wada

1953. Discharge-inducing concentrations of acids and bases for the nematocysts of sea-anemone. Nat. Sci. Report, Ochanomizu Univ., 4(1): 112-118.

1954. Effects of trypsin and thioglycolate upon the nematocysts of the sea anemone. Nature, 173: 171.

1959. Physiological mechanism of nematocyst responses in sea-anemone. VI. A note on the microscopical structure of acontium, with special reference to the situation of cnidae within its surface. Cytologia, 24(1): 81-97.

Yonge, C. M.

1930. A year on the Great Barrier Reef. London: Putnam.

Yonge, C. M.

1957. C. Symbioses. *In*: J. W. Hedgpeth [Ed.]. Treatise on marine ecology and paleoecology, vol. 1. Ecology. Mem. Geol. Soc. Amer., 67(1): 429-442.

Zahl, P. A.

1952. Man-of-War fleet attacks Bimini. *In*: J. O. La Gorce [Ed.]. The book of fishes. Nat. Geog. Soc., Washington, D. C.

Genetics and general fish folders

Box 1

1. genetics -philosophical, taxonomy, evolution
2. genetics - fish evolution
3. genetics - fish - distribution through the world
4. genetics - fish - behavior
5. genetics - fish - manipulation
6. genetics - fish research & National Science Foundation grant proposals
7. genetics - California gene resource conservation program - anadromous salmonid plan
7. genetics - workshop on salmon & steel-head conservation and enhancement