

# THE ADJUSTMENT OF FLATFISHES TO VARIOUS BACKGROUNDS:

## A STUDY OF ADAPTIVE COLOR CHANGE<sup>1</sup>

FRANCIS B. SUMNER

*From the Naples Zoölogical Station and the U. S. Fisheries Laboratory, Woods Hole, Mass.*

### THIRTEEN PLATES

#### 1. INTRODUCTION

That many fishes are strikingly adapted to their surroundings in respect to their general coloration is a fact familiar to all. A casual inspection of any well-stocked aquarium will reveal numerous examples. This adaptation is probably exhibited with greatest constancy by the flounders and other bottom-dwelling species, though some very striking examples are to be found among fishes which inhabit marine algae. In the latter class, a noteworthy instance is the 'sargassum fish,' *Pterophryne histrio* (Linn.), which dwells among the fronds of the 'gulf-weed' and with it occasionally drifts to our New England shores.

It has likewise long been known to naturalists that certain fishes possess the power of changing their colors more or less rapidly in conformity to variations in the color or the shade of the background. Those, for example, who have had much to do with the common 'minnow,' *Fundulus heteroclitus* (Linn.), in our laboratories at Woods Hole, realize that this fish becomes far paler when kept in a white vessel than when kept in a dark one.

<sup>1</sup> I take pleasure in acknowledging my indebtedness to the director and staff of the Stazione Zoologica at Naples, and particularly to Dr. Victor Bauer and Dr. Richard Burian, for abundant facilities and valuable advice. To Columbia University I owe the privilege of occupying the table maintained by that institution at the Naples Station. Finally, my thanks are due to the United States Commissioner of Fisheries for permission to publish herewith the results of work conducted at the Fisheries Laboratory at Woods Hole.

The work of Pouchet<sup>2</sup> and a number of subsequent investigators has shown that the stimuli which call forth these responses are received through the eyes, since fishes which have been deprived of their sight no longer change adaptively. Blind fishes may, it is true, undergo changes of color, but these changes bear no relation to the optical properties of the environment. And indeed normal fishes may exhibit rapid changes of color, as a result of what have been not very appropriately called 'psychic' stimuli, *e.g.*, fright, sexual excitement, etc. Thus Newman<sup>3</sup> has given us an account of the play of colors in *Fundulus majalis* during 'courtship' and Townsend<sup>4</sup> has described and figured the color changes which he has observed in fishes of a number of species in the New York Aquarium. But changes such as these do not, so far as we know, have any adaptive significance whatever. They are probably of no more utility to the animal than are blushing and various other indications of emotional disturbance in ourselves.

It now seems to be fairly certain that the immediate cause of the color changes of fishes, as well as those of many other animals, is a movement of the pigment granules within the chromatophores of the skin, and not an actual contraction and expansion of the chromatophores themselves. The work of Pouchet, Van Rynberk<sup>5</sup> and others has shown that the efferent nerve-tracts which control this action of the color-cells pass through the sympathetic trunks. Section of the spinal cord alone will not result in a paralysis of the chromatophore function below this level; section of the sympathetic chain will do so. But just as muscle or gland cells may be called into activity by stimuli applied directly, without the intervention of nerve fibers, so the chromatophores may undergo a

<sup>2</sup> The most important of this writer's contributions to the anatomy and physiology of the chromatophores are presented in the "Journal de l'Anatomie et de la Physiologie," 1876, pp. 1-90 and 113-165.

<sup>3</sup> Biological Bulletin, April, 1907.

<sup>4</sup> Thirteenth Annual Report of the New York Zoölogical Society, 1909.

<sup>5</sup> Van Rynberk (*Ergebnisse der Physiologie*, Bd. 5, 1906) presents copious abstracts of the work of the principal previous investigators in the field of color change among animals; likewise what seems to be a fairly exhaustive bibliography of the subject up to the date of his publication. For this reason, I have not thought it necessary to cite many of these earlier papers myself.

concentration of their pigment granules as a result of mechanical stimuli, the electric current, etc. From the mechanism of color change, we should naturally expect that the chromatophores in their resting condition would be darker than when subjected to stimulus, and this appears to be the rule.

Such, in brief, are the main facts which have been recorded regarding the physiology of color change among fishes. It is my purpose in the present paper to give the results of some experiments which were conducted by me at Naples during the earlier months of the year 1910, and which were continued at Woods Hole during the succeeding summer.<sup>6</sup> In these studies, I have been chiefly concerned with the relations between the stimulus and the response. Very little attention has been given by me to the physiological mechanism of this response, though experiments with blinded fishes have, it is true, been performed.

While viewing specimens of one of the common European turbot, *Rhombus maximus* (Linn.), in the aquarium of the Naples station, I was impressed by the detailed resemblance which obtained between the markings of the skin and the appearance of the gravel on which the fish rested. Now although the pattern of the animal was such as to harmonize very strikingly with this gravel, it would not have harmonized particularly well with fine sand, even if similarly colored, nor would it have been well suited to a bottom of large stones. The query at once suggested itself: Is it a mere coincidence, this detailed agreement of the fish with its present background, or does the fish have the power of controlling the color pattern as well as the general color tone of the body?

Curiously enough, I have found scarcely any references in the literature to adaptive change in the color pattern of fishes,<sup>7</sup>

<sup>6</sup> A report upon some of these results, illustrated by lantern slides, was presented before the research seminar of the Woods Hole laboratories last summer, and similar reports have been read before the American Fisheries Society, New York, September, 1910 (published in the 'Transactions'), and before the American Society of Zoölogists, at Ithaca, December, 1910. A brief popular statement, with five illustrations was published in the *Zoölogical Society Bulletin* (N. Y. Zoöl. Soc.), November, 1910.

<sup>7</sup> The only direct reference which I have found to differences of color pattern displayed by the same fish on bottoms of different texture, is contained in Cun-

though changes of color tone, both adaptive and non-adaptive, have been discussed by a large number of writers. That changes of the former class actually occur will be evident to anyone who devotes a moment to the inspection of my figures. Indeed they are, in many instances, so striking that it is impossible to believe that they have been wholly overlooked in the past.<sup>8</sup>

The fish from which I obtained the most favorable results was a small species of flounder, *Rhomboidichthys podas* (Delaroche)<sup>9</sup> belonging to the Psettinae or turbot tribe. This species occurs in various parts of the Mediterranean Sea, but unfortunately it is not so common in the Bay of Naples as one might desire for experimental purposes. Less than forty<sup>10</sup> specimens were at my disposal during a period of about four months; and during the latter part of my stay the supply gave out completely. For this reason, certain important tests were left untouched.

Two larger species of turbot, *Rhombus maximus* (Linn.) and *R. laevis* Rondelet, were used in a limited number of my Naples experiments; and gobies and several species of soles were likewise tried, but without any results worth recording.

At Woods Hole, my observations have been confined almost wholly to the common 'sand-dab' or 'window-pane,' *Lophopsetta maculata* (Mitchill), which, like *Rhomboidichthys*, is a representative of the turbot group. Casual observations upon the 'sum-

ningham's "Treatise on the Common Sole," (Plymouth, '90, part iii, chapt. iii). The author here describes and figures a spotted condition which is said to be manifested by this fish upon bottoms of gravel; but he later asserts: "All the changes are evidently due to the action of light and depend on the quantity of light acting on the sole, not on the tint or texture of the ground on which it rests."

<sup>8</sup> Townsend (op. cit.) mentions and figures cases in which the markings of various fishes appeared and disappeared under different conditions; and Pouchet (op. cit., p. 81-82) had earlier described a conspicuous, but apparently non-adaptive, change of color-pattern in *Callionymus lyra*. Indeed certain instances of this phenomenon are doubtless familiar to many persons, but most of such changes probably do not have any adaptive significance.

<sup>9</sup> This species was one of those employed by Van Rynberk (op. cit., p. 549). Strangely enough, he makes no mention (at least in the work cited, which alone is accessible to me) of the extraordinary changes of pattern displayed by this fish.

<sup>10</sup> Of these a considerable proportion died within the first few days of captivity. Some specimens, on the other hand, lived for many weeks, and from such my best results were obtained.

mer flounder,' *Paralichthys dentatus* (Mitchill), and the 'winter flounder' *Pseudopleuronectes americanus* (Walbaum), made it evident that these, likewise, manifested interesting pigment changes of an adaptive nature, but no systematic experiments were performed.

In the ensuing text, I shall first discuss the experiments with *Rhomboidichthys*, and the less searching ones upon *Rhombus*, at Naples; later the experiments upon *Lophopsetta* at Woods Hole.

## 2. EXPERIMENTS WITH RHOMBOIDICHTHYS PODAS.<sup>11</sup>

### *General description*

When first brought into the laboratory by the collectors, the fishes were more commonly of a rather dark brown color, with inconspicuous darker and lighter markings (fig. 3c). This fact makes it seem likely that they were generally taken upon the dark, mixed sand, composed of finely divided lava and tufa, which is so common in the Bay of Naples. On the other hand, some specimens were fairly light when received, though never of a shade even approaching the maximum degree of pallor which they attained under experimental conditions. In a few instances, the intra-annular areas (see below) were white or nearly so in the freshly received specimen, giving to the latter a conspicuously mottled appearance (fig. 7). Such specimens, if we may judge from the results of my experiments, had probably come from a bottom diversified by white shell fragments.

<sup>11</sup> The collectors of the Stazione Zoologica recognize but one species of *Rhomboidichthys*, and Van Rynberk (*op. cit.*) refers to the species upon which he worked as *Rhomboidichthys (manus seu podas)*. On the other hand, Canestrini and others list two species, '*Rhombus podas*' and '*Rhombus rhomboides*,' which are said to be very similar, differing chiefly in the distance between the eyes. Moreau (*Manuel d'Ichthyologie Francaise*, '92, p. 469), under '*Bothus podas*,' cites Steindachner to the effect that there is but a single species of which '*B. rhomboides*' is the male and '*B. podas*' the female. I have followed the usage of the Naples Station in referring all my specimens to the same species, although marked differences are to be noted in the shape, and especially in the distance between the eyes. Compare, for example, specimens 3 and 4, plates 6 and 7.

For an understanding of the color changes undergone by this species, some account is necessary of the permanent markings or aggregations of visible pigment. These markings are so complex in their arrangement that a satisfactory account of their condition in any one color phase would be a most laborious task, and an adequate description of their changes under various circumstances would be practically impossible. These markings may, however, be referred to several rather distinct types according to their general appearance and behavior.

1 We have a considerable number of circular, elliptical or pear-shaped spots, each bounded by a series of small white dots. The areas within these dotted outlines vary in shade, according to conditions, from a nearly pure white to a shade uniform with the ground color of the fish, however dark that color may happen to be. Some of the most striking alterations of appearance which are manifested by this fish are due to the changes undergone by this first type of spots. The rings of dots bounding these areas I shall call the 'annuli,' the areas within the latter being the 'intra-annular areas.' For the sake of brevity, I shall refer to the markings thus constituted as the 'pale spots,' where no confusion will result from this designation. So far as I have observed, the white dots making up the annuli never wholly disappear, even in the darkest condition assumed by the fish on any bottom (figs. 1c, 9d). At times, the entire areas inclosed by them are almost pure white, but the central region usually remains somewhat darker. Under certain conditions some of these spots have a rather striking resemblance to patches of lichen.

The markings of this type are arranged with a considerable degree of regularity, and it is likely that their disposition is essentially similar in all members of the species. They may be distinguished as marginal and central, according to their position. A regular alternation of annuli of different sizes (primary, secondary and tertiary) will be noted along the margin of the body. The inner edges of certain of the largest marginal annuli expand into conspicuous white crescent shaped areas. This is particularly true of one pair of primary annuli lying some distance behind the middle of the body.

Especial mention must here be made of one spot, differing in some respects from the foregoing, and lying just behind the base of the pectoral fin. This spot is elliptical in shape, and bounded by a paler outline, in which the dots are commonly not very distinct. It undergoes great and oftentimes very rapid changes of shade, and is frequently the most conspicuous white spot upon the fish. Under certain conditions of extreme contrast in the skin pattern, this spot is found to merge into adjacent white areas, so as to form an irregular white blotch of considerable size (figs. 1j, 1l, etc.).

2. Small, nearly circular spots, more regular in outline than those of the preceding type, and in some respects just the reverse of the last. Each consists of a dark ring, inclosing a center which is usually somewhat paler than itself, and the spot as a whole is usually somewhat darker than the ground-color of the fish. These spots are generally much less conspicuous than are the pale spots, and at times they practically disappear from view. At other times, however, they stand out as dark brown circles against a paler background (figs. 2c, 3a). It is probable that these spots, like those first considered, are fairly constant in their arrangement for all members of the species.

3. Large dark blotches of variable occurrence, which may better be characterized as 'permanent possibilities' than as constant features of the pigment pattern of the fish. These large blotches appear, in every case, to form around one of the spots of the preceding type (2) as a nucleus. They are conspicuous features of the skin pattern, in all cases where a blotched or highly contrasted appearance is exhibited, and it is probable that they always reappear in the same positions. On the other hand, they may be wholly wanting when the animal assumes a homogeneous or fine-grained appearance. The most nearly permanent blotches of this type are three which occur along the lateral line. The second of these, lying about two thirds of the distance from the snout to the base of the caudal fin, is the most constant of the three, and in some specimens probably never wholly disappears, even when the fish is in the most extreme con-

dition of pallor. But it is likely that dark areas may form on occasions around any of the spots of the second type.

4. As a phenomenon parallel to that last mentioned, the intra-annular areas seem at times to overflow their boundaries, thus producing larger pale blotches (figs. 1*l*, 4*d*). This fact has already been pointed out in speaking of the elliptical pale spot behind the pectoral fin.

There remain still more vague and impermanent arrangements of the pigment, which are very difficult to describe. Moreover, aside from these various types of spots and blotches, the remainder of the skin surface does not present a homogeneous coloration, but exhibits at times more or less well defined areas differing from one another in shade. Frequently, too, the outlines of the scales are conspicuously visible, contributing materially to the 'grain' of the surface.

Allowance must, of course, be made for the superficial character of the foregoing description. This crude classification of the markings of the fish is based upon external appearances only, no histological study of the skin having been undertaken. Indeed, it is probable that much of the diversity in the distribution of visible pigment in the skin of *Rhomboidichthys* is "functional" rather than "organic." Or, better stated, it may result not so much from diversity in the *distribution* of the chromatophores, as from local differences in their tonus, under the influence of the nervous system, these last being determined perhaps by the distribution of the efferent nerve fibers.<sup>12</sup>

Regarding the color of *Rhomboidichthys*, little need be said at present, since this will be discussed in relation to the various phases assumed by the fish. I need only state here that the animal is almost wholly restricted to black, white and various shades of gray, brown and yellow. It must be added, furthermore, that the browns and yellows are scarcely ever brilliant in quality, being dull tones, of a low degree of saturation. Thus they depart little, if at all, from the various hues which we encounter among the

<sup>12</sup> Mayerhofer (Archiv für Entwicklungsmechanik der Organismen, 1909) states that the chromatophores of the pike (*Esox lucius*) are distributed uniformly without reference to the dark crossbands of the body.



fragments of lava, tufa, shells and pottery, constituting the seabottom in the vicinity of Naples.<sup>13</sup>

In considering the appearance of this fish upon a given bottom, it must be borne in mind that the marginal fins (homologous with the dorsal and anal) are translucent, or indeed at times nearly transparent, and that through them the underlying bottom may commonly be seen distinctly. In this way, the harmony of appearance between fish and bottom is oftentimes greatly enhanced. When resting upon a bottom of sand or fine gravel, the fish frequently covers over the marginal fins, and sometimes more or less of the remaining skin surface, with the material at hand. This it does by a rapid undulatory movement of the body, by which it stirs up the sand or gravel and settles down into it.

### *Methods*

The specimens were kept in glass jars, either circular or rectangular in form, and commonly supplied with sea-water from a large tank by means of siphons. When natural materials were employed for the background,<sup>14</sup> these were emptied directly into the bottom of the jar. Artificial backgrounds were produced by painting the bottom of the jar directly, or by painting glass plates which could be inserted at pleasure. An account of the different types of background employed in these experiments will be deferred until I come to a consideration of the results which were obtained.

The fishes were kept for longer or shorter periods under the various experimental conditions, notes and descriptions being made from time to time. Since verbal descriptions of such phenomena are necessarily quite inadequate, frequent photographs were made. In order that the colors assumed might be recorded with approximate accuracy, reference was in many cases made to the

<sup>13</sup> I do not mean by this to imply that there is any specific adaptation to this particular locality. Sands and gravels of a very similar appearance, though differing widely in their mineralogical composition, are doubtless to be found all over the world. Samples of gravel which I brought back with me may be matched, as regards their general appearance, by gravels collected in the vicinity of Woods Hole.

<sup>14</sup> I have throughout used the word background to designate the surface upon which the fish lay.

'Code des Couleurs' of Klincksieck and Valette (Paris, '08). Differences of color (as distinguished from shade) played, however, a minor part in my observations, partly because no very striking changes of color occurred, partly because of the difficulty of reproducing changes of this sort.

*Photography.*<sup>15</sup> The camera used<sup>16</sup> was mounted vertically upon a frame made for the purpose, the jar containing the fish being placed upon a horizontal platform below. With a few exceptions, the bellows of the camera was always drawn out to the same point, so that practically all of my photographs are in the same scale. This is slightly over two-thirds (69 hundredths) of the natural size. In the present reproductions, this has been reduced to approximately one-half of the natural size.

Fortunately *Rhomboidichthys podas* is ordinarily a quiet fish and may generally be depended upon to remain still long enough to allow of a satisfactory exposure being made. The time required for this varied, depending upon the light, from a small fraction of a second to one minute or more. The intensity of sunlight, during an average spring day in Naples, varies enormously from hour to hour, and even from minute to minute, a fact which made it very difficult in many cases for me to estimate the proper time required for the exposure. It would have been much better, had it been practicable, if an artificial light of constant intensity had been employed, and the conditions of exposure, development and printing had been identical in all cases. Thus alone would the different pictures have been strictly comparable.

As is well known by anyone at all familiar with photography, quite different appearances may be given to the same object by the use of varying technique. This is particularly true of the relative values of light and shade. An object of intermediate

<sup>15</sup> I must confess to having had no experience with this sort of photography prior to the work in hand, a fact to which, I fear, some of my results bear abundant witness. My profound thanks are due to Dr. Victor Bauer, of the station staff, for much assistance and instruction.

<sup>16</sup> This camera was one made by Curt Bentzien, Goerlitz, and the lens by Voigtlander and Son ('Major'). Lumière and Son's 'Blue Label' plates were used, commonly 9x12 cm. in size, though in some cases 13x18 cm.

shade, lying upon a white or a black background may be caused to vary in appearance from pale gray to nearly black, without in the least affecting the value of the background. In the case of the present subject, not only might the shade of the fish as a whole be caused to vary enormously, but spots which were in reality very conspicuous could be toned down, almost to the point of disappearance. Thus it would be quite possible to produce some (though by no means all) of the differences which appear in my plates by differences of exposure, development or printing.<sup>17</sup> There is therefore abundant opportunity for self-deception and unintentional exaggeration of one's results, unless this source of error is guarded against. The precautions taken, in my own case, were as follows:

1. My notes upon the experiments give important clues, in respect to fishes to be compared, as for example, when one is said to be "much darker" than the other, or to have become "much paler" in the course of 24 hours. After considerable experience, one acquires fairly accurate standards of comparison and is able to pass such judgments with confidence.

2. The negative was usually developed very soon after the exposure was made, and frequently while the fish still remained upon the bottom which had been employed. Thus it was possible either to compare the negative directly with the object, or at least to pass upon the former while the appearance of the latter was fresh in memory. Likewise, prints were generally made before the lapse of many days.

3. In some cases, fishes which were to be compared were photographed together upon the same plate (*e.g.*, some of the figures on plates 12 and 13, and many others which I have not included as illustrations).

<sup>17</sup> For example, as I know by actual experience, such differences as those shown in fig. 1*j* and 1*l*, plate 3, or between fig. 4*d* and 4*e* plate 7 might be brought about very readily by differences of printing; and in such a case, the backgrounds would afford little evidence of this misrepresentation. On the other hand, differences such as those between the skin patterns assumed upon gravel and upon sand or between the latter and the highly contrasted effects assumed upon some of the checker patterns would be utterly impossible to bring about by any differences of photographic manipulation.

4. Certain of the bottoms, notably the natural sands and gravels, form very good standards of comparison in judging of two negatives. If, for example, the familiar dark mixed sand of my experiments has the same value in two cases (either in negatives or prints) it is likely that the relative shades of the fishes have been preserved sufficiently well. Samples of these sands and gravels were saved by me and were referred to during the preparation of this paper.

5. While making some of my exposures, I included a strip of white opaque glass, painted so as to be divided into three bands, white, black and gray respectively. This was of considerable value in certain cases, but its application was rather limited.

6. Finally, a plate commonly bears in itself evidence of its having been over or under-exposed or developed, and this may be allowed for in printing.

In spite of such errors as may have crept in, owing to imperfect technique in photography, I cannot believe that the value of my results has been very materially impaired. Furthermore, I believe that the consequence of such defects of technique has, on the whole, been rather to decrease than to exaggerate the differences of pigmentation which are portrayed in my illustrations, and to minimize many of these instances of adaptation. For the color (as distinguished from the shade) was frequently an important element in the adaptation and this, of course, is not indicated in the figures. Again, the condition of extreme pallor assumed by many of the specimens upon a white background is impossible to reproduce by ordinary photographic processes,<sup>18</sup> since the skin of the fish always retains a certain amount of yellow, and this, as is well known, looks disproportionately dark in a photograph. Thus figures 1*k*, 10*a*, etc., give a very imperfect idea of the degree of blanching which these fishes had undergone upon a white bottom, and fig. 4*i* greatly minimizes the extent of the adaptation of this specimen to its gray background. According to my notes the appearance of the two harmonized very well at the time, but the photograph represents that of the former as

<sup>18</sup> A color screen might have been used, but this was not done.

much darker. Notwithstanding the justifiability of such a procedure in some cases, I have not taken the liberty of altering either the plates or the prints by pen or brush, not even (with a few unimportant exceptions) for the purpose of correcting imperfections or blemishes. I have, however, 'intensified' a number of negatives which had been underexposed.

In order to supplement these photographic illustrations, and to give an idea of the actual color of this species in two different phases, I reproduce (plate 6) two water-color sketches by Mr. V. Serino, one of the artists of the Naples station.<sup>19</sup> The artist has done well with a very difficult subject, but the constant slight changes in the disposition of the pigment of this fish proved to be extremely baffling. Moreover, the specimen chosen for these sketches, of which I have given photographic reproductions in figs. 3*a* and 3*b*, did not prove to possess the power of color adaptation in as high a degree as did many others. Thus the difference between the 'sand' and the 'gravel' phase is not nearly as striking as that shown by some other specimens. (Cf. figures 2*e* and 2*f*, plate 5).

#### *Responses to the various backgrounds*

To commence with the natural backgrounds, we have:

1. A rather coarse, mixed sand, consisting of particles of lava, tufa, shells and other materials. The general tone of this sand was very dark, since it consisted largely of jet black particles (probably magnetite, in part), but it contained abundant white and pale gray specks, which contrasted strongly with the rest. This material is of frequent occurrence in the bay, in the vicinity of Naples. Probably the majority of the fishes, as already stated, harmonized fairly well with this sand, when first brought into the laboratory. When kept upon this material, the harmony oftentimes became quite striking (figs. 2*f*, 4*c*, 9*a*). The resemblance consisted not only in the general similarity of color-tone, but in the granulated appearance of the fish's surface, and the presence of the white specks of the 'annuli' (see p. 414), which matched

<sup>19</sup> One of the many courtesies for which I have to thank the director of the station was the placing at my disposal of the services of Mr. Serino for a number of days.

the minute white particles (shell and tufa) of the sand. There was, nevertheless, nothing which could be regarded as very specific in this resemblance. It was a harmony of the same sort that we meet with frequently, both among land and water animals.

2. A fine gravel of a predominantly gray tone, apparently composed of about the same materials as the last, but much coarser, and containing a larger proportion of the paler ingredients. For the latter reason it was, on the whole, of a considerably lighter shade. The particles ranged in size from a few millimeters to about a centimeter in diameter, and in shade from pale gray or white to black. The general appearance was thus diversified, and this effect was heightened by the presence of yellow and red fragments. Upon gravel of this type the adaptation of the fish was often very striking (figs. 1*b*, 2*e*, 5). Here it is plain that no single color or shade, disposed homogeneously throughout the animal's surface, would have rendered it inconspicuous to any such extent as this. It was necessary that the diversity of the background should be matched by a corresponding diversity on the part of the fish. The way in which this was brought to pass is difficult to analyze in detail, but the results are indicated in the figures. It is evident that the annuli have come conspicuously into view, the intra-annular areas being pale, but commonly broken up more or less by darker shading. The brown spots of the second type (p. 415) have also become rather conspicuous, and the general ground color of the skin, which had earlier been dark and fairly uniform, is now diversified by various sized patches of contrasting shades. One of the striking features of the present skin pattern is the curious appearance of transparency which is often manifested, as if we were actually looking through the body of the fish and saw the gravel underneath.<sup>20</sup> This effect is heightened, in some cases, by the appearance of certain of the dark spots, which are darkest at the center, and shade off into a paler margin. These spots convey the impression of depressions among the pebbles which seem to surround them. This appearance may be merely one of those

<sup>20</sup> This, of course, is true of the marginal fins, but is not at all true of the body proper. Moreover, even the marginal fins undergo pigment changes which contribute to the general harmony of appearance (Fig. 2*e*).

'accidents' of nature, of which we hear so much, but it is hard to suppress the belief that it is an integral part of the process of adaptation which we are considering.

3. A coarse gravel, composed of stones ranging from 2 to 3 or 4 cm. in diameter. This is not strictly to be included among the natural types of background, since much mud and sand had to be sifted away in order to obtain it. The stones ranged in shade from nearly white to nearly black, and the diversity was increased by the occurrence in small numbers of reddish or brown pieces. In most of my experiments, white shells and smooth fragments of marble were added in order to heighten the contrasts. This type of bottom was used with only four specimens, but rather impressive results were obtained from two or three of these. In the most striking of these (fig. 1e) most of the annuli became inconspicuous, as well as the finer elements of the skin pattern generally, and certain large dark areas came into view, giving to the fish a coarsely marbled appearance. This effect rapidly disappeared, in large degree, when the fish was transferred to a background of white glass, but reappeared upon its being returned to the coarse gravel. A similar appearance was manifested by this specimen upon certain of the other backgrounds (see below), and the same large dark areas may be distinguished in a number of the figures.<sup>21</sup> But the 'marbled' effect came into view clearly only in cases in which it was appropriate, *i. e.*, upon a field having a coarsely blotched appearance.

Another specimen, which had been kept for 11 days upon the coarse gravel became in time—though rather gradually—quite strikingly adapted. Unfortunately the fish escaped from the jar and died, before any photographs were taken, but my notes state that: "for past few days mottled effect had become quite striking, showing a fusion both of darker and lighter areas into larger spots."<sup>22</sup> One of the other specimens, on the contrary, assumed an appearance which though plainly a mottled and 'gravelly' one, was more nearly adapted to the fine gravel than to the coarse. As

<sup>21</sup> This specimen seemed predisposed to the production of these effects, since the coarse blotching was dimly evident when the fish was first received.

<sup>22</sup> This is probably not a very accurate account of the origin of these larger spots.

regards the fourth of these specimens (no. 2), it will be seen by a comparison of figs. 2*c* and 2*e* that the appearance upon the coarse gravel was somewhat different from that upon the fine, and that the difference, so far as it went, seemed to be in the direction of a greater adaptation to the former. The case is not, however, a particularly striking one, since we should regard the appearance of the fish in fig. 2*c* as tolerably well adapted to the finer material. It is interesting that the coarsely blotched effect is here produced in a somewhat different manner from that shown in fig. 1*e*, since, in the present case, the pale spots are clearly in view all over the surface, and form a conspicuous part of the skin pattern.

Certain other materials were employed as backgrounds, 'which, although 'natural,' in the sense of occurring in nature, were not found in any part of the possible habitat of the species under consideration.<sup>23</sup> As the most important of these, we have:

4. A very fine, jet-black sand, composed almost wholly of crystals of magnetite. This was found in the bed of a stream in the island of Ischia, and had to be separated by means of considerable washing from the paler sand and mud with which it was mixed. Although of nearly a jet-black shade, these crystals gleam so much in certain lights that the sand may appear to the observer to be far from black (fig. 1*c*). My chief object in using this material was to test the question whether on a bottom devoid of white particles<sup>24</sup> the white specks forming the annuli would completely disappear. Three specimens were put to this test. One of these was the individual which I have designated as no. 1, this being a specimen which had yielded some of my most striking results. Fig. 1*c* shows the condition of the fish after a stay of four days<sup>25</sup>

<sup>23</sup> This is particularly true of the magnetite sand. On account of the high specific gravity of this substance, any other ingredients with which it was mixed,—and these were all much lighter in color—tended to separate out and come to the surface. It thus seems improbable that an uncovered bed of such material should be formed anywhere upon the sea-bottom, and could ever constitute a part of the normal environment of any fish.

<sup>24</sup> This could of course be likewise tested by placing the fish on a black painted bottom. But the consistency of the sand seemed better adapted to calling forth normal reactions.

<sup>25</sup> According to my notes, the maximum effect was attained after two days.



upon the magnetite, following seven days upon the coarse dark sand already referred to. As will be seen by comparison with fig. 1*a*, the fish became considerably darker than it had been while upon the preceding background. The general shade of the body became darker than at any other time during my experiments, and the intra-annular areas were little if any paler than the rest of the body. The annuli themselves, however, were still clearly visible, the minute, much contracted white specks being in conspicuous contrast to the rest of the surface. Whether or not even these specks would have finally disappeared remains problematic, though I regard it as improbable, in the case of this specimen, at least. After four days, white pebbles of about the size of a bean were scattered at considerable intervals over the black surface. I thought it likely that the pale spots of the fish would come more distinctly into view under the circumstances. This did not happen, however, at least in the course of two days—an interval which was usually more than sufficient in the case of this specimen.

Two other fishes (no. 10 and no. 11) were also tested with the magnetite sand, the former for a period of six days, the latter for twelve days. The results are shown in figs. 10*d* and 11*e* respectively. It is probable that neither of these specimens became any darker than upon the ordinary dark sand. It must be stated, however, that prior to their transfer to the magnetite sand, one of these specimens had been kept all of the time, and the other most of the time, during a period of two months, upon white or pale gray backgrounds. Owing to this cause, the pale condition had become in a certain sense fixed, as later experiments showed (p. 446).

5. A very coarse sand (perhaps better, a fine gravel) composed of white, gray and dark red particles. The latter gave the material much more color than was possessed by any of the preceding materials. This sand was taken from a beach, and was not, therefore, a submarine deposit. It was employed in only a few cases. One of these was my fish no. 1, which was, as stated, a particularly adaptable one. This specimen adjusted its skin pattern very well to the texture and the general shade of the material (fig. 1*d*), but the reddish color of the sand exerted little or no effect upon the animal,

even during a stay of eight days upon this material. Another specimen (fig. 6c) assumed much of the color as well as the texture of the sand. This fish which, my notes state, had exhibited very little red in its composition when kept on other backgrounds assumed, after six days on the sand, a general tone resembling the no. 122 of Klineksieck and Valette. Fig. 6c does scant justice to the extent of the harmony. A third fish (no. 4) was kept upon this sand for a period of six days. Although, in general, this specimen had been a highly adaptable one, it proved to be entirely refractory upon this material, changing little, if any, from its previous condition, which was quite ill-adapted to the present type of bottom.

A very coarse gravel, likewise containing considerable red in its composition, was employed, but only one or two specimens were tested upon this, and the results were negative.

6. A white sand-like preparation obtained by grinding up fragments of marble. Upon this, certain specimens became very much paler, though none of the three fishes tested attained the same degree of pallor as those which were kept upon the marble bottom of a large aquarium or upon white glass plates. Indeed, one of the three did not undergo any striking change, even after 11 days.

7. In another experiment, large, rounded fragments of nearly black lava were used in combination with this white artificial sand, giving a vividly contrasted effect. The result, in the case of specimen no. 1 (the only one tried) was the appearance of large dark blotches and a coarsely mottled effect, resembling that shown in figure 1e or figure 1f.

8. A background just the reverse of the last was obtained by the use of rounded fragments of white marble imbedded in the coarse dark sand (1) or in the magnetite sand. The only experiment in which the latter combination was employed gave negative results, as has already been stated. The marble fragments and coarse dark sand were used with specimen no. 6, and the effect is shown in figure 6b. A considerable measure of contrast was brought about in the skin of the fish, but on the whole less than I had expected. The pale spots were at no time even approximately white.

The remaining backgrounds to be considered consisted of hard, smooth surfaces, differing thus from all of the preceding ones, which consisted of more or less finely divided materials. Thus we have:

9. The white marble bottom of a large aquarium, and strips of white opaque glass, used in the bottom of smaller jars. Under the influence of such backgrounds, all normal specimens became considerably paler in the course of a few days at the most. A number of specimens which were kept in the large aquarium for a period of 14 of 15 days became extremely pale, some of them matching very well the marble bottom, which at the end of this period was considerably discolored by a deposit of diatoms or other microscopic plants. A pure white, or even a very close approach to this, was not, however, assumed by any of my specimens, even upon bottoms of opaque white glass.<sup>26</sup> The closest approximation to this was a very pale yellow or straw color, not very different from the '128 D' of the 'Code des Couleurs.'<sup>27</sup>

10. Nearly black bottoms, made of slate or glass, painted with asphalt varnish. Upon such backgrounds several of the fishes assumed an appearance which was as dark or darker than that displayed on the dark mixed sand. In no case, however, was there in such cases a very close approach to black, while one of the fishes, although apparently normal, remained of a pale brown hue for several days.

11. A tank, much larger than the rectangular jars used in most of these experiments, having glass walls and a glass bottom, through which light was reflected from below by a mirror, inclined at an angle of about 45°. The lateral walls of the tank were covered with black cloth, and the top by a sheet of galvanized iron, painted black within. In looking into this tank from above, the observer of course perceived a well-lighted field, practically coextensive with the entire bottom. Upon first thought, it

<sup>26</sup> No. 11 was kept for thirty-three days uninterruptedly upon marble and white glass.

<sup>27</sup> This comparison was made in the case of one specimen (No. 12), which, however, probably did not become quite as pale as no. 11 and possibly some others.

would seem that the fishes should behave in such a tank much the same as upon an ordinary white bottom of opaque material illuminated from above. As a matter of fact, however, only one<sup>28</sup> out of seven specimens which were used actually became paler, even after a stay of several (in one case 10) days in this tank. All the other specimens either become darker, if they had previously been pale, or remained dark, if taken from a dark bottom. An examination of the actual conditions of illumination showed the reason for this apparent anomaly. In order to see an illuminated surface below, it was necessary that one should look directly downward, *i.e.*, in a direction nearly perpendicular to the glass. The fish, however, necessarily viewed the bottom at a very obtuse angle, and perceived, not the illuminated surface of the mirror below, but a surface of total reflection, where the glass bottom met the air. This surface itself acted as a mirror, reflecting the darkened walls of the tank, rising above it. What the fish actually saw, therefore, was a dark surface, not a bright one. This could be verified by the observer himself by viewing the bottom at a proper angle.<sup>29</sup>

12. A few tests were made with glass strips painted with rather bright shades of yellow and red.<sup>30</sup> The two fishes used (no. 12 and no. 4) were ones which had, under some other conditions, shown a high degree of adaptability. One of these was kept for five days upon the red and an equal length of time upon the yellow, without any approach to the color of the background. The other was kept for 10 days upon the red, with equally negative results,

<sup>28</sup> This one later showed various other anomalies in its reactions.

<sup>29</sup> This same optical principle was responsible for another anomaly in my results which at first baffled me. I had, in the beginning, prepared my black and white patterns with paper and cardboard, mounted between two strips of glass, which included, of course, a film of air. Viewed from above, the pattern was perfectly clear and distinct, as seen through the water; but beyond a certain angle, one saw nothing but a shining mirror. I was surprised by the complete failure of the fishes to adjust themselves to these patterns, until I chanced to view one of the latter, at an appropriate angle, through the side of the jar. For further references to this point see p. 478, below.

<sup>30</sup> The red was of a shade closely approaching the no. 61 of Klincksieck and Valette, the yellow of a shade similar to no. 226.

as regards color. It became of a homogeneous tone, however, having previously shown a pattern with considerable contrast.<sup>31</sup>

It was with various painted patterns, in black and white, that perhaps the most striking of all my results were obtained. The following backgrounds of this sort were employed:—

13. Squares of black and white, alternating as in a checker-board. These were of four sizes, viz. 2 mm., 1 cm., 2 cm. and  $4\frac{1}{2}$  cm. square, respectively. One of the most interesting of my results is the difference in the appearance assumed by the same fish upon the 2 mm. squares and the 1 cm. squares. (Compare fig. 1*h* and 1*i*; also figs. 4*a* and 4*b*). In each case, the skin presents a much more fine-grained appearance when the animal is upon the smaller squares. The effect is much as if a draughtsman had taken fig. 1*h*, or fig. 4*b* and 'stippled' the pale areas with dark ink, thus breaking them up into smaller subdivisions; at the same time doing exactly the reverse with the dark areas, by filling them in with pale dots. Thus the *degree of subdivision* of the background—independently of the relative amounts of black and white—is shown to be an important factor in the stimulus.

The 2 cm. squares, which were painted rather crudely upon the bottom of a glass vessel, called forth a somewhat interesting appearance in specimen no. 1, the only one which was used for the purpose (fig. 1*f*). The same large dark blotches will be seen to have come into view, as were manifested by this fish upon the coarse gravel. But the pale spots, in the present instance, are likewise conspicuous, so that there is now more contrast between the lightest and darkest portions of the surface.

The effect of the  $4\frac{1}{2}$  cm. squares was tested with specimens 1 and 4. The former fish was kept upon this pattern for a period of seven days. During most of this time the animal seemed ill at ease, swimming around the jar at frequent intervals, and seldom lying upon the bottom in the attitude of complete rest. This

<sup>31</sup> These experiments are confessedly too few, and their duration too brief, to permit of our forming any final opinions, even as regards this species. Other observers have recorded radical changes of color in fishes, as witness the effects of monochromatic light upon *Nemachilus*, as reported by Secérov (Archiv für Entwicklungsmechanik, 1909).

was in contrast to the behavior of other fishes in the room, and in noteworthy contrast to its own previous and subsequent behavior. Upon being transferred later to the 1 cm. squares, it became tranquil at once. Equally interesting was the condition of the chromatophores while the fish was kept on these largest squares. Although this was the same specimen which had shown the coarsely blotched appearance upon the 2 cm. squares, the skin now took on a nearly homogeneous appearance (fig. 1*g*). This was nearly or quite of the same as the appearance of this and some other specimens while swimming. Specimen no. 4 did not exhibit so complete an effacement of its previous pattern when transferred to these largest squares, but the contrasts were greatly reduced. (Fig. 4*f*, *not* fig. 4*g*, which represents the condition at the commencement of active movement). The results from the tests with this pattern are perhaps such as might have been expected on the assumption that the areas were too large to admit of their undergoing a synthesis in the creature's brain. The animal's attention has perhaps vacillated between the light and the dark areas, with a resulting indecision as to what to do.<sup>32</sup>

14. White (or black) circular spots, upon a background of the opposite shade. The spots were of such a diameter, and spaced in such a manner, that their aggregate area was about one fourth that of the background. These patterns were used to determine to what extent differences in the proportional amounts of black and white in the underlying surface would lead to corresponding differences in the skin of the fish. Specimens 1 and 4 were again used for this purpose, and figs. 1*j*, 1*l*, 4*d*, and 4*e* give a decisive answer to this question. The appearance of no. 4 upon the darker of these two patterns (fig. 4*e*) was, indeed, one of the most picturesque results which I obtained in the course of my experiments. Despite the difference between the two in the form of the spots, and the fact that the intra-annular areas were not of as pure a white as on some other occasions, the animal merged almost insensibly into its background, and was scarcely visible

<sup>32</sup> The reader is at liberty to substitute less 'anthropomorphic' language, if his sensibilities are jarred by these words.

when viewed from a short distance. This seems especially remarkable when we consider that the vividly contrasted black and white condition of the fish was probably quite foreign to its experience prior to captivity.

15. Parallel alternating bands of black and white, each 1 centimeter in width. Upon these the fishes assumed an appearance (figs. 1*m* and 4*h*) not very different from that displayed on the 1-centimeter squares, *i. e.* the dark and light areas were highly contrasted. Nothing approaching a banded condition was manifested, and this was hardly to be expected, considering the disposition of the permanent pigment areas of the animal.<sup>33</sup>

16. A white plate, bearing patches of dark sand, cemented in place with Canada balsam. One fish (no. 11), after a sojourn of fifteen days on white marble, was kept upon this spotted plate for a period of eighteen days. A photograph, which was taken after thirteen days (fig. 11*b*) exhibits what would seem to be significant differences, in comparison with the appearance which had been manifested upon the uniformly white bottom (fig. 11*a*). I am not certain, however, that the somewhat speckled appearance shown in the former figure did in reality result from the character of the background; first, because these dark specks were of inconstant occurrence, coming into view on occasions and then disappearing again, and second because much the same appearance could be produced by disturbing the fish, even when the latter was on a clear white bottom. In favor of the influence of the spotted plate, on the other hand, is the fact that another specimen (no. 4) displayed a yet more conspicuously spotted surface, in the presence of scattered flakes of asphalt varnish, which had fallen upon the white bottom of the jar. The fish had previously been in the condition of extreme pallor, and devoid of prominent markings.

Upon these artificial patterns of black and white, the fishes used (most of all no. 4) lost, in large degree, the brown and yellow tints which they naturally possessed, and themselves became

<sup>33</sup> Of course such a banding, even if possible, would have been of cryptic value, only if the fish lay in the same position relative to the bands, which, in fact, it did not do.

nearly black and white. Such intermediate shades as appeared were chiefly of uncolored gray. The glaringly contrasted appearance which was manifested in some cases differed very significantly from the almost complete monotone which was frequently assumed upon homogeneous backgrounds. Such natural backgrounds as the variegated sands and gravels which were used produced an intermediate effect. A more or less specific skin pattern was evoked, but this did not commonly consist of areas which contrasted very highly.

Although the capacity of the fish to assume one or another pigment pattern was obviously curtailed in large degree by a fixed arrangement of the chromatophores, and doubtless by other morphological conditions, the possibilities of reaction, within these limits, were certainly striking. Perhaps the most startling example of this diversity in spite of sameness is to be found by comparing the effects of the 1-centimeter and the 2-millimeter squares (fig. 1*h*, 1*i*, 4*a*, 4*b*). An analysis of how these various appearances were produced, from a merely descriptive point of view, would be difficult and not very profitable. Enough illustrations are here given to enable anyone to make the attempt, if he feels so inclined.

At this point, it would be well for me to qualify the impression which the reader may have received from an examination of my figures and text. It must be admitted that such changes as I have described were not of universal occurrence. In the case of some fishes, indeed, the capacity for adaptation was found to be very slight, though I do not think that it was completely wanting in a single uninjured specimen. Again, some individuals were found to undergo certain changes quite readily, while completely baffled by others. For example, specimen no. 4 'balked' most persistently when placed upon the coarse reddish sand (p. 425), and, after six days on this material, remained in much the same condition as it had been when on the banded black and white background (fig. 4*h*). The pale spots were distinct, and the general appearance was one of conspicuous contrasts, with little trace of red. Now this fish had throughout been one of my 'star performers,' and later showed that its capacity for change was unim-



paired. I can offer no explanation for such an utter failure to respond to a new background, on the part of a fish so well endowed with this power. Certain other specimens, as already stated, reacted adaptively to this material, one to its texture only, the other apparently to its color as well.

Another instance of the same phenomenon was offered by specimen no. 6, which, after undergoing adaptive changes on a number of bottoms (including the just mentioned red sand), finally refused to adapt itself further, and remained for thirteen days conspicuously out of harmony upon two of the artificial backgrounds.

No. 8,<sup>34</sup> likewise, after having adapted itself strikingly to gravel (fig. 8*a*), and later responding unmistakably to black and to white bottoms, remained for nineteen days in the pale condition which was induced by the last, almost regardless of successive changes to a black-bottomed jar, colored gravel, and even the familiar dark sand. Whether or not the later condition of this fish was a pathological one I cannot state, since an accident brought its life to an end. At all events, the animal could see, as was shown by its following moving objects with the eye.

Again, it frequently happened that the degree of adaptation, even after the maximum effect had been reached, varied from time to time, and sometimes became reduced to nil, even while the fish remained undisturbed. This was noticed, for example, with specimen no. 1, upon such large patterns or stones as called forth the coarsely blotched appearance. These blotches were at times scarcely distinguishable. It was thought at the time that some of these changes in the extent of the adaptedness bore a direct relation to the degree of illumination, since it was on dark cloudy days that certain of these cases of disappearing pattern were recorded. I was not, however, able to verify this conjecture.<sup>35</sup>

Lastly, in a few cases, after the maximum effect had been reached, the resemblance to the background seemed actually to undergo a permanent decline. This appears to have been the

<sup>34</sup> Cf. p. 438.

<sup>35</sup> Pouchet (op. cit., p. 130 et seq.) had already observed such fluctuations in the degree of adaptedness, and these he was inclined to attribute to differences in the brightness of the day.

case with no. 6, upon the background of dark sand and white pebbles (fig. 6b). According to my notes, the pale spots of the fish were probably more conspicuously pale two or three days after the transfer of the latter to this bottom, than they were several days later.

In spite of these admissions, it must not be supposed that my illustrations represent occasional or exceptional instances. They naturally include, among others, my best results in the way of color adaptation. But it must be stated emphatically that most of those specimens which remained in health for a long enough period exhibited these changes in a marked degree. That my most striking results were obtained from comparatively few specimens is owing to the fact that comparatively few lived for more than a few weeks in the laboratory.

#### *Time required for these changes*

This time ranged from a few seconds to several days. A change involving the almost complete withdrawal from view of the skin pigments in a dark specimen probably required the longest period. Some of the best effects which were obtained in this direction, starting with dark fishes, were observed at the close of about two weeks, when three out of five specimens which had been put in together were found to harmonize very well with the somewhat discolored marbled bottom of the large tank. The other two specimens were very pale, though still somewhat mottled. Since I was absent during the whole of this period, I do not know how soon the maximum effect appeared.

In another experiment, two specimens were recorded as being 'far from white' after nine and ten days respectively on the marble bottom, though they were 'noticeably paler' within an hour or less after being transferred to the latter. On the other hand one fish (no. 12) attained nearly or quite the extreme condition of pallor after four days in a white jar, but this had been preceded by about two weeks on various pale homogeneous bottoms.

In general, it may be said that in the experiments with natural bottoms and with certain of the patterns, the maximum effect was

commonly attained within one or two days at the most, after which no further change was manifested. The fact already pointed out by Pouchet<sup>36</sup> and Van Rynberk<sup>37</sup> that 'practice' or habituation to these changes, greatly reduces the time required, was clearly shown in my experiments with *Rhomboidichthys*. Certain specimens, after several changes of background, were found to adapt themselves in almost full measure to one of these within a fraction of a minute. The first of these changes had required some hours.

A case worth citing here is that of specimen 11, which had been kept for two months upon white and pale gray backgrounds. This fish, after transfer to the pure black magnetite sand, did not reach a medium shade in less than five days,<sup>38</sup> and continued to become darker for some days thereafter. Now this, it must be remembered, was a change toward what would ordinarily have been the normal shade. On the other hand, return to a pale gray bottom resulted in the fish becoming appreciably paler within an hour, and decidedly pale in the course of a day, although this change was away from the condition normal to ordinary specimens.

#### *Direction of the stimulus*

Before considering the question as to what part of the visual field was most effective in calling forth these transformations, a few words are necessary regarding the eyes of *Rhomboidichthys*. These are extremely protuberant, being virtually mounted on the ends of stalks like those of many crustacea. They are extremely motile, following moving objects in a rather uncanny fashion, or even turning without any apparent stimulus. During these movements the eye-stalks undergo an axial rotation, working together in such a manner that the two eyes nearly always look in exactly

<sup>36</sup> Op. cit., p. 73.

<sup>37</sup> Op. cit., p. 549.

<sup>38</sup> A. Agassiz (Bull. Mus. Comp. Zoölogy, 1892) records the production of "permanent albinos" in *Gasterosteus*, as a result of keeping these fishes on a white bottom. The time required for such a change is not stated, however, and no evidence is offered to prove that the alteration really was permanent.

opposite directions. The pupil of the eye is crescentic in form, owing to a semicircular projection from the dorsal side of the iris. This must largely eclipse the visual field overhead, though, as will be pointed out presently, the fish can see in this direction, even without any special movement of the eye.

In most of these experiments, glass jars were used, whose bottom areas were not large in comparison with the size of the fish.<sup>39</sup> Except in special cases, the walls of these jars were left unpainted. Since the fish commonly lay close to one or another side of the jar, and its head was never more than a few centimeters distant from one of the vertical walls, the animal's visual field necessarily included much that lay outside of the jar altogether. The different portions of this 'landscape' must have varied greatly in their degree of illumination, from the bright side toward the window, to the comparatively dark side viewed in the opposite direction. That the fishes actually did, at times, give attention to things seen through the walls of the jar, was evident from the fact that their eyes frequently followed my hand or other moving objects held in their vicinity. It was likewise found that the fishes could see objects directly overhead, since they sometimes rose with great celerity to take food which was dropped in from above, even in a larger tank with 25 or 30 cm. of water, and certain more timid specimens became agitated whenever I moved objects directly over them, although at a considerable distance above the surface of the water.

In the experiments thus far described, reference has been made to the bottom alone. In some cases the fish itself covered a fourth, or even more, of this bottom, while another large part of the animal's visual field was necessarily occupied by the vertical walls of the jar, together with the lights and shades of the room

<sup>39</sup> Most of the rectangular jars used had bottom dimensions of 15 by 20 cm. (These are the external measurements. In reality, the movable plates were somewhat smaller). Rectangular jars of a larger size were used, measuring 20 by 30 cm. at the bottom, the artificial patterns being 17 × 27 cm. The cylindrical jars employed had a diameter of 20 cm., and a height of 12 cm. The fishes ranged in length from 8.2 cm. to 19 cm. No. 1 had a length of 11.4 cm., no. 4 a length of 11.2 cm., no. 11 a length of 8.9 cm.

outside. Add to this the view overhead, which, as we have seen, was not wholly ignored, and it is truly a matter for surprise that the bottom was the surface chiefly concerned in evoking these pigment changes. To what degree, if any, surfaces lying in other planes might influence the fish was tested by special experiments.

A fish (no. 8) which had first been photographed on a gravel bottom (fig. 8a) was used in a series of such tests. This specimen, whose length was 12.4 cm., was placed in a glass jar having a bottom diameter of 20 cm. The bottom of the jar was painted black, but the walls were left transparent. Thus when this vessel was set into a larger jar and surrounded by gravel,<sup>40</sup> the latter could be clearly seen by the fish. In this contrivance, the animal became much darker in the course of the next few days, the annuli being reduced to rings of white dots. These last remained conspicuously pale, however, so that the fish was far from being concealed on this bottom. (Fig. 8b represents the condition at the close of seven days.)

The same specimen was now transferred to a contrivance exactly the reverse of the last, *i.e.*, one having the walls painted black, and the gravel visible through the bottom. A partial return to the gravel appearance was noted in the course of one day, and this increased during the next day or two, although the original appearance was not resumed in full, even after the lapse of ten days<sup>41</sup> (fig. 8c).

The fish was next transferred to a jar having a white bottom, 20 cm. in diameter, and black walls. Within two days it was noticeably lighter, and after three days "very much lighter and more homogeneous." It is doubtful whether any further change oc-

<sup>40</sup> Under water, of course, so that total reflection from the walls of the jar was avoided.

<sup>41</sup> The fish, after seven days, had been changed to a smaller jar, having a diameter of only 16 cm., but no certain change was noted. Gravel was now (after ten days,) placed in the bottom of the dish, so that the fish lay upon this directly, rather than upon a glass bottom. It is probable that some further change took place in the direction of adaptation to the gravel, for my notes state later that the fish now harmonized quite well. I do not believe, however, that this higher degree of adaptation had any relation to the tactile stimuli derived from direct contact with the gravel, but rather to an alteration of the visual stimuli.

curred in the next six days, at the end of which it was photographed, after being transferred to a jar having a black bottom and white walls (fig. 8*d*). By this time, however, the fish appeared to have wholly lost its power of response, for it changed but slightly during a stay of six days in this jar, six days in a jar whose walls and bottom were both black, five days upon a coarse reddish gravel, and two days upon the dark, mixed sand.<sup>42</sup>

Similar experiments were tried with a number of specimens, but several of them became blind or otherwise diseased before decisive results were obtained. The most pronounced success was achieved in the case of fish no. 9. In fig. 9*a*, this fish is shown lying upon the bottom of dark mixed sand, on which it had been kept for two days.<sup>43</sup> The tests to which it was further subjected were as follows.

It was first put into a dish 16 cm. in diameter and 7 cm. deep, having the vertical walls painted black, and the bottom covered with fine gravel, cemented in place with plaster of Paris.<sup>44</sup> The length of the fish was about 15 centimeters, and it must have covered from one-third to one-half of this bottom, while the head must at all times have nearly or quite touched the black vertical wall of the jar. In the course of a few hours, notwithstanding, the fish had changed somewhat in the direction of harmony with the gravel, while fig. 9*b* shows its condition on the following day. The appearance is certainly quite different from that manifested upon the sand, and is not ill-adapted to the new bottom, though it is recorded as "somewhat darker in appearance than the gravel, and gravel pattern not particularly good."

Transfer to a larger jar (20 cm. diameter, 12 cm. high), also with black walls and gravel bottom, did not result in any appreciable change, but upon removal to a large open tank, having gravel of the same sort at the bottom, the fish resumed the maximum degree of resemblance within a few hours. The animal was

<sup>42</sup> Cf. p. 433, above.

<sup>43</sup> It had previously been well adapted to the fine gravel. After transfer to sand, it changed considerably within an hour or less, and the maximum effect probably resulted within a day or less.

<sup>44</sup> This was done in order to prevent the animal from covering itself with the gravel.

then returned to the larger jar used previously (20 cm. diameter, with black walls and gravel bottom), but the maximum gravel effect now persisted for two days, when the fish was again removed.

Later, this same specimen was put into another jar (20 cm. diameter) having a black bottom and white walls. After five days (no observations being made in the meantime) the fish was of a "pale brown or buff, with pale spots still lighter" (fig. 9c). My record says: "not only not black, but not a dark fish."

The animal was next transferred to a jar of the same size with bottom and walls both black. Within less than a day there was a very pronounced change: "Fish so dark and so devoid of conspicuous markings as to be pretty well concealed in jar. Not noticed at first" (fig. 9d). The transfer was again made to the white-bottomed jar, and back again to the all-black one, with similar results in each case.

From the records of the two foregoing specimens, as well as of many others, it is quite plain that the bottom, even when it is of very limited area, and largely concealed by the fish itself, may exert a predominant influence in determining the appearance assumed by the latter. On the other hand, it seems plain from the later behavior of the second of these specimens that the vertical wall may also exert an important influence upon the animal. A comparison of fig. 9c and fig. 9d will sufficiently illustrate this point for the present. This entire question was much more searchingly tested with *Lophopsetta maculata* (see below).

In order to determine whether a surface directly overhead would have any effect upon the color-pattern of *Rhomboidichthys* specimens were placed in the large tank (p. 427), lighted from below by means of a mirror. A plate of opaque white glass, of the same size as the bottom of the tank, was covered with small, irregular blotches of black paint. Four corks, 35 mm. long, were fastened to the painted surface of this plate, one near each corner, and served as legs when the contrivance was placed at the bottom of the tank. In this position, the spotted side faced downward, at a distance of about 3 cm. above the eyes of the fishes.

The three specimens used in this experiment had all been unmistakably influenced by this spotted plate when this was placed

*beneath* them, assuming a much blotched appearance resembling that which was commonly shown upon a bottom of fine gravel. Upon the removal of the plate from beneath them, they had returned to a nearly unspotted condition. The spotted plate, now mounted on corks, as above described, was next inserted above the fishes (under the surface of the water, of course). The plate, in its present position, was brightly lighted by the mirror below. That the fishes could see this spotted surface cannot be doubted. Nevertheless, not one of the specimens showed any appreciable influence, even after several days.<sup>45</sup> Return of the spotted plate to the bottom of the tank, beneath the fishes, resulted in each case in a resumption of the blotched condition within a few hours at the most.

With two specimens an attempt was made to force the animal to look directly upward. The eyes, or rather the eye-stalks, were tied together by means of threads stitched through the skin. This drastic treatment resulted in the blindness of the fishes, and no significant results were obtained.

*Relation between the degree of illumination and the character of the response*

The foregoing experiments were conducted in a laboratory room of medium size, lighted from one side only. Different jars were exposed to very different amounts of light, and the degree of illumination for all of them varied greatly, of course, with the weather and with the time of day. Nevertheless, no undoubted relation was discovered between the intensity of the light and the rapidity or extent of the adaptive changes. In a few instances, it is true, certain of the pigment patterns were found to be much less conspicuous on dark, cloudy days. It has been pointed out, however, that the completeness of these adaptations varied at different times in the same individual, even when no external cause was discoverable. And even if some specimens were actually affected at times by the intensity of the illumination, this was certainly not

<sup>45</sup> The fishes were observed through the walls of the tank, by raising the dark curtains; also by removing the spotted plate.



the rule. The dark tone assumed by the fish upon the dark sand did not give way to a lighter shade when the animal was brought into direct sunlight; while fishes on a white bottom acquired the maximum degree of pallor, even though this white bottom was heavily shaded.

This state of affairs has already been pointed out by other observers,<sup>46</sup> and indeed it would seem to be a necessary one in order that the color should be adaptive or cryptic. For it is obvious that the fish itself is shaded or lighted equally with the surface on which it lies, so that the relation between the two remains unaffected by the degree of illumination.

A rather curious corollary may be drawn from this last principle. Suppose that we have two aquaria side by side, one with its inner surfaces painted white, the other painted a perfectly neutral gray. Suppose, now, that the white aquarium is heavily shaded, so as to admit comparatively little light, while the gray aquarium is well illuminated. Under these conditions, the fishes in the white tank should, according to hypothesis, assume the maximum degree of pallor, while those in the gray tank should continue to display some of their dark pigment, in amount depending upon the shade of gray employed.<sup>47</sup> Now experiment shows that this is precisely what happens. The fishes in the shaded white tank blanch to their fullest extent, while those in the gray tank become gray. It is obvious, however, that the dimly illuminated white bottom of the one tank may be actually *darker* than the brightly illuminated gray bottom of the other, in the sense that the former may reflect an absolutely smaller amount of light to the observer than the latter. The theoretical bearings of these facts will be discussed in a later section. At present, I shall confine myself to an account of certain experiments upon Rhomboidichthys.

Two glass jars, 20 cm. in diameter and 12 cm. deep, were used. The bottom of one of these was painted gray of a shade nearly match-

<sup>46</sup> Most clearly by Keeble and Gamble for schizopod and decapod crustacea (Phil. Trans. Roy. Soc., Series B, vol. 196, 1904, pp. 353 et seq.); likewise by Bauer for isopods (Centralblatt für Physiologie, 1906, p. 459).

<sup>47</sup> It is needless to point out that gray is not a color. If pure, it reflects white light, though of reduced intensity.

ing that produced on a color-wheel by combining two parts of black and one part of white.<sup>48</sup> The gray was not, it is true, perfectly neutral, being somewhat 'cold,' *i.e.*, tinged with blue. That this fact played no part in the results seems likely from my later experiments (p. 461). The side of the jar toward the window was left transparent, the opposite side being covered with white cardboard to increase, by reflection, the illumination of the bottom. In addition to this, a reflecting screen of white cloth, inclined at a suitable angle, was poised above.

The white-bottomed jar had walls which also were painted white, but the light was largely cut off from its interior by a cylinder of sheet iron, painted black, which encircled the jar and projected upward for a distance of 12 cm. above its top.

That the bottom of the gray tank was actually far lighter than that of the white tank, *i.e.*, reflected far more light, is readily seen from fig. 11f-12b (plate 13), which reproduces a photograph taken in the laboratory with the jars arranged as nearly as possible in the same manner as during the test.

Several experiments were made with these jars, with more or less instructive results. Only one of these tests, however, was so clear cut and decisive that it deserves to be described in detail. Specimen no. 11, which had previously been kept for a long period upon white and other pale backgrounds, but was in the present case taken from the black magnetite sand (after twelve days) was placed in the gray-bottomed jar. It became appreciably paler within an hour, much paler within a day, and, after two days "probably no darker than the gray bottom." Specimen no. 12 which had likewise been on various backgrounds, but came, in this instance, directly from gray, was placed in the (shaded) white jar. This specimen grew noticeably paler in the course of a day, and the pallor increased for a day or two more. (The color-book was here referred to for comparison.)

At the end of four days, the two specimens were examined under identical conditions of illumination, when it was found that no. 11 (on the gray bottom) was decidedly darker than no. 12 (on

<sup>48</sup> Contrary to what one might suppose, such a gray is far from being dark.

the white bottom). Photographs were now made, in which the two fishes were taken together, first on the gray bottom (fig. 11g-12c, plate 13), then on the white bottom. Both of these showed very plainly the difference of shade between the two fishes.

The specimens were then transposed, no. 11 being placed upon the white bottom, no. 12 being placed upon the gray bottom. After two days, no. 11 appeared to be paler than 12, and after four days it was certainly so. They were compared, as before, and again photographed together, first upon the gray bottom (fig. 11h-12d), then upon the white bottom. The relative shade of the two fishes had obviously been reversed.

The two animals were once more transposed, and with similar results, though no photographs were taken.

*Is the behavior of the fish influenced by the degree of its adaptation to the background?*

As has already been pointed out, most specimens covered themselves more or less with the gravel or sand in which they lay. In some cases, the marginal fins only were concealed; but in a few instances the entire body was buried, only the eyes protruding. So far as my observations go, the fish was just as likely to cover itself with the bottom material when its color and pattern were highly adapted to this as it was when they were glaringly ill-adapted. When specimen no. 10 was taken from a pale background and placed in black sand, it buried itself with extreme rapidity, and remained completely concealed. In this instance the fish was at the outset utterly out of harmony with the bottom. It was noted, however, that this tendency to hasty concealment beneath the sand was just as marked after the fish had assumed a shade not far different from that of the latter.

In contrast to the last example, specimen no. 11, though even more conspicuously out of harmony with its background, did not, at first, make any endeavor to bury itself when placed on the magnetite sand.

In order to test the question whether the fish, when offered the choice, tended to select a background in harmony with its own

shade, a plate of glass was employed as a bottom, having an area of 17 x 27 cm., and divided transversely into a black and a white half. Fishes nos. 11 and 12 were used in these experiments. Both were healthy and active. The former was, at the time, adapted to a very pale bottom, the latter to the dark sand. The fishes, one at a time, were placed upon this background, in the neighborhood of the division between the white and black halves, and in such a position that they could plainly see both. This experiment was repeated a number of times with each fish, the latter being left in some cases for more than an hour upon this bottom. No preference was shown for one surface more than the other. The fish commonly remained very near to where it was placed, whether or not it was adapted to the surface which immediately surrounded it, and in no instance crossed over into the opposite side. On the contrary, it happened that in more than one case, the dark fish moved further back into the white area, and vice versa.

Each of these fishes was then placed upon bottoms of dark and of white sand. No. 11 showed no disposition to burrow in either. No. 12 covered itself very little with either sand, and with one no more than with the other.

Such experiments are of course not entirely conclusive, but, when taken in connection with other observations, they at least render it improbable that the fish exercises much selection in respect to the shade of its background. The behavior of this animal is thus not at all in accord with that of the decapod crustacean *Hippolyte varians*, as described by Gamble and Keeble.<sup>4</sup>

#### *The rôle of sight in these reactions*

Various previous observers<sup>50</sup> have recorded that blind fishes failed to undergo adaptive color changes, and it has been pointed out that both specimens which have become blind through natural causes,

<sup>49</sup> Quarterly Journal of Microscopical Science, 1900, p. 601. (See especially plates 32 and 33.)

<sup>50</sup> *E.g.* Pouchet, Mayerhofer and Secérov, in works already cited.

and those which have been deprived of their sight experimentally, cease to adjust themselves to the shade of their background.

Certain of my own fishes which failed to respond adaptively to changes of bottom were found to have become diseased in one or both eyes, although, as has been stated, some of the most refractory individuals had not lost their sight. One of the fishes, both of whose eyes were affected, acquired a peculiar appearance which was not noted in any normal specimen. It assumed a rich brown color, with specks of orange, the whole effect being much more decorative than the somber hues ordinarily displayed by this species. Another specimen, one of whose eyes had already become blind, took on almost precisely the same appearance after I had cut the optic nerve of the sound eye. In both cases the fishes remained conspicuously out of harmony with the gravel or sand on which they were kept.

My most complete experiments in blinding fishes were later made upon *Lophopsetta*, but a few which were made with *Rhomboidichthys* deserve recording. It was at first my endeavor to cover the eyes with some opaque coating, without thereby causing any injury.<sup>51</sup> This proving impracticable, I next tried the effect of searing the corneas with a red-hot platinum wire. The results, with specimens no. 10 and 11, are detailed in the next paragraph. The effect of cutting the optic nerve has already been described for one specimen<sup>52</sup>. I will add that this fish was subsequently kept for 22 days upon a white marble bottom. A slight paling was noted at first, and this, as subsequent experiments showed, might have occurred equally well on any bottom. Thereafter, no change was noted, and the fish remained fairly dark as long as kept under observation.

One result of blinding, manifested in two of the foregoing specimens, is of peculiar interest. Specimen no. 10, which had been

<sup>51</sup> Mixtures of lampblack with certain fatty substances were tried, but it was found that these would not adhere for more than a very few minutes.

<sup>52</sup> Aside from the resulting loss of sight, it is probable that there is a distinct shock effect from the cutting of the optic nerves. Thus specimen no 10 (see below), when in a pale condition after the searing of the corneas, turned dark immediately, upon the cutting of the optic nerves, and this dark condition persisted until the death of the fish four days later.

kept most of the time during a period of two months upon white and pale gray bottoms, was transferred to the black magnetite sand for a period of six days. At the end of this time the fish was nearly or quite as dark (fig. 10*d*) as are most of these fishes when adapted to a very dark bottom. The animal was then blinded by searing the corneas with a red-hot platinum wire. The effect was a conspicuous paling of the body (fig. 10*e*), which became evident in a short time and persisted for some days, after which the darker condition began to return.

Substantially the same results were obtained from specimen no. 11, which had been kept for an even larger proportion of the preceding two months upon pale bottoms, and had been only 3 days upon the black sand at the time of blinding. Within a few hours, the fish returned completely, or nearly so, to the extremely pale condition which it had acquired upon its earlier backgrounds, and remained in this condition for a day, after which the observations were brought to an end.

These results are readily intelligible on the assumption that the pale condition had, to a certain extent, become fixed in the nervous mechanism during the long sojourn of the fish upon such bottoms. The transfer to a dark bottom resulted, without much delay, in the acquirement of a darker appearance, but this condition was not, at first, a stable one, and its maintenance seemed to depend upon the continuance of visual stimuli. There are, it is true, certain facts which seem irreconcilable with this hypothesis, as we shall see later. But the foregoing experiments have been repeated upon two other species, and the facts themselves are beyond question. Moreover, fishes which had undergone no extended sojourn upon a pale bottom did not (with a single exception) become pale when blinded.

#### *Changes having no relations to visual stimuli*

As stated in an earlier paragraph, decided changes occur in the disposition of the skin pigment, which have no relation to the background or, indeed, to any visual stimulus whatever. Certain very conspicuous phenomena of this sort were observed

during the course of the present experiments. The fishes commonly assumed a very different appearance when disturbed or when swimming 'voluntarily' in the aquarium from that displayed when at rest.<sup>53</sup> Such changes generally followed certain laws, though there were abundant exceptions to these.

1. A fish of pale or medium shade generally became darker<sup>54</sup> when disturbed, and at such times dark spots or blotches commonly came into view.<sup>55</sup> In a few specimens highly colored red specks appeared at such times. The resting condition was resumed in a few minutes or seconds after the fish settled upon the bottom. These phenomena were manifested even by those blinded specimens which had secondarily become pale.

2. In certain cases very dark fishes, which had recently been considerably paler, assumed a lighter hue when caused to swim around. These changes were so inconspicuous that I was not at first certain of their reality, but their occurrence was confirmed by observations upon at least three fishes, after transfer to the magnetite sand.

3. When the fish was in the highly contrasted condition, with conspicuous white and black areas, this appearance commonly diminished, or even wholly disappeared, when the animal was disturbed. Its skin then assumed a medium shade, and the markings became inconspicuous. The same monotone was commonly assumed when these fishes swam about without known external stimulus. Indeed, in the case of certain specimens, I found it a very easy matter to discern the fish's 'intention' to begin swimming by the disappearance of the spots and the assumption of this monotone. Thus fig. 4*g* was taken upon such an occasion. Upon settling down upon the bottom, the skin pattern gradually came into view, and generally attained its maximum distinctness within comparatively few seconds. The effect of these latter changes

<sup>53</sup> Pouchet, Van Rynberk, Townsend (op. cit.), and others, have called attention to pronounced color differences, in some species, between the resting condition and conditions of activity or excitement.

<sup>54</sup> This darkening, under the influence of disturbance, is the only change of this sort recorded by Van Rynberk, who believes it to be of constant occurrence.

<sup>55</sup> Pouchet (op. cit., p. 76) records the appearance of such spots in the turbot.

upon the observer was much like that which one experiences in watching the development of a photographic plate. Indeed it not infrequently happened, in those cases in which the maximum adaptive effect was not displayed by the fish at the time of its being disturbed, that this maximum effect appeared for a brief period after the animal settled down, only to diminish again after a few moments.

### 3. EXPERIMENTS UPON RHOMBUS

Although *Rhombus maximus* was the species which first arrested my attention in the show aquarium by its extraordinary adaptation to the gravel bottom, no striking results were obtained in the laboratory from the single specimen which I used. Moreover, the species was too large for convenient manipulation.

Two specimens of *Rhombus laevis* were, however, used with some interesting results. Both of the specimens showed a high degree of adaptation to the fine gravel, used in the foregoing experiments, and one of them (the other was not tested) likewise acquired a high degree of harmony with the dark sand. Both specimens became much paler when placed upon the white marble bottom of a large aquarium, though neither attained such an extreme condition of pallor as did *Rhomboidichthys*. One of the two, at the end of a stay of forty-six days, "harmonized pretty well with the now much stained marble bottom," though the maximum degree of adaptation had probably been brought about long before this. Even after this extended sojourn upon the marble, however, I note of this specimen, after transfer to gravel, that "within a short time, certainly in less than an hour, the spots had come distinctly into view, and on the same afternoon the fish harmonized pretty well with the gravel."

After a short sojourn on the gravel, the corneas of this fish were rendered opaque by the application of silver nitrate, the animal being then returned to the same bottom. After the lapse of a day, the fish was very much paler than before the operation, and not far different from the condition when on marble. After two days, however, the gravel condition (*i.e.* the darker, spotted



condition) had, to a considerable extent, reappeared. Subsequent experiments with this fish led to the suspicion that enough light still passed through the corneas to influence the changes. After complete extirpation of the eyes, the fish, which was finally returned to the marble-bottomed tank, remained "rusty brown, with inconspicuous markings."

#### 4. *LOPHOPSETTA MACULATA*

Since certain important points were left in an unsatisfactory state by the experiments at Naples, this line of work was resumed during the following summer in the laboratory of the Bureau of Fisheries at Woods Hole. The fish which was chiefly employed in these later experiments was the common 'window-pane' or 'sand-dab,' *Lophopsetta maculata* (Mitchill), another member of the turbot group. *Lophopsetta* proved to be a far less favorable object for studies of this sort, since, on a white surface, it never attained such an extreme degree of pallor as did *Rhomboidichthys*, and its capacity for displaying adaptive skin patterns, though far from wanting, was much more restricted.<sup>56</sup> The experiments with this species were therefore concerned chiefly with the relative influence of different portions of the visual field, the time of reaction, effect of blinding, etc. Especial attention was likewise given to the problem of how the fish is able to conform the shade of its skin to that of its background, irrespective of the degree of illumination.

A few experiments with natural bottoms (gravel and sand) were also tried, but without any very striking results. In the large exhibition aquaria the adaptive reactions were, however, sometimes rather impressive. Some specimens assumed a characteristic appearance upon gravel, which was decidedly different from that displayed upon sand, and the changes were sometimes fairly rapid. Upon the former material, spots, both light and dark, came into view rather conspicuously, while upon the latter,

<sup>56</sup> Indeed, of the nine species of *Pleuronectidae* and *Soleidae* which have been observed by the writer, *Rhomboidichthys podas* appears to possess by far the highest capacity for adaptive changes of this sort.

a fairly homogeneous brown or buff tone was commonly assumed. The adaptations of *Lophopsetta* are not to be compared, however, with such appearances as those exhibited by *Rhomboidichthys*. The rich mosaic effect sometimes displayed by the Mediterranean species would seem to be structurally impossible in the American one. As a compensating advantage, from the experimenter's point of view, the latter may be obtained in far greater numbers.

The experiments with this fish were nearly all performed in the cod-hatching boxes of the Woods Hole station. These are wooden boxes, with a bottom area of 30 x 70 centimeters, and containing water to a depth of 18 centimeters. They are built in rows of 12 each. In the course of the present investigations, they were painted variously, as will be described in connection with the separate experiments. No photographs of *Lophopsetta* were taken.

#### *Blotched surfaces*

A few experiments were tried to test the capacity of this species to adapt itself to a highly contrasted pattern. Four specimens were placed (two at a time) in one of the boxes just described, the walls and bottom of which had been painted white with small irregular daubs of black scattered throughout the entire surface. All of these fishes responded unmistakably to this stimulus, the ground-color becoming (or remaining) medium pale, while certain stellate or irregular black blotches came distinctly into view. The fishes thus acquired a piebald appearance, quite different from anything which was observed on a background of uniform shade.

Another interesting case was noted, in which these dark blotches appeared upon an extremely pale specimen which had been kept for three days in a box having white (unspotted) walls and bottom. It was found, in this instance, that patches of very dark vegetable debris had accumulated at the bottom of the box in the neighborhood of the fish's head. Removal of this debris resulted in the disappearance of the spots, while a later accumulation led to their return. It must be remarked, however, that in the specimen under

consideration the dark blotches were vaguely visible much of the time, even when the fish was on a homogeneous ground. The presence of dark spots in its neighborhood merely served to accentuate these.

*Direction of the stimulus*

A point which was tested much more thoroughly than at Naples was the relative influence of the bottom and of the vertical walls of the receptacle in determining the changes of shade on the part of the fish. The bottoms employed were, as just stated, 70 centimeters long and 30 centimeters wide. The length of the fishes varied from 24 to 35 centimeters, and their area probably ranged from 200 to 400 square centimeters, or from 10 to 20 per cent of the area of the bottom. The fishes lay, much of the time, near one or another wall of the box, and the larger specimens naturally could not at any time reach a position very far removed from the latter.

Boxes were employed having 1, walls and bottom painted black; 2, walls and bottom white; 3, walls black, bottom white; 4, walls white, bottom black. In addition to this, false walls of galvanized iron were made, which were painted white or black or both. These could be inserted into any of the boxes without disturbing the fishes.

1. In boxes of the first type, the fish became (or remained) as dark as it was capable of being. The shade varied, of course, with the specimen, but was usually a very dark brown, and fairly homogeneous, though certain small white spots sometimes showed distinctly. Usually the fishes were very inconspicuous in the black boxes.

2. In the white boxes, the fishes commonly attained a considerable degree of pallor, assuming a shade which may perhaps best be characterized as buff, *i.e.*, a pale yellowish or brownish gray. In this condition, while of course far less conspicuous than previously, they could not be regarded as very well concealed, at least from a nearby observer. The harmony with the pale bottom was furthered by the fact that, with the withdrawal from view of the dark pigment, not only the marginal fins (already partially transparent), but the adjacent portions of the body proper, be-

came fairly translucent, so that the underlying surface was more or less visible through them.

3. In the black-walled, white-bottomed box, different fishes behaved differently, depending upon the individual peculiarities of the specimens, or upon their previous treatment. When placed here in the dark condition, most specimens remained fairly dark, even after a lapse of some days. But they were, notwithstanding, commonly affected somewhat by the white bottom, being noticeably paler than those in an all-black box, and in some cases exhibiting a peculiar blotched or marbled appearance, as if attempting to adapt themselves to black and to white at the same time.<sup>57</sup> In one instance, a fish became nearly as pale as did the average specimen in an all-white box.

Two fishes which had been placed in this box in the dark condition, and which had remained dark for four days, were transferred to an all-white box. In the latter they attained nearly or quite the maximum degree of pallor within a single day. Upon being returned to the black-walled, white-bottomed box, they remained pale for two days, *i.e.*, as long as they were kept there.

Two other specimens, which had remained dark for two days in this box, became pale in seven hours or less when the white movable wall was inserted. Upon removal of the latter, at the end of one day, however, the fishes promptly began to darken, and became nearly or quite as dark as before. Yet another two, which were put in when pale, remained so for two days.

Thus, while there can be no doubt as to the influence either of the white bottom or of the black walls in these experiments, the relative importance of the horizontal and vertical surfaces seems to differ in different cases. The same is seen to be true of the next sort of box considered.

4. In the white-walled, black-bottomed box, dark fishes in every case remained fairly dark, though they were in some cases influenced by the white surfaces around them, for about half of

<sup>57</sup> No such contrasts were here produced, however, as were shown upon the spotted bottom. (See above.)

the specimens took on a somewhat paler shade, looking as if a very thin 'wash' of white had been spread over their bodies.<sup>53</sup>

Pale fishes placed in this box either became nearly as dark as when kept in an all-black box (three specimens), or at least of a medium shade (one specimen). One of these specimens acquired the mottled appearance referred to above.

5. The movable walls, when painted uniformly, were used in order to change the outlook of the fish without otherwise disturbing it. The results obtained from their use were the same as those following the transfer of the animals from one tank to another. They need not detain us here. Highly interesting results were obtained, however, with a wall painted partly black and partly white, the line of division between the two areas being horizontal. In the first experiments the white and black portions were of equal extent, that is to say, the wall, which was 18 centimeters high, was divided into a white and a black half. Later, it was painted so that the white band occupied only a fourth of the height of the wall.

The movable wall, thus painted, was used only in the white-bottomed, black-walled box. It served, therefore, to add a certain amount of white to the vertical surfaces of the box. Some of the results from its use seem worth recording in detail.

Two fishes (dealt with together) which had remained dark in this box, were found to become pale when an all-white movable wall was introduced, returning to the dark condition, however, when this was removed. The half-white, half-black wall was then inserted, the white half being uppermost. No change occurred, even after 8 hours. Upon the reversal of the wall (white half now

<sup>53</sup> Here, and in all similar cases, it was absolutely necessary to place fishes together in the same box before comparing them. The white walls, in the present case, reflected enough light upon the surface of the animal to give it a paler appearance than when in an all-black box. Accordingly, specimens from one of the latter were transferred to the present box, and a comparison made with the fishes which had been kept in this for some time. The reverse change was likewise made, both lots being compared together in all-black tank. A mirror was also used in examining specimens kept in dark boxes, the fishes being illuminated by reflected light. Without such precautions, one may easily be led into error in judging of the less pronounced changes of shade.

down) the fishes became decidedly pale within an hour. A second inversion of the wall resulted in the fishes becoming much darker (about medium shade) in  $4\frac{1}{2}$  hours. It would seem, however, that even in this position the white surface did have some influence, since the fishes did not become very dark until the removal of the wall (leaving the vertical surfaces entirely black), when they became so within two hours.

Two other specimens were, at the outset, subjected to the same tests as the preceding ones, and with substantially the same results. After several further changes of the visual stimulus, they were again subjected to the influence of the black-walled, white-bottomed tank, in which they now displayed a somewhat intermediate shade. The black-and-white metal wall was next put in (now one-quarter white), the white band being below. After twenty minutes, one fish had acquired nearly the maximum degree of pallor, but the other had undergone no change.

Two more fishes kept in this box for two days, remained dark, one being of about maximum darkness, the other somewhat paler. The black-and-white wall (one-quarter white) was now inserted, the white band, as before, being below. After two days, both fishes had become pale, though not of maximum pallor. After removal of the wall, they remained in this condition for a day.

Thus, it is interesting to note that when the bottom and the adjacent zone upon the vertical walls were white, even though this zone were no broader than  $4\frac{1}{2}$  centimeters, the fishes reacted much (though not quite) the same is in an all-white tank. When, on the other hand, the bottom was white, and the adjacent zone upon the vertical walls was black, even the presence of an overlying band of white, 9 centimeters wide, was not sufficient to call forth a truly pale condition in any of the four specimens thus tested.

It would hence seem, at first glance, that quantitative relations alone could not determine which of these two components of the visual stimulus should prove effective. In endeavoring to decide this point, however, one must distinguish between the potential and the actual visual fields. What the fish, from a given position,

*can* see is not necessarily the same as what it commonly *does* see. It may well be that the animal's attention is chiefly centered upon areas which do not rise much above a horizontal plane. I shall discuss this point more fully later.

*Rapidity of these changes*

The average time required by *Lophopsetta* to attain the highest degree of pallor, commencing with the dark state<sup>59</sup> was probably less than two days, and the change was commonly noticeable within a single day. One particularly refractory specimen was kept for four days in a white box before any undoubted change occurred. The change, when it did come, was rather abrupt, though the highest degree of pallor was not attained until the lapse of 6 to 7 days. Specimens were found, on the other hand, which changed decidedly within a few hours, when placed for the first time in a white tank, and, in one case at least, the maximum degree of pallor was assumed in less than twenty-four hours.

After the first experience of this sort, it happened, in many cases at least, that subsequent changes were undergone much more rapidly. Thus specimens which required several days for the first change to the pale shade often completed this change within a few hours, after one or more such transpositions. One dark fish, for example, when placed for the first time in an all-white box, showed little or no evidence of paling after one day, and did not blanch to the fullest extent until the lapse of about three days. After being returned to black, it was recorded, at the end of 19 hours, as being nearly or quite as dark as originally. When transferred to the white box for a second time, the fish became decidedly paler in less than a minute, and within an hour was nearly or quite as pale as at any time previously.

Whether or not a similar shortening of the reaction-time may be brought about in the case of the reverse change, *i.e.*, from light to dark, was not fully determined. A change in this direction is, in

<sup>59</sup> Nearly all of the specimens, when first brought into the laboratory, were much nearer the darkest than the lightest condition. They were, too, frequently kept for some days before being used, in a large stock tank, painted black within.

most cases, a return to a more nearly normal state, and presupposes a previous (commonly recent) change from an original dark condition.

*Condition in total darkness*

The fishes were examined at night, after three hours or more of darkness, by means of an electric flash-light. This was done on two different occasions, and with a considerable number of fishes in various conditions. With one or two possible exceptions, these fishes were of nearly or quite the same shade as when last observed in the daytime.<sup>60</sup> Even specimens which had but recently assumed the pale condition were found to have retained this after the withdrawal of the visual stimulus. Certain observers have reported among fishes characteristic differences of color during 'sleep' or at least at night.<sup>61</sup> I have found no evidence of such in the case of *Lophopsetta*.

Experiments were tried in which fishes of different shades were shut up in a light-proof box. In the first of these, two specimens which had become very pale and two of maximum darkness were put into the box together. After five days the two dark ones were found to be dead. The other two, though much darker than when put in, still remained distinctly paler than those kept in neighboring black boxes. They assumed the darkest condition after a few hours' exposure to light in such a box.

In the next experiment, one pale and one dark fish were kept in the light-proof box for a period of seven days. The pale specimen had previously passed 6 days in an all-white box. When the fishes were examined at the end of their stay in darkness, the dark specimen was found to be as dark as before; the other, though now fairly dark, was distinctly paler than the former. It acquired the darkest shade, however, after a few hours' exposure to light in a black box.

<sup>60</sup> In making such comparisons, I could only refer to my own notes describing the condition of these fishes in the daytime, and to my recollection of this. Differences may have appeared which escaped me.

<sup>61</sup> *E. g.* Verrill (*American Journal of Science*, 1897, p. 135). Verrill's observations were made by dim gas-light, mainly between midnight and 2 a.m.



Thus it is plain that the shade assumed by the fish under the influence of visual stimuli tends to be retained for a considerable period after the latter are withdrawn.<sup>62</sup>

*Experiments with blinded fishes*

Any method of permanently destroying the sight of an animal must necessarily involve a considerable nervous shock, and it might be fairly objected, in the lack of further evidence on this point, that such results as are described below may be due, in part at least, to this shock, rather than to the loss of sight alone. Thus any mere failure to respond adaptively after the operation is not, in itself, a decisive proof that vision is a necessary element in the reaction. Such doubts are, to be sure, greatly weakened in the present instance by the fact that the blinding of one eye was found to have little or no effect upon most specimens.

In order to meet fully this objection that we may have to reckon here with a 'shock' effect, I endeavored in the first place to use a bandage of black cloth, fastened over the eyes. It was necessary, however, to stitch this bandage to the margin of the head, and this, of course, involved an injury to the fish. Moreover, the friction or pressure of the cloth soon damaged the eyes and led to blindness.

Accordingly, I gave up all attempt to blind the animals without inflicting injury,<sup>63</sup> and adopted the plan of cauterizing the surface of the eyes with silver nitrate. This resulted at once in an opacity of the cornea. After the lapse of a few days, the latter fell from the eye, exposing its interior to the surrounding water. Even in this condition, the retina (or optic nerve) frequently remained for some days (7 or 8, in certain cases) decidedly sensitive to light, as was shown by reflecting daylight upon the head with a mirror, or by the

<sup>62</sup> For the pike, Mayerhofer (op. cit.) regards darkness as a "strong stimulus to an extreme contraction of the chromatophores," since fishes which were thus kept became much paler after a few days. On the other hand, Secérov and some others report the acquirement of a deeper shade in total darkness.

<sup>63</sup> The use of a coating of opaque material had been found to be impracticable with *Rhomboidichthys*.

use of a flash-light at night. In many cases the eyes moved unmistakably, or the fish even swam away, as a result of the stimulus.

Altogether, 16 specimens were deprived of the sight of both eyes by cautery, while three others were blindfolded. Of this total, 8 fishes were in the dark condition at the time of the blinding; 9 were in the pale condition, and two others in an intermediate state. As regards results, the following general statements may be made:

1. Dark specimens, excepting those having the history specified below (3), remained dark after the destruction of sight.

2. Pale specimens, after blinding, remained as pale as before for about a day, after which they gradually grew darker, and became indistinguishable from those which had been blinded when in the dark state. The duration of this persistence of the pale condition after blinding seemed to bear little relation to the length of the previous sojourn upon a pale background. Thus fishes which had been kept in white boxes for only two days before being blinded retained the pale condition about as long as specimens which had been thus kept for fourteen or seventeen days.

3. Specimens which had passed considerable periods (seventeen to twenty-five days) in a white or pale gray box, and then, before blinding, returned to black just long enough to cause them to resume the earlier dark shade (twenty-four hours, or less), became pale again within a few hours after blinding, and remained thus for about a day, after which they gradually became dark again. Three of the four specimens thus treated reverted, after blinding, to nearly or quite the maximum degree of pallor; the fourth became distinctly paler, though not so pale as it had been. The results of these experiments upon *Lophopsetta* are thus in complete agreement with those obtained from the use of *Rhomboidichthys* and *Rhombus*. On the other hand, with a single exception (see below), none of the ordinary dark specimens became paler as the immediate result of blinding.

4. The shade assumed by the blinded specimens was not thereafter influenced in any appreciable degree by the background.<sup>64</sup>

<sup>64</sup> One apparent exception is to be recorded among all the specimens used. This fish was of a fairly dark shade at the time of blinding. Some hours after transfer

Change from all-black to all-white boxes called forth no visible response.

5. Whatever the original shade of the fish, that which was finally assumed was, as already stated, a dark one. But the final condition was not, in the majority of cases, that of maximum darkness. It was frequently a shade distinctly paler than this, though in all cases one nearer to the darkest than the palest condition. Certain blinded specimens displayed a distinctly abnormal appearance which I never observed in an uninjured fish. On the other hand, some specimens remained very dark, and of normal appearance, to the end. For example, one fish (pale when blinded) was of about the maximum degree of darkness, even after forty-one days.<sup>65</sup>

With six specimens, the sight of one eye only was destroyed. In three cases, this was the right eye, in three others the left. Since the two eyes are rather differently directed with reference to the bottom, I thought it worth while to look for a possible difference in the effect of the two operations. Of these six specimens, four retained the power of adaptive change nearly or quite unimpaired. Indeed one of these, for rapidity and completeness of the adjustment, remained one of the most favorable specimens which I encountered.

Of the two remaining fishes, one appeared to have very largely lost the power of change while in the other, this was considerably

to a white receptacle, the animal was found to be very pale. It must be borne in mind, however, that the immediate result of cauterizing the eyes was not complete blindness, but that the corneas were merely rendered opaque. In this exceptional specimen the opacity might not have been complete.

<sup>65</sup> According to Pouchet, the shade assumed by a blinded turbot was always an intermediate one. Mayerhofer, experimenting upon pike, found that the immediate effect of blinding was a paling of the fish, this being followed by the assumption of a more intensely colored condition than before the operation, accompanied by a disappearance of the dark bands. The further history of the specimen depended upon whether it was kept in the dark or in the light. If the former, the pigment tended to disappear. If the latter, the pigment cells not only persisted on the back and sides, but developed upon the (normally pale) ventral surface. This last phenomenon suggests the artificial production of pigment upon the lower side of flounders in Cunningham's well-known experiments.

impaired. In both of these cases, it was the right eye<sup>66</sup> which had been destroyed, but I do not regard this fact as of any significance, since in the third specimen thus treated there was little or no impairment of the pigment reactions.

Since a very decided inhibition of these reactions was also noticed in certain specimens which were injured in other ways, without being blinded (p. 465), it seems probable that the shock of injury and not the loss of the sight of one eye was responsible for such impairment of the chromatophore function as was observed in these last cases. This, of course, is reason for suspecting a similar shock effect, perhaps an even greater one, in the case of those fishes both of whose eyes had been destroyed. Certain facts which I have recorded above may indeed be referred to this cause. But it must not be forgotten that we have, quite apart from these blinding experiments, conclusive evidence of the part played by sight in these reactions.

*Relation between the degree of illumination and the shade assumed*

In discussing the experiments upon *Rhomboidichthys*, I pointed out that the degree of illumination of the background had little or no effect upon the reaction which the fish underwent. As a special illustration of this principle, it was shown that a fish became paler upon a white bottom, even though this was heavily shaded, than upon a gray bottom exposed to a considerable measure of light. The latter surface, in my experiments with *Rhomboidichthys*, was shown photographically to be very much lighter than the former.

Identical results were obtained with *Lophopsetta*. One of the boxes was painted gray of a shade close to no. 499 of Klincksieck

<sup>66</sup> *I.e.*, the eye which belonged morphologically to the lower, unpigmented side of the body. Pouchet (op. cit., p. 88) had just the opposite experience, finding that one turbot whose left eye was destroyed failed to respond as well as previously, though no such impairment was observed in a specimen whose right eye was destroyed. He suggested a possible physiological correlation between the left eye and the skin of this (the upper) side.

and Valette.<sup>67</sup> The gray paint used was not perfectly neutral, it is true, being, when fresh, slightly tinted with blue. After exposure to sea-water, however, it changed somewhat, becoming 'warm' (*i.e.*, slightly yellow) instead of 'cold.' It was probably in this condition during most of the period of the experiments.<sup>68</sup>

The gray box was situated near the window and was well lighted throughout much of the day, though not exposed to direct sunlight.

Another box was painted white within, but its interior was rather heavily shaded by a tent-shaped contrivance of galvanized iron. This was painted black within, and had a long cleft in the top, partly for the admission of light, partly to permit of observations. The cleft was largely closed by strips of wood, the amount and distribution of the light being thus controlled.

No photographs were taken of the surfaces upon which the fishes lay, but I feel sure that the difference in the amount of light reflected from the two bottoms was as great, or greater, than in the experiment with *Rhomboidichthys*.

Four fishes were used in the present experiment. Two specimens at once were kept in each of the two boxes. From time to time, those from one box were transferred to the other box, for brief periods, in order that all four might be compared directly under identical conditions of illumination and of background. Such direct comparisons were also made with other pale fishes kept in a neighboring white tank which was well lighted.

At the close of the first phase of the experiment, the two specimens in the gray box were found to be decidedly darker than those in the shaded white box. More pigment was visible in the skins of the former than in those of the latter, and they were of a gray appearance, in contrast to the yellowish or slightly pinkish appearance of those in the white box. The latter, moreover, were

<sup>67</sup> Prof. Yerkes, who kindly matched a sample of this paint upon a color wheel, reports that 75% of black and 25% of white gave the desired shade.

<sup>68</sup> If anyone wishes to maintain that this slight element of color (aside from shade) probably played some part in the results, I cannot absolutely refute him. I can only say that my experiments as a whole make this seem to me highly improbable.

found to show no appreciable differences of color or shade from specimens which were kept in a well lighted box, having a white interior.

The two sets of fishes, which had now been in their respective boxes for six to nine days, were next transposed, *i.e.*, those from the gray box were transferred to the covered white one, and vice-versa. At the end of 5 days, the relations in respect to pigmentation were found to be reversed, those which had formerly been darker now being paler and vice-versa. One of those which had previously been very pale was now (when on gray) recorded as "one of the best cases of resemblance in respect to general color tone which I have had."<sup>69</sup>

Reference should be made here to one exceptional specimen which, when dark, was placed in the shaded white box for three days with little or no effect. Upon being removed, to an *unshaded* white box, on the contrary, some change was noticeable during the same day, while on the next day the fish was very pale. In the case of this specimen, therefore, it would seem that the scant illumination of the interior of the former box had exerted an inhibitory influence.<sup>70</sup> On the other hand, this result may have been due merely to my having dealt with a rather refractory specimen, which was on the point of changing at the time of removal from the shaded box, and would have done so if left there.

*How is the fish able to adjust itself to a bottom of given shade,  
independently of the degree of illumination?*

As was pointed out earlier, (p. 441) it is plain that, in order that the change of shade on the part of fish should be *adaptive*, the latter would have to behave exactly as described. When, however, we begin to inquire as to the visual stimuli responsible

<sup>69</sup> Indeed, a number of specimens, aside from those employed in the present experiment, harmonized quite strikingly with this and other gray bottoms which were used. This harmony was enhanced by the transparency of the fins and marginal portions of the body, but was also due, in no small measure, to a disappearance of the yellow and brown tones and the assumption of a nearly pure gray.

<sup>70</sup> It may well be that the degree of illumination at times affects the *rate* of adjustment (Cf. Mayerhofer, *op. cit.*, p. 554), but not its *character*.

for the changes just recorded, the case becomes decidedly puzzling. For anyone with any knowledge of optics knows that gray—at least a perfectly neutral gray—is not a color. Such a gray reflects all the components of white light in their normal proportions. It differs from white only in this, that it reflects a smaller fraction of the total quantity of light which falls upon its surface. Gray is thus relatively darker than white, but not always absolutely darker. When we ourselves judge of an object as being gray or white we make an allowance for the degree of illumination to which it is subjected, and this last is inferred from the totality of the visual field.

But how about the fish? It is not in the position of an outside observer, with abundant standards of comparison at hand. This tank, with its painted surfaces, would seem to constitute for the time being its entire environment. How, then, if the walls of the shaded white box reflect absolutely less light to the animal's eyes than do those of the brightly lighted gray box, does the creature take on a lighter shade in the former than in the latter?

So far as I can see, we are limited to two alternative explanations: either (1) the fish takes into account the degree of illumination, just as we do, and makes due allowance for this in judging of the paleness or darkness of the background; or (2) it makes a direct visual comparison between its own surface and that of the background and endeavors to bring the former into harmony with the latter.<sup>71</sup> In this second case, since the body of the fish itself is lighted or shaded to an equal extent with the background, it would have to become fully white in order to conform even to a dimly lighted white background.

Let us take up the latter of the foregoing alternatives first. In order to test the question whether the fish compares its own appearance with that of its background, I have tried the expedient of concealing from the view of the animal its own skin color. For

<sup>71</sup> Such hopelessly 'anthropomorphic' language may shock the sensibilities of the ultra-mechanistic reader. I therefore hasten to explain that no consciously reasoned mental processes are here implied. The whole chain of events could doubtless be stated in purely physiological terms, were we more familiar with the facts, but so, for that matter, might our own behavior.

this purpose, I have employed two methods, that of staining the skin of the fish and that of covering it with a cloth, stitched along the margin of the body.<sup>72</sup> At first I made a full-length 'swimming suit' for the animal, but this did not seem necessary, since from the position of its eyes, only the anterior portion of the body can fall within its range of vision. Accordingly, a mask only was employed in my later experiments, apertures being made for the eyes.

Now I have devoted considerable time and trouble to experiments of this sort. Eighteen fishes were provided with cloth masks or coverings for the body, and 8 others were stained in various ways.<sup>73</sup> Fully satisfactory tests were, however, found to be difficult, if not, indeed, impracticable. It was, for example, very hard to cover the head completely with cloth, and at the same time permit of an unobstructed view for the eyes. In the earlier experiments, the body alone was covered, leaving the head, or most of it, exposed. The results from such are, I think, wholly inconclusive. Stains, unless rubbed in with considerable force, were found to affect only the mucus covering the body, and to be removed with the discharge of this secretion.

Moreover, all of the methods employed were open to one serious objection: they injured and sooner or later killed the fish. Under such circumstances, it would be expected that disturbances of the normal reactions should occur, and such was indeed the case. A merely negative result in any instance, *i.e.*, the failure to respond to a given stimulus, cannot therefore be regarded as of great importance. We cannot, on the other hand, deny the significance of any positive results which were obtained, if the experiments were otherwise above criticism.

Suppose, now, that the anterior parts of a dark flounder be covered with a white mask, and that the animal be placed in a white tank. The fish would see itself as white. According to the hypothesis we are testing, there would seem to be no reason for change. The converse experiment might be performed with a pale

<sup>72</sup> This suggestion of covering the fish with a cloth I owe to Professor Parker.

<sup>73</sup> Potassium permanganate and silver nitrate were the stains chiefly used. Both imparted a very dark shade to the skin. A white stain proved to be impracticable.



fish wearing a black mask and placed in a dark-walled tank. In this case, likewise, no change of pigmentation should occur, if a visual comparison between the animal's skin and the surrounding bottom is a necessary element in the reaction. Yet such changes did occur in a considerable number of my experiments, and in several cases they occurred under such circumstances as to go far, I believe, toward refuting the hypothesis in question.

In two such instances, where a white mask was employed, the fish (at first dark) did become pale upon a white bottom, and this reaction, in the case of each specimen, occurred again after a second trial.

Once more, a pale fish, which had been kept for ten days on white, was stained (anterior parts only) with potassium permanganate. This produced a continuous dark brown mask, covering as much of the animal's skin as it was enabled to see without bending the body. The fish, after return to the white box for a while, was later transferred to a black one. It became plainly darker in five hours and fairly dark in eight hours. The next day it died. Another specimen gave similar results, though not so well marked.

It must be allowed that in none of these cases was the shade assumed as pale (or as dark), as in normal specimens, but this I believe was due to the inhibitory effect of such severe treatment. That the latter is the true explanation is rendered probable by the fact that reactions were quite as likely to be inhibited which conformed to the requirements of the visual comparison hypothesis as were those which were contradictory to it. Thus one dark fish, which was covered with a *dark* mask and then transferred to white showed little or no change in the course of three days.

Fairness compels the mention of a case in which the reaction (in this instance to a white bottom) was almost wholly inhibited for two days by the presence of a white mask, but occurred within the next few hours after removal of the latter. In this case, the stitches and marginal portions of the cloth were left in situ, and it cannot be said that the effects of injury had been lessened by removing the other parts of the mask. This result, which was obtained much less conclusively with two other specimens, may be held to support the view that what the animal sees of its body is a deter-

mining factor in the reaction. I believe, however, that the inhibitory influence of the mask, in all these experiments, was due not only to the injury inflicted by needle and thread, but to the interference of the cloth with the respiratory movements of the operculum. This interference would of course cease with the removal of the overlying portion of the mask.

One test of the hypothesis in question, which was made unintentionally with *Rhomboidichthys* at Naples, must be referred to at this point, for I regard it as of greater significance than all of these experiments with artificial masks and stains. Specimen no. 10, which had been kept for fifteen or sixteen days in a marble-bottomed tank, and had in consequence assumed a high degree of pallor, was transferred to the coarse dark sand used in so many of my experiments. The fish immediately buried itself with great rapidity, and remained so, with only its eyes protruding, during its entire sojourn upon this bottom. It is probable that it never emerged (in the daytime, at least) except when forced to do so by myself, and at such times it concealed itself with extreme rapidity. Nevertheless, after two days, this specimen was nearly as dark as the sand, and after five days it was described in my notes as harmonizing almost perfectly with this material. After another extended sojourn (twenty-six days) upon white and pale gray backgrounds, the fish was placed upon the jet-black magnetite sand. In this, it displayed the same tendency toward concealment, remaining buried, except when forced to leave cover. Nevertheless, the fish was quite plainly darker after the lapse of a single day, and of a very dark shade after the lapse of six days (fig. 10*d*), although my notes state that "when placed here, the fish seemed almost white in comparison with the sand." There surely had been little opportunity in this case for the fish to observe the appearance of its own body.

The foregoing experiments with these two species of fish, although not free from contradictions, certainly do not bear out the visual comparison hypothesis, but rather come very near to refuting it altogether. A really satisfactory test of the alternate hypothesis seems likewise very difficult in practice, and, although I have devoted much time to the matter, I have, at the present writing,

no experimental results of interest to offer. The essential requirement for such a test would seem to be that the background to which the fish is to cause its own shade to conform shall be illuminated from a source of light independent of that which falls upon the animal's eyes from overhead. Thus this background might be made to appear dark or the contrary, relatively to the light which *seemed* to illuminate it. A human observer, under similar circumstances, would be deceived, and would misjudge the shade of the surface in question. Would not a fish do the same?<sup>74</sup>

After considerable experimenting, I believe that I have devised an apparatus calculated to fulfil these conditions. This apparatus I will not describe here, since I am not prepared to report upon any results from its use. Owing to a lack of flounders of the right species, the experiments must be deferred until the coming summer, when, I hope, it will be possible to settle the question at issue by a few decisive tests.

#### SUMMARY AND CONCLUSIONS

Flounders of several species were found to undergo marked changes in their color pattern or their general shade, when transferred from one type of bottom to another. The range and character of these pigment changes, and the nature of the stimuli which provoked them, were subjected to considerable experimental inquiry. The following are some of the principal facts which were revealed through these investigations:

1. Fishes became very pale (in one species extremely so) upon a white background; dark brown or nearly black upon a black one, and of various intermediate shades upon bottoms of gray, brown, etc.

2. The animals appeared to be limited in their capacity for adjustment almost wholly to black, white, brown and gray tones. Bright red or yellow backgrounds, for example, failed to call forth adaptive responses, at least during periods quite sufficient

<sup>74</sup> Again the spectre of 'anthropomorphism' may seem to rear its head. But no. An optical illusion does not presuppose intelligent judgment (or misjudgment), any more than does an ordinary normal perception.

for the other changes which are here described. In other words, the skin pigments which were displayed seemed to be restricted to components of the more habitual backgrounds encountered by such fishes.

3. Upon a homogeneous ground, the pigment of the skin was commonly much more uniformly distributed than upon a background having a diversified appearance.

4. Upon a mixed background, such as was afforded by one of the ordinary sands or gravels of its customary habitat, the fish took on a definite color pattern, which varied with the texture of the material, and was oftentimes in striking harmony with the latter.

5. Artificial backgrounds, containing variously distributed areas of pure black and white, called forth far more contrast in the skin patterns than did the less contrasted tones of the sand and gravel.

6. The principal markings constituting these various skin patterns were found to be permanent, in the sense that they always reappeared in the same positions, and even when the animal adapted itself to a homogeneous background, the outlines of most of these spots were still distinguishable. In the case of *Rhomboidichthys podas*, the arrangement of these spots was, in its essentials, constant for all members of the species. Regarding the other fishes used, I cannot speak with the same certainty.

7. The patterns assumed were consequently limited, in great degree, by fixed morphological conditions. Thus squares, cross-bands, circles, etc., were never copied in any true sense, by the fishes.

8. Within the limits thus imposed, the capacity of one of these species (*Rhomboidichthys podas*) to adapt itself in respect to the distribution of its skin pigments was often remarkable. For example, experiments with painted squares and circles of black and white showed that the resulting skin patterns depended not only upon the relative *amounts* of black and white in the background, but upon the *degree of subdivision* of the areas of the latter. As an example of this last point, when the background was divided into areas 2 millimeters square, a finer grained appearance was produced in the fish than when 1-centimeter squares were used.

9. Thus, while the adaptation was most complete upon such backgrounds as formed a part of the natural habitat of the species, it was plainly not restricted to these cases, and the pigment was at times disposed in ways which, it seems likely, were quite foreign to the previous experience either of the individual or the race. For example, the extremely pale, and perhaps also the very darkest conditions; likewise the vividly contrasted black-and-white condition, without intermediate shades, which was assumed by certain specimens upon some of the artificial backgrounds. Accordingly, the notion that the fish is limited to a few stereotyped responses, representing the most familiar types of habitat, must be rejected at once.

10. Fishes of the same species differed greatly in their individual powers of adaptation, and some seemingly normal specimens possessed this power in a very limited degree. Again the same fish acquired with practice (if this word may be allowed) the power of changing much more rapidly than before. The time required for a radical change of shade or of pattern ranged from a fraction of a minute to several days.

11. In the case of *Rhomboidichthys*, the underlying surface (more strictly, that part of the bottom immediately surrounding the fish) appeared to be the one chiefly effective in calling forth these changes. The influence of the vertical walls of the vessel commonly seemed to be a subordinate one, even in cases where the fish was so large that it covered a considerable fraction of the bottom, and was obliged to lie constantly with its eyes close to one or another side of the jar. Fairly conclusive evidence was offered, however, of the influence of the vertical walls of the latter, even upon this species. What the fish saw directly overhead seemed, on the contrary, to exert a negligible influence upon the color pattern.

12. With the sand-dab, much clearer evidence was obtained of the influence of the vertical walls of the receptacle. These, at times, appeared to have an effect as great as, if not, indeed, greater than, that exerted by the bottom. It must be noted here that this difference between the two species is perhaps to be attributed to the differing positions of their eyes. Those of *Rhomboidich-*

thys are situated at the ends of movable stalks, so that this fish must be able to obtain a much nearer view of the bottom than is possible for *Lophopsetta*.

13. Within very wide limits, the degree of illumination of the background was found to have little or no effect upon the shade assumed by the fish. As a special example of this principle, fishes in a white receptacle, even when the latter was heavily shaded, became paler than fishes in a gray receptacle, even when this was exposed to bright light. In such cases, the dimly lighted white bottom of the one tank was actually darker than the brightly lighted gray bottom of the other, in the sense that the former reflected an absolutely smaller amount of light to the observer—whether human or piscine—than the latter. A rather curious problem was raised by a consideration of these facts, which was dealt with at some length and was made the object of special tests.

14. A specimen of *Rhomboidichthys* which was transferred while extremely pale to black sand, acquired a very dark shade, even though the fish remained persistently buried in this material, with only its eyes protruding. Again, specimens of *Lophopsetta* having their skin deeply stained, or wearing masks of cloth, were found, in some cases, to undergo pronounced adaptive changes, despite the fact that their body surface was disguised in this way. It is thus rendered highly improbable that any direct visual comparison on the part of the fish between its own body surface and the surrounding background is an essential factor in the production of these changes.

15. Fishes (*Rhomboidichthys*), when given the choice of two backgrounds, displayed no preference for the one which conformed more nearly to their own shade at the time. Likewise, specimens which were glaringly out of harmony with a given shade of sand appeared no more likely to conceal themselves beneath its surface than when their skin color was adjusted very closely to this.

16. When examined at night, after several hours of complete darkness, the fishes (*Lophopsetta*) were found to be in the same condition of pigmentation as when previously observed by daylight. Pale specimens, which were kept 5 to 7 days in a black-painted, light-proof box, became considerably darker during this

period, though remaining distinctly paler than dark control specimens with which they were compared. They acquired the same shade as the latter, however, after a few hours' exposure to light in the same box.

17. Experiments with fishes which had been deprived of their sight confirmed the findings of earlier investigators that the unimpaired functioning of at least one eye is necessary for the adjustment of the animal to its background. If blinded when in the dark condition, the fishes ordinarily remained dark, though they did not always permanently retain the darkest shade which is displayed by a normal specimen. If blinded when pale, they remained pale for about a day, but reverted to a darker condition, representing more nearly the resting state of the chromatophores. An interesting special case was discussed of fishes which had been adapted for a considerable period to a pale background, and afterwards for a brief period to a dark background. These reverted to the pale condition after blinding, though this later gave place once more to the dark state.

18. Destruction of the sight of one eye (whether the left or the right) had little or no effect upon the chromatic reactions of the majority of specimens of *Lophopsetta*.

19. Tactile stimuli, if effective at all, certainly played a quite subordinate part in evoking color changes of an adaptive nature, for the fishes responded as promptly to patterns painted upon the under side of strips of glass as to bottoms of stones and gravel whose complexity could be discerned by touch as well as by sight.

20. Very decided changes in the markings, as well as the general color-tone of the body were at times called forth by tactile or other non-visual stimuli, and the fish, when swimming, commonly presented a decidedly different aspect from that shown in the resting condition. But such changes as these belong to quite a different class from those which form the chief subject of the present paper.

Certain of the facts above summarized, deserve further discussion than was devoted to them in the body of the text.

We have seen that the skin of some of these fishes commonly assumes a nearly homogeneous tone upon a bottom of uniform color and shade, while presenting a more or less pronounced pattern upon a bottom of diversified appearance. Abbot Thayer<sup>75</sup> has pointed out that the breaking up of a uniform color tone by markings of any sort makes for concealment, and this is particularly true against a diversified background. This principle, without question, accounts for much of the effectiveness of the various patterns assumed by *Rhomboidichthys* and other flounders, and we must not be in too great haste to point out specific resemblances to particular backgrounds, merely because the fish ceases to be conspicuous upon these. I think, however, that a careful consideration of the experiments as a whole, and particularly of the facts referred to in paragraph 8 of the summary, forces us to the belief that there may be very specific relations between the distribution of light and shade in the background and the pigment pattern assumed by the fish.

Had we to do here merely with a general paling or darkening of the entire body surface, affecting spots and ground color to an equal extent, or even were there at the disposal of the fish one of two of these pigment patterns, corresponding to certain of the most frequent types of bottom, we might ascribe this power to a few comparatively simple reflexes. But we have seen that the responses are far from being as stereotyped as this. Certain areas become paler and others become darker, each more or less independently, and in varying degrees, depending upon the circumstances. At one time we have a large dark blotch covering a given portion of the surface; at another time, the pigment of this blotch has practically disappeared from view; at another yet this area has become broken up and diversified by the appearance of paler specks within it. Most of this change, too, is brought about by variations in the conspicuousness of groups of pigment cells

<sup>75</sup> Popular Science Monthly, December, 1909; also book by Gerald Thayer entitled "Concealing Coloration in the Animal Kingdom. A Summary of Abbot H. Thayer's Discoveries," N. Y., 1909. It is likely that few biologists can follow Mr. Thayer in the unbridled zeal with which he strives to universalize this and the other important principles of animal coloration which he has discovered.



which never wholly fade from view. The pale specks which serve to "stipple" the dark blotches and give to them a fine-grained appearance (fig. 4a) may, in large part, be distinguished in the nearly solid blotches of the coarser pattern (fig. 4b).<sup>76</sup>

When we add to this complexity, the additional complexity due to differences of color proper (as distinguished from shade), it is difficult indeed to conceive of a nervous mechanism competent to bring about such changes. But conceivability is surely a poor criterion of possibility in biology, and we cannot see that a non-mechanical (*i.e.*, vitalistic) interpretation of these phenomena would help us in the least. For, on the sensory and motor sides, this baffling complexity of mechanism would have to be granted in any case, and the only thing which the vitalist could do would be to posit a non-mechanical coordinating agency, which adapted the means to the end. But this, as has so often been pointed out, is a merely formal solution of the difficulty, and one totally impotent as a principle of scientific explanation.

That the stimuli which call forth these changes are visual rather than tactile has been shown, in my experiments, by the use of perfectly smooth glass plates, having the pattern painted upon the lower surface. That these stimuli are received through the eyes, rather than through the skin is, of course, not wholly proved by destroying the animal's sight, since the objection may always be raised that we have to do with inhibition through shock. On the other hand, the recent experiments of Parker<sup>77</sup> show pretty conclusively that the skin of at least some marine fishes is insensitive to light, even when the latter is of very high intensity. Were it proved, however, that such a general sensitiveness to light and shade was highly developed in the skin, it is impossible to see how responses to a *pattern* could be brought about through any organs except the eyes, for these alone are provided with the lenses necessary for the production of images.

<sup>76</sup> As stated earlier (p. 416), the chromatophores themselves are probably distributed with much greater uniformity than the complexity of pattern would at first lead us to suppose. The position of the spots—actual and potential—may be largely determined by the position of the nerve termini.

<sup>77</sup> American Journal of Physiology, October, 1909. Fishes of nine species were used in Parker's experiments.

But aside from the evidence which they afford of the rôle played by the eyes in these *changes* of color, the blinding experiments seem to show that vision is necessary in order that the pigment cells shall remain in a given state of *tonus*, exception being made to the case of those fishes which are blinded in a uniformly dark state, representing most nearly the resting condition of the chromatophores. Continued adaptation to a less usual background, *e.g.*, a very pale one, may result in the new condition becoming more or less fixed. The latter may persist for a time after loss of sight, but the more habitual state of *tonus* finally reasserts itself. The cases mentioned at the close of section 17 of the summary might be explained by supposing that the pale condition had become in considerable measure fixed, so as to reappear after the stimuli responsible for the secondary dark condition had been withdrawn by destruction of the sight. The ultimate return to the dark state would be intelligible here as in the case of fishes which are blinded when pale. But if the foregoing interpretation is correct, it is hard to understand why any unusual state of the chromatophores which has but recently been acquired should not give place to the more habitual condition as soon as the light of day is withdrawn (*e.g.*, at night). But this was found not to be the case. Here, as so often happens, the simple and obvious explanation does not seem to contain the whole truth.

Evidence has been offered which seems to show conclusively that the plane in which a given surface lies with relation to the fish determines in some cases, whether or not it shall be effective in calling forth a given change. It was not made certain, however, that even in such cases, the matter was not decided by purely quantitative relations within the visual field. For, as was pointed out, we must distinguish between the potential and the actual visual fields. That the horizontal surface lying immediately about the fish is the one which is generally most potent in determining the reactions of *Rhomboidichthys*, might be due entirely to the fact that the animal's gaze is commonly turned in this direction. In experiments upon *Lophopsetta*, we found (p. 454) that when the bottom, plus the *upper* half of the vertical walls, were white, while the lower half of these walls was black,

the dark fishes which were used did not turn pale. On the other hand, the white bottom, plus the white *lower* half, or even lower fourth were found to call forth this change. These facts, which at first thought would seem to indicate the operation of some other factor than the relative amounts of black and white, do not in themselves force us to such a conclusion. If we assume that the animal's field of attention (due to the position of the eyes or otherwise) extends but little above the horizontal plane, the facts may, indeed, be explained on a purely quantitative basis. But this is probably not the whole truth. For it seems to follow from the considerations offered below that differences in the direction of different portions of the visual field probably condition the reactions of the fish in another important respect.

This problem is more clearly allied than might at first be supposed to another one which has received considerable attention in the present paper. I refer to the *modus operandi* of the stimuli which lead the fish to become very pale on a white surface and gray upon a gray surface, irrespective of the degree of illumination.<sup>78</sup> As I have already pointed out (probably quite needlessly), a surface of pure gray reflects white light, with no alteration except a diminution of its intensity. A human observer distinguishes a given object as gray, rather than white, only by reference to the degree of illumination to which it is subjected, and this last he infers from the appearance of the remainder of the visual field. Suppose, for example, that our visual field should for the moment consist of a single uniform surface, of which we had no prior knowledge, illuminated by a light of unknown intensity. Under such circumstances, we should be at a loss to say whether the surface was gray or white.<sup>79</sup> Once we have an idea of the degree of illumination, however, and we make the necessary correction for this, as, for example, when we view a piece of white paper in the twilight, we commonly pronounce it to be white, despite the abso-

<sup>78</sup> The reader, if interested in this part of the discussion, is advised to refer directly to the treatment of this question in the body of the text, particularly pp. 440-443 and 460-467. It would be impossible, without much undesirable repetition, for me to restate the entire problem here.

<sup>79</sup> Colors, of course, would still be distinguished.

lutely small amount of light reflected from it. In the same way, the interiors of the white vessels used in my experiments seemed to the outside observer<sup>80</sup> to be white, and those of the gray vessels to be gray, despite the fact that the latter actually appeared far lighter in a photograph.

Are the perceptions of the fish similarly determined? How can such a thing be possible, in cases where the uniform walls of the receptacle constitute practically the entire visual field of the animal? Without any outside standard of comparison, how can a heavily shaded surface of white appear paler than a brightly lighted surface of gray?

We have seen that one simple solution of this difficulty would be to assume that the fish makes a direct visual comparison between its own body surface and the bottom on which it lies. If the former is adjusted to the latter, the absolute degree of illumination which is common to the two is a matter of no possible consequence, for the object of this adjustment is the concealment of the animal. This hypothesis was, however, rejected, in view of pretty conclusive experimental evidence. Furthermore, it does not accord well with the fact (p. 443) that the behavior of the fish does not seem to be influenced in other ways by the color-phase in which the animal happens to be.

What, then, is the standard of comparison by which the fish (or its unconscious nervous mechanism, if the reader prefers) determines the shade to which the skin is to conform? In other words, if, as has been demonstrated, the absolute amount of light reflected from the background is not the only factor in the effective stimulus, what other one is there? As just stated, the human observer would decide the point by reference to other elements of the visual field. From the fish's point of view, the only other element of the visual field, besides the bottom and walls of its tank, is the illuminated area overhead, representing the source of light—commonly sunlight reflected from objects outside the tank. May not, then, the ratio between the light reflected from the near-

<sup>80</sup> At least they did so to me. It is quite possible that one who did not appreciate the density of the shadow might have judged otherwise.

by surfaces within the tank and the light which enters the latter from above be that factor of the total stimulus which renders possible these accurate adjustments of the shade of the fish's body to that of its background?<sup>81</sup> I think that this is the true solution of the problem, and I hope, with apparatus already constructed, to put the question to experimental test, as soon as material is available.

That such a relation between the light intensities of two portions of the visual field may form an integral part of the immediate perception, without the necessity of rational mental processes, I think will be granted by all. Now naturally the fish knows nothing of the distinction between the source of the light and that part of the environment which is illuminated by it. There is for the animal but one continuous visual field, though this may not all be apprehended at once. The latter is constituted by various areas, differing in luminosity or in color. Those portions of this field which lie below, or but little above, a horizontal plane passing through the animal itself are the ones to which the appearance of the latter is adjusted. It is these which, as already seen, probably occupy the focus of attention most of the time. Those portions which lie more nearly overhead, and thus ordinarily beyond the focus of attention, must, however, serve in some way as a criterion by which the shade of the rest of the visual field is apprehended. With a given amount of light from outside the tank, a greater or a less amount of reflected light from the bottom would of course imply a lighter or a darker shade in the latter. On the other hand, with a given (absolute) amount of light reflected from the bottom, the occurrence of a low degree of illumination overhead would lead the animal to attribute a paler shade to this bottom (*i.e.*, *to see it as paler*) than if the source of light were a brilliant one.

<sup>81</sup> These words, and in fact my entire discussion of this problem, down to the end of the next paragraph, were written before I had any knowledge of the almost identical hypothesis which was put forward some years ago by Keeble and Gamble (Phil. Trans. Roy. Soc., Series B, vol. 196, 1904). Under these circumstances, such a verbal coincidence as is to be noted in comparing their statement with mine is rather surprising. On p. 358, these authors state: ". . . on the white and black grounds the animal . . . appeals for pigment-guidance to the amount of light *scattered* or *absorbed* from the ground; or, as we put it previously, it is a reaction to the ratio  $\frac{\text{direct}}{\text{reflected}}$  light."

Experiment alone (see p. 467) can place beyond question the accuracy of this interpretation. What is needed especially is a satisfactory determination of just which elements of the visual field it is to which the animal conforms its own appearance, and which ones it is that serve as a criterion by which the shade of the background is apprehended. So far as I can see, differences of *direction from the animal's eyes* are the only ones which can be invoked in differentiating these two sets of stimuli, and Keeble and Gamble (whose treatment of this problem was unknown to me when the foregoing discussion was written<sup>82</sup> incline to the same opinion. They hold (p. 354) that "in some way, the eye differentiates between the direct and the irregularly scattered light, in other words, it displays a certain dorsi-ventrality." Under ordinary conditions, the background is below and the source of light above. But the authors find that, if the conditions of illumination be artificially reversed, the "background" being above the animal and the light entering from below, the reaction to the former is the same as when it lies beneath them. Thus, they hold, "the dorsi-ventrality is probably not due to a permanent structural difference in the two sides of the eye." It is not clear, however, from their account of this experiment, that the conditions of illumination were not complicated by total reflection from the bottom of the jar. Unless the animals looked directly downward, or at least within a certain angle with the bottom, they would see, not a brightly lighted field below them, but the reflections of objects in the upper portions of the tank (pp. 427, 428 of the present paper).<sup>83</sup>

<sup>82</sup> See foot-note 81

<sup>83</sup> I cannot feel quite sure that the experiment of Bauer (*Centralblatt für Physiologie*, 1906), in which he used electric lights, placed above and below the glass container, is not open to the same objection. From this experiment and others, Bauer concluded that the assumption of a dark shade by *Idotea* was determined by "Simultankontrast," irrespective of the position of the contrasting portions of the visual field. This is certainly not true of fishes, as is shown by my experiments. (See particularly p. 451 et seq.)

The experiments of Mayerhofer, likewise, (op. cit., pp. 553, 554) in which a mirror was placed below the glass container, inclined at an angle of 45°, appear to me to be inconclusive, owing to the same apparent technical defect; and it is significant in this connection to note that fishes lighted from below, in this way, assumed the same shade as those kept in total darkness.

A word in regard to the utility of this power of color change in the life of the organism. Despite the recent reaction against extravagant applications of the protective coloration principle, it is difficult to doubt, in the present instance, either that this faculty has some use, or that it has been developed in some way because of its use. The end to be attained seems to be *concealment* and nothing else. No appeal to thermal regulation,<sup>84</sup> to possible "photoreceptive" or "photosynthetic" functions of the skin pigments, nor any other purely physiological explanation of the phenomena seems adequate. A complete explanation must regard ecological factors as well. Whether the utility of these changes to the fish consists primarily in their concealing the latter from its enemies or from its prey cannot, however, be stated without a greater familiarity with the bionomics of these species than the present writer possesses. I learn from several trustworthy observers that flounders of various kinds are preyed upon by sharks and other large fishes. The only information which I have relating directly to the enemies of any of the species which have been discussed in this paper, is the statement of Mr. Vinal Edwards that he has taken sand-dabs, along with other flounders, from the stomach of the cod. It is quite probable *a priori* that all of the species are similarly preyed upon.

As regard the prey of these fishes, I can but offer my own observation that specimens of *Lophopsetta*, when recently brought into the laboratory, frequently regurgitated the 'sand-launce' (*Ammodytes americanus*), sometimes in considerable numbers. It is not unlikely, therefore, that the cryptic coloration of flounders is of advantage in concealing them from smaller fishes<sup>85</sup> until the latter come within easy range.

These few meagre statements of course illustrate the paucity of our direct evidence upon the whole question of the utility of cryptic coloration, and indicate the inferential nature of most of our conclusions in this field.

February 23, 1911.

<sup>84</sup> As suggested by Max Weber et al. (Van Rynberk, op. cit., p. 568 et seq.)

<sup>85</sup> Invertebrate food may perhaps be left out of consideration here.

## EXPLANATION OF PLATES

The photographs, with the exception of 1e (by Dr. Victor Bauer), were all taken by the author. The water-color sketches (plate 6) are the work of Mr. V. Serino, an artist in the employ of the Naples Station.

The figures all relate to a single species, *Rhomboidichthys podas* (Delaroche), and all are reduced to approximately one half the natural size.

Figures bearing the same number represent different views of the same fish. These are arranged with a view to easy comparison. Thus the order in which the views of a single specimen are presented does not necessarily bear any relation to the order in which the corresponding changes were undergone in the course of the experiments.

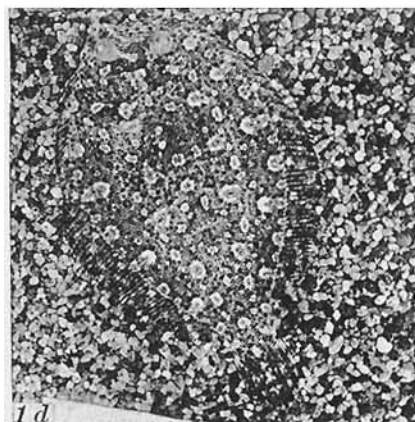
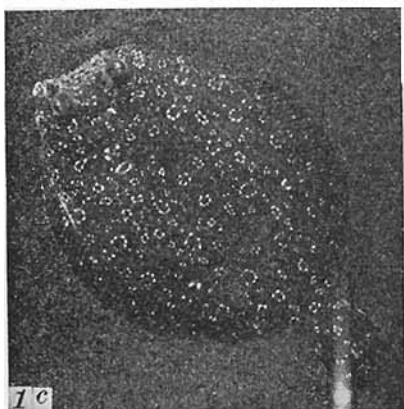
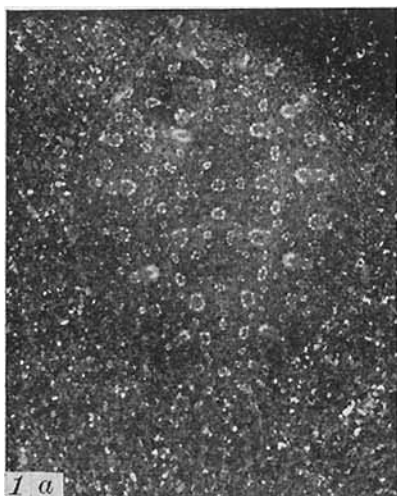
For an account of the photographic methods employed see pp. 418-421 of the text.

## PLATE 1

### EXPLANATION OF FIGURES

Views of specimen no. 1: *a*, on a dark, mixed sand (after one day); *b*, on fine gravel (after one day); *c*, on fine jet-black (magnetite) sand (after four days); *d*, on a very coarse reddish sand (after eight days); *e*, on a coarse gravel, devoid of sand (after two days).

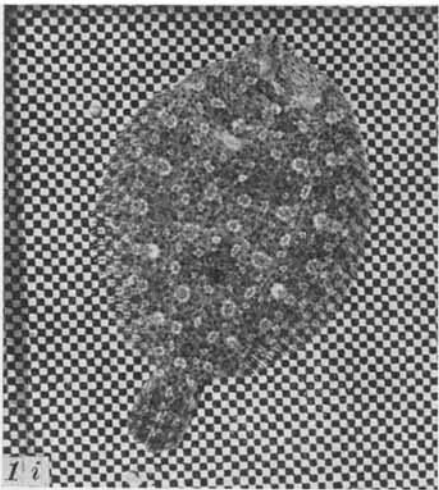
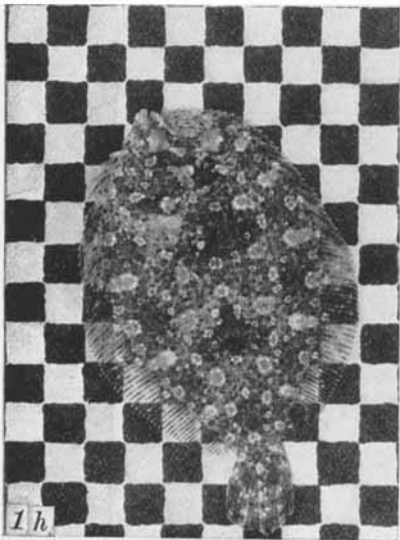
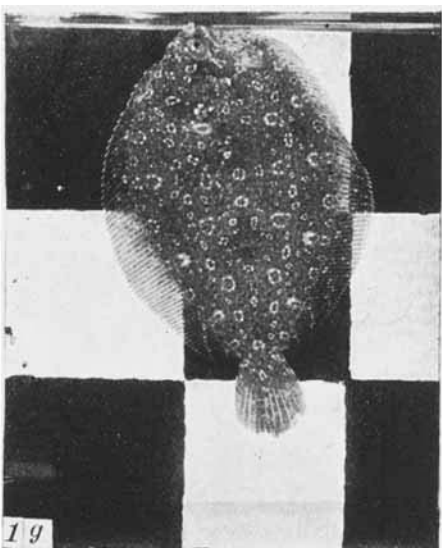
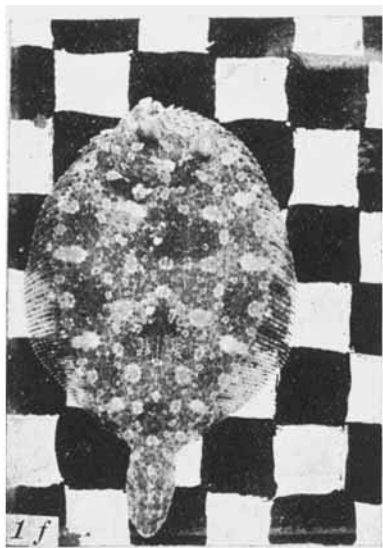




## PLATE 2

### EXPLANATION OF FIGURES

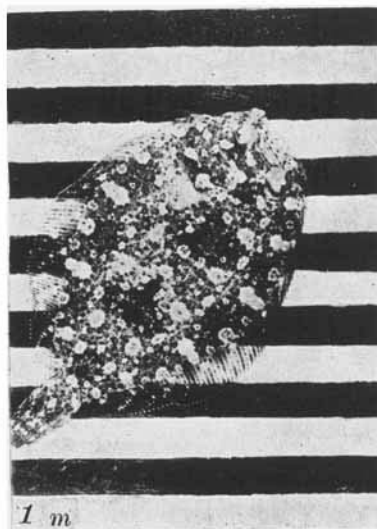
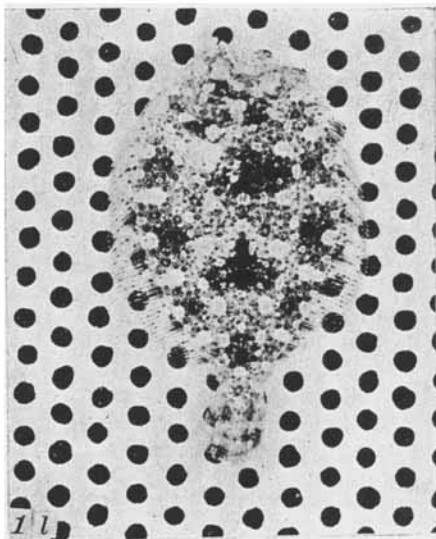
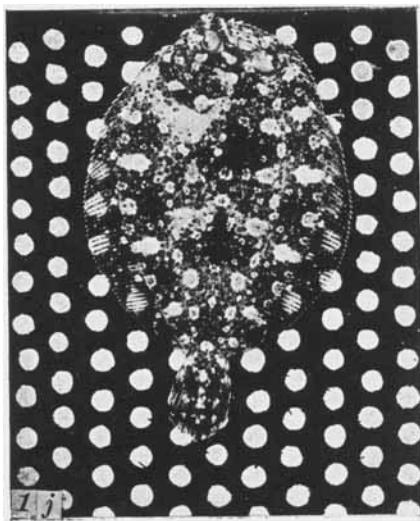
Views of specimen no. 1: *f*, on painted squares, 2 cm. sq. (after four days); *g*, do.,  $4\frac{1}{2}$  cm. sq. (after seven days); *h*, do., 1 cm. sq. (after four days); *i*, do., 2 mm. sq. (after one day).



### PLATE 3

#### EXPLANATION OF FIGURES

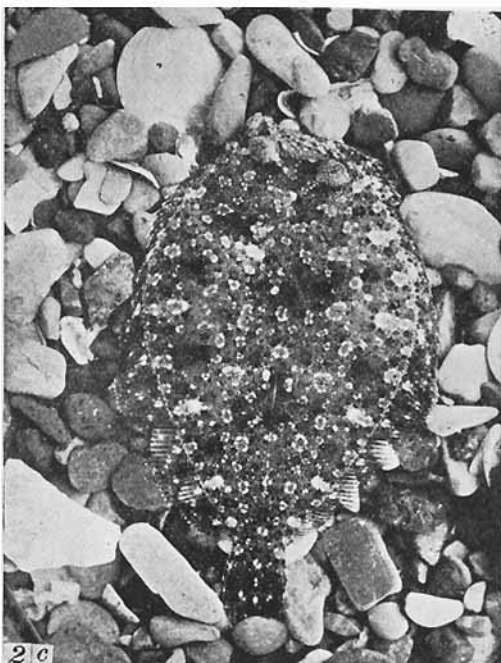
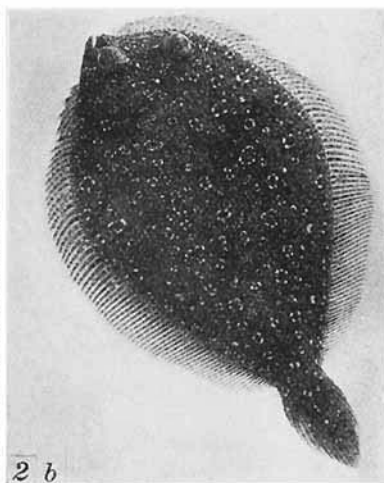
Views of specimen no. 1: *j*, after three days on background figured; *k*, after fourteen days on white marble bottom (the fish was in reality much paler than the photograph would seem to indicate); *l*, after three days on the background figured; *m*, after six days on the background figured.



## PLATE 4

### EXPLANATION OF FIGURES

Views of specimen no. 2: *a*, on dark mixed sand, partly covered with this material (after two days); *b*, on white glass plate, shortly after transfer to this following sojourn on dark sand; *c*, on coarse gravel (after two days); *d*, on white glass plate, shortly after transfer to this, following sojourn on coarse gravel. (Compare this with *b*. In *d*, the gravel pattern has persisted to some degree, despite an immediate partial disappearance of this).



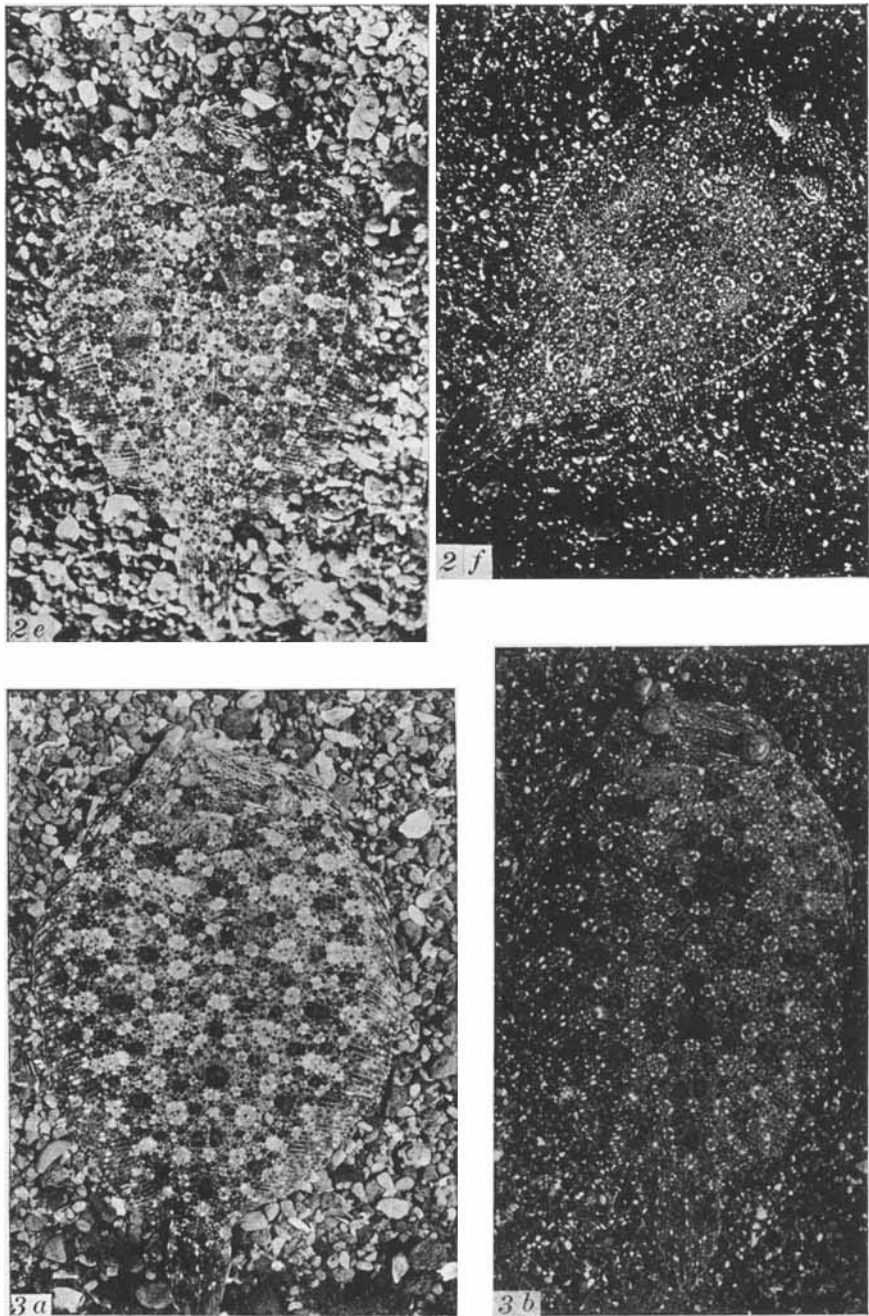
## PLATE 5

### EXPLANATION OF FIGURES

Views of specimen no. 2: *e*, upon fine gravel (after two or three days); *f*, upon dark, mixed sand (after two days).

Views of specimen no. 3: *a*, after one day on present ground; *b*, taken on the day when first placed on this sand. (Note the inferior power of adaptation shown by this fish, as compared with the last. The harmony with the backgrounds increased little if any beyond the condition shown in the photographs).





## PLATE 6

### EXPLANATION OF FIGURES

Views of specimen no. 3, in the 'sand' and 'gravel' phases. Unfortunately, the capacity of this specimen for such adaptations proved to be comparatively small.



3 c

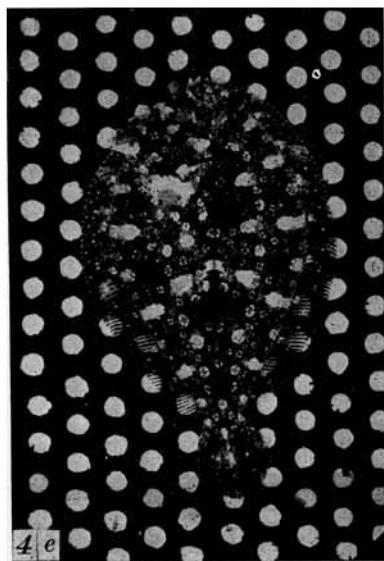
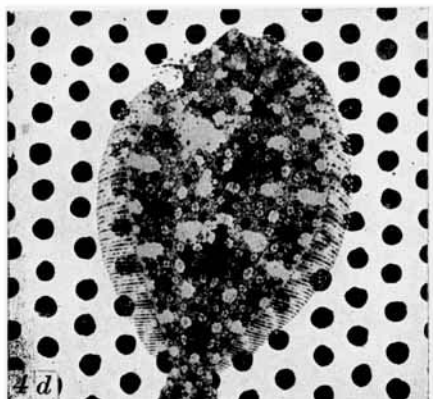
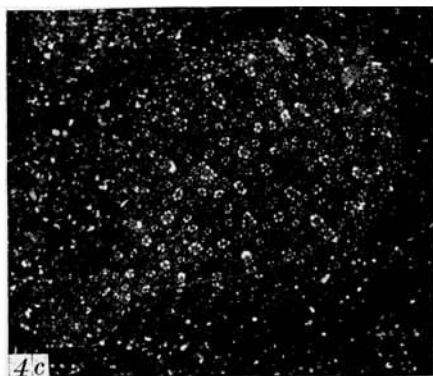
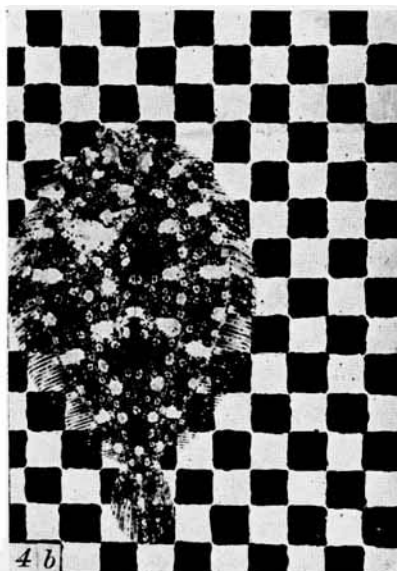
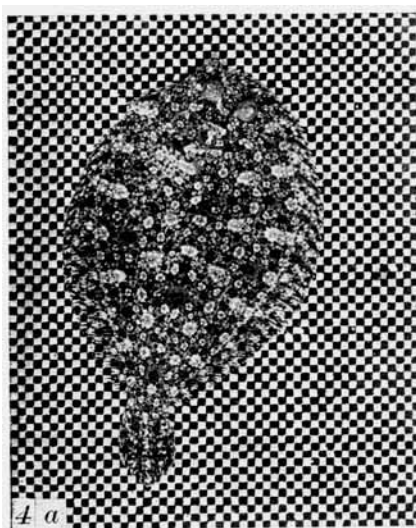


3 d

## PLATE 7

### EXPLANATION OF FIGURES

Views of specimen no. 4: *a*, after six days on pattern shown; *b*, after three days on pattern shown (compare minutely with last); *c*, after nine days on the dark sand; *d*, after three days on the pattern shown; *e*, after three days on the pattern shown.

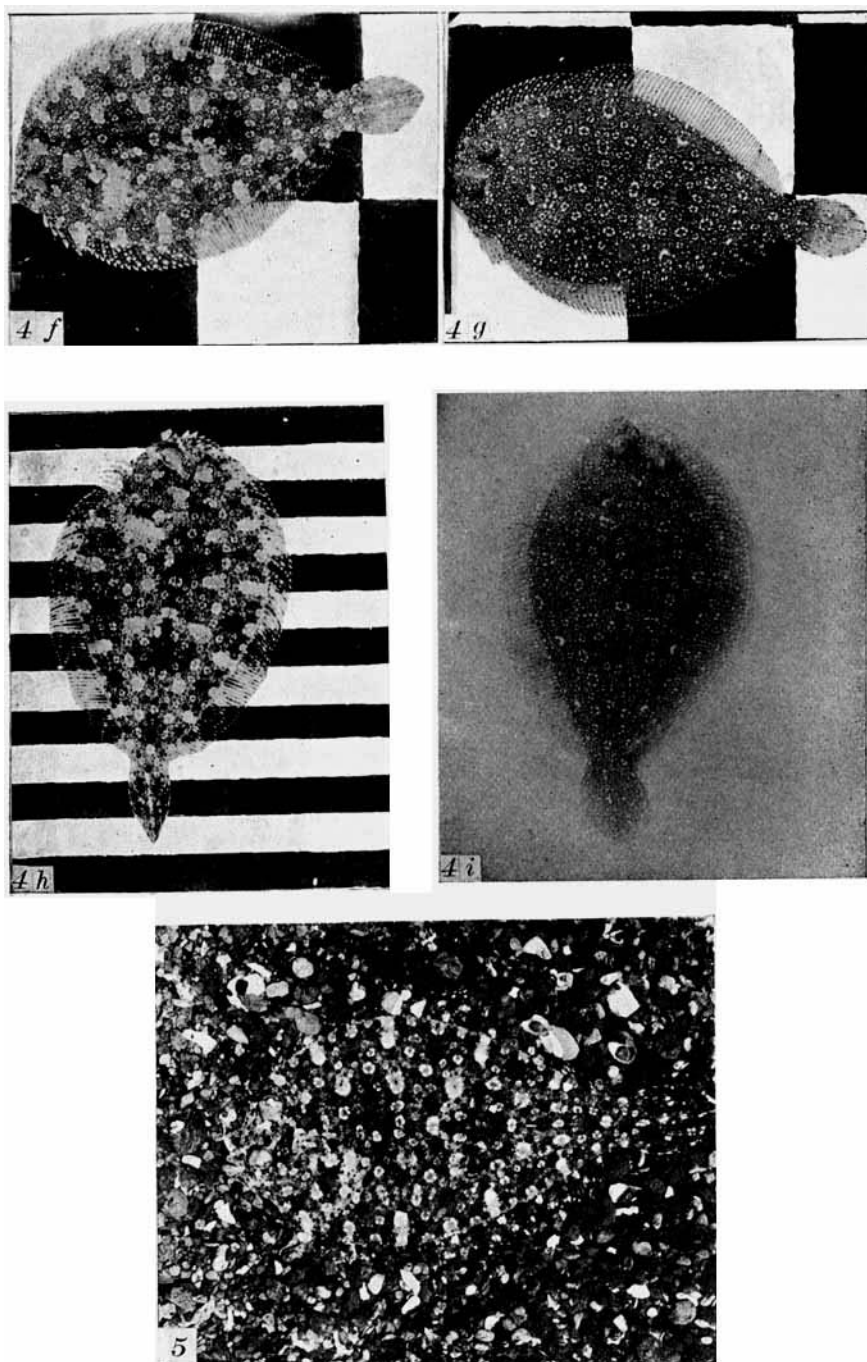


## PLATE 8

### EXPLANATION OF FIGURES

Views of specimen no. 4: *f*, after seven days on present background (condition of rest); *g*, same, when preparing to swim; *h*, after one day on present background; *i*, after three days on a background of gray, of a shade approximately matching that produced on a color-wheel by the use of two parts of black and one of white. (The harmony between the fish and the bottom was really much greater than would seem to be the case from this photograph, which has made the fish seem darker).

Specimen no. 5: view inserted to show a particularly striking gravel pattern (taken after eight days). (There are in reality a few particles of gravel on the back of the fish).



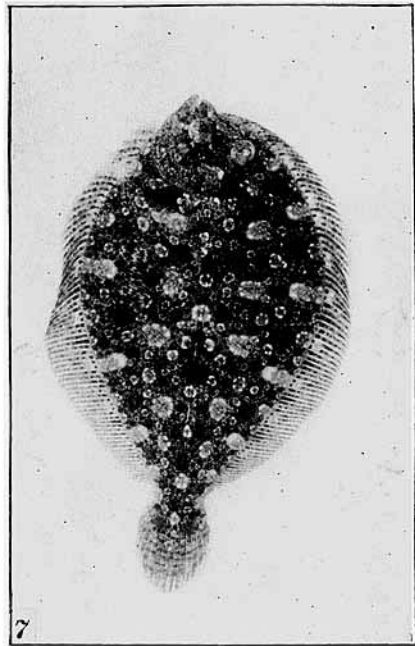
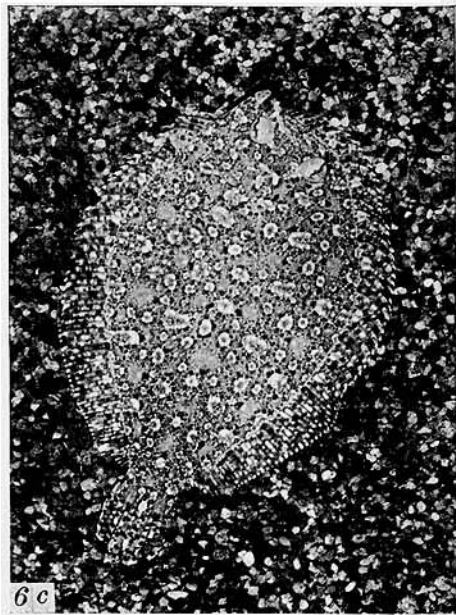
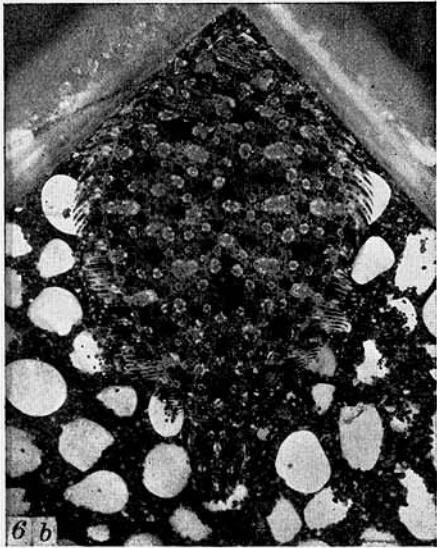
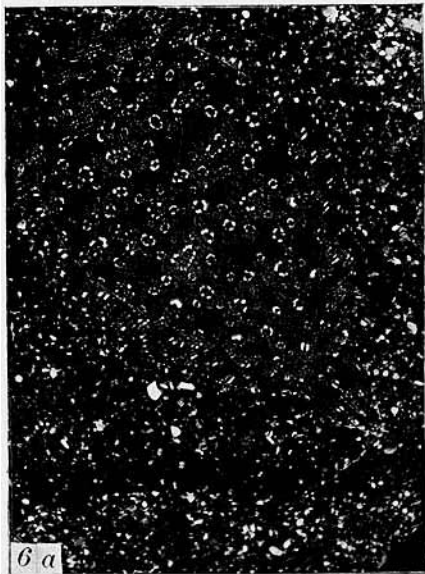
## PLATE 9

### EXPLANATION OF FIGURES

Views of specimen no. 6: *a*, upon dark, mixed sand (after one day); *b*, upon the same sand, with the addition of white pebbles (after three days); *c*, on coarse, reddish sand (after six days).

Specimen no. 5: showing conspicuously mottled appearance, unusual in a specimen just brought to the laboratory.

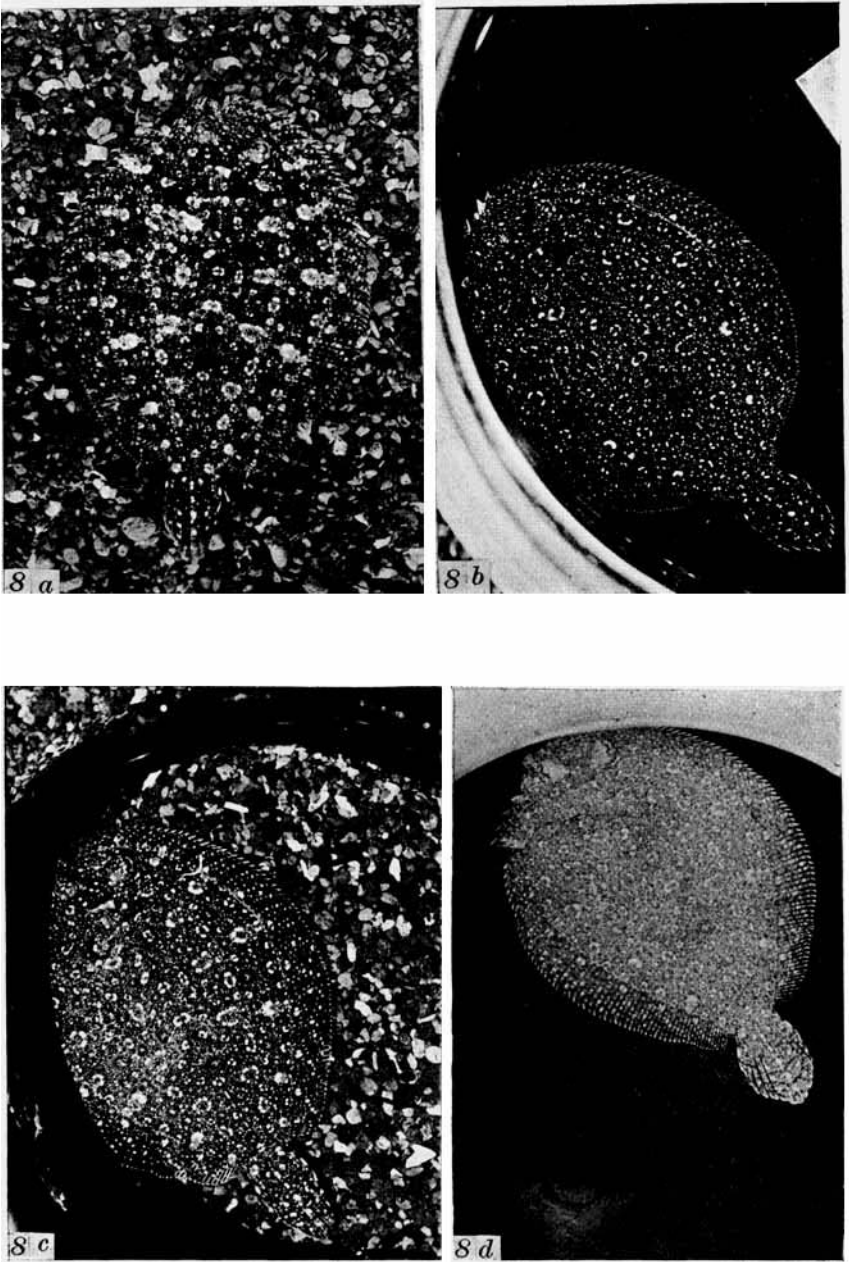




## PLATE 10

### EXPLANATION OF FIGURES

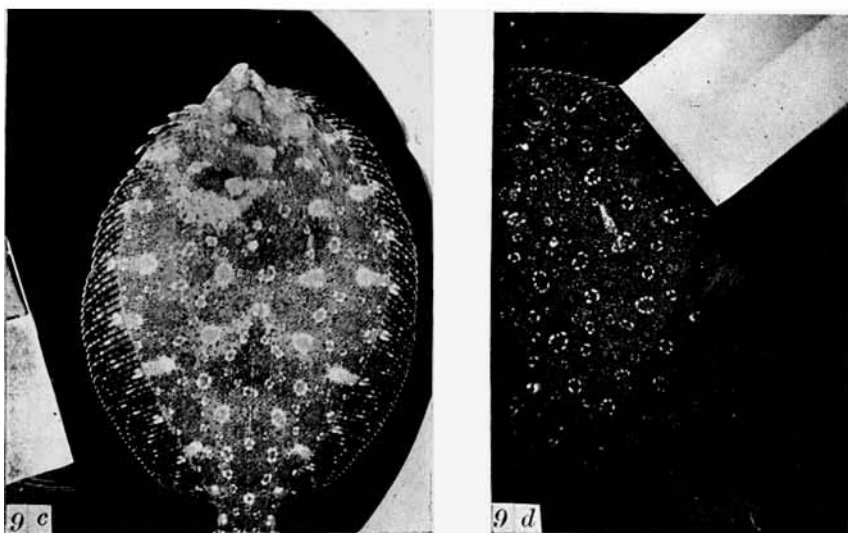
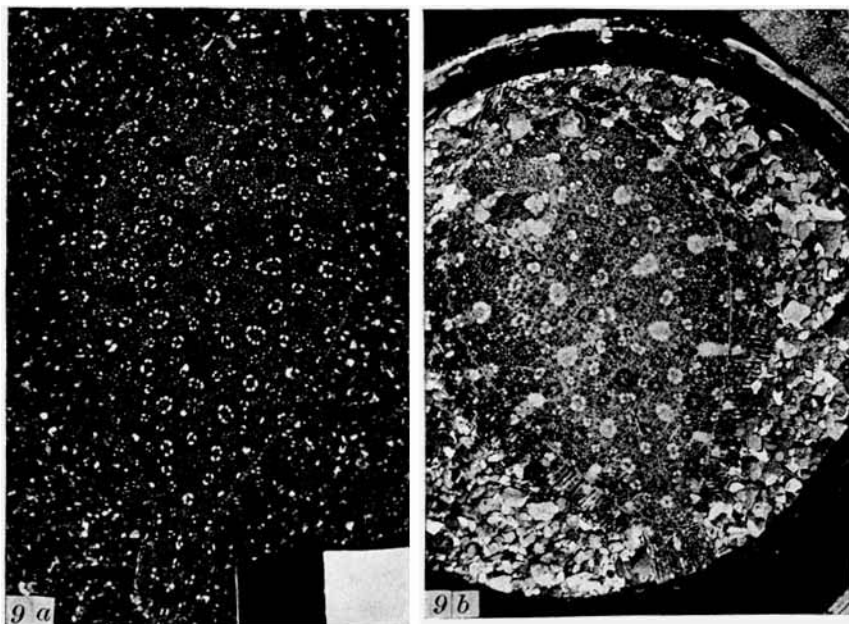
Views of specimen no. 8: *a*, after four days on material shown; *b*, in jar having black bottom, and transparent walls, surrounded by gravel (after seven days); *c*, in jar having black walls and transparent bottom, with gravel underneath (after ten days); *d*, taken on a black bottom, immediately after transfer from a white-bottomed, black-walled jar, in which the fish had remained 9 days.



## PLATE 11

### EXPLANATION OF FIGURES

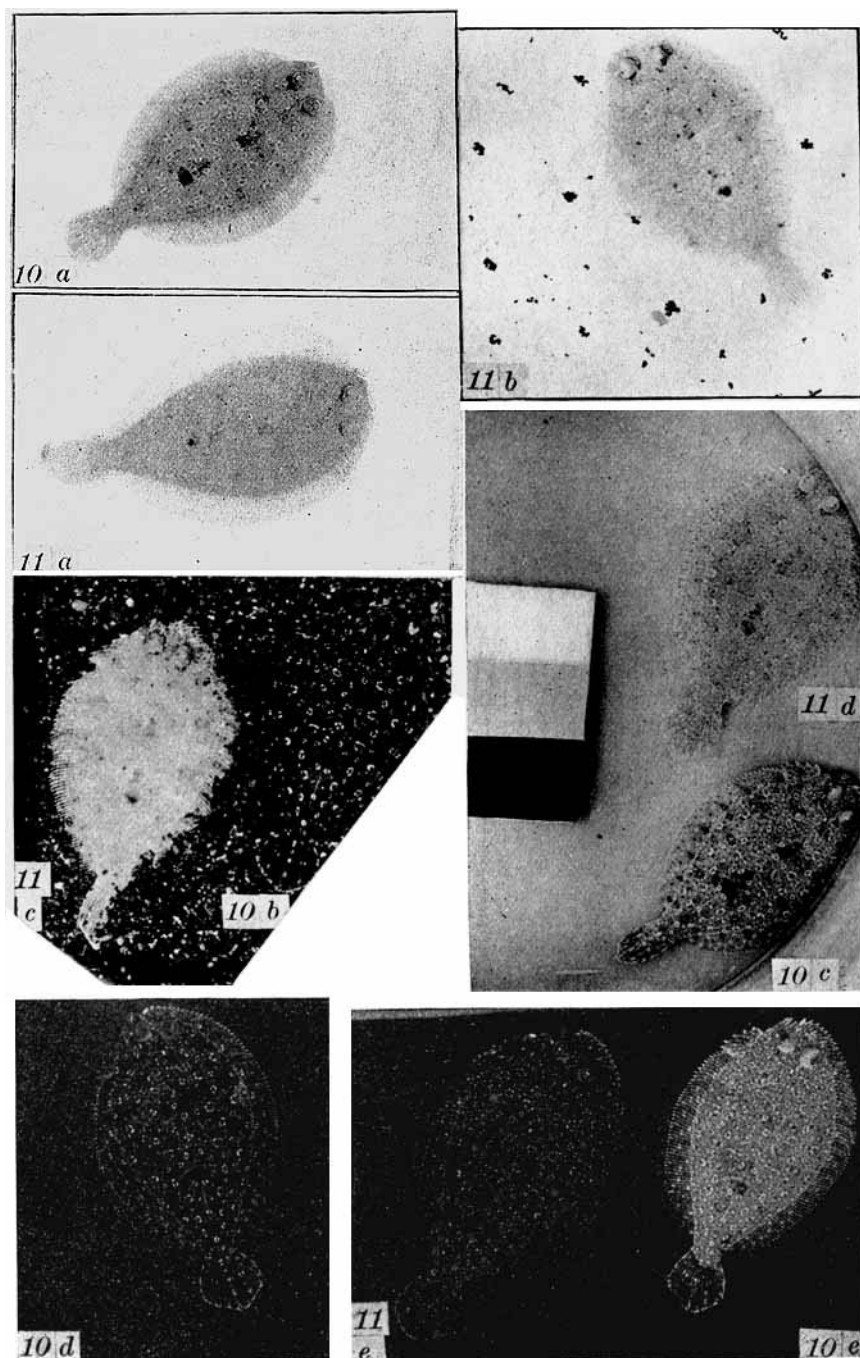
Views of specimen no. 9: *a*, on dark, mixed sand (after two days); *b*, in jar having black walls and gravel bottom (after two days); *c*, in jar having white walls and black bottom (after five days); *d*, in jar having black walls and black bottom (after one day); (Comparison between the last two shows plainly the effect of the white walls in the former case).



## PLATE 12

### VIEWS OF SPECIMENS 10 AND 11

- 10 *a* After fourteen days on white marble bottom.
- 11 *a* After fifteen days on white marble bottom. (Both of these fishes appear much too dark).
- 11 *b* Showing possible effects of black specks in the white field.
- 10 *b*-11 *c* Showing condition of former fish, after thirteen days on the dark sand as compared with the latter, which had just been transferred to this.
- 10 *c*-11 *d* Taken on gray bottom (gray of the same shade as in 4*i*).
- 10 *d* After six days on jet-black (magnetite) sand, following long sojourn on white and gray bottoms.
- 10 *e* After blinding, during recently acquired dark condition, following long sojourn on pale bottoms. The result is a return to the pale phase.
- 11 *e* After eleven days on jet-black sand



## PLATE 13

### VIEWS OF SPECIMENS 11 AND 12

12 *a* Against background of gray (same gray as in 4 *i*), immediately after transfer from dark sand.

11 *f*-12 *b* Showing conditions of illumination in the white and gray jars, used in the experiment described on pp. 440-443. The bottom of the white jar appears much darker than that of the gray jar.

11 *g*-12 *c* Showing condition of these two fishes (photographed together on gray bottom), after former had been kept four days on the (lighted) gray bottom and the latter four days on the (shaded) white bottom.

11 *h*-12 *d* Appearance of the same two fishes, four days after the reversal of the above conditions (11 being in white jar, 12 in gray). (The reader must not be misled by the altered positions of the two fishes in the later picture. The identity of each specimen is revealed by its size, no. 12 being the larger).



