

ON THE RELATIONSHIP OF SOCIAL  
BEHAVIOR TO PIGMENTATION  
IN TROPICAL SHORE FISHES

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## INTRODUCTION

THAT THE COLORATION of animals bears a close but sometimes complex relationship to the various elements that go to make up the environment is well known. In fishes most of the studies of activity of the pigmentary system have been made in reference to the inanimate elements of their environments or in reference to sexual activity. There are few data on the details of interplay between social behavior and the pigmentary system in this group of animals. Evidently this has been partly because superficially social behavior appears to be less definite and direct than the other two mentioned. On consideration, this apparent diffuse vagueness of many items of social behavior would seem to be merely a deceptive appearance because of greater complexity. The validity of this point of view is developed later by means of an analytical table which considers the various possible responses open to fishes.

In three areas of study there has developed a considerable literature, but each with little reference to the others. These three are (1) social behavior, (2) reactions and physiology of the pigmentary system, and (3) field observations of a miscellaneous sort on general natural history. One of the purposes of the present communication is to discuss these in mutual reference, with especial consideration of the physical possibilities open to fishes and of the organic restrictions of the fishes themselves.

In addition to a consideration of data bearing on the problem that may be found in the literature, some new items that have not been previously reported are here presented. The bulk of the data and the new items are based mostly on tropical shore fishes. Most of these observations were made at the Lerner Marine Laboratory on the island of Bimini. Here, in extraordinarily clear sea water, a large number of species have their being, compete with one another, and are readily accessible for observational and experimental purposes. In fact, this location was chosen for the laboratory largely because it is possible to find fishes living side by side that demonstrate a wide variety of successful solutions to the problem of living.

The general activities of fishes, as well

as other animals, as has been indicated above, may be considered in terms of the possibilities open to them. That is to say, confronted with a given stimulus, only a few broad types of reaction are possible, both on an *a priori*, theoretical basis and on an observational basis. Table 1 serves to make this clear. For purposes of simplicity, and as unnecessary in the present connection, items purely concerned with reproduction, parental care, and pathology have been omitted. It covers the other aspects of fish behavior, including their attitudes towards danger, food, their fellows, environment, and "emotional state," as well as time and space in general terms.

It is understood that any given fish, theoretically at least, may change from one kind of reaction to another and that thus listing them does not imply any particular rigidity of reaction. Actually both extremes exist, reaching from practically a fixed pattern to cases where the changes from one type of reaction to another occur with startling rapidity. It is, in fact, the main purpose of this paper to compare actual observed behavior in a variety of fishes living in the same environment with this list of possible reactions open to fishes.

A consideration of this list leads to the conclusion that much of fish behavior is the interaction of these various elements in a somewhat kaleidoscopic pattern. It is to be noted that the first three items are, in a broad sense, all of a locomotor nature and therefore under the direct control of the skeletal musculature and of a "voluntary" nature. The fourth, controlled by light and intermediated by way of hormones and the autonomic nervous system, is evidently not under such "voluntary" control. As will be developed, however, the interactions of the two types of control are such that a discussion of them in these terms becomes rather pointless.

Before specific cases are considered, some explanation of table 1 should be made in order to clarify what is to follow. In item 1 all responses to attack are typically found in various species, excepting only the last, counterattack, which represents a special case and is not the typical reaction of any

known species. In item 2 all four manners of taking food are used typically by one species or another and need no especial explanation. In item 3 all social attitudes are to be found typically, except possibly the second, indifference. It is doubtful if any real fish in normal health is actually "indifferent" to the presence or absence of its fellows. In item 4 all cases listed are to be found actually occurring in a state of nature. It is here that much confusion has arisen because some fishes at one time are colored in reference to background and at others to something other than background, evidently internal and here called, loosely, "emotional state." In item 5 the continual alternation of light and darkness forms the basic, short-term, temporal changes. In item 6 altitudinal position in reference to surface and bottom is evident as a prime positional differentiation. When this difference in behavior is considered in terms of other concomitant acts the entire phenomenon becomes much more understandable, as do a variety of other interactions which will be discussed in reference to the species concerned. More exact definitions of these terms will be found in the discussion.

Other aspects of fish reactions not listed in table 1, such as territoriality, hierarchies, and social facilitation, are evidently the working out of these various items as listed, to which are often added elements of sexual behavior. These will be referred to at the proper places.

Thanks are due Mr. James W. Atz for critically reading the manuscript.

TABLE 1

THEORETICALLY POSSIBLE USEFUL REACTIONS  
OPEN TO FISHES IN RESPONSE TO VARIOUS  
ELEMENTS IN THEIR ENVIRONMENT

1. Possible reactions to attack
  - A. Flight
  - B. Hiding
  - C. Freezing
  - D. Corporal metamorphosis
  - E. Counterattack
2. Possible reactions to feeding requirements
  - A. Overtaking prey
  - B. Stalking prey
  - C. Attracting prey
  - D. Sifting out prey
3. Possible social reactions
  - A. Solitary
  - B. Indifferent
  - C. Aggregating
  - D. Schooling
  - E. Attached
4. Possible pigmentary reactions
  - A. In reference to background
    - i. Matching background
      1. In general tone
      2. In pattern detail
    - ii. Opposing background
    - iii. Indifference to background
  - B. In reference to emotional state
    - i. Unvarying with state
    - ii. Varying with state
5. Possible temporal reactions
  - A. Diurnal
  - B. Nocturnal
  - C. Aperiodic
6. Possible altitudinal reactions
  - A. Surface
  - B. Midwater
  - C. Bottom
  - D. Indifferent



## OBSERVED BEHAVIOR

ACTUAL OBSERVATIONS on a variety of Bimini shore species bearing on the preceding general considerations follow. This descriptive part, perhaps seemingly scattered, represents to some extent new data and confirmation of the observations of others. Other items of biological interest are noted for purposes of record. The bearing of each item on the present thesis is taken up in the discussion.

### *Manta birostris* (Walbaum)

A young individual of this species was placed in the larger stockade on February 17 and lived until July. It recovered rapidly from a harpoon wound in one pectoral and evidently obtained sufficient plankton natural to these waters for sustaining life, as no ground fish and similar material which was offered was given the slightest attention. It was estimated to be about 8 feet wide. The cephalic appendages are evidently used in steering, as they would be turned appropriately when sharp turns were negotiated but were usually left symmetrically disposed when slow or wide turns were made. Sometimes they were carried, one or both, curled lightly into a "horn." The color of the dorsal surface was uniform by day, but a light patch on each pectoral was shown at night. These were ill-defined areas extending forward from the rear edges of the pectorals at about their center. These areas would seem to have no relevance to the white shoulder patches discussed at length by Beebe and Tee-Van (1941). However, since they were unable to settle the question of the puzzling presence or absence of this pattern, it would seem possible, in the light of the diurnal color change shown by this individual, that there is a much wider change of pigmentation in these fishes than had been supposed and that the patterns as found may in fact represent responses of individuals to specific but as yet unknown stimuli.

A small echeneid of about 4 inches, which evidently came along with the manta, picked at the harpoon wound more or less continually, but in spite of this the wound healed completely in a short time. Under such conditions these fishes could probably be considered as facultative parasites instead of mere riders.

### *Strongylura notata* (Poey)

Several moderate-sized examples confined in a concrete tank supplied with running sea water showed an inversion of the color differential on dark, moonless nights. That is, the dorsum would become very pale and the ventrum would become very dark, almost black in some instances. This reaction is closely parallel to that shown by *Sphyræna* discussed by Breder (1948). In both it can be seen only momentarily in the beam of a flashlight, as they quickly revert to the daytime coloration in this illumination. This doubtless explains why those taken about a submerged light do not show this inversion, for long before they come within the range of good visibility they have adjusted their color differential accordingly.

### *Hippocampus punctulatus* Guichenot

One large female kept in an aquarium showed a dark, nearly black uniform color by day but at night displayed a series of lighter bars. Four smaller, not quite half-grown, individuals remained in the dark phase at all times.

They all fed well on plankton which came in with the water supply or was especially given to them. Much of their time was spent at a distance from the mouth of the inlet tube, evidently appropriate for feeding purposes. A few small *Eucinostomus*, about 1 cm. in over-all length, were placed in this aquarium for safekeeping. Surprisingly the large sea horse was able to stalk and catch them and was successful in downing them through its long tube-like mouth. It was, however, a feat near its possible limits. Since these *Eucinostomus* are fairly deep bodied, the sea horse managed to pass them down its tube-like mouth by crushing them to some extent. This was not accomplished by the small jaws but evidently by the sides of the mouth after the greatest depth of the fish had passed the oral opening.

### *Hepsetia stipes* (Müller and Troschel)

This common species, which may be seen in small aggregations during the day, is one of the first to appear about a submerged light at the end of the laboratory dock at night.

Although mostly silvery during the daytime, those taken at night have the tips of the caudal lobes dusky to black, and the dark lateral streak, mostly obliterated in the daytime, is prominent. This observation was checked on aquarium material, and the individuals all regularly showed this change with the coming of darkness. This effect is most marked in the fully adult individuals. They come to the light singly but sometimes form aggregations amounting almost to schools under its influence.

A group of about 40 half-grown examples were caught singly as they appeared at the night light and were confined in a common aquarium. They immediately formed a well-organized school. This persisted for about nine days, by which time it gradually broke up. Evidently this type of aggregation, despite its persistence, is a fright school.

***Mugil trichodon* (Poey)**

A single individual of this species was confined in an aquarium with a *Canthigaster rostratus* of approximately equal length. Although in the open sea *Mugil* is a schooling or closely aggregating form, it has not been seen to attempt to form associations with other than its own kind. This solitary individual, however, continually attempted to school with the *Canthigaster*. It is shown doing so in plate 4. The latter invariably sought to avoid the mullet's attentions. This species is not an aggregating type of fish. At night the mullet would "roost" in some seaweed after dark.

It is to be noted especially that the mullet is a uniformly silvery fish, of a type common to so many schooling forms, whereas the puffer is not in the least silvery, but is marked with a variety of definite and distinct chromatic and pattern characteristics.

***Sphyraena barracuda* (Walbaum)**

Some notes on the color and pattern change shown by this species have already been indicated by Breder (1948) in reference to light and dark backgrounds. Further study shows that the series of color reactions are considerably more complicated than might be suggested by the remarks in that paper. Since those observations were made, the edge of a hurricane changed the bottom consider-

ably, and at this writing there are no longer such large areas of clean white sand near the laboratory dock as were to be seen at that time, the bottom being now more evenly covered with darker colored objects in the form of litter. No individuals were seen to take on the very simple and pale pattern described in that paper as associated with clean, light sand bottoms.

A single individual of about 15 cm. was confined in a concrete tank provided with running sea water and which measured 6 by 3 by 2 feet. This fish rapidly became accommodated to its quarters and fed freely from the hand and showed evident growth. The tank was new and the color of gray concrete when the fish was first established. In this it showed a very light phase, but at all times there was some evidence of faint cross bars. When startled, these immediately became intensified. A black card was placed on the bottom of the tank and whenever the fish swam over it the bars were also intensified, although at this time there was no evidence of any fright being associated with the reaction. A dense growth of algae soon darkened the walls of the tank, and the fish kept pace with this, darkening its general overtone and no longer going into the very light phase at any time. Although these color reactions can hardly be considered as close background matching, they evidently perform in a manner characteristic of fishes that do match closely. Evidently the responses to dark objects in the environment are exceedingly delicate, and only when a very large area of clear white sand completely fills the visual field does the extreme lightening discussed in the earlier paper make itself apparent.

On dark moonless nights this individual showed the inversion of the color differential, previously discussed for the larger fishes. The blackening of the ventral surface was more intense in this younger example.

A large individual is shown in plate 3 as it appeared in one of the enclosures with a light sand bottom. The very dark back is typical under such conditions with a dark surface in view of the fish, in this case the enclosing wall of piling, not included in the photograph. In the same plate a *Tarpon atlanticus* (Cuvier and Valenciennes) is shown



under identical circumstances as well as a group of *Caranx sexfasciatus* Quoy and Gaimard. These species when over light sand but with no dark objects within their range of sight are much lighter.

Examples of barracuda about 15 mm. long may be taken resting under sargassum weed in August at least. These are very often found resting in some position other than the horizontal with the head either up or down. The angle most frequently encountered is about 30° from the horizontal but may range up to nearly 90°. The most usual coloration is with a light black and dark sides and ventrum, against either a light or dark background. Typical examples are shown in plate 4.

#### *Coryphaena hippurus* Linnaeus

Four individuals, each of about 3 feet in length, were established in the larger stockade. From the shapes of the heads, two were judged to be mature males and two, females. These fish at no time crashed into the walls as do so many truly oceanic species. They became accommodated to captivity in a surprisingly short time, and in a few days fed avidly, freely taking food from the feeder's hand. They behaved more like pond-reared carp than in a manner one would expect from oceanic species.

When later the *Manta* was placed in the same pool, they gave it considerable attention. They swam about it and repeatedly "scratched" themselves on its broad back. To this the *Manta* gave not the slightest heed, as though it were accustomed to such behavior. It would seem possible that *Coryphaena* regularly makes use of such objects in their natural state for this purpose where there would be little otherwise for them to rub against. Bottom-dwelling species often make such use of rocks, and Breder (1932) suggested that such a function might be served by open-water fishes which leap over small sticks, striking them in passing. Possibly *Manta*, large turtles, and similar submerged objects are so regularly used by dolphin.

#### *Apogonichthys stellatus* Cope

An individual of this species lived well in an aquarium without any living mollusk

for refuge. It was provided with an empty *Strombus* shell which it used as a retreat during the daytime, when it showed its darkest phase. At night it would prowl about the aquarium and show its lightest, very pale phase. This was suffused with a metallic greenish sheen on the upper parts of the sides and head, a coloration that was completely invisible by day. This behavior and fading at night are in agreement with Longley and Hildebrand (1941). The specimen was taken in daylight, however, in a small dredge which brought up no conchs, so evidently this one was swimming freely during the daytime. A second specimen, taken from a *Strombus*, was introduced into the same aquarium. It dislodged the first from its shelter, which thereafter found shelter in a corner of the aquarium. Evidently the new fish immediately took control of the territory, although in size it was scarcely larger than the first. The fishes kept well away from each other. After this happened, the first fish no longer took on its pale night phase but maintained its dark phase continually and often slipped into the conch shell when the second was prowling about at night. There was some chasing about once at nightfall, and both fish showed the dark phase. The dislodged fish eventually jumped out of the aquarium.

Plate 5 shows a single individual in its daytime, dark, hiding phase and in its night-time, light, prowling phase.

#### *Pomacentrus leucostictus* Müller and Troschel

It was noted by Breder (1948) that this species always retreats into a shell or other protective cavity at night. This was reconfirmed for a large variety of sizes. Longley and Hildebrand (1941) remarked, in connection with sexual differences in coloration, that "At night sexes become alike in appearance, both becoming uniform gray above. The light color extends from the eye posterodorsally to mid-level on the side, straight back, and then upward just behind the soft dorsal; anterior margins of pectoral, anal, and soft dorsal blue; a blue sheen on the soft dorsal, anal, and caudal." A point which they do not note is that this change actually makes the upper part of the fish lighter than the lower in most normally colored adults, which, is, of course, a reversal of the normal color

differential of the generality of fishes and of this species in daylight.

The well-known habit these fishes have of modifying their territorial holding in various ways was demonstrated in rather striking fashion in one aquarium which contained a single half-grown individual. A glass inlet tube one-quarter inch in inside diameter rested diagonally in this aquarium and because of its connection with the main supply by means of a flexible rubber tube could be moved about fairly freely. It was noted that when this tube was displaced from a certain position the fish would always put it back to a certain spot resting against one of the side walls. As the end of the tube rested in the sand, the flowing water excavating a depression, it was necessary for the fish to push the tube with the tube's end dragging through the sand. Thus considerable physical effort was required to move the tube. The small jaws were opened and, pressing its open mouth against the tube, accompanied by vigorous swimming efforts, the fish effected the movement. The effort was such that the entire operation could seldom be accomplished in one attempt. Most often it took three separate pushes to return it to the original position. The intervals between the attempts were mostly spent by the fish in swimming about the tube and viewing it from various angles. The eye movements accompanying these "inspections" were unmistakable. Thus it was clear that not only did the fish remove this nearly unmanageable object from an "undesired" location, but maneuvered the object to a very exact place. This behavior was tested at least once a day for a period of three weeks with surprisingly uniform results. Sometimes the reaction would be immediate and at others delayed occasionally up to as much as 15 minutes.

***Abudefduf saxatilis* (Linnaeus)**

A number of species of rather distinctive patterns and coloration show a simple fading of their daytime colors at night. This species is marked in this direction, and along with it should be listed *Abudefduf analogus* (Gill), *Halichoeres bivittatus* (Bloch), *Thalassoma bifasciatum* (Bloch), and *Holocentrus ascensionis* (Osbeck). The latter, bright red by

day, becomes nearly white, but differs from the others listed by being active nocturnally.

***Doratonotus megalepis* Günther**

This species is common amid the *Thalassia* beds and shows a considerable range of color from brilliant green to a brownish red. In an aquarium planted with *Thalassia* a specimen was noted to spend much of its time huddled against a blade of this plant. There was considerable variation in the colors presented by this foliage, from bright green to the brown of dead leaves. It was especially noted that, when resting, the fish always rested against a portion of a leaf of almost its exact shade of green. Seen to be active only by day.

***Erotelis smaragdus* (Cuvier and Valenciennes)**

A single specimen was taken from an empty conch shell. This fish showed mostly a light tan back with darker sides not unlike a certain phase of *Eleotris pisonis* (Gmelin). This pattern became intensified with the coming of nightfall. It would sometimes rest in an empty shell but was noted to prowl about the aquarium both day and night.

***Bathygobius soporator* (Cuvier and Valenciennes)**

Various comments on the general nature of color and pattern change in this goby have been given by Beebe (1931) and Breder (1948). Certain comments by the latter become clearer in the light of present data. At times specimens may be bottom matching and at other times, bottom opposed, and as he noted, "There seemed to be a general tendency for the darker fish to dominate the bottom-matching light-colored fish in daylight." After considerable observation on fishes kept in aquaria, in varying numbers but with no other species, it became clear that under conditions of great fright, such as handling in a net, the fishes assumed a light coloration which more or less made them inconspicuous. Individuals which set up territory, after being well established in an aquarium, ordinarily showed similar inconspicuous patterns. However, the sight of another individual would be followed by a rapid flashing up of a dark, mostly black, coloration in such individuals. These two types of pattern are shown in plate 6, figures



1 and 2, together with figure 3 which shows the dominant black fish which has chased the dominated light fish out of its sight for the moment. The black chin and light cheeks are well indicated. In the case of two dark fish meeting, the vanquished, i.e., the one that finally flees from the other, loses its black pattern and takes on the bottom-matching one. There is thus in this species a very pretty demonstration of the interplay of bottom-matching and bottom-opposing patterns in association with social behavior. It is not to be thought, however, that this is all there is to the behavior and pattern changes of these fishes, as it was clear in making the above observations that the described patterns were only the main themes running through a complicated set of interrelationships in which many minor and as yet not clear smaller differences played varying roles.

#### *Gnatholepis thompsoni* Jordan

This well-marked species has been hitherto reported only from the type locality—Tortugas, Florida. The description of its behavior as given by Longley and Hildebrand (1941) checks closely with the present observations made on a single specimen in an aquarium. The distinctive dark vertical line through the eye was noted to be present only during the daylight periods. It showed little color change during a sojourn of about two months in the aquarium, remaining in a light phase during that period. As soon as established in the aquarium it prepared three retreats, one under each of three pieces of *Porites* excavated in such a manner as not to cause the coral to fall into them. These retreats consisted of long troughs under the branches of the coral, leaving supporting amounts of sand at each end. In no place was the burrow so constructed that the fish could not see out, or be seen from the outside. On alarm it would dash for the nearest retreat and at other times rest quietly in one or the other. Much time was spent during the day searching for food. It paid not the slightest attention to bits of fish dropped in for other fishes, in this case *Hepsetia*, but contented itself in feeding after the manner described by Longley and Hildebrand (1941) who wrote, "The mouth is protrusible and sucker-like, and much sand

is taken up, from which the material the species seems to feed upon is sorted." In actual detail the fish would gather a mouthful of sand and detritus and then with a very rapid fluttering of the opercular apparatus eject through each gill cleft a fine stream of the inedible material. This would be repeated again and again as the fish moved from place to place in quick, almost insect-like movements. It became quickly accommodated to aquarium life and, through a hand lens, could be watched feeding. The material leaving the two gill openings in tiny jets was ejected with considerable force, forming tiny twin piles of sand on either side of the fish about midway between head and tail. Such observations did not, however, reveal by what mechanism the actual sorting took place. The sand supported a sparse growth of some green algae amid which lived a variety of micro-organisms. Evidently the materials gathered were adequate, for the fish was obviously in vigorous health and grew considerably during its time of aquarium residence. This fish is shown in plate 7 together with its excavations.

During August two much larger examples were seen about the laboratory dock making similar burrows in the sand under various objects. It was suspected that they were a mated pair on the basis of their attitude towards each other, but no nest cavity could be found.

#### *Stathmonotus hemphillii* Bean

This species, hitherto known only from the Florida Keys, can be freely dredged from water of about 20 feet in depth off the western beach. Mostly they are solid black except for the characteristic white markings on the dorsal and anal. In agreement with Longley and Hildebrand (1941) who wrote, "The fish's motion is eel-like," at first glance they were thought to be small morays. When placed in an aquarium it was expected that they would quickly hide away in some shell or crevice in more or less moray fashion. However, they would have nothing to do with such places and rested conspicuously on the white sand in plain sight. As the species is considerably flattened it manages to rest upright on its ventral surface by throwing the body into a more or less S-shaped curve.

When thus posed its essentially blenny nature became apparent. While there are insufficient data, these observations being based on about half a dozen fish, of a species known to vary considerably in coloration, it may be that this phase represents yet another case of background contrasting coloration.

***Dinematchthys cayorum* (Evermann  
and Kendall)**

A single gravid individual gave premature birth to a number of young in a laboratory aquarium. This light-colored, almost pale pink fish was distinctly nocturnal, remaining hidden all day in a shell but swimming about vigorously after dark.

***Alutera scripta* (Osbeck)**

A small example of this species was noted to perform in a manner similar to that described by Beebe (1928). On the introduction of a new object into its aquarium it would stand on its head and press its chin to the bottom by vigorously waving its transparent and all but invisible dorsal and anal fins. This was generally an immediate reaction to the introduction of a new and larger fish to the aquarium. Actually it did not always press its chin to the bottom, but a favorite place was against the vertical drain pipe of the aquarium as shown in plate 4. This aquarium was bare of fittings, but under a natural environment it is not hard to imagine how such behavior would help to conceal the fish.

***Canthigaster rostratus* (Bloch)**

Small examples of this species are not uncommon in sheltered places at Bimini. In an aquarium they showed very little tendency to change color or pattern, and handling did not cause them to inflate. They were seen to be strictly diurnal in habit, "roosting" quietly, closely pressed into the corner of the aquarium and always with the head up at night.

***Histrio gibba* (Mitchill)**

As noted by authors, this species can disappear in full view by optically merging with a clump of sargasso weed. It, too, can change its coloration to some extent to match the exact shade of the weed it inhabits, but this change does not take place rapidly.

Also well known are the prodigious appetites of these fishes and that only one can ordinarily be kept in a single aquarium, for if two or more are so confined the population is quickly reduced to one. Usually the largest engulfs the smaller, but not necessarily so as they are able to engulf a fish considerably larger than themselves because of the tremendously distensible stomach. Experimentally, a specimen of about 4 inches in length with its tail missing, evidently from some prior misadventure, was fed on bits of fish flesh continuously until it finally refused food. By that time it contained a mass of food considerably greater than its own bulk. However, during the following night it regurgitated the entire mass and then refused food for a few days.

This fish, a female, although kept alone repeatedly shed eggs. The first mass was abnormal in that the rolled-up agglutinated eggs did not swell but sank to the bottom as a small solid clump, which nevertheless showed the peculiar double roll in which these eggs are wrapped. The subsequent masses were normal in all respects. These water hardened and floated in great wavy sheets. The remarkable part of these later normal egg masses was the frequency with which they were produced. The dates are given in the following tabulation:

Date of production of egg masses:

March 13 (eggs abnormal)

April 12

April 17

April 22

April 26

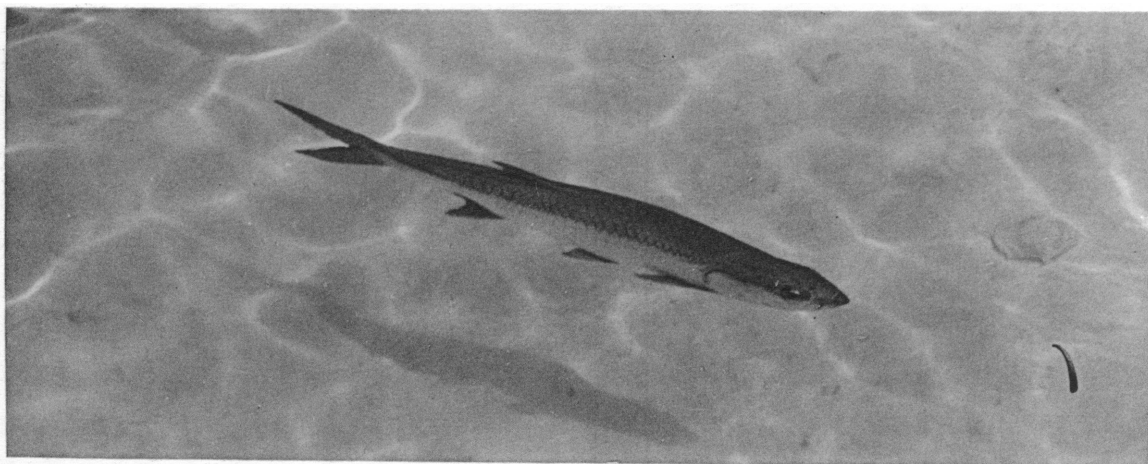
May 2

May 5

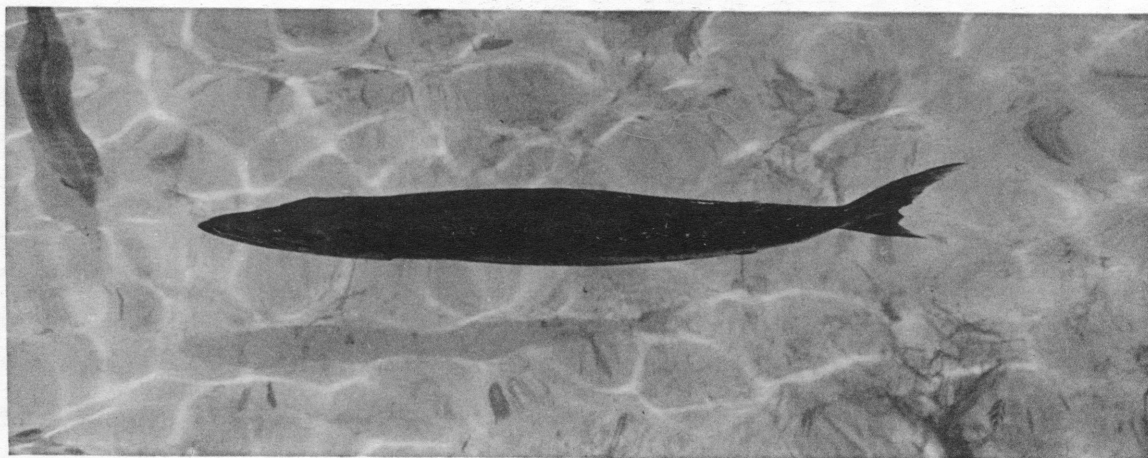
May 17

Accidentally destroyed June 4

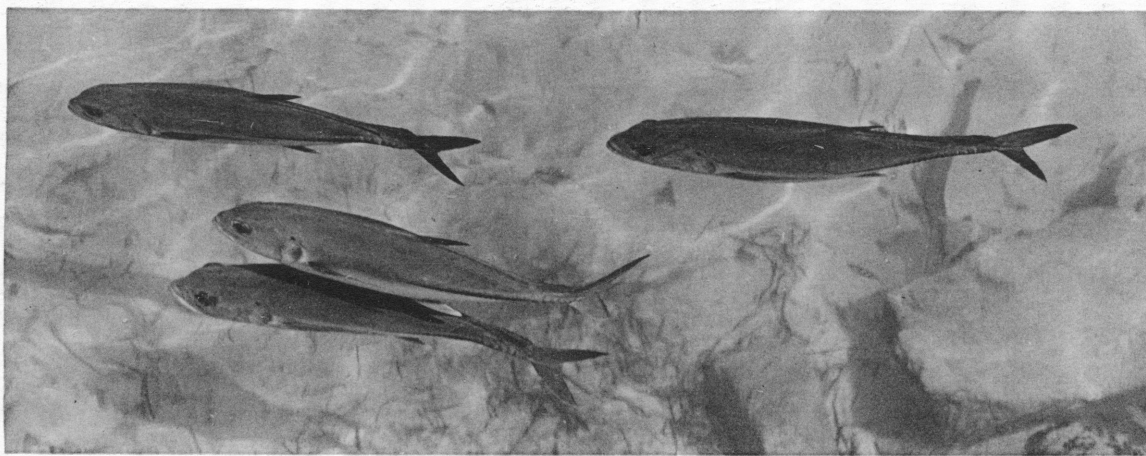
In the period of 35 days, covering the laying of six masses of normal eggs, the intervals between oviposition ranged from a minimum of three to a maximum of 12 days. This fish fed freely on cut-up fish and would take virtually anything offered including the experimenter's fingers which it attempted to choke down in spite of the fact that they were attached to a hand too large even for such a fish. In the same aquarium was a small *Pomacentrus* which seemed not to pay any heed to the voracious *Histrio*, nor was the



1



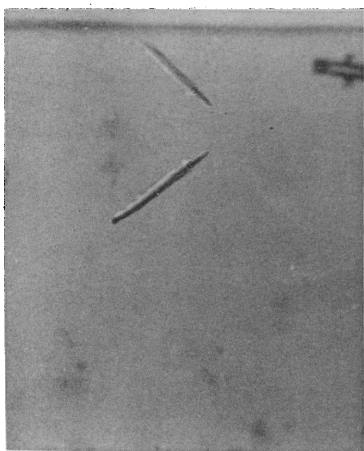
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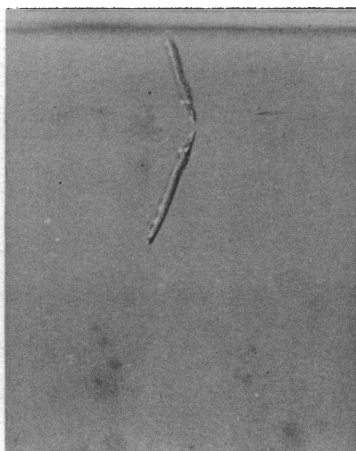
3

Large fishes over a light sand bottom. 1. *Tarpon atlanticus*. 2. *Sphyræna barracuda*. 3. *Caranx sexfasciatus*





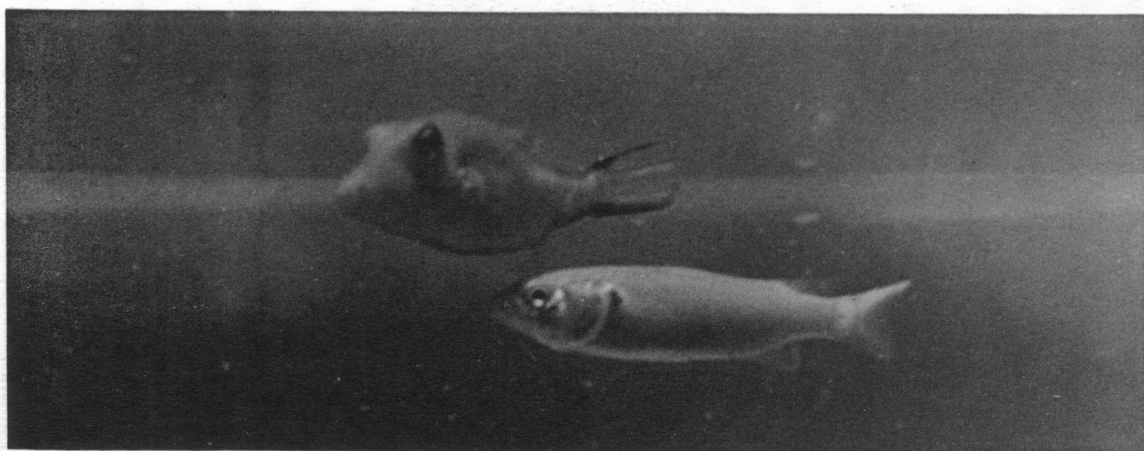
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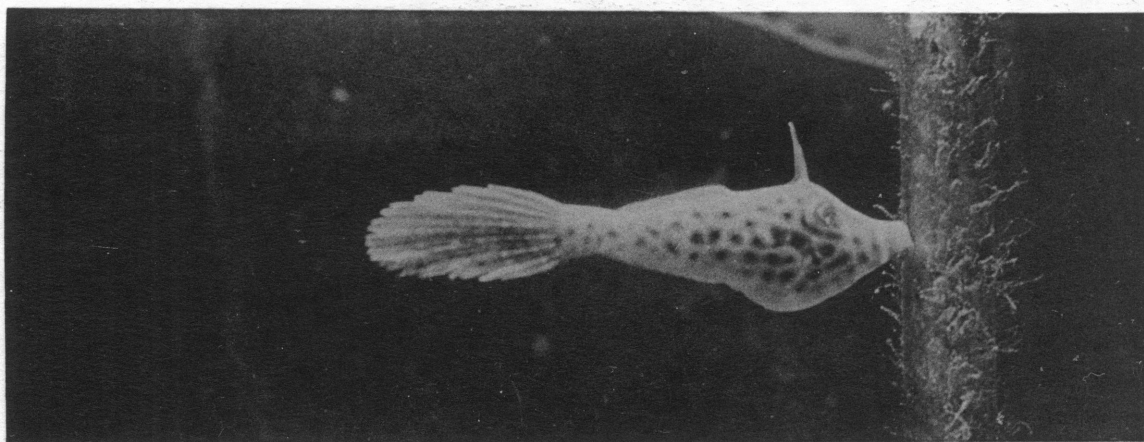
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3



4

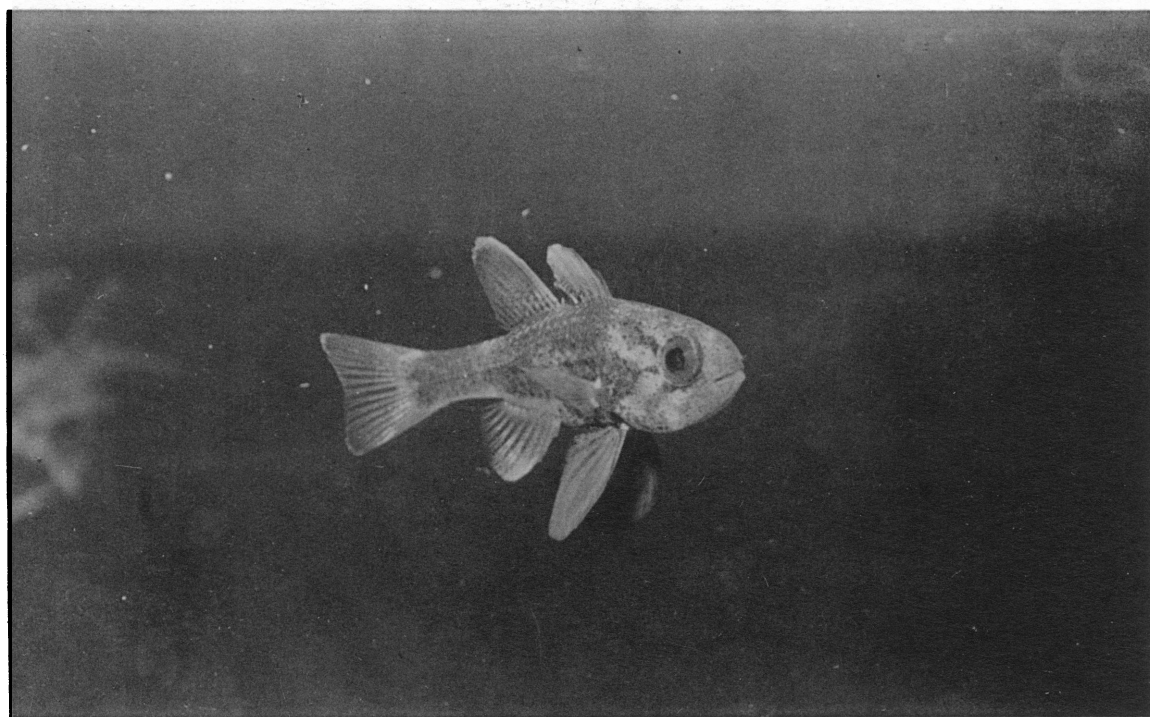


5

1, 2, 3. Three typical resting poses of young *Sphyræna barracuda*, showing the light back and dark sides against both a light and a dark background. 4. An isolated *Mugil trichodon* attempting to school with a *Canthigaster rosstratus*. 5. A young *Alutera scripta* in its "hiding" pose

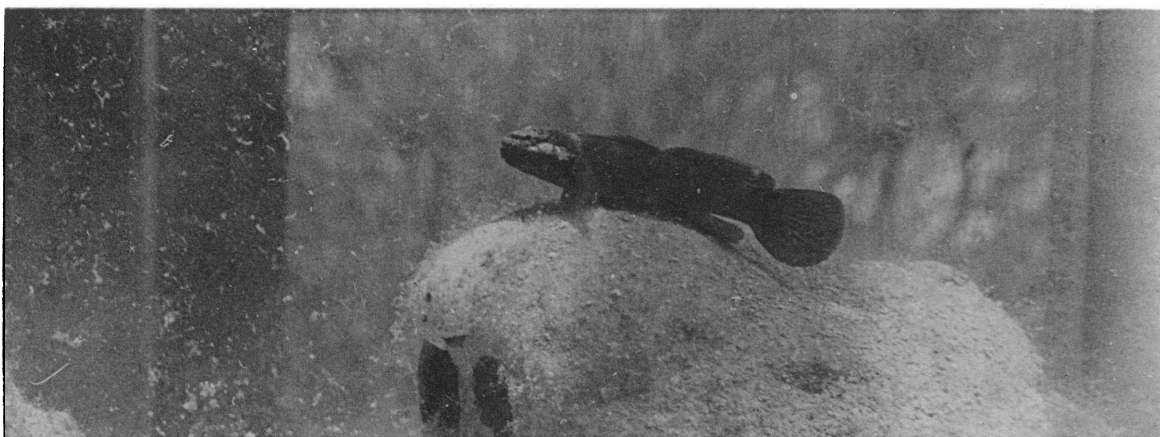


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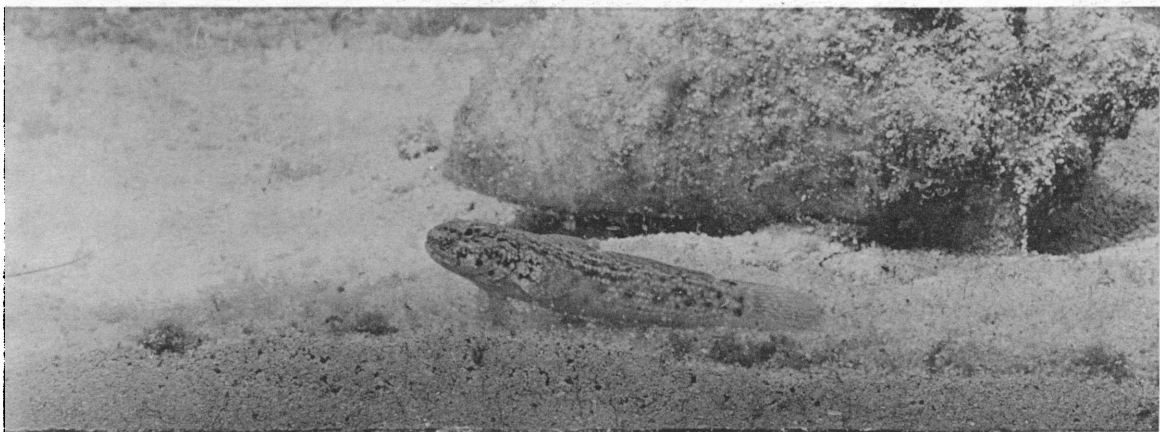


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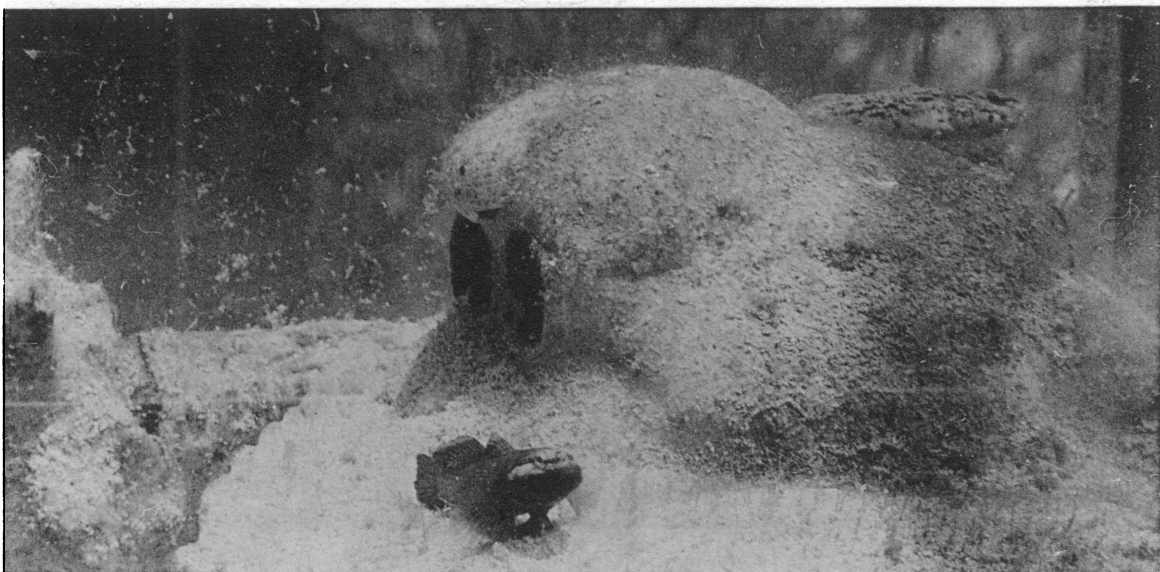
*Apogonichthys stellatus*. 1. Dark daytime phase accompanied by hiding in shell. 2. Light night-time phase while active. Both photographs show the same individual



1



2



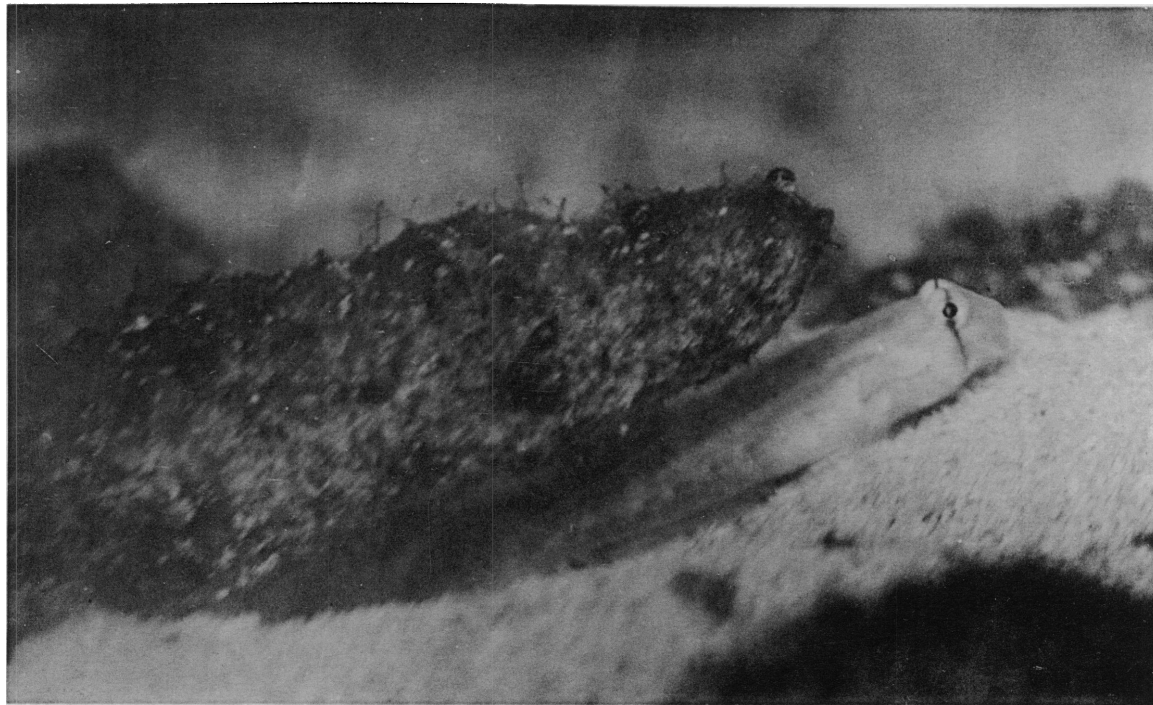
3

*Bathygobius soporator*. 1. Dark contrasting phase of dominant territory-holding fish. 2. Light inconspicuous phase of non-territory-holding fish. 3. Frontal view of dark phase and light subjugated fish just driven from the sight of the dominant





1



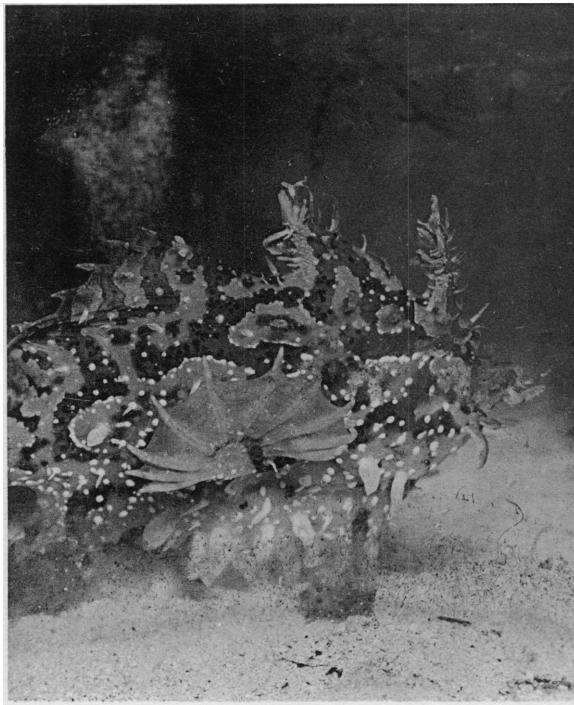
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*Gnatholepis thompsoni*. 1. Showing light phase shown by this individual. 2. Resting in the entrance of one of its retreats

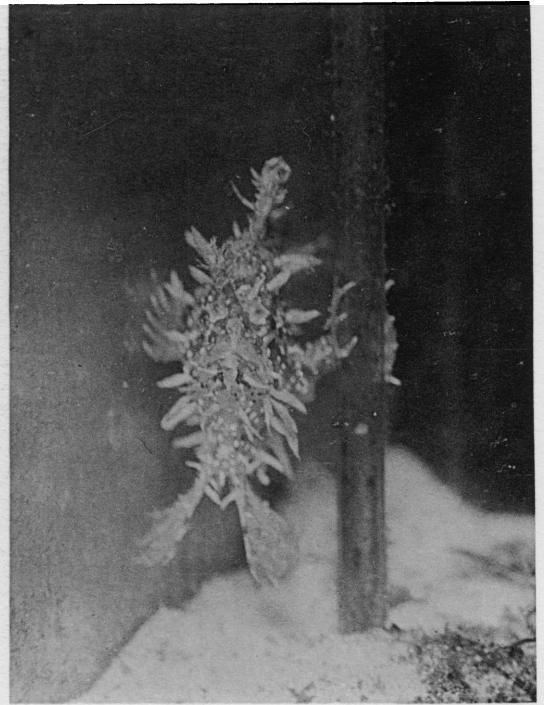




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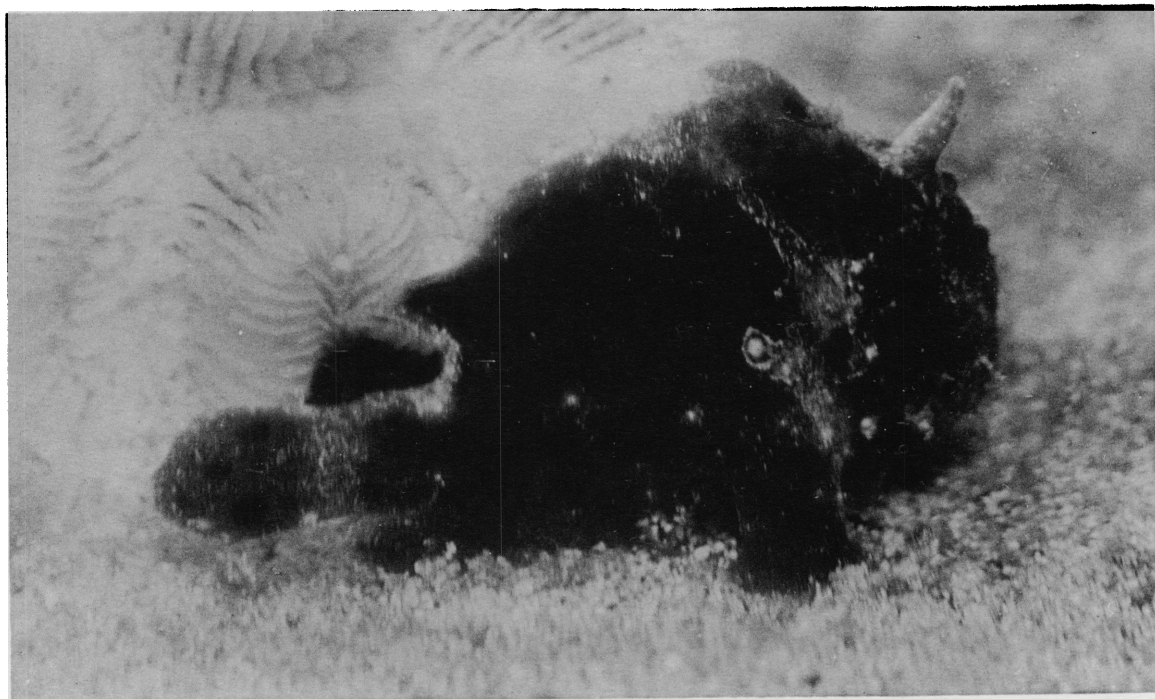


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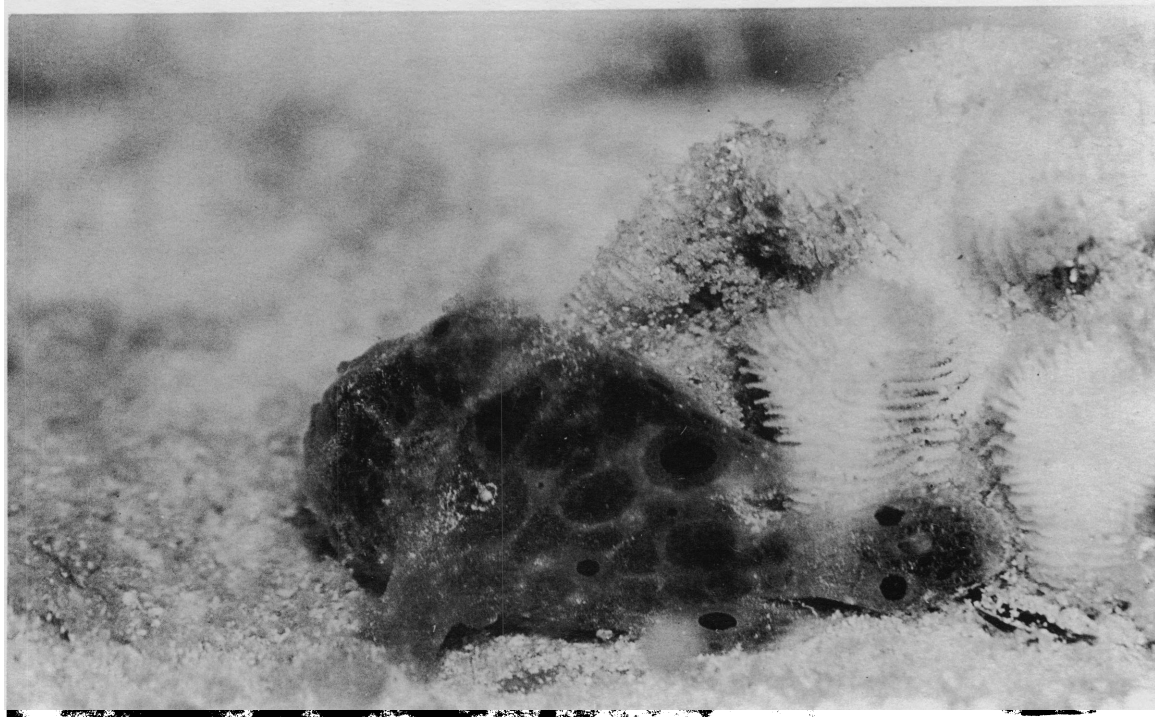


3

*Histrio gibba*. 1. Frontal view of fish in sargasso weed. 2. Right pectoral spread to hold position against glass wall of aquarium. 3. Frontal view showing right pectoral braced against aquarium side and left pectoral grasping aquarium stand pipe



1

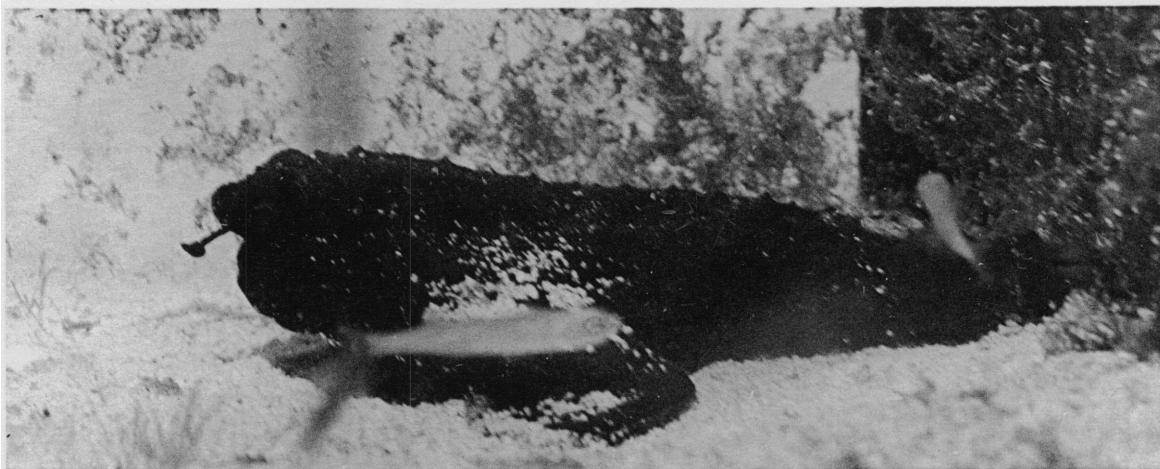


2

*Antennarius multiocellatus*. 1. Dark phase, shown when disturbed. 2. Light spotted phase, shown when at rest



1



2



3



4

*Ogcocephalus radiatus*. 1. Individual with sand thrown over pectoral, just before the commencement of angling. 2. Bait thrust out in angling posture. 3. Direct rear view from which the bait cannot be seen. 4. Rear quartering view showing how far to back the bait is still visible

latter seen at any time to attempt to stalk it. In another aquarium, a small *Histrio* would stalk fairly large *Bathygobius* with extreme persistence, sometimes continuously for all the daylight hours, and would occasionally catch one.

The large female is shown in three poses in plate 8. Its apparent merging with a clump of sargassum weed is well indicated, as is the remarkable hand-like use it makes of its pectorals, including an actual grasping of solid objects.

***Antennarius multiocellatus* (Cuvier and Valenciennes)**

A single example when taken was almost entirely black and resting on white sand and in its peculiarly inert fashion resembled a fish in no discernible manner but showed a striking similarity to a very small logger-head sponge. Barbour (1942) notes such resemblances in considerable detail and remarks on the extreme variability of this form. Later, it would at times take on a paler phase and become a dirty gray, when it would show dark round spots arranged like those described for this species as well as the characteristic light saddle on the peduncle. The light phase was shown when the fish was hiding in the shelter of a shell. When chased out onto white sand it immediately reverted to its dark phase. These color changes are indicated in plate 9. The "fishing pole and bait" is as ordinarily described for the species except that on one side there protruded an almost worm-like appendage which resembled that of *A. scaber* (Cuvier) but from which it is distinct on other bases. This kind of variability casts doubt on the reliability of this character for taxonomic purposes and suggests that accidental injury, perhaps during the angling operations, may modify the form of the "bait" considerably.

When actively fishing, it angles for comparatively short intervals between changes of position. During its travels from place to place it glides along very slowly and very much after the manner of many gastropods. The impression is enhanced because at such times it bends the second and third dorsal spines, which are stout, to opposite sides of the body and moves them slowly, very like the exploring eye stalks of such a mollusk.

The short pectorals are used, within their limitations, very like those of *Histrio* and actually grasp shells and other solids. It is evidently entirely diurnal.

***Ogcocephalus radiatus* (Mitchill)**

A single individual was kept in an aquarium for about three weeks. Evidently the form is not common, as the natives did not know the fish. Its curious quadripedal locomotion was given some study. Actually it may operate its four "legs" in various manners, not being confined to a single fixed gait. At times its locomotion is basically rabbit-like, that is, the pectorals far to the rear thrust it forward as do a rabbit's hind legs while it lands on its pelvics which are far forward. At other times this motion seems to be more toad-like, while at still others it "trots" after the fashion of a dog with alternate fore and hind limbs moving together. Obviously here, too, the pelvics are functioning like the fore limbs of a dog and the pectorals like its hind limbs.

For the most part the fish remained an intense black, so much so that it was only with difficulty that any of the ordinarily visible fish structures could be seen. Thus the pupil, iris, and skin about the eye were so much the same that none of the details could ordinarily be seen at all. The inside of the mouth and the membranes shown when "yawning" were at all times a rich mahogany and very contrasting to the entirely black fish. At night on a few occasions the iris became mahogany colored, and vague lighter bands appeared across the back.

This fish, and probably most if not all of the family Ogcocephalidae, angle with their so-called rostral tentacles, very much after the manner of the Antennariidae, an item that has apparently not been noted before. Both this species and the *Antennarius* already discussed freeze on fright, and both seem to represent further cases of fishes contrasting to their background but more or less resembling objects that might be present in such an environment. Before fishing, this fish not only froze but with its paddle-like pectorals threw sand over itself so as partially to bury the large pectoral expanses. The "fishing rod and bait" were just as black as the rest of the animal. The "rod" would first



be tentatively thrust out slowly, later the tiny "bait" would be extended from the swollen tip of the rod and fluttered rapidly for a moment, and then the whole apparatus would disappear under the overhanging rostrum. This behavior could be elicited only by placing some small fish in the same aquarium. When none could be seen by the fish there would be no attempts at fishing. Usually the bait is thrust straight forward, but at times

it is thrust alternately a little to the right and left to an angle of about  $30^{\circ}$  on either side of the mid-line. It may be more than accidental that this amount of excursion of the bait keeps it just about within the evident limits of the visual field, as may be judged from the illustrations in plate 10. Thus its bait at no time is exposed to view in the sector of the rearward blind area.

## DISCUSSION

ACTUAL FIELD OBSERVATIONS, data obtained from experimental procedures and from the literature bearing on the behavior of fishes of various kinds, are here brought together and considered in connection with the preceding general considerations as set forth in table 1. Unless stated otherwise, these fishes form part of the shore fish association at Bimini. They are considered in sequence under each of the six headings of table 1.

### 1. ACTUAL REACTIONS TO ATTACK

Undoubtedly more fishes react by flight to an attack or approach than by any other manner. The word is used here in the simple sense of putting distance between the object causing the reaction and the subject. Whole groups appear to use this method alone, and at first it might seem to have a considerable phylogenetic significance. It is, however, such a widespread and primary phenomenon among animals generally that only departures from it can be thought of as possibly showing a clear phylogenetic bearing. It is scarcely necessary to go into specific details except to note where it is replaced by some other behavior. Often, in fact, individuals show alternately hiding, burying themselves, or flight as a reaction to attack. Since these other modes of escape depend on certain environmental features that may or may not be present the only recourse at all possible may be flight. If, for example, there is nothing to hide behind and the species does not react by burying itself, flight alone is left, or if the bottom precludes burying a similar situation arises. In the case of open-water fishes, flight or freezing is the only recourse normally present except in the presence of drift. Under such conditions flight is often resorted to after freezing has failed. It is such considerations that led Breder and Halpern (1946) to write, "Benthonic fishes of defenseless types are given to hiding, apparently because there is present in their habitat something to hide behind, alongside of, or under. Surface fishes of a similar nature are given to similar behavior in so far as their cover is adequate. The behavior of goldfish in a well-planted lily pool will demonstrate this. When not close to some shelter, they seek protection in flight, but

otherwise they hide under lily pads. Oceanic pelagic fishes show the same sort of behavior, except that there is little for them to hide behind except each other. Even so, floating trash, seaweed, boxes and barrels, large jellyfish, sharks, etc., at sea are generally attended by various species of small fish."

In the elasmobranchs, flight is typical except in the depressed skates and rays where both freezing and burying themselves may alternate with flight. They generally give the impression of using all three or being unable to determine clearly which is the most appropriate reaction. The Isospondyles, of which there are so many open-water forms, are given to flight, in its simple sense for escape, including such forms as *Albula*, *Elops*, *Tarpon*, *Sardinella*, *Harengula*, *Jenkinsia*, and *Anchoviella* with representatives at Bimini. In fact it is not until some of the fresh-water forms are considered that other behavior is encountered, including some degree of hiding as seen in the Salmonidae. The eels, especially in clear marine waters, are thoroughly cryptic by day and are active only nocturnally. *Synodus* with some bottom-matching ability is apt to flee and freeze, and this behavior is evidently associated with its relatively slight natatorial abilities. The synentognaths as adults all have recourse to fleeing and in some cases actual flight through the surface of the water. Many of the young, however, freeze or hide, and some show remarkable modifications for such purposes. See Breder (1946) for a detailed discussion of some of the more striking types.

A very special condition is that of corporal metamorphosis wherein an attacked animal radically changes its form, usually with considerable enlargement. It is found in the swell shark, *Cephaloscyllium* (see Clark, 1947), and in various tetrapods, such as some Salientia, as well as in some birds and mammals that increase their size by fluffing up their feathers or fur. However, only in the plectognaths does this response to attack reach truly impressive proportions. In this highly specialized teleost offshoot, two separate methods are employed: inflating with water as seen in the puffers, and enlarging the outline by erecting a ventral flap as seen most

strikingly in *Triodon*. These features have been discussed in detail by Breder and Clark (1947). Accompanying the change in shape, there is often the erection of an elaborate spiny armature, such as seen in *Diodon*. This feature is notable here only because of the accompanying change of form, since all fishes with erectile spines, whether they hide or flee, regularly erect what they have under conditions of stress.

## 2. ACTUAL REACTIONS TO FEEDING REQUIREMENTS

As with the previous item, by far the simplest and most widespread reaction is that of the actual locomotor pursuit in the simple sense, ranging from capture of active prey down to the feeding on sluggish forms or even sessile organisms of either plant or animal nature. It is widespread throughout organisms, and only departures from it need be discussed in detail. The stalking of prey, such as seen in the *Sphyræna* or in *Esox*, may be thought of as feeding expressions of "hiding" and "freezing." Attracting prey is a very special attainment and in most cases is simple angling in a very true sense. This seems to be confined to that one extremely specialized group, the *Pediculati*, and in the light of present data it may be assumed that all that possess a developed ilicium use it for attracting their food. Such behavior has been well known or suspected among all but the *ogcocephalids* which are here shown to have such behavior as well. Gudger (1945) summarizes data on this type of feeding but shows that there were up to then actual observations on only two genera, *Lophius* and *Antennarius*.

The fourth type of basic feeding is that of sifting out materials either from the water itself or from various types of bottom detritus. The plankton feeders would represent the first, and such forms as *Mugil* and the herein-described *Gnatholepis* would represent the latter.

## 3. ACTUAL SOCIAL REACTIONS

The question is often raised as to whether solitary life or schooling is the primitive condition in fishes. Since species showing both tendencies and various intermediates

occur in both primitive and advanced groups a clear phylogenetic sequence is not present. Since population structure is based on both aggregating tendencies and dispersal tendencies, which are antagonistic, the above question may lack a true answer. Animals must disperse to some extent, primarily for mechanical reasons but mostly for reasons of food finding and sanitation. How widely they disperse, or how little, is determined by their own physiological requirements and the nature of the environment in which they find themselves.

Animals cannot disperse completely or there can be no reproduction. Consequently they must either remain within touch of each other or foregather at some place during the reproductive period. Secondary influences cover such items as social facilitation and psychic needs.

Thus from the earliest times a brood of organisms either dispersed or hung together, depending on their innate tendencies and the environmental restrictions, and as soon as species began to differentiate probably some showed a tendency in one direction and others in the other. At the very least this must have had a profound effect when a bisexual condition became established, so that long before there were any vertebrates, species were already showing differential social attitudes. Certainly in existing invertebrates such behavior is to be found, including both solitary and aggregating tendencies.

What was the attitude of the form that gave rise to chordates at the time of this evolutionary development is of course a question that cannot be answered. No one can say just what kind of organisms became the first chordate, and, even if we knew, fossil evidence is woefully inadequate to give even hints of the social attitudes of the material. It remains a reasonable guess, however, that if we could uncover all this data it is likely that, during the evolutionary changes going on to establish a chordate, it would be found that the social attitudes of the line of succession changed frequently both with organic changes and environmental modification, while the numerous collateral branches which did not lead to vertebrates showed similar or opposite social attitudes.

In fishes today, four of the five conditions listed are met with. As noted in the Introduction, there is no case of record in which it has been shown that a species of fish actually is socially indifferent. It remains a mere theoretical possibility and one that is unlikely of real occurrence. Perhaps approaching this condition is the behavior of the blind cave fish *Anoptichthys* when not reproductively active. These have been studied by Breder and Rasquin (1943) and Breder and Roemhild (1947). However, in all normal forms, which had not been operated upon, they found a statistically significant difference from pure random movement. The nature of the solitary, aggregating, and schooling attitudes of fishes has been recently summarized and discussed by Breder and Halpern (1946) and need not be repeated here.

The one remaining case, attachment, is again in the *Pediculati*, where in the deep sea ceratoids the males become permanently attached and live a parasitic life on the much larger females. This, while presumably of primarily a sexual significance, forces small groups into continual and close association.

#### 4. ACTUAL PIGMENTARY REACTIONS

Perhaps the most common, or at least the most easily recognized, pigmentary reaction shown by fishes is that of lightening on a light background and darkening on a dark background, which is associated with the albedo rather than with light intensity, as has been shown by Sumner (1939). Such behavior has been studied in a number of mostly freshwater fishes, e.g., in the poeciliid *Gambusia* by Sumner (1934, 1935a, 1935b, 1943), Sumner and Wells (1933), Sumner and Doudoroff (1938), and Breder (1947), in the cyprinid *Ericymba* by Brown and Thompson (1937), in the silurid *Ameiurus* by Odiorne (1937, 1948), and in the cyprinodont *Fundulus* by Odiorne (1933, 1936, 1937). Such fishes as the pleuronectids, which go farther in this direction, have similarly been studied by Sumner (1911) and Mast (1916). Longley and Hildebrand (1941) call attention to general and specific background matching by a wide variety of reef fishes, while the very extreme forms which so closely resemble other objects

in the environment as to be notably deceptive have been reviewed by Breder (1946). Naturally these latter, while matching a specific object, are usually in contrast or opposed to the general tone of the environment but nevertheless effectively obscured. Others, such as the *Ogcocephalus* mentioned in this paper and moderate-sized *Chaetodipterus* mentioned by Breder (1948), while opposed to the background may resemble nothing in particular but nevertheless be effectively hidden. As can be seen from the above, very little attention has been given to this latter type of background response which clearly calls for a physiological reaction pattern different from that used by fishes which match the general background.

Other fishes show little or no change in coloration in reference to the background. The goldfish, *Carassius*, may represent such a type, as indicated by Breder and Halpern (1946), and many of the more brilliantly colored reef fishes show no changes directly associated with the background, although they may have a wide variety of color and pattern change associated with their own behavior or that of their fellows. Such changes are referred to the "emotional state" of the animal, as they are evidently associated with an effect produced by the activity of a fellow fish or with the physiological state of the individual, most conspicuously connected with reproduction or territoriality. The case of *Bathygobius* discussed herein may serve as an illustration of this type of pigmentary response. *Lachnolaimus*, with its rapid interplay of color and pattern change, would be well worth study in this connection.

Many fishes, on the other hand, show no pigmentary response associated with their activity and may or may not be responsive to the background. In cases where fishes are responsive to both alternately, the most bewildering changes take place. It is possible that with meticulous study all fishes could be shown to demonstrate some trace of both types of behavior, although it is certain that in some either or both are reduced to practically nil. This condition may perhaps be better visualized by the following tabulation in which reaction to background is listed against reaction to emotional state:



REACTION TO BACKGROUND	REACTION TO EMOTIONAL STATE	
	VARIES WITH	UNVARYING
Matches generally	<i>Bathygobius</i>	<i>Gambusia</i>
Matches in detail	?	<i>Paralichthys</i>
Opposes	<i>Bathygobius</i>	<i>Ogcocephalus</i>
Indifferent to	<i>Lachnolaimus</i>	<i>Carassius</i>

The illustrations in the column showing the reactions of fishes that are not known to vary their pattern and coloration with emotional states are clear, but in the column of those that do vary with emotional state one is seen to illustrate two background reactions (*Bathygobius*). This indicates that the species alters its attitude towards background or other matters and in effect has two different sets of reactions. The single case marked with a question may mean only that there has been insufficient study to uncover a case that matches the background in detail and at other times opposes the background because of emotional state, or it may mean that all fishes that have developed a close approximation of background have abandoned a reactivity of pigmentation to emotional state.

#### 5. ACTUAL TEMPORAL REACTIONS

Perhaps the majority of fish species are either strongly diurnal or nocturnal rather than aperiodic. At least vast numbers are strongly one way or another. The pigmentary change associated with light or darkness is even more difficult of interpretation than the daytime differences between the pigmental behavior of various species. The changes that may come with a considerably lowered intensity of illumination have not been studied in sufficient detail nor have any been found to be striking enough to indicate any clear-cut reactions. However, the changes that have been noted and are discussed herein refer to absolute or near absolute darkness. Here, *a priori*, it should make no difference what the pigmentation was like for it could not be seen in any case. However, it is under just such conditions that certain fishes show their most profound color changes and in which there is a strong tendency to invert the ordinary countershading common to most. Such diverse forms as *Strongylura*, *Sphyræna*, and *Pomacentrus* prominently show such changes. If one attempts to ascribe some subtle importance to the first two be-

cause of the open-water locations in which they are to be found day and night, this will hardly do for the third, as this species hides completely in an empty shell or similar cavity on the fading of light. It is extremely difficult to try to imagine some direct biological significance that this reaction could have. If some sort of fatigue could be ascribed to the light-induced condition in which the chromatophores are held, a reversal of this condition in the absence of light might be thought of as being physiologically useful. Unfortunately we have no reason to suppose that there is such a fatigue effect involved in any case.

#### 6. ACTUAL ALTITUDINAL REACTIONS

Aquatic organisms have three basic types of environment available to them, one at the air-water interface, another at the water-earth interface, and a third, where the water is deep enough, a non-interface environment between the first two. While many fishes regularly or at special times in their ontogeny have recourse to two or all three, many, if not most, are for large parts of their adult life chiefly concerned with only one of the possible three. It is doubtful if any are ever indifferent. All of these niches are inhabited by various of the species discussed herein. Certain features of each have already been noted in reference to individual species. It is evidently not accidental that the surface and mid-water fishes show a monotony of general pigmentation and corporal form not to be found in the bottom forms. Both surface and mid-water environments are similarly "monotonous" and have little in the way of objects to relieve them. As soon as one enters a surface area where this is not true, such as in the presence of floating sargassum weed, the fishes take on a resemblance to bottom forms and show wide variations in form and pattern. It is clear that both these features of fish life are closely associated with materials of a diversified kind.

#### INTERACTION OF ACTUAL REACTIONS

It is well enough to point out these various prominent features of fishes' behavior, as has been done under the six preceding items, but the chief interest in so doing is preparatory to a consideration of them in reference to one

another. Certain of the interrelations have already been foreshadowed in some of the preceding material, but it is not a simple matter to attempt to synthesize these various components, for with a little consideration it becomes clear that they represent a complicated set of interrelations. However, it is at least possible at this time to indicate some main threads of consistency running through a complicated maze of structural modifications and behavioral changes. The difficulty in ascribing utilitarian functions to these various items should not be surprising under such a condition of complicated interactions.

The color patterns and color changes of fishes well illustrate this complexity. Sumner (1934) showed experimentally that under special conditions *Gambusia* that did not match the background shade were caught more readily by predatory birds, but Breder (1947) showed that under natural conditions a large differential in the behavior of matching and non-matching fish of this species tended to compensate for the color differences even to the point that made him speculate as to which fish actually were the better protected. Coupled with this is the fact that *Antennarius* changes to a dark phase on light sand as herein discussed and *Chaetodipterus* behaves similarly (Breder, 1948), a reaction that is opposite in sign to that of *Gambusia*. Nevertheless both reactions tend to make the fishes less conspicuous. With such a situation and the additional fact that some fishes will operate in one way under certain conditions and the other under other influences, it is clear why such behavior in various species casually observed has led to complete confusion as to the utility or lack of utility of these vagaries of behavior of the pigmentary systems. There is, however, enough miscellaneous data now accumulated on these matters to make it evident that an understanding of the functional utility of such pigmentary behavior can be understood only in terms of the total pattern of behavior of a given species, throughout its ontogeny.

Phylogenetically it may be considered that the whole gamut of possibilities, such as outlined in their basic features in table 1, would be open for evolutionary exploration. Then fishes as they exist today represent the successful results of such "exploration." How

many and which ones of these items in any given fish are of real utility and survival value and how many are relics or accidental, can be worked out only with detailed study of a given species. It does not follow that because a condition can be shown to be valuable to one species it has the same, or any, value if present in another.

Under the term "protective coloration" and similar qualitative and variously charged words and phrases, the ability of many animals to "hide" in the open has long been discussed by naturalists in usually the most superficial manner. In an attempt to consolidate some of these concepts, most recently, Breder (1946) extended a table in which various attributes were considered. These included items that make it more difficult for any animal to be seen, covering both the static aspects such as coloration and form and dynamic aspects such as posturing and certain movements. The term here used, protective appearances, serves to cover all of these and is to be used in contradistinction to "protective behavior" such as is employed in actually hiding under some object or openly fleeing, and is not concerned with becoming difficult to see in the ordinary sense.

Obviously, on a theoretical basis at least, an organism could be conceived of which depended entirely on protective appearances alone to escape destruction and to which its other behavior contributed nothing whatsoever. Contrariwise, another could be conceived of in which the reverse were true, such as a very conspicuously colored animal which depended alone on flight for escape from enemies. These two would represent either extreme of a series. A little consideration would show that actually most animals are somewhere between these two extremes. For example, a rabbit clearly uses both open and obvious flight as well as freezing with consequent merging into the landscape. A pseudo-mathematical description of this condition may serve to clarify this concept. If scales are laid off on coordinates with "protective appearances" on the *Y* axis and "protective behavior" on the *X* axis then points may be plotted in terms of *X* and *Y*, as is shown in figure 1. Since, because of the way the graph is constructed, an increase in either value indicates an increase in the degree of the pro-

tection that a given case possesses, certain postulates may be made. If we call 100 the minimum amount of protection necessary to the survival of an animal, then the following conditions obtain:

Survival follows where  $Y+X=100+a$   
 Neutrality follows where  $Y+X=100$   
 Destruction follows where  $Y+X=100-a$

$a$ =net gain in protection. Thus a line drawn from  $Y=100, X=0$  to  $X=100, Y=0$ , as in figure 1, contains all the points at the line of division between successful protection (or survival) and failure. This covers all cases from complete protection by behavior to complete protection by appearances. In other words, if protection by one is not 100, then the difference must be made up by the other to the extent of that deficiency. In graphic terms, this means that any sum of  $X$  and  $Y$  falling within the  $45^\circ$  triangle will fail of survival and any exterior to it will succeed.

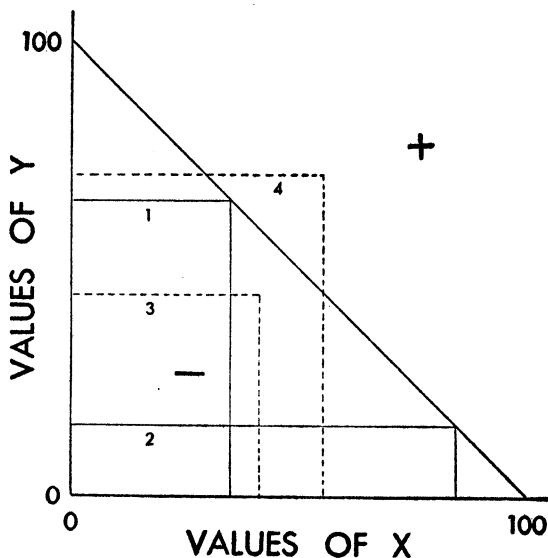


FIG. 1. Relationship of two factors that supplement each other, such as protective behavior and protective appearance. 1. Minimum protection where protective appearance is large and protective behavior small.  $X+Y=100$ . 2. Minimum protection where protective behavior is great and protective appearance is slight.  $X+Y=100$ . 3. Less than minimum protection but where both components are about equal.  $X+Y=100-a$ . 4. More than minimum protection but where both components are about equal.  $X+Y=100+a$ .

The greater this excess the more heavily protected the organism becomes.

Since organisms are essentially energy exchange mechanisms, it follows that to obtain a net energy increase for growth, reproduction, and so forth, there must be an excess of energy intake over the expenditure necessary to obtain the new energy. That is to say, the food captured must exceed in energy the amount expended for its capture. This may be illustrated by figure 2 in which  $Y$ , the energy gained, is plotted against  $X$ , the energy expended. Equal values for  $X$  and  $Y$  yield a 0 gain and fall along a line from the origin at  $45^\circ$  so that any absolute value of the energy expended equals that gained.

Successful feeding follows

where  $X < Y$   $Y-X = +b$   
 Neutrality follows where  $X = Y$   $Y-X = 0$   
 Starvation follows where  $X > Y$   $Y-X = -b$

$b$ =net gain in energy. Thus, points above the diagonal line show a net gain in energy and those below it a net loss. Obviously a successful animal shows values above this diagonal, and its food must be obtainable in such terms. The more remote such points be-

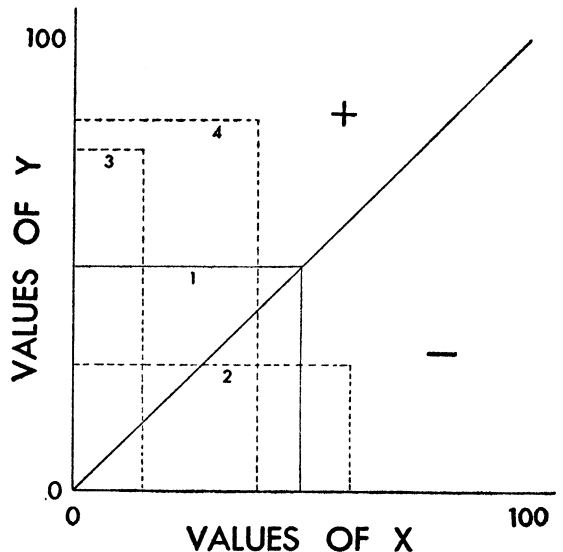


FIG. 2. Relationship of two factors that oppose each other, such as energy gained and energy expended. 1. Intake equals outgo.  $Y-X=0$ . 2. Intake is less than outgo. Starvation.  $Y-X=-b$ . 3. Intake exceeds outgo but is less than  $100-X$ .  $Y-X=+b$ . 4. Intake exceeds outgo and is more than  $100-X$ .  $Y-X=50-b$ .

come from the diagonal the more available its food becomes up to the limiting value of possibility of ingestion. If we postulate that 50 units are a minimum requirement, then in addition to the negative area already indicated, it extends to the  $Y$  axis along the ordinate of 50.

Another item bearing strongly on the present considerations is the fecundity of a form in relation to the amount of destruction. Figure 2 may also serve to show this relationship.

Population increases where  $X < Y$   $Y - X = +c$   
Population static where  $X = Y$   $Y - X = 0$   
Population decreases where  $X > Y$   $Y - X = -c$

$c$  = gain in population. Since normal populations of many animals are usually relatively static or fluctuating slightly about a mean, it follows that this differs from the two preceding cases in that the usual condition is that

where  $X = Y$ . In order for this to be realized, since it is based on a positive value for  $b$ , it follows that the usual condition for energy intake is for  $X < Y$ .

Since the absolute population size is of importance for the continued success of a population and there is some lower value below which a population may not be reduced without destruction, for present purposes a minimum value for  $Y$  may be set at 50. Then for graphic purposes figure 2 serves as it did for the prior case and what has been said for the former applies equally to the latter, with appropriate changes in the names for which the values stand.

From these illustrations it should be evident that a great many items could be paired and considered in terms of either figure 1 or figure 2 depending on whether  $X$  and  $Y$  supplement or oppose each other.



## SUMMARY

1. THE POSSIBLE REACTIONS open to fishes in regard to attack, feeding needs, social behavior, pigmentation, time, and space may be conveniently tabulated in theoretical terms.

2. The actual reactions observed in a variety of fishes compared with the theoretical tabulation show that illustrations filling nearly every category exist.

3. Included in such illustrative material are new data on the pigmentary and associated behavioral reactions of *Manta*, *Strongylura*, *Hippocampus*, *Hepsetia*, *Sphyræna*, *Coryphaena*, *Apogonichthys*, *Pomacentrus*, *Abudefduf*, *Halichoeres*, *Thalassoma*, *Holocentrus*, *Bathygobius*, *Gnatholepis*, *Stethmono-*

*tus*, *Canthigaster*, *Histrio*, *Antennarius*, and *Ogcocephalus*.

4. These data indicate that study in greater and more exact detail must be made of the total behavior of a given species in reference to its pigmentary changes before any clear picture can be had of the full significance of the activity of the pigmentary system.

5. A scheme for representing the relationships between various factors in the survival of organisms, covering cases where pairs of factors are supplementary and cases where they are opposed, is found convenient when discussing their various reactive patterns.

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