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THE BEHAVIOR OF THE LARVAL AND ADOLESCENT STAGES OF THE AMERICAN LOBSTER (HOMARUS AMERICANUS).[1]

BY

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WITH TWENTY-TWO FIGURES.

OUTLINE OF CONTENTS.

[1] The present paper is the last of the series of four in which the author has attempted to analyze the behavior of the larval and early adolescent stages of the lobster. The papers already published are the following, references to which may be found in the bibliography at the end of the present work: (1) The relation of optical stimuli to rheotaxis in the American lobster; (2) Galvanotaxis in larvæ of the American lobster; (3) The reaction of blinded lobsters to light.

I. INTRODUCTION AND HISTORICAL SUMMARY.

Every year is bringing new and valuable additions to our knowledge of the behavior of the Crustacea. Most of the investigations dealing with this subject are concerned, however, with the Entomostraca, while the behavior of the higher forms has been less studied. It is apparent, moreover, that the experimental work done has been chiefly upon adults, while little attention has been given to the behavior of the larval forms of those Crustacea, as the macrurous decapods, which undergo an extensive metamorphosis. It is the aim of the present paper to demonstrate certain phases in the reactions of larval and early adolescent stages of the American lobster (Homarus americanus) to light, and to analyze these reactions, so far as possible, into their constituent factors.

In the study of reactions to light it is apparent that the lack of a satisfactory terminology has led to considerable confusion. This is manifest when we attempt to apply the definition of positive or negative phototaxis, as given by LOEB, to the types of behavior which we find, for instance, in the lobster and in the shrimp, Palemonetes (LYON 1907). LOEB (1905, p. 29) states that "positively heliotropic animals are compelled to turn their oral pole toward the source of light and move in the direction of the rays to its source." In the larval lobsters, however, there may be a difference between the signs of body-orientation and what may be called progressive orientation. In body-orientation the animal in question *turns* with reference to the source of light; in progressive orientation it moves toward or from the source of light. Employing these terms, we may say that the body-orientation of the larval lobster under stimulation by light is invariably negative, whereas the progressive orientation may be either positive or negative, as the conditions of the case determine.

Secondly, what do we mean by intensity and by direction of light? Are we justified in assuming that a stimulus such as light can be effective in causing either kind of orientation through its directive quality? The answer to these questions depends largely upon arbitrary definitions. YERKES' (1903) exposition of what constitutes a phototactic reaction as differentiated from a photopathic reaction indicates very nearly the meaning that will be given to these terms in the present paper. Attention may be called to one difference, however. It is inferred by YERKES that the sign of the phototactic response is dependent upon the previously assumed body-orientation of the organism. This is by no means necessarily true, for in the case of the larval lobster, it is clear that the orientation of the body has absolutely nothing to do with the sign of the consequent progressive orientation. For our present purposes we may, therefore, slightly modify the definition of YERKES by describing *a phototactic reaction as one in which the organism tends to place the longitudinal axis of the body parallel to the direction of the rays and to approach or recede from the source of those rays.*

If we so limit the meaning of a phototactic response, what shall we say regarding the nature of the so-called photopathic response? It is entirely possible (and indeed in the case of the larval lobsters, most probable) that again the view of YERKES (1903), that a photopathic reaction is one in which an organism "selects" a particular intensity of light, and confines its movements to the region illuminated by that intensity, is correct. But it is not so certain that the photopathic responses of the lobster larvæ are brought about by means of slight phototactic reactions, as YERKES (1903, p. 1) suggests for Daphnia. Therefore, for present needs, we may conclude that *a photopathic reaction is one in which an organism, without previous assumption of a body-orientation, "selects" regions of optimal light-intensity.* In the following account of experiments and observations, we shall see to what extent the behavior of the lobster larvæ conforms to these definitions of phototactic and photopathic reactions.

The movements of Entomostraca toward or from a source of light, and their reactions to rays of different wave lengths have been made the subject of investigation by many naturalists. In the earlier investigations it was commonly concluded that the intensity of light was the most important factor, and that organisms "chose" an optimal intensity. LUBBOCK (1881) and GRABER (1884) found that Daphnia gather in areas of greater light intensity. SCHOUTEDEN (1902) found that older individuals are negatively phototropic. These experiments, as repeated by DAVENPORT and CANNON (1897), YERKES (1899, 1903), and PARKER (1902), showed that Daphnia also manifests phototactic reaction. It was assumed, therefore, that some organisms may react either phototactically or photopathically. Later work of American investigators has demonstrated that the Crustacea are more influenced by the directive factor of the light rays than by the intensity, and, more recently still, KEEBLE and GAMBLE (1904), in their excellent work on the color physiology of the higher Crustacea, have shown that the nature of the background may be an important factor in determining the reaction of many species.

The Malacostraca have received less attention than have the Entomostraca, and it is only for a comparatively short time that anything has been known concerning the reactions of either the larvæ or the adults of decapod Crustacea. With the adult forms of the decapods results have been readily obtained. HOLMES (1901) found that several species of terrestrial amphipods manifest a strong positive phototactic reaction, while all aquatic species are negatively phototactic. We know further from KEEBLE and GAMBLE (1904) that the adult form of Palemon is negatively phototropic and that Hippolyte is positively phototropic. Hippolyte, according to KEEBLE and GAMBLE, not only moves toward the light, but also "prefers" a white to a black background. Macromysis inermis reacts positively or negatively in accordance with the character of the background or the nature of the physical environment. It is positively phototropic on a white background, and negatively phototropic on a black background. Furthermore, when a choice of background is made possible, Macromysis "selects" the black. In the case of Hippolyte, the larvæ respond positively to light, as do the adults. BELL (1906) states that the adult crayfish is "somewhat negatively phototactic" and that difference in the intensity of light made but slight difference in the reactions. Other investigators have shown that the adults of several species of Crustacea react either positively or negatively to light. Very few investigators, however, have studied systematically the reactions of Crustacea in the larval stages. Among the first, LOEB (1893) reported the reactions to light of Limulus in the "trilobite stage." These larvæ, he said, are at first positive, and later, negative. PEARL (1904), by repeating LOEB's experiments, ascertained that this larval stage of Limulus manifests at first a negative reaction, and that later, a relatively small number of individuals gives a positive reaction. It was learned by KEEBLE and GAMBLE (loc. cit.) that the response of the larvæ of Palemon is the direct opposite of the reaction of the adults. BOHN (1905) discovered that the larvæ of the European lobster (Homarus vulgaris), although at first positive in their reaction to light, may later undergo certain changes. HERRICK (1896) states that larvæ of the American lobster react positively to light. BOHN (1905) learned that the reaction of Artemia salina was similar to that of Homarus vulgaris; and the writer has ascertained that the larvæ of the green crab, Carcinus granulatus, react sometimes positively and sometimes negatively, and behave very much like the larvæ of the lobster. The writer can verify the conclusions published by LYON (1906) that the larvæ of Palemon may react either positively or negatively to light.

The results of the small number of investigations which have been made upon the reactions of Crustacea in the larval stages, indicate the desirability of further systematic study of these reactions. PEARL (1904) has well pointed out the value of studying the "ontogeny of reaction," and of applying the knowledge thereby gained to the investigation of the more complex forms of response exhibited by adult individuals. Although the writer has not yet had an opportunity to study the behavior of the adult lobster, the present work shows that in the larval stages there are found diverse types of reaction, differing from one moment to another, and depending upon conditions which, even in the nicest experiments, are by no means readily discoverable; and, furthermore, that it is only by a systematic study of the reactions *through the developmental stages*, that many contradictory points can be cleared up, and the more complex behavior of the older animals explained.

II. BIOLOGY OF THE LOBSTER.

A brief résumé of the biology of the lobster will facilitate the understanding of later considerations. The life of the lobster consists of a series of stages or stage-periods, each of which represents the span of life between two successive moults, or castings of its shell. Of these stage-periods, the first four are passed through very rapidly, since the young creature usually moults four times in the first twenty days of its existence. These first few quickly passed stages (called the larval stages because they denote the successive emergence of one from another) include the most important changes in form, color, and manner of behavior, that the lobster undergoes. In each successive stage the animal is larger than before. The larvæ grow at the time of moulting, but never between moults. From the fourth stage on, each successive stage-period is of longer duration and the changes which the adolescent lobster thenceforth undergoes are correspondingly less significant, being characterized chiefly by alterations in internal morphology as the adult functional type is gradually approximated. The first three stages of the lobster are free-swimming stages, and the activities are without apparent

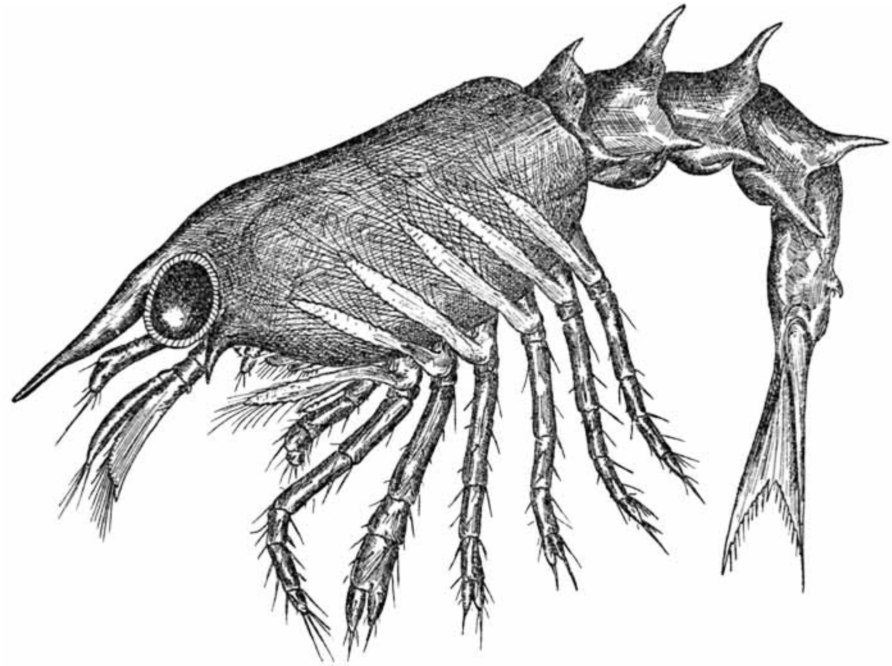

FIG. 1. Showing a young first-stage larval lobster about two days old. The eyes are large and prominent. The exopodites of the thoracic appendages are represented at the beginning of the downward stroke. This figure shows the typical swimming position of larvæ in the first three stages, the plane of the cephalo-thorax bent down at an angle of about 30° from horizontal.

coördination or aim. The larvæ are swept here and there by the tide and possess no power to evade the attacks of numerous enemies.

The swimming of the lobsters of the first three stages is accomplished by means of the feathered exopodites, or outer branches of the thoracic appendages (Fig. 1). These exopodites beat the water with short vibratory strokes, which tend to carry the larva backward or forward or upward as the case may be,[2] and allowing it to sink toward the bottom when their motion ceases. The progressive movement and the body-orientation of the lobster in the first three stages are almost wholly dependent upon the activity of these organs. Occasionally, darting backward movements, caused by the sudden contraction of the abdomen, appear, but these are of slight importance in the reaction to light.

When the lobster moults to the fourth stage, the exopodites are lost. Consequently the forward swimming during and after the fourth stage is dependent upon the action of swimming appendages which after the second stage make their appearance on the under sides of the second, third, fourth and fifth abdominal segments. The fourth-stage lobsters swim with directness and precision, usually near the surface of the water. This surface-swimming may be due to stimulation by light, but, as the writer has suggested elsewhere (1906b), it is not improbable that this form of behavior is due in part to the food-seeking impulse. During the latter part of the fourth stage, contact-irritability begins to play an important rôle in determining the behavior of the young lobster. Now, as in the fifth and later stages, the creature no longer swims at the surface of the water, but seeks the bottom and attempts to burrow in the sand or beneath any object that presents itself. After the fifth stage, the adolescent lobster shows the same type of behavior as during the fifth stage, but with a gradual increase in the tendency to avoid light. Its reactions have now become fixed in every way.

III. APPARATUS AND METHOD OF PROCEDURE.

The manipulation of the various pieces of apparatus here described will be spoken of when the particular experiments in which they are used are mentioned. The room in which the experiments were conducted contained on two of the opposite walls windows 2 feet high and 8 feet long, before which extended work benches or tables. The two windows, which opened respectively to the east and west, were the only source of daylight, and, as occasion required, were heavily screened with black paper or cloth. At appropriate places in these screens were cut openings which could be readily closed. On the table before one of the windows was

[2] For details on method of swimming, see p. 258.

placed a box 2 feet high, 3 feet wide, and 2 feet deep, lined on the inside with black cloth, and containing, on the window side, slits or openings to correspond with the openings in the screen outside the box. On the room side, the box was fitted with a movable black curtain, which permitted the operator to move the jars or other apparatus contained within the box. This arrangement served to control the light falling upon the larvæ, which were put in suitable containers and placed inside the box.

Other pieces of apparatus may be described as follows: *Glass box A*. Of glass boxes two types were used for studying the photopathic and phototactic reactions of the larvæ. One was a rectangular wooden box having glass "windows" in each end and in the bottom. This box, which was 12 inches long, 6 inches wide, and 3 inches deep, was painted dull black on the inside and fitted with a light-tight cover. It was used in experiments which required illumination from the end, from below, or both.

Glass box B—This box was similar in most respects to box *A* (see Fig. 7). It was 12 inches long, 6 inches wide, and 5 inches deep. It had "windows" on each end and along one side. Like box *A*, it was painted black on the inside and was fitted with a light-tight cover. This cover contained three slits so arranged that diaphragms of wood or glass might, in an instant, be slid into place to divide the box transversely into four chambers of equal extent. Then the cover of the box might be removed if desired, leaving the partitions in place. The object of this arrangement was to make it possible to imprison the young lobsters wherever they chanced to be at any given time and so to ascertain, by count, in what manner and in what relative numbers they had responded to certain stimuli.

Of these two boxes, the former, while oftener placed in a level position on a laboratory table, was sometimes used in another way to study the photopathic reaction alone, or the photopathic and the phototactic reactions together. In these cases the box was placed over a light-shaft, which was merely a rectangular tube lined with black cloth, with a height of 18 inches and with a cross section of the same size as the bottom of the box. Over the upper end of this tube or shaft, the glass bottom of box A exactly fitted. At the bottom of the shaft was either a sheet of white paper or a mirror which was so placed as to reflect the rays of light coming from the window up through the shaft to the glass bottom of the over-lying box. The rays that thus passed through the black-lined shaft and entered the box were practically parallel and at right angles to the plane of the bottom of the box. It is clear that, when the water in the box was very shallow, the rays of light passing up the shaft and striking the larvæ could have no directive influence, and that, when they passed through the graded light screens or through plates of colored glass, placed just beneath the glass bottom of the box, they could be effective only through difference in intensity.

Besides these boxes, use was made of certain glass jars, known as museum or brain jars, which were for the most part cylindrical in shape and varied in diameter from 20 to 25 centimeters. For certain experiments these were covered wholly or partially about their circumference with black paper, and the light was made to come from the top, bottom, or through a "window" in the side, as the case might require.

In addition to the apparatus mentioned above, several kinds of glass tubes were employed. Some were ordinary 15 centimeter laboratory test tubes, while others had a length of 40 centimeters and a diameter of 4 centimeters. These tubes were made with rounded ends so that there would be no obstruction to the light striking the tubes even at a slight angle, and the lobsters were introduced through an opening in the top. Another type of tube employed was the Y-tube, constructed of glass tubing, 4 centimeters in diameter as shown in Fig. 5. These proved exceedingly useful in testing the reactions of young lobsters, both to the intensity and the directive influence of the light rays, since the arms of the Y-tube could be readily covered with colored glass plates or fitted with black or white backgrounds, thus producing different conditions of light in each arm of the Y.

In many of the experiments it was desirable to use graded light screens. These were made by adding india ink to a solution of gelatine and allowing this to harden in the form of a wedge. The wedge-shaped screen permitted light to pass through in diminishing amount, from the thin edge to the thick edge, which was quite opaque. Graded light screens of red and blue were also made by adding to the gelatine a solution of eosin or methylene blue. It was by means of these, together with the colored glass plates that differences in the intensity of light were secured.

Since a particular response to light is often interpretable only when the conditions previous to the hour of experimentation are taken into account, it was found desirable to secure such conditions for experiment that all influences which might be instrumental in determining the final reaction of the larvæ either before or during the time of actual experimentation should be clearly recognized. Accordingly, the data to be presented show not only the nature of the reaction of the larval lobsters at a few chosen periods in their life history, but they also make it possible to trace modifications in reaction as the young animals pass on from stage to stage and gradually approach the adult type. Numerical results were usually obtained by counting the larvæ which had been imprisoned in different compartments of the box by the sliding partitions. In other cases a large number of larvæ were put into a glass jar and the reaction of the majority was observed. The separation and selection of larvæ which gave either a positive or a negative reaction to the same stimulus was thus possible, but conclusions have been drawn only after a careful study of the exact accounts of many groups of larvæ. The exact intensity of light used in the experiments was not known, but the experiments were performed on such days and at such times as would make the conditions uniform. Before entering upon a detailed consideration of the experiments as a whole, it will be appropriate to state some ground for assuming that lobster larvæ react both to the intensity and to the directive influence of light. The preliminary experiments which led to this view may be presented as follows:

IV. PRELIMINARY EXPERIMENTS.

Experiment I—Glass tubes 15 centimeters long and 2 centimeters in diameter were filled with salt water and in each were placed six first-stage lobsters two days old. When the tubes were held vertically, there was no tendency shown for the larvæ to gather in any particular region of the tubes. When, however, a strip of black paper was wound in such a manner as to cover the upper half of a tube (Fig. 2) and records were taken every minute, the larvæ became distributed as follows:

NUMBER OF LARVAE PRESENT AFTER	UNSHADED AREA.	AREA WHERE LIGHT AND DARK MEET.	SHADED AREA.
1 minute	5	1	0
2 minutes	6	0	0
3 minutes	6	0	0
4 minutes	6	0	0
5 minutes	5	1	0
Total	28	2	0

It will be seen that the larvæ "seek" the light area. Next the paper was so arranged that the shaded part was below, as shown in Fig. 3. In this case the larvæ were always found uniformly in the unshaded area. In all cases the body-orientation of the larvæ was determined by the direction of the rays of light, which struck the tube at right angles; but at no time, it would seem, could this directive influence alone have been instrumental in causing the larvæ to remain in the region of greater light-intensity. The same general results were obtained when the tubes were laid horizontally on the table (Fig. 4) but still at right angles to the direction of the incident light rays which came from the side. These tests of the reaction of larvæ in glass tubes appeared at first sight to demonstrate that larvæ of a certain age and stage show a tendency to group themselves in regions of greater illumination, irrespective of the directive influence of light or of reaction to gravity. This, however, is not the only possible conclusion to be drawn from these facts.

To take, for instance, the case of the horizontally lying tube (Fig. 4), in which the larvæ gathered in the illuminated ends (the region of greatest light-intensity), and there oriented to the directive influence of the light. In the darkened area of the tube the larvæ did not undergo body-orientation, but swam about in many directions. When occasionally, they entered the more brightly illuminated end of the tube, they at once oriented to the directive influence of the rays and took the position shown in Fig. 4. Furthermore, the larvæ usually manifested a tendency to retain their body-orientation and thus to remain in the illuminated region when once they had entered it. Here, then, we have a case where the apparent reaction to the intensity of light is, in reality, determined, and maintained, partly at least, by the orienting response to the directive influence of light. In other words, the larvæ did not, in this instance, "select" the region of greater light-intensity because of the intensity *per se*, but because they became imprisoned in it through orientation as a result of the directive stimulus. It is only through rays which strike the larvæ directly from above or from below that an approximately non-directive influence can be obtained.

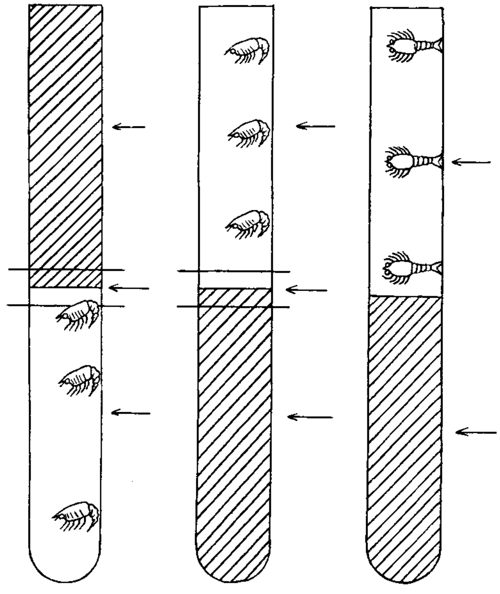

FIG. 2. FIG. 3. FIG. 4.

FIGS. 2 and 3 show the orientation of the larvæ in tubes standing in the vertical position; Fig. 4, in the horizontal. The arrows represent the direction of the light rays striking the tubes from the side. The cross hatching represents the parts of the tubes covered with black paper.

Experiment 2. Reaction to intensity of light—In this experiment use was made of the glass-bottomed box *A* with the light-shaft, and the colored-glass plates or graded light screens. First the glass plates were arranged over the top of the light-shaft in the order blue, green, orange, red. The box was filled with salt water to a depth of 15 mm., and ten first-stage larvæ were placed therein. The light-tight cover was then put in place and the larvæ were allowed five or more minutes to become acquainted with their new environment. The result was as follows:

TIME.	BLUE.	GREEN.	ORANGE.	RED.
After 5 minutes	10	0	0	0
After 10 minutes	10	0	0	0
After 14 minutes	9	1	0	0
After 17 minutes	9	0	0	1
After 19 minutes	9	0	1	0
Totals	47	1	1	1

The results of these tests and others in which the order of the glass plates was changed, demonstrate the tendency of the larvæ to group themselves in the blue, which was the more brightly illumined region. Similar experiments were performed with graded light-screens (strips of paper of different thickness or a gelatine wedge) substituted for the glass plates. The results in every case indicated that here also the larvæ reacted to difference in intensity. These experiments were performed with a belief that it is the refrangible rays of the spectrum alone that are active in determining the phototropic reactions of animals and plants. MINKIEWICZ (1906), however, has found that, although positively heliotropic animals usually react positively to the rays of shortest wave-length (violet or blue), and negatively heliotropic animals usually react to the rays of greatest wave-length (red or yellow), these phenomena of positive phototropism and positive chromotropism are not necessarily found together in the same organism. It is uncertain whether or not the larvæ of Homarus manifest chromotaxis. At the present time it can be said that the observed reactions of the larvæ to colored lights agree so well with the reactions to lights of varying intensity as determined by light screens, that they may fairly be considered responses to difference in intensity of light.

Experiment 3. Reaction to the directive influence of the rays—To demonstrate the response of the larvæ to the directive influence of the light rays the description of a single experiment will suffice. Similar experiments will be recorded later, in another connection. The conditions of this experiment are like those described in Experiment 2, i. e., box *A* was mounted over the light-shaft on the colored glass plates arranged in the order blue, green, orange, red. The ten first-stage larvæ contained in the box were more or less constantly oriented in the region of greatest light intensity, that is over the blue glass. Next, the small window situated at the red extremity of the box was opened to the diffuse light of the room. The result was that the larvæ immediately oriented to the new rays, left the region of greatest light-intensity, the blue area, and moved backward in the direction of the incident light rays toward the source of the weaker light and, at the same time, into a region of lesser light-intensity at the red end of the box.[3] The distribution at the end of 19 minutes was as follows: blue, 4 individuals; green, 1; orange, 1; red, 24. Here it appears that the larvæ, which at the beginning of the experiment were grouped in the area of greatest illumination under the influence of non-directive rays, were forced by the directive influence of the new rays to move from a region of greater into one of diminished light-intensity. As will be observed later, this experiment was tried under a great variety of conditions, and with larvæ of different stages and ages, with uniform results. Whenever the larvæ had an opportunity to move in the direction of the rays, they would do so, notwithstanding the fact that they thus passed from a region of greater to one of less illumination.

In the paragraphs immediately preceding, the purpose has been merely to indicate that in the behavior of the lobster larvæ we may observe reactions both to the intensity of light and to the directive influence of the light rays. The latter depends, first, upon the unequal stimulation of the two eyes, and second, upon the degree of illumination which affects both eyes. The conclusions which have been drawn from these few experiments receive further support from other experiments. But first, it is necessary to know whether there is any form of reaction common to all larval lobsters. To answer this question, which is of primary importance, it will be necessary to report in detail a series of tests, which were made upon many groups of lobsters during different periods of their metamorphosis and under different conditions of stimulation by light.

Experiment 4. Case 1—In several instances larvæ which had been hatched from one-half hour to one hour were put in a glass jar, which was in turn placed in the dark box and submitted to illumination on one side from a narrow window. In every case

[3] If this experiment appears uncritical because of the lack of information regarding the exact intensities of light at the opposite ends of the box, it may be answered that the intensity of light was measured by the only method available. Sensitized paper was placed inside the box, one strip over the end window, the other over the bottom at the blue end. The results showed that the light entering the blue end through the bottom of the box was much stronger than that entering the end window from the room.

the young larvæ at once swam backwards toward the source of light and grouped themselves closely together at the window side of the glass jar. So perfect was this orientation on the part of the newly hatched larvæ that, out of 100 individuals, not one showed a negative reaction.

Case 2—When the same larvæ were put in one of the long 40-centimeter glass tubes so placed in the dark box that the tube was parallel to the direction of the incident rays, the young lobsters in every case swam rapidly to the end of the tube nearest the window and remained there until the tube was reversed, when they again swam toward the window. These reversals might be continued for hours.

Case 3—When the same individuals, or other larvæ of the same group, were placed in box *B*, and this was turned with one end toward the window, the reaction of Case 2 occurred. They swam backward toward the window.

Case 4—Another group of fifty first-stage larvæ three days old was placed in a glass jar in the dark box and illuminated from the small window. All were definitely positive. Next, the circumference of the jar, except a vertical strip three inches wide on the light side, was covered with black paper, and the jar was so placed that direct sunlight had access to the open side. The larvæ immediately gathered on the darker side of the jar and remained there for one and a half minutes, after which they again returned to the sunlit side and remained there in bright sunlight as long as they were observed.

Experiment 6.—July 19, 3:30 p.m. Fifty first-stage larvæ, two days old, were put in a glass jar and this was placed in the dark box. Though the light was not bright at this time in the afternoon all the larvæ gave a positive reaction. The jar now was placed on a black background in the bright sunlight on the west table. Evey lobster moved to the room side of the dish away from the light. Within two minutes, many began to go back to the window side, and this continued until all were again gathered there. After four minutes, however, they again returned to the room side and remained there for ten minutes, at the expiration of which time they were about equally divided between the room side and the window side of the jar. They were now put back in the dark box, and with the slight intensity of light at 7 o'clock in the evening, all were reacting positively. By 8:30 the box was fairly dark and the orientation of the larvæ was indefinite. Suddenly the rays of a powerful acetylene light were thrown upon the jar. Immediately a negative reaction took place and continued for two minutes, when some of the larvæ began to return to the light. At the expiration of four minutes all the larvæ were reacting positively, and this reaction continued for several hours.

Experiment 7—July 22, 9:30 a.m. Forty-four second-stage lobsters, six days old, were placed in the glass jar, in the dark box. Eleven came at once to the room side of the jar. The jar now was moved nearer the small (three by three inch) window. As a result seventeen out of forty-four individuals gathered on the room side, but the definiteness of the positive reaction on the part of the window-side lobsters was lessened by desultory swimming. The jar was next placed on the west table, the room side and top of the jar being shielded by black paper. All the larvæ came to the room side of the jar. When replaced in the dark box (in light of much lesser intensity), the reaction again became uniformly positive.

Experiment 8—July 23, 9 a.m. Forty second-stage larvæ, seven days old, were placed in the glass jar on the east table, and exposed to strong light. All the larvæ at once oriented on the room (darker) side of the jar. These lobsters were next placed on the west table where the negative reaction continued throughout the afternoon. From 6 to 8 o'clock in the evening the light faded gradually. At 7:35 the body-orientation was nearly lost, but the orientation on the room side of the jar with diminishing definiteness remained in effect until 7:50, when the light had faded quite away and the lobsters were scattered throughout the jar.

Experiment 9—July 28, 9:30 a.m. Twenty third-stage lobsters, twelve days old, were placed in the glass jar in the dark box on a white background and submitted to light of slight intensity coming through the small window. All showed a strong positive reaction, and gathered on the window side of the jar. The next day in the afternoon, about fifty third-stage larvæ of the same group, now thirteen days old, were placed in the glass jar in the dark box on white background and submitted to light of medium intensity. Nearly all of the larvæ oriented on the room side of the jar, thus demonstrating a definite negative reaction.

Experiment 10. Case 1—June 26, 9 a.m. Ten fourth-stage lobsters, fifteen days old, were placed in the glass jar in the dark box and submitted to light of medium intensity from the small window. There was no appreciable tendency to undergo either body or progressive orientation. The lobsters were much engaged in eating one another.

Case 2—The fourth-stage lobsters mentioned in the preceding paragraph were fed on chopped clam meat and placed in box *A* with the black interior. Light was admitted through the end window. Records of four tests made at two-minute intervals show that while nine were neutral in reaction, six were positive, and twenty-five were negative. The box was next lined with white paper and the same fourth-stage lobsters were submitted to the same external light conditions. The results show twenty-six positive, twelve neutral, and twelve negative individuals.

Case 3—August 7, 2:30 p.m. When twenty fifth-stage lobsters, twenty-five days old, were put in box *A* and illuminated through the end window, all, without exception, oriented in the dark end of the box.

Conclusions concerning the permanence of these reactions through the stages—In explanation of the ten experiments recorded above, it should be stated that the writer had at his command large numbers of larval lobsters of approximately the same age and stage which had been subjected throughout the whole of their early life to the same conditions of environment. Therefore it was possible to make a detailed systematic study, not of a few isolated individuals alone, but of whole groups. The result of this study is expressed in these experiments.

Whatever else the foregoing facts may demonstrate, the answer to our first question is evident. *There is no constant form of reaction on the part of the larval lobsters to the directive influence of the light rays.* For this reason one has no warrant for saying, without reservation, that the larval lobster is either positively or negatively phototactic. If it had been necessary to depend for material upon a few individuals of uncertain age, and to draw conclusions regarding the general behavior of all the larvæ after observing the behavior of these few individuals, the outcome would of course be far less satisfactory than in the present instance. It is to be regretted, perhaps, that no means were at hand to make a critical determination of the exact intensities of light to which the larval lobsters gave their recorded reactions, but it is apparent that such a refinement of method would not change the general conclusions reached.

With the foregoing facts in mind, it is clear that the problem before us becomes, not, what reactions do the larval lobsters in general give to light, but *how do the lobster larvæ of a certain age react to light under certain known conditions?* To this rather more complex question attention will now be given.

V. SYSTEMATIC ACCOUNT OF THE REACTIONS TO LIGHT OF LOBSTERS IN THE LARVAL STAGES.

What is the nature of the reactions to light through the successive developmental stages, and by what conditions is it determined? Regarding the first of these points, it should be borne in mind that the subject matter concerned cannot be treated concretely, but that it is necessarily scattered through the long series of observations which follows, and that it is only from a consideration of the series *as a whole* that a clear idea of the gradual modifications in the reactions from the first to the sixth stage of the lobster's life can be obtained. As to the second point of inquiry, it is at once perceived that the conditions or factors which we seek to discover are of two sorts:

1. Conditions which are peculiar to a certain definite age or stage in the development of the larva, and which may be designated as physiological conditions.

2. All outside influences, including the intensity and multiplicity of stimuli brought to bear upon the animals.

In the following discussion it will be found of advantage to consider these two kinds of modifying conditions together; for they are found to be very much inter-related when a consideration of their mutual importance in bringing about any orientation of the young lobsters is involved.

It may be appropriate to mention at this point the method of securing the data here presented. The futility of taking young larvæ at random from the hatching bags without knowledge of their age or previous history was recognized early in the course of the investigation. It was considered advisable to work only with those lobsters whose previous history was definitely known. To this end the exact time of hatching of certain groups of larvæ was noted. In the large canvas hatching bags, used at the Wickford Station, hundreds of larvæ hatch in a single hour, and observations were made, as a rule, twice each day (morning and afternoon), upon individuals taken from these groups, whose age was accurately known. During the course of the study, the history and the daily reactions of three groups of larvæ were followed and recorded. For the following account of the reactions of the first-stage larvæ, for instance, the records of these three groups for the first day, the second day, the third day, etc., were used. Only the reactions which appeared to be the most constant and typical have been introduced here. Therefore, although many variations in reactions were found to occur, the following section describes the typical daily reactions of the larval lobsters from the time of hatching through the fifth stage of their existence.

1. First Larval Stage.

As has been shown by preliminary observations and the experiments already mentioned, the lobsters of the first larval stage are usually strongly positive both in their photopathic and in their phototactic reactions. These reactions are manifested strongly in the few hours directly after hatching, when, as we shall presently see, the young lobsters react definitely, and to very slight differences in the intensity of illumination. When half-hour old lobsters were placed in the glass jar, and submitted to any kind or intensity of light (daylight, artificial, or colored), they responded well (especially when the intensity was increased by a white background) to slight differences in illumination; and reacted uniformly and invariably by moving, tail foremost, toward the source of light. In case of two sources of light, on opposite sides of the jar, the larvæ would respond to the rays which were the more intense. If the rays from two sources of light were introduced at right angles to each other, the resultant reaction, as has been shown for other organisms by many investigators, was determined according to the law of the parallelogram of forces.

It would appear that, in the behavior of the first-stage larvæ, we have the most delicate reactions to slight differences in light intensity that occur throughout the life of the lobster. During the early hours of the first larval stage, no individuals reacted negatively to the directive stimulus of the light, while in the later stages, although a majority of the larvæ manifested definitely one reaction or another, there were usually a few individuals which gave responses that were either indefinite or opposite to the rule.

Experiment 11. Case 1—Ten first-stage larvæ, five hours old, were placed in a glass tube 40 cm. long, and this was laid on the table at right angles to the plane of the window and parallel to the light rays entering through a narrow slit in the screen. All of the larvæ at once oriented themselves at the window end of the tube. Next, blue, green, and yellow glass plates were placed successively over the end of the tube next the window, leaving the opposite end clear, but none of these changed the definiteness of the positive reaction. When, however, an orange glass was used, the larvæ paused midway in the tube, at the border line of the orange light, and in their final orientation were scattered between this region and the orange end of the tube. When a red glass was superimposed, all the larvæ took a position at the border line of the red and the clear glass, this region representing the junction of the areas of strong and weak illumination.

Experiment 12. Case 1—In this experiment the glass bottomed box *A* was set up over the light-shaft with the colored glass plates arranged in the order, red, orange, green, blue, as described on p. 207. The box was filled to a depth of one inch with water and first-stage larvæ, twenty-four hours old, were introduced. Five minutes was allowed for the larvæ to become acquainted with the new environment. Records of four tests then made showed that while thirty-eight larvæ gathered in the blue area, only one was found in the red, one in the orange, and none in the green. Changing the order of the glasses in no way changed the results. This apparently demonstrates that there is a definite tendency on the part of these larvæ to orient themselves over the glass plates which admit the brightest light; and that the precise order of the plates makes no difference in orientation.

Case 2—In this instance the order of the glass plates was red, orange, green, blue. The same larvæ used in the above tests were employed, but the conditions of the experiment were changed. The window in the end of the box corresponding to the red glass was uncovered and the diffuse light from the room was allowed to stream through the box longitudinally. The object of this was to discover whether the larvæ which had previously given so definitely the positive photopathic reaction, could be induced to enter the region of diminished light intensity (at the red end of the box). In other words, whether the phototactic reaction could be made to overcome the photopathic. Between each of the successive tests mentioned below, the light from the room and the light through the shaft were cut off in order that a scattering of the larvæ through the box might occur. In other cases the position of the box was reversed; and in still others both the position of the box and the order of glass slides, changed. The results of four tests are as follows (the arrow represents the direction of the light entering the end window of the box):

TEST.	AFTER	DISTRIBUTION OF LARVAE.			
		→ Red.	Orange.	Green.	Blue.
1	45 minutes	8	0	0	2
2	9 minutes	8	0	0	2
3	14 minutes	8	1	0	1
4	18 minutes	9	0	1	0
Totals		33	1	1	5

Case 3—In this instance the red and orange glass plates were removed and black paper substituted. The photopathic reaction was found to be definitely positive, the young larvæ grouping in the blue area. Now, as before, the window at the end of the box corresponding to that overlying the black paper was opened to the subdued light of the room, while brilliant daylight entered the blue end of the box. As will be observed, the conditions of this experiment are similar to those of Experiment 11, save that, in this instance, a greater difference between the intensity of light at opposite ends of the box existed. Between tests the light from both sources was cut off and the larvæ were allowed to scatter. The results, which may receive the same interpretation as those of Experiment 11, are tabulated below (the arrow indicates the direction of light entering the end window of the box):

TEST.	AFTER	DISTRIBUTION OF LARVAE.		
		→ Black.	Green.	Blue.
1	5 minutes	10	0	0
2	7 minutes	7	3	0
3	10 minutes	10	0	0
Totals..............................		27	3	0

Conclusions from Experiments 11 and 12: In the results of the foregoing experiments, we have further evidence to support the conclusions drawn from Experiment 3. In Experiment 12 the larvæ passed from a region of greater (blue) to one of lesser (the red, or in Case 3, the black) light-intensity in moving toward the source of light in the direction of the incident rays. It must be assumed that in Case 3, there was a much greater difference in the intensity of light at the two ends of the box (overlying the blue glass and the black paper respectively) than in Case 2, or in Experiment 3. These experiments were performed many times, under several different conditions of light, and with larvæ of ages varying from a few hours to two days. The same results were obtained in every case, except that in the older first-stage larvæ the reactions were not so definite (more individual variations) and a stronger light was required to bring about the same responses as were manifested by larvæ under four hours old. In these cases, as also in Experiment 3, rays of lesser intensity (but in a horizontal plane) which struck the larvæ in such a way as to cause a body-orientation in which a normal swimming position was still maintained, were more influential in determining a progressive orientation than were the more intense rays which struck both eyes equally, but which came from below, and had a tendency (as will be shown in detail later) to throw the larvæ out of their normal swimming position. As the writer has shown elsewhere (1907a), galvanotactic reactions in the young lobsters occurred only when the tail or the back was turned wholly or partly toward the anode. Although at first sight it appears that the causes for this condition of reaction can have nothing in common with the causes which determine a progressive orientation to the directive influence of light rays only when the swimming position is favorable, it may not be inappropriate to suggest that here also the direction of the impact of light with reference to the axis of the body of the larva, may have some influence on the reaction.

Experiment 13. Case 1—Ten larvæ, twelve days old, were placed in box *A*, mounted over the light-shaft. When the glass plates were arranged in the order designated below, the photopathic reaction was as follows:

Test.	After	Distribution of larvae.			
		Red.	Orange.	Green.	Blue.
1	5 minutes	0	1	2	7
2	10 minutes	1	1	1	7
3	15 minutes	1	1	2	6
4	20 minutes	2	0	0	8
5	25 minutes	0	1	0	9
Totals....................		4	4	5	37

Case 2—When the order of the glass plates was changed to red, blue, orange, green, the following results were obtained: Red, 3; blue, 31; orange, 3; green, 3.

Case 3—After redistribution of the larvæ had taken place, the small window opening at the green end of the box was uncovered to the diffuse light of the room. The resulting reactions were as follows:

Test.	After	Distribution of larvae.			
		Red.	Blue.	Orange.	Green.
4	2 minutes	0	3	3	4
2	4 minutes	1	3	3	3
3	7 minutes	1	3	1	5
4	10 minutes	1	2	3	4
Totals		3	11	10	16

Case 4—Once more the order of the glass plates was changed to blue, green, orange, red, and the window at the red end was uncovered to the light of the room. The results of the three sets of tests were: Blue, 9; green, 5; orange, 3; red, 13.

Experiment 14—The following observations deal with cases of larvæ suddenly submitted to a light of great intensity, as for instance when they are brought from subdued daylight into full sunlight, or when the brilliant rays from an acetylene lamp fall upon larvæ which had been for sometime in darkness.

Case 1—July 18, 4 p.m. Fifty first-stage larvæ, about thirty hours old, which had been reacting positively in lights of low or medium intensity, were placed (in a glass jar) in the bright sunlight of the west table. Every larva at once moved to the room side of the jar. Within a few minutes, however, all returned to the window side of the jar. Ten minutes later they were divided about equally on each side. Next they were returned to the dark box and submitted to the weak light from the small window. Here they manifested a definite positive reaction which continued until evening. At 8:30 these fifty larvæ were suddenly submitted to the intense rays of an acetylene light. The result was a universal negative reaction. Within two or three minutes, however, a few larvæ began to return toward the light, and within four minutes all had become positive in their reaction.

Case 2—A group of fourth-day first-stage larvæ in the glass jar was subjected to light of low intensity and found to manifest a positive reaction; when subjected to a much stronger light the same larvæ were still universally positive. This reaction, once established, endured through the period of gradually diminishing intensity of light accompanying the coming of night. The next morning these (now fifth-day) larvæ were found to be negative in reaction. It was feared, however, that the manner of reaction might have been changed because of the long period of confinement which they had undergone. For this reason a fresh lot of twenty-five larvæ from the same group (fifth-day, of the first and second stages), was secured. It was observed at this time that about a third of the number of those in the hatching bag had moulted into the second stage, and that the others were very near the moulting-period. When these larvæ were put in the glass jar, placed in the dark box and submitted to subdued light from the small window, six tests showed fifty-five to be negative, and ninety-five positive. When these same larvæ (now thirteen first-stage and twelve second-stage), under the conditions of stimulation stated above, were subjected to light of still greater intensity by placing the jar nearer the small window of the dark box the results showed that fifty-nine were negative and forty-one were positive.

At 3:30 p.m. these same larvæ were removed from the dark box and placed (in the glass jar) on the west table, where they were suddenly subjected to the bright afternoon sunlight. Every larva came to the room side of the jar and remained there so long as observed.

Case 3—The larvæ mentioned above were liberated and another lot of twenty-five (of the same group, but all in the second stage) was secured at 8 o'clock in the evening. The intense rays of the acetylene light were suddenly directed upon one side of the jar.

This resulted in a sudden and universal positive reaction which, however, soon became indefinite. The larvæ gradually returned to the darker side of the jar and, as in the case mentioned above, remained there so long as observed.

Case 4—When, on the other hand, another group of larvæ which was reacting positively to a light of low intensity, was brought by slow degrees into a light of great intensity, there resulted no sudden, temporary change of reaction such as that observed above. The reaction usually remained unmodified, but if it was reversed it remained permanently so. The same statement holds for larvæ which had been reacting negatively to light of low intensity. When they were brought by slow degrees into light of great intensity, seldom did a sudden temporary change in reaction result.

Conclusions from Experiment 14: The stimulation brought about by suddenly submitting larvæ to intense light may cause at least two kinds of response: first, in the case of early first-stage lobsters (about thirty hours old, and manifesting previously a positive reaction), a definite and universal, though temporary, negative response; second, in the case of early second-stage larvæ (about five days old, and giving previously a negative reaction), a definite and universal, though temporary, positive response. From Case 4 it appears that a gradual change of intensity (extending over an equal or even a greater range of intensities) may not bring about a similar result, although a permanent reversion in the reaction may sometimes ensue.

Larvæ which have recently moulted are most susceptible to slight differences in light-intensity; and the reaction of such larvæ is frequently negative, while the reaction of larvæ which are approaching the moulting-period is more often indefinite or positive.

Experiment 15. Case 1—The following experiment involved the use of the Y-tubes described on p. 207. Ten positively reacting lobsters, five hours old, were placed in the tube at the end designated *a* (Fig. 5, *B*). The Y-tube was then placed in position in the dark. Over one arm was laid a red glass, over the other arm an orange glass, and then the screen was drawn from the window to allow the light rays to strike the tube in the direction shown in Fig. *B*. Tests were made about five minutes apart. After each, the return of the lobsters to the (*a*) end of the tube was induced merely by reversing the tube so that the end (*a*) was toward the window; the position of the red and orange glass was also reversed. The distribution at the end of each test was as follows:

Test.	Red arm.	Stem.	Orange arm.
1	0	0	10
2	0	1	9
3	0	1	9
4	0	2	8
Totals	0	4	36

Case 2—Next, green and blue glass plates were substituted for the red and orange, the method of the experiment otherwise remaining the same, and the green and the blue glasses were reversed in position at the end of each test. A series of four tests showed the following results: Green arm, 11; stem, 2; blue arm, 27.

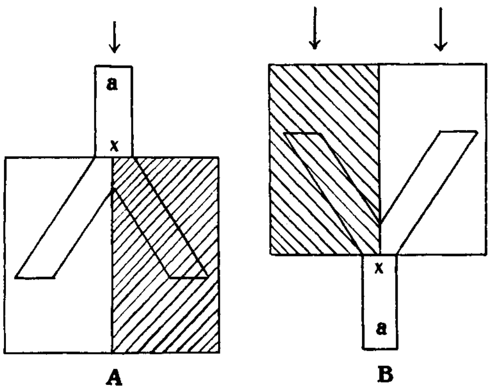

Fig. 5. Showing the Y-tubes as set up for experiment. The arrows indicate the direction of the light rays. The cross-hatched areas represent the glass plates of the darker color laid over the arms of the tubes. The ends designated *a*, represent the starting point for the negatively reacting (A), or the positiyely reacting (B), larvæ.

Case 3—One more test of the reaction of this group of positive larvæ was made at this time, which was far more delicate than either of the preceding, for the difference in the intensity of the glass plates used was less. In making a selection of glass slides two were chosen which had been purchased for "red glass." On close inspection, however, and by test with sensitized paper, it was observed that one slide was somewhat lighter in color tone than the other. These glasses were used in the next experiment. The darker of them may be designated as red, the lighter as ruby. The results of four tests were as follows: Ruby arm, 21; stem, 10; red arm, 9. In the last experiment, with this group of larvæ, it was found that a great intensity of light, striking the red slides, was required to bring about reaction; and that, even then, several larvæ would remain in the region designated *x* (Fig. 5, *B*), near the junction of light and dark. These experiments were repeated with both black and white backgrounds for the arms of the Y-tube. The results agreed with great uniformity, differing only in the length of time required for the reaction. From these last experiments we may conclude that the first-stage lobsters, at the age of five hours or less, are extremely sensitive to slight differences in the intensity of light, more so in fact than older lobsters of the first and later stages; for it was seldom with these older lobsters that the delicate reaction to the ruby and the red glasses observed in Experiment 15, Case 3, could be induced.

Experiment 16. Twenty first-stage larvæ, slightly over two days old (for which to light of nearly all intensities reactions on the first and second day had been positive), were put in the glass jar, and this in turn was placed in the dark box. They were submitted to light from a small window one inch wide and two inches high, before which the colored glass plates could be placed so as to illuminate one side of the jar with red, blue, green, or orange rays, as the case might be. The reaction in each of these lights was as follows:

LIGHT.	POSITIVE.	NEGATIVE.
Red	20	0
Orange	20	0
Green	19	1
Blue	18	2
White*	15	5
Day	3	17

* Subdued daylight passing through one or two thicknesses of white paper.

Here it is shown that the negative reaction to lights of great intensity, which was first discovered in larvæ thirty hours old (Experiment 14, Case 1), and which, as we shall see, persists for a variable length of time, has become accentuated and remains for the time permanent. The next series of observations were made upon lobster larvæ on the fourth day after hatching. Many of them were earing the moulting-period and preparing to pass into the second stage.

Experiment 17—July 17, 8:30 a.m. About one hundred fourth-day, first-stage lobsters (Group A) were taken from one of the hatching bags and placed in the glass jar in the dark box. The majority reacted positively to daylight through the small window. At 1 o'clock, when examined again, about one-half of them were reacting negatively. The jar was then removed and placed in the light of the west window where the intensity was greater. At once every larva became negative in reaction.

In order to determine whether this mode of reaction was a natural incident in the life of the larvæ of this age, or whether the response had been induced as a result of their having been so long subjected to experimentation, twenty-five first-stage larvæ (Group B) were removed from the same group as that from which the larvæ mentioned above were taken. When these twenty-five were put in a glass jar and placed in the west window beside the group mentioned above, they gave a positive reaction. After five minutes, half were positive and half negative. At 5:30 the sun was low and the light weak, but all the larvæ gave a negative reaction, which persisted, as did the negative response in Group A mentioned above, until far into the twilight.

It may be further noted in this connection, that five of the larvæ which reacted negatively in the afternoon were placed in absolute darkness for four and a half hours. It was believed that the positive reaction might be renewed; but this was not the case when they were again brought into daylight of several intensities.

Experiment 18. Case 1—July 20, 4 p.m. A number of fourth-day, first-stage larvæ were removed from the hatching bag and put in the glass jar. This was placed in the dark box and the larvæ submitted to red light through the three by three inch window. The resulting reaction was positive and remained so even when the intensity was still further diminished by inserting numerous sheets of paper behind the red glass. Finally, a point was reached where the positive orientation was lost and a homogeneous scattering occurred. When the intensity of the light was again increased, the positive orientation returned; but, with a still greater increase in intensity, this response became again less definite, and finally, in the more intense blue and white light, the negative reaction again appeared.

Case 2—In the evening, when other observations were made upon the same group under the influence of the acetylene light, burning dimly, the reaction in the glass jar was positive under all the colored glass plates. When the intensity was increased by substituting a lamp which burned more brightly, the group divided, half going to the positive and half to the negative side. When the intensity was increased still further (reinforced by a brilliant oil burner and reflector) a greater number gave a negative reaction. As it afterward transpired, the larvæ used in these last tests did not moult to the second stage until on or after the fifth day.

Case 3—July 23, 1:20 p.m. Fifty fourth-day, first-stage larvæ were put in the glass jar and placed in the dark box. In the red light the reaction was definitely positive. The reaction under the different intensities obtained by colored glass plates may be tabulated as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red	50	0
Orange	47	3
Green	43	7
Blue	36	14
White	23	27

Case 4—July 31, 10 a.m. Twenty-eight first-stage and second stage larvæ of the fifth day (all nearly ready to moult to the second stage) were put in the glass jar and placed in the dark box. Under lights of different intensities the results were as follows:

LIGHT.	POSITIVE.	NEGATIVE.
Red	28	0
Orange	22	6
Green	18	10
Blue	12	16
White	14	14
Daylight	0	28

In this particular case it was observed that under the orange light the negative larvæ were of the second stage, while those which retained for the longest time the positive reaction (in the case of the blue and white glasses), were the lobsters which were nearest to the moulting-period. When fresh, clean larvæ, which had moulted into the second stage within a very few hours, were selected and submitted to several different intensities of light, they invariably gave the negative reaction.

Case 5—July 23, 1 p.m. Twenty fifth-day, second-stage larvæ were taken from one of the hatching bags and put in the glass jar. This was placed in the dark box and the larvæ were submitted to illumination from the red light. There was some random swimming, but the general reaction was positive, except in white light, in which three were positive and seventeen negative. Next, the jar was removed from the dark box and placed on the west table in subdued sunlight. Here the reaction was definitely negative. At 4:30 when the jar was returned to the box (at this time in the afternoon the light was much less intense than earlier) a positive reaction was obtained in red, orange and green light.

Conclusions from Experiments 16, 17, 18: From the result of the last three experiments the following tentative conclusions may be drawn. The general negative reaction to light of great intensity, begins on about the third day of the first stage, continues for the most part uninterruptedly until the moulting-period is near; just before the moult the reaction becomes indefinite or, more often, positive; directly after the moult into the second stage (which occurs on the fourth or fifth day of the first-stage-period), the reaction to lights of nearly all intensities again becomes definitely negative.

2. *Second Larval Stage.*

Experiment 19. Case 1—July 19, 8:30 a.m. Observation of a group of sixth-day, recently moulted second-stage larvæ demonstrated that a negative reaction took place when the larvæ were put in the glass jar and placed in the dark box. This was true for daylight coming through the three by three inch window, and in both blue and green light. In the case of orange and yellow light, however, the reaction was similar to that in either yellow or orange, but perhaps less definite. It may be here recorded that a group of first-stage larvæ, about one and a half days old, subjected at the same time to these conditions, gave a positive reaction, not only in orange, but also in blue, and even to white light. These reactions took place on both black and white backgrounds, but they were more definite on white. But when the stimulus of the orange rays was continued for ten minutes or more, in this case also, the negative reaction began to appear again and many larvæ came to the room side of the jar.

Case 2—July 23, 5 p.m. The larvæ used in this case were of the seventh-day group of the second stage, having been taken from the hatching bag at 9 a.m. At 5 p.m. under red, orange, green, blue and white lights, entering through the three by three inch window, all were definitely negative. They had also shown a negative reaction in several intensities of light in the morning. At 7 p.m. further observations were made on the same group of larvæ. The following quotation is from the daily note book.

"July 23, 7 p.m. One of the best demonstrations of the persistency of the negative reaction of these seventh-day larvæ was exhibited this evening. Larvæ taken from the hatching bags at 9 a.m. have reacted negatively at every observation during the day. At 7 p.m. it was observed that this group, which still remained in the glass jar near the west window, continued to present a definite negative reaction. This negative response continued until 7:55 p.m., when the light became too faint to determine either a body or a progressive orientation. Here it is to be observed that the negative reaction on the part of these second-stage larvæ was continued through a long series of gradually diminishing intensities of light. After all signs of body-orientation or progressive orientation had vanished in the case of the group of larvæ mentioned above, the intense light from the acetylene lantern was suddenly thrown open one side of the glass jar. A most definite negative reaction resulted. This response, it will be observed, is different from that recorded in Experiment 14, Case 3, for in the latter case the sudden illumination determined a definite positive reaction."

Experiment 20. Case 1—July 24, 9 a.m. Thirty eight-day, second-stage larvæ were taken from one of the large bags and put in the glass jar in the dark box. The time of moulting into the third stage was near at hand, and many of the individuals were already "fuzzy" and sluggish in their movements. Illumination through the three by three inch window, by the colored lights, gave these reactions:

COLOR.	POSITIVE.	NEGATIVE.
Red	30	0
Orange	27	3
Green	17	13
Blue	13	17
Day	13	17

Before we state the next case, one consideration must be noted. In the previous pages, use has been made of such terms as "third-day," "seventh-day," and "eighth-day" larvæ, to distinguish the age, and roughly the stage, of certain groups of lobsters. Because of the use of these terms, it must not be supposed that there is always a constant relation between the age and the stage of the larvæ. Among the larvæ of a single group which have been hatched and have developed under similar conditions, a fairly constant relation between the age and stage is invariably maintained. But for different groups of larvæ, this correlation does not necessarily exist, for it is entirely possible, and indeed it very frequently happens, that a group of seventh-day larvæ may be in the third stage, while a lot of eight-day individuals are in the second stage. The differences in rate of development are due to such factors as water density, temperature, food-supply, and conditions of light and darkness, which, as the writer has shown (HADLEY '06b), may act either directly upon the body processes, or indirectly by favoring or preventing the growth of various body parasites such as diatoms, protozoa, and algæ that naturally develop in profusion on the bodies of the young larvæ. This explanation will perhaps make clear why, in the following case, we apparently retrace our steps to consider the case of seventh-day larvæ. In point of fact, these larvæ were, at the time of experimentation, somewhat further developed than were the eighth-day larvæ mentioned in Case 1.

Case 2—July 20, 9 a.m. Twenty seventh-day larvæ (eight second-stage, twelve third-stage) were removed from the hatching bag, put in the glass jar, placed in the dark box and illuminated by the light through the three by one inch window. After a half hour, observation showed that the larvæ were equally divided between the window side and the room side of the jar. After five minutes' exposure to red light, thirteen larvæ were positive and seven were negative. When, however, the amount of light was increased by opening the large three by three inch window, only three larvæ remained positive while seventeen became negative. This proportionate reaction endured for several hours, or until observation ceased.

Case 3—July 20, 8 p.m. Twenty seventh-day, early third-stage larvæ were taken from one of the hatching bags, placed in the glass jar, and illuminated by an acetylene light. A more or less scattering negative reaction at first resulted. When the amount of light was increased by supplementing the acetylene with a brilliant oil burner the response was more definitely negative.

Case 4—July 21, 9 a.m. Twenty-two eighth-day, early third-stage larvæ were taken from one of the hatching bags and put in the glass jar in the dark box. When subjected to subdued daylight through the three by one inch window, sixteen out of twenty-two gave the negative reaction. In orange light the reaction was seventeen negative, five positive; in red light eighteen negative, four positive. Here attention may be called to the fact that these third-stage larvæ gave a negative reaction to practically the same intensity of light as determined a positive response for larvæ in the late second stage.

Case 5—August 3, 2 p.m. Twenty eighth-day, early third-stage larvæ were taken from the hatching bags and put in the glass jar in the dark box. They were submitted to the colored lights, with results as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red	8	12
Orange	6	14
Green	3	17
Blue	2	18
White	6	14
Day	0	20

Conclusions from Experiments 19 and 20: The conclusions which we draw from the two foregoing experiments support further those formulated for Experiments 16, 17 and 18, on p. 228. In Experiment 20, Case 1, was observed the definite positive response which was manifested toward the end of the second larval stage when the moulting-period was near. In Case 2, where a group of larvæ which included individuals of both the second and third stages was used, it was observed that the reaction was either positive or negative; and that those larvæ which gave the negative reaction most definitely or gave it first were usually the larvæ of the early third stage. In Cases 4 and 5, in which only third-stage larvæ were employed, it was observed that, in general, the reactions to lights of nearly all intensities were negative. As in the case of the first-stage larvæ, it was found that the reaction of second-stage larvæ, just before the moulting-period, usually changed from negative to positive, and again became negative at the beginning of the third larval state.

3. Third Larval Stage.

By the ninth day it is only in exceptional cases that the larvæ have not entered the third stage; and it frequently happens that they are nearly ready to enter the fourth. The swimming of the third-stage larvæ is much like that of the earlier stages except that in the third stage there is greater difficulty in using the swimmerets of the thoracic appendages, especially during the last part of the stage. One reason for this is the fact that, as the larvæ grow older and larger, they more often play the host to multitudes of diatoms, algæ and protozoa which gather in such quantities as seriously to interfere with the processes of swimming and eating. In the preparation for the moult from the third to the fourth stage, moreover, occur the most important changes that the young lobster undergoes in the course of its life. These changes appertain not alone to modifications in the external form of the body and to the form and functions of many of the body appendages, but also to points of internal structure. Among the changes during this period of metamorphosis we may enumerate the following as important in connection with our study of behavior: (1) The loss, in the moult from the third stage, of all functional swimming attachments of the thoracic appendages; (2) the great development of both the first and second pairs of antennæ and of the chelipeds; (3) the accession of functioning swimmerets on the under side of the second to sixth abdominal segments; (4) a great change in the form of the body, and a consequent modification of the manner of swimming.

In view of these important changes, which are taking place in the anatomy of the lobsters as they pass from the third into the fourth stage, it does not appear unjustifiable to believe that these processes have an influence on the behavior of the larvæ even before they emerge in approximately the adult structural type, endowed with a new body form, new functional apparatus and new reactions. We shall now undertake a study of the behavior of the third-stage larvæ as they approach and finally pass this most critical period of their life history.

Experiment 21. Case 1—July 22, 9:30 a.m. Thirty ninth-day, third-stage larvæ were removed from the hatching bag, put in the glass jar and placed in the dark box. Under stimulation by the red rays, although there was no definite positive reaction, most of the larvæ swam about at random on the window side of the jar. When orange glass was substituted for red, half of them came to the room side of the jar. In the case of green glass, a few more reacted negatively, and when blue glass was substituted for green, all but five larvæ gave a negative response. These five did not manifest a definite positive reaction, but swam at random on the window side of the jar. When the colored glasses were removed and the larvæ were submitted to the influence of diffuse daylight through the small window, all reacted negatively.

Case 2—August 4, 9 a.m. Twenty ninth-day, third-stage larvæ were taken from one of the hatching bags and placed in the dark box. Stimulation by the colored light resulted as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red	6	14
Orange	3	17
Green	2	18
Blue	2	18
White	0	20
Daylight	0	20

Case 3—In the present case it was attempted to learn whether the sign of the photopathic reaction in the larvæ of this stage corresponds to the sign of their phototactic reaction. To this end, ten ninth-day, third-stage larvæ, fresh from the hatching bag, were placed in the glass-bottomed box *B*, which was set over the light-shaft and mounted upon colored glass plates. After each observation either a period of five minutes was allowed for a uniform distribution of the larvæ to take place, or the box itself was reversed, leaving the glass plates in the same order. In other instances the order of the glass plates was changed. During this experiment the water in the box was eighteen to twenty mm. deep. The results are presented below:

RED.	ORANGE.	GREEN.	BLUE.
4	0	1	5
1	0	2	7
RED.	ORANGE.	BLUE.	GREEN.
2	1	3	4
1	1	4	4
RED.	BLUE.	GREEN.	ORANGE.
1	5	3	1
2	2	3	3
BLUE.	RED.	GREEN.	ORANGE.
6	0	3	1
5	1	2	2

The larvæ which were used as stated above, and which presented a positive photopathic reaction in every instance, were next transferred to the glass jar and placed in the dark box. Here, and in tubes, the assumed phototactic reaction was uniformly and definitely negative; and this was true in the case of lights which were both of greater and of lesser intensity than in the tests above mentioned.

Case 4—To confirm the results obtained in Case 3, similar tests were made with another group of ninth-day, third-stage larvæ, fresh from the hatching bag. Notwithstanding the fact that this series of observations was not started until 5 o'clock in the afternoon when the light was fading, the results were similar to those obtained in Case 3. That is to say, the photopathic reaction was definitely positive, but the phototactic reaction, as shown when the larvæ were transferred to the glass jar in the dark box, was as definitely negative.

Experiment 22—The following experiment and observations concern the tenth-day, third-stage larvæ. Most of these lobsters were well along in the third stage, and many were covered with body parasites.

Case 1—July 23, 9 a.m. Thirty tenth-day, third-stage larvæ were transferred from one of the hatching bags to the glass jar and placed in the dark box. After having been submitted for one-half hour to light coming through the red glass (three by one inch window), the reaction was uniformly negative. In the case of orange, yellow, green, blue and white light the results were the same. In all of these reactions, however, one fact was noticeable, the body-orientation of these larvæ was much less definite than in any previous case of the same or earlier stages.

Case 2—July 26, 9 a.m. A mixed lot of thirty third-stage larvæ, most of which were ten days old, although some were older and some younger, were transferred from the hatching bag to the glass jar. When submitted to the colored lights in the dark box, the following results were obtained:

Color.	Positive.	Negative.
Red	3	27
Orange	13	17
Green	8	22
Blue	13	17
White	0	20

In consideration of the apparent fluctuations in the sign of reaction manifested by the above-mentioned larvæ, it may be noted that these lobsters represented a group in which some were "early," others "advanced," third-stage larvæ. Indeed many were approaching the third moulting-period; the significance of this for the behavior of the larvæ we shall consider in the next few cases.

Case 3—July 27, 2 p.m. Thirty eleventh-day, third-stage larvæ were transferred to the glass jar and placed in the dark box. Under colored lights, although the general reaction was negative, many were positive. Experiments made upon the larvæ in the glass-bottomed box *B* to determine the photopathic reaction at this time, showed that the larvæ gave neither a definitely positive nor a definitely negative reaction. Other tests indicated a definitely positive reaction. When, however, light was admitted to the box through the end window (as well as through the bottom), first from the red end, then from the blue end, of the box, there resulted a definite negative phototactic response. The arrows show the direction in which the light entered the box.

→ RED.	BLUE.	ORANGE.	GREEN.
1	2	1	6
1	1	0	9
0	0	0	10

→ RED.	ORANGE.	GREEN.	BLUE.
0	0	0	10
0	0	1	9

RED.	ORANGE.	GREEN.	BLUE. ←
5	1	2	2
6	0	2	2
9	1	0	0

The foregoing cases demonstrate that these larvæ manifested a definitely negative phototactic reaction under the conditions of illumination described; and that, by those rays which had a directive influence, they could be driven into a region of either greater or lesser light intensity, as represented by the blue and by the red ends of the box, respectively. It might be argued that, so long as the eyes of the larvæ are homolaterally stimulated, variations in intensity can not cause or change the orientation, and that orientation results only from a heterolateral stimulation. But this is by no means true, for it has been noted in the foregoing pages, and it will be further demonstrated, that slight differences in intensity, when coincident with a homolateral stimulation, may even reverse the index of progressive orientation.

Case 4—July 24, 9 a.m. Thirty-five eleventh-day, third-stage larvæ were transferred from the hatching bag to the glass jar and placed in the dark box. The reactions to the colored lights were as follows:

Color.	Positive.	Negative.
Red	15	20
Orange	16	19
Green	8	27
Blue	8	27
White	7	28

Next, the jar was placed in full daylight, on the table before the west window. All larvæ came to the room side. In this case there were seven larvæ which became the special object of observation, since they invariably manifested a positive reaction until they encountered daylight. This group was set aside, and before night four of the seven had moulted into the fourth stage; consequently their exceptional behavior was due to the fact that they were in a different physiological condition than the majority of the group used in Case 4.

Experiment 23. Case 1—In this experiment is continued the examination of the reactions of other twelfth-day larvæ which were approaching the third moulting-period. Twenty-three larvæ were placed in the glass jar and observed under the influence of the colored lights in the dark box. The results were as follows:

Color.	Positive.	Negative.
Red	6	17
Orange	15	8
Green	6	17
Blue	4	19
White	3	20

Case 2—At 3:30 p.m. Ten larvæ from the above groups were transferred to the glass-bottomed box *B*, which was set up over the light-shaft upon the colored glass plates. The results were as follows: Blue, 19; green, 3; orange, 4; red, 4. During the course of the day, many of these ten larvæ moulted to the fourth-stage.

Case 3—July 29, 9 a.m. By this date there were very few third-stage larvæ left in any of the groups whose actual age was known. Indeed there are few cases in which the development is so slow that the third-stage larvæ endures to the thirteenth or fourteenth day. In this particular instance, twenty larvæ were transferred to the glass jar and placed in the dark box. The resulting reactions to the colored lights were as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red	16	4
Orange	16	4
Green		
Blue	13	7
White	9	11
Day	0	20

It may be observed in the account of the last three experiments how the general reaction of the third-stage larvæ has gradually changed from negative to positive; and how it requires an increasingly greater intensity of light to determine a negative response in the larvæ which are approaching the fourth stage. In the next case the culmination of this gradual change is reached, since the third-stage larvæ almost uniformly manifest a positive reaction which is as definite as that of the newly-hatched larvæ.

Case 4—July 30, 2 p.m. Thirty fourteenth-day, third-stage larvæ secured from a group in which nearly all had entered the fourth stage, were transferred from the hatching bag to the glass jar and placed in the dark box under the influence of colored lights:

COLOR.	POSITIVE.	NEGATIVE.
Red	30	0
Orange	30	0
Green	30	0
Blue	30	0
White	28	2
Day	23	7

It is here observed that, when as indicated above, the jar was removed from the dark box and placed on the west table in daylight, only seven larvæ became negative. All the others remained positive, even in this light of great intensity. This case represents the strongest and most definite maintenance of the positive reaction in late third-stage larvæ ever observed by the writer. These larvæ moulted into the fourth stage very soon after the above observations were made.

Case 5—In the following test other members of the group of larvæ used in the previous case were employed. The aim was to learn whether or not the photopathic reaction in these larvæ was in agreement with the phototactic reaction described in Case

6. The larvæ were placed in the glass-bottomed box over the light-shaft; fifteen minutes was allowed for the first orientation, and five minutes was given for each of the others:

After	Blue.	Green.	Orange.	Red.
15 minutes	6	2	2	0
20 minutes	6	1	1	2
25 minutes	4	1	5	0
30 minutes	4	5	0	1
35 minutes	3	7	0	0
40 minutes	2	7	0	1
Totals	25	23	8	4

It thus appears that the photopathic reaction of the larvæ was definitely positive. After this series of observations the larvæ were returned to the glass jar and placed on the west table. In the faint daylight which remained, the positive reaction was manifested and continued as long as the light lasted.

Conclusions from Experiments 20, 21, 22 and 23: As has been noted, these experiments deal with the reaction of larvæ as they pass through the third and enter the fourth stage. In Experiment 20 (Cases 2, 3, 4 and 5) it was shown that, in general, the majority of early third-stage larvæ reacted negatively, frequently to light of weak intensity, and invariably to light of greater intensity. In Experiment 21 it appears (1) that this negative response was fairly characteristic of the early third-stage larvæ; (2) that, notwithstanding this negative phototactic reaction, the photopathic response might be definitely positive (Experiment 21, Case 3) thus appearing to indicate that, at least at a certain period in the life of the third-stage larvæ, a positive photopathic reaction and a negative phototactic response may be given by the same individual. Experiment 22 demonstrates (1) that, as the third-stage advanced, the positive reaction, was more frequently and more easily determined by light of all intensities (Case 2), and that an increasingly strong illumination was required to bring about a negative reaction (Case 4); (2) that the photopathic response, if anything, remains throughout the stage, positive (Case 3), while the sign of the phototactic response may change with the intensity of the light (Cases 2 and 4).

In Experiment 23 it is observed that the negative reaction to strong light was still prominent in the behavior of the twelfth-day larvæ (Case 1), while on the thirteenth and fourteenth days, as the moulting-period to the fourth stage approached, the negative reaction was less easily determined (Cases 3 and 4). It was observed furthermore, that these larvæ continued to manifest a very definite positive photopathic response (Case 5), and that this was maintained until the end of the stage-period.

General conclusions on the behavior of larvæ of the first three stages—As the larvæ, after the very definite positive photopathic and phototactic reactions characteristic of the first part of the first larval stage, pass on through the first stage-period, lights of low intensity (red, orange, twilight, etc.), gradually lose their efficiency in bringing about a positive phototactic reaction, while, on the other hand, lights of a greater intensity (green, blue, daylight, etc.) determine, more and more easily, a negative response. This negative phototactic response, which may enter on the third day of the first stage-period, changes again to positive as the first-stage larvæ draw near the first moulting-period. At this time, the lights of low intensity are again effective in bringing about a positive reaction, which is maintained until the larvæ have moulted into the second stage.

While the photopathic reaction of newly moulted second-stage larvæ remains positive, the phototactic response is more often negative, and this negative response is commonly maintained until toward the end of the second stage-period. At this time, as was observed in the first stage-period, a positive reaction again becomes manifest as the larvæ approach the period of moulting into the third stage.

While the positive photopathic reaction still obtains, the newly moulted third-stage larvæ commonly manifest a negative phototactic reaction, and this, as was the case with the second-stage larvæ, is retained until the moulting-period into the fourth stage approaches. At this time the reaction again becomes positive, and continues so until the larvæ have entered the fourth stage. These general points in the behavior may be illustrated by the following diagram (Fig. 6).

The foregoing facts serve to emphasize further the statement made on an earlier page, that we can not justly say that the larvæ of Homarus are positive to light or negative to light, or that they react in this way to intensity, and in that way to the directive influence of the light rays. But these observations do show that the larval lobsters manifest a type of behavior which includes widely varying kinds of reaction, even to the same stimulus. The point has been, not to learn what reaction the lobster larvæ give to light, but to ascertain the conditions which so play upon the mechanism of these organisms as to produce the wide ange of responses observed. The causes of the daily and the hourly variations in the kinds of reactions manifested by organisms is a field which is, even at the present day, largely given up to speculation, and all sorts of explanations have been brought forward from the view of the rhythmical succession of certain movements resulting from purely internal stimuli, to the view of cycles of change in certain metabolic products under the influence of external stimulation, and their consequent reaction upon the nervous processes of the organism. The fact of variations in the reactions of larvæ of the European lobster (Homarus vulgaris) has been noted by

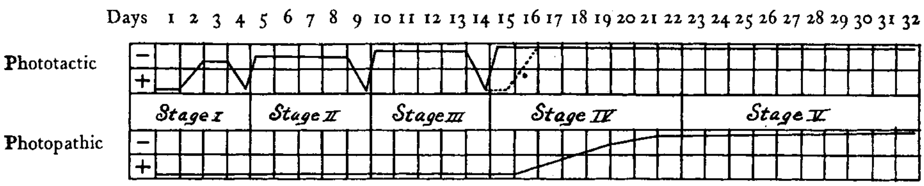

Fig. 6. Diagram recapitulating the nature of the phototactic and photopathic reactions of lobsters in the first five stages. The dotted line in the upper series indicates that the early fourth-stage lobster may give a positive phototactic reaction to light of very great intensity. For further explanation, see General Conclusions on p. 239.

Bohn (1905, p. 10). After having made several observations upon recently hatched larvæ, he comes to the following conclusion. "De ces diverses observations, il semble résulter que *le sens de deplacement des larves de homard subit des variations occellantes de signe*, qui, bien que influencées par l'éclairement actuel sont en relation avec les heures de la journée."

Although certain phases of behavior in some marine animals may be explainable on the ground of rhythmically recurring reactions which bear a certain relation to the hours of the day, the present writer's experience with larvæ of all ages and stages of the American lobster makes it quite impossible to attribute the variations in the reaction of lobster larvæ to such causes. The hours of the day, except as they are accompanied by corresponding differences in the intensity of light, have nothing to do with the form of reaction displayed by the lobster larvæ. This is readily shown, first, by the fact that, at any corresponding time on two successive days (and especially when a moult has intervened), the reactions of the same larvæ may be quite dissimilar. Here the reactions are explainable on the grounds of (1) the stage of the larvæ and their age in the stage-period; and (2) the intensity of the light and of other stimuli which are brought to bear. This conclusion is shown furthermore by the fact that larvæ at corresponding times in the different stage-periods usually manifest similar types of reaction. Thus does it appear that, although the diverse forms of reaction are partly due to the differences of intensity in actual illumination, the underlying cause is some physiological change which the larvæ undergo as they gradually approach and pass the crises of their moulting-periods.

4. Fourth Stage.

We come now to a consideration of the reactions to light of the fourth-stage lobsters. It has been observed in previous pages that the most striking change, not only in body-form but also in life-habits, which takes place in the life of the lobster, occurs during the transition from the third to the fourth stage. It is the aim of the present section to analyze the reactions of the fourth-stage larvæ and to exhibit the conditions which determine or modify these reactions.

In the previous pages the lobsters under consideration have been referred to as the "second-day" or the "fifth-day" larvæ, etc., as the case might be, and this terminology was of advantage, because the first three stage-periods are so brief that changes may occur even in two consecutive days. The fourth stage-period, however, is much longer (usually eight to twelve days) and the differences in reaction on two consecutive days may be slight or inappreciable. For this reason, then, in the following consideration we shall divide the fourth stage-period into three parts, viz: the early, the mid, and the late fourth stage-period.

Experiment 24. Reactions of early fourth-stage lobsters. Case 1. Photopathic reactions—July 28, 10 a.m. Ten early fourth-stage larvæ were put in the glass-bottomed box *B* and this was placed over the light-shaft. The arrangement of the colored plates and the resulting orientations were as follows. The results indicate that the early fourth-stage lobsters show a slight tendency to remain in the more brightly illuminated areas.

Red.	Orange.	Green.	Blue.
1	1	2	6
2	2	1	5
2	3	2	3
5	6	5	14

Red.	Orange.	Blue.	Green.
4	1	2	3
2	2	2	4
0	2	5	3
0	1	4	5
6	6	13	15

Green.	Blue.	Orange.	Red.
2	4	1	3
1	4	2	3
3	3	2	2
6	11	5	8

Totals.

Blue.	Green.	Orange.	Red.
38	26	17	19

Case 2. Phototactic reaction—August 7, 5:30 p.m. Ten early fourth-stage larvæ were placed in box *B* and the end window of the box was opened to the diffuse light of the west window. As has been explained, this box was so constructed that in a moment glass plates could be slid through the cover, and into such position that they would divide the floor area of the box between the ends into four equal parts. Beginning with the end toward the light these may be numbered 1, 2, 3, 4, respectively, and the results showing the imprisonment of the larvæ in two instances, may be recorded as follows:

1.	*2.*	*3.*	*4.*
2	2	0	6
7	0	0	3
2	0	2	6
0	0	2	8
11	2	4	23

1.	*2.*	*3.*	*4.*
2	1	2	5
0	1	2	7
0	0	1	9
0	0	3	7
2	2	8	28

In the second of these instances an acetylene light was used, the intensity being diminished by inserting a red glass between the burner and the window in the end of the box toward the light.

Case 3. Phototactic reaction—August 9, 3:40 p.m. Ten early fourth-stage lobsters were transferred from the confining bag to box *B*, and this was placed with the end toward the west light. In this case, colored glass plates were placed at intervals in front of the end window to modify the intensity of the light entering the box. A five-minute intermission was allowed between observations. The results, which clearly establish a negative phototactic reaction, are presented in the following table:

COLOR.	*1.*	*2.*	*3.*	*4.*
	2	1	2	5
	1	1	2	6
	2	1	3	4
	0	0	2	8
Orange	5	3	9	23
	0	1	2	7
	0	1	4	5
	1	3	2	4
	0	1	1	8
Red	1	6	9	34
	1	0	1	8
	0	0	0	10
	1	1	0	8
	1	2	2	5
Green	3	3	3	31
Totals	9	12	21	78

Case 4. Phototactic reaction—In the following case, in which the same lobsters were used the source of illumination was the acetylene light and the intensity of the light which entered the end window of box *B* was modified in two ways: (1) by the colored glass plates placed between the light and the window in the end of the box; (2) by the distance of the light from the box. The results, which demonstrate a definite negative phototaxis, were as follows (in all cases the figure *1* indicates the division of the box nearest the light; *4* the division farthest from the light):

Color.	Distance.	1.	2.	3.	4.
Red	2 inches	3	1	2	4
		1	0	1	8
		1	2	3	4
		1	1	1	5
	Totals	6	4	9	21
Red	6 inches	2	1	1	6
		1	3	2	4
		3	0	1	6
		1	2	2	5
	Totals	7	6	6	21
Red	12 inches	3	1	2	3
		4	2	1	3
		1	3	2	4
		2	4	4	2
	Totals	10	8	9	12
Blue	12 inches	0	1	4	5
		1	1	3	5
		3	2	0	5
		2	2	0	6
	Totals	6	6	7	21
Blue	2 inches	2	0	1	7
		1	1	2	6
		2	1	2	5
		2	1	3	4
	Totals	7	3	8	22
Totals		36	27	39	97

Case 5—One observation on the behavior of the early fourth-stage lobsters is difficult to harmonize with the reactions mentioned in the previous cases. When at night the rays from an acetylene light were brought to bear upon very early fourth-stage lobsters, swimming in the confinement bags, they would sometimes swim directly toward the light. This reaction was often so strongly manifested that the natural rheotactic response to the influence of the water current circulating in the bags was quite obscured in the areas of greatest illumination, because the young lobsters followed—so to speak—the course of the rays from the acetylene lantern. If this reaction represents a true phototactic response, then it must be said that very early fourth-stage lobsters may, under appropriate conditions of stimulation, respond positively to the directive influence of light, not, as do the earlier stages or the late fourth-stage by turning from the light, but by "heading"

into it. In an earlier paper (HADLEY 1906b), the writer has assumed this to be a true phototactic response. One other instance which appears to support this view may be recorded as follows.

Case 6—Ten sixteenth-day, fourth-stage lobsters were placed in a large slender dish, which was set in the dark box. The larvæ manifested no tendency to undergo either body-orientation or progressive orientation. Next, the same lobsters were placed in the glass-bottomed box, now lined with white paper, which greatly intensified the light within. This box was put with the end window toward the bright sunlight, and the records of five trials (ten larvæ in each) indicated that, when the light was sufficiently intense, the early fourth-stage lobsters might give a positive phototactic reaction. In this instance twenty-six larvæ were positive, twelve negative, and twelve neutral.

When the white paper was removed, and four more tests were made, the results showed that twenty-five larvæ were negative, six positive, and nine neutral.

Experiment 25. Reaction of mid-fourth-stage lobsters. Case 1. Phototactic reaction—August 10, 3:30 p.m. Ten mid-fourth-stage lobsters were transferred from the hatching bags to box *B*, and the experiment was continued in daylight as in Experiment 24, Case 2. The results show a definite negative phototactic reaction, and may be tabulated as follows (similar results were obtained when a white lining in the box was used, though in this case, they showed a less definitely negative reaction):

COLOR.	*1.*	*2.*	*3.*	*4.*
Orange	1	1	1	7
	0	1	2	7
	0	0	1	9
	1	1	2	6
Totals	2	3	6	29
Blue	0	1	2	7
	1	0	1	8
	1	1	2	6
	1	1	1	7
Totals	3	3	6	28
Ruby	0	0	1	9
	0	2	1	7
	1	1	4	4
	1	0	3	5
Totals	2	3	9	25
Grand Totals	7	9	21	82

Case 2. Photopathic reaction—August 9, 3:30 p.m. Ten fourth-stage lobsters were removed from one of the confinement bags and placed in 16 mm. of water in the glass-bottomed box. The glass plates were arranged in the order given below, and tests were made at five-minute intervals. The results, which showed a diminished tendency to remain in the areas of greatest illumination, are represented in the following table:

Red.	Orange.	Green.	Blue.
3	2	1	4
4	0	3	3
1	2	1	6
2	2	4	2
2	4	2	2
12	10	11	17

When, some hours later, the same lobsters were tested again the results of five trials were as follows: Blue, 13; green, 9; orange, 7; red, 21; apparently in this instance it can not be said that the mid-fourth-stage lobsters were either positively or negatively photopathic. Yet the last instance shows a tendency toward a negative reaction.

Experiment 26. Reaction of late fourth-stage lobsters. Case 1. Photopathic reaction—August 12, 2 p.m. Ten late fourth-stage lobsters were transferred from one of the confinement bags (where the majority had already entered the fifth stage) to the glass-bottomed box which was placed over the light-shaft in order to test the photopathic reaction. In this case nine consecutive tests were made, three minutes being allowed for each orientation. The results, which are characteristic of all other tests, and which show a tendency on the part of the lobsters to avoid the light, may be recorded as follows:

No.	Blue.	Green.	Orange.	Red.
1	1	2	1	6
2	1	0	3	6
3	3	0	2	5
4	3	4	1	2
5	1	2	1	6
6	3	1	0	6
7	5	3	0	2
8	1	1	1	7
9	4	2	2	2
Totals	22	15	11	42

Case 2. Phototactic reaction—August 10, 3:30 p.m. Ten late fourth-stage lobsters were taken from one of the hatching bags and put in box *B*, which was placed in the dark box so that the end window faced the light, the intensity of light being modified in each case by interposing colored glass plates between the end window and the light. The tests, which were made at three-minute intervals, and which showed a very definite negative reaction, were as follows (in the fourth tests of the first and last sets respectively, one lobster was accidently killed, thus making the totals incomplete):

COLOR.	*1.*	*2.*	*3.*	*4.*
	1	1	1	7
	0	1	2	7
	0	0	1	9
	1	0	2	6
Orange........................	2	2	6	29
	0	1	2	7
	1	0	1	8
	1	1	2	6
	1	1	1	7
Blue..........................	3	3	6	28
	0	0	1	9
	0	2	1	7
	1	1	4	4
	1	0	3	5
Red...........................	2	3	9	25
Totals........................	2	8	21	82

Conclusions on the reaction of fourth-stage lobsters—The observations thus far made upon the behavior of fourth-stage lobsters appear to demonstrate the following points: (1) Throughout the entire fourth stage-period (with the exceptions noted under Experiment 24, Cases 5 and 6), the lobsters manifest a negative phototactic reaction, which is accentuated in the latter part of this stage. This behavior is quite different from the positive reaction which supersedes the negative in the case of second and third-stage larvæ just previous to their moult into the third and fourth stages respectively; (2) This type of reaction after the first part of the fourth stage-period, cannot be reversed or modified, as was the case in earlier stages, by using different intensities of light (3) The photopathic reaction, which in the early fourth-stage lobsters is definitely positive, changes by the latter part of the stage to negative in the majority of individuals. Thus it can be observed that, just as the third-stage larvæ might at the same time (or successively) manifest both a negative phototactic and a positive photopathic reaction, so may the lobsters of the fourth stage. Other points regarding the behavior of fourth-stage lobsters will receive consideration in connection with the subject of contact-irritability.

5. Fifth Stage.

The body-form of the fifth-stage lobster is similar to that in the fourth-stage, and we might therefore expect to find similar types of reaction. It will be seen, however, that there are many points of difference in behavior which are of such a nature that they can not be attributed, either wholly or in part, to changes in body-form or in the swimming appendages. The changes are doubtless the consequence of modifications which have taken place in the body-processes or in the physiological states of the lobsters themselves, and which have resulted from the cumulative stimulation during the earlier life of the lobsters. Generally speaking, it may be said that the reactions of the fifth-stage lobsters are fairly typical for the adult form, and are especially characterized by the light-shunning tendency. This form of behavior could be observed readily by watching the lobsters in their confinement cars; but, for the sake of certainty, the same experiments, to which the larvæ of earlier stages had been subjected, were repeated with the fifth-stage lobsters. Since the reactions did not appear to undergo any noticeable modification as the lobsters passed through the fifth stage, there is no need for considering the early, mid and late fifth stage-periods separately, as was done for fourth-stage lobsters. The type of reaction presented in the early fifth stage-period differs in no way from the behavior of lobsters in the late fifth stage-period; and both are characteristic of the behavior in all later stages.

Experiment 27. Case 1. Photopathic reaction—In the first instance, ten fifth-stage lobsters were transferred from one of the confinement bags to the glass-bottomed box and this was placed over the light-shaft. The method used was the same as in previous experiments. In the second instance the blue glass was removed, and the space where it had lain was left clear, thus permitting the reflected daylight to enter this area of the bottom of the box. The results of both tests show a negative reaction which was more definite in the second instance.

BLUE.	GREEN.	ORANGE.	RED.
2	1	2	6
2	1	2	5
3	1	1	5
2	3	2	3
8	6	7	19

DAYLIGHT.	GREEN.	ORANGE.	RED.
0	2	2	6
0	3	2	5
1	2	2	5
0	2	2	6
1	1	3	5
0	2	4	4
2	12	15	30

Case 2. Phototactic reaction—Further demonstration of the definitely negative phototactic response of fifth-stage lobsters was given by the experiments on contact-irritability (Exp. 29, p. 256). Here is clearly shown the extreme manifestation of this negative phototactic response, which frequently would have culminated in fatal results by driving the lobsters from deep to shallow water and leaving them stranded where they would certainly have died had they not been returned to the water at the end of the experiments. Here, as has been found in the case of many animals, the total behavior is completely dominated by the light influence. It may be said further that in the case of the fifth-stage lobsters light of different intensities does not cause a change of reaction from positive to negative, or from negative to positive, as was the case in the earlier stages; nor do we ever find the individuals "heading" into the light, as may be the case in the fourth-stage larvæ. For the fifth-stage lobsters any intensity of light which influences their behavior in any degree, determines, under experimental conditions, both a negative body-orientation and a negative progressive orientation.

In the foregoing pages it has been shown that larvæ which were positively photopathic could be made to pass from regions of greater to regions of lesser light intensity by submitting them to the directive influence of light of sufficient strength. In these cases, it was observed that the photopathic reaction was invariably subservient to the phototactic, although the latter was also very dependent upon a certain optimal intensity for bringing about a positive or negative response. In the following instance we shall observe that, although the directive influence of the light rays is capable of modifying the orientations which relative intensities of light have determined, still the directive influence can not quite obliterate the evidence of a photopathic reaction, as was possible in the younger larvæ. In other words *the tendency of the fifth-stage lobster to "select" the darker regions has become almost as firmly fixed as has the tendency to react negatively to the directive influence of the light rays.* In the first larval stages the photopathic response invariably gives way to the phototactic. In the fifth the two tendencies clash; and the resulting orientation of the lobster is determined, not by one, but by both of these factors.

(*A.*) *Case 3. Photopathy versus phototaxis*—Ten fifth-stage lobsters were put in box *B*. This was mounted upon the colored glass plates over the light-shaft as in previous experiments. The preliminary observation showed that there was a definite tendency for the lobsters to congregate at the red end of the series of glass plates, thus demonstrating a negative photopathic reaction. Now the window at the red end was opened to diffuse light. After a period of ten minutes, observations of the position of the lobsters were begun, and continued at five-minute intervals. The following results show that, although the negative phototactic response is still manifested, it has been greatly modified by the tendency on the part of the lobsters to avoid the brightly illumined area at the end of the box:

Daylight.	Green.	Orange.	Red.
1	4	2	3
1	3	3	3
2	3	3	2
1	3	4	2
1	2	4	3
2	3	3	2
8	18	19	15

In the next case, the end of the glass plate series, which in the previous instance admitted reflected daylight, was covered with a blue glass and the illumination of this area thus rendered less intense, while the end window of the box (at the red end) remained open, as in the last experiment. The results, which demonstrate that the phototactic reaction had still further overcome the photopathic, were as follows:

BLUE.	GREEN.	ORANGE.	RED.
2	2	4	2
1	3	2	4
3	2	3	2
3	2	2	3
4	3	2	1
2	3	2	3
15	15	15	15

In the last two instances it becomes apparent that the fifth-stage lobsters, unlike the early-stage larvæ, could not be forced, by the directive influence of the light rays, into an area of greater light-intensity. In other words, the tendency to manifest a negative phototactic reaction was not sufficiently strong to overcome the tendency to give a negative photopathic response.

(*B.*) *Experiment 28. Phototaxis leading to fatal results*—Before bringing to a close this consideration of the reactions to light in lobsters of the fourth and fifth stages, it may be appropriate to introduce the results of some experiments whose aim was to show the extreme nature of some phototactic reactions. In other words, attempt was made to determine whether or not the strong directive influence of the light rays could compel the larvæ so to act that they would do injury to themselves as in the familiar case of the moth that flies into the flame, or of Ranatra, mentioned by HOLMES (1906). The reactions of the fourth-stage and fifth-stage lobsters will be considered together.

Case 1. Fourth-stage lobsters—For this series of experiments box *B* was set up as represented in Fig. 7, being supported at one end so that the bottom of the box made an angle of about fifteen degrees with the table. The box was filled with water so that when it was slanted, the water-line did not quite reach the angle made by the bottom and upper end, *B*. In this way there was created an inclined plane, slanting from the window end, *A*, of the box to the higher end, *B*. The water consequently diminished in depth as the end, *B*, was approached. At this end there was an inch or more of the bottom of the box not covered by water. The light from the window, *L*, was reflected into the box by the mirror, *M*, for the purpose of discovering whether the larvæ in presenting their negative phototactic reaction, would allow themselves to be driven into the shallow water. By means of a hole in the bottom of the box, the water could be withdrawn very gradually (a few drops a minute), so that if the larvæ persisted in remaining in the

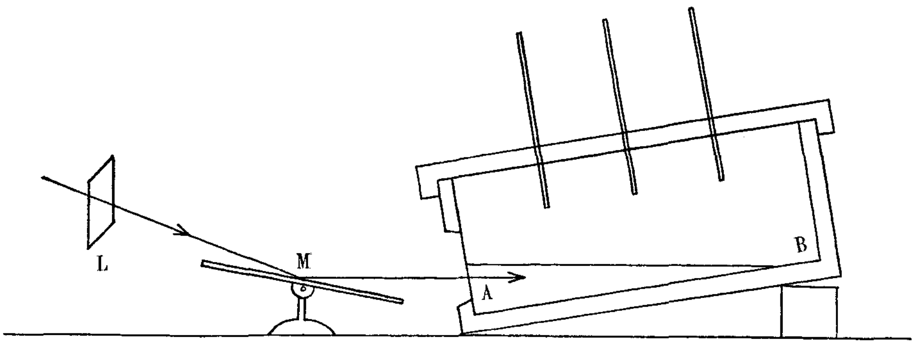

FIG. 7. Diagram of apparatus as set up to test the extreme phototactic reactions, leading, in the case of fourth and fifth-stage lobsters, to fatal results. *L*, source of light; *M*, reflecting mirror; *A*, end of box adjacent to "window;" *B*, end of box not covered with water, where the lobsters were stranded. In the cover of the box are shown the sliding partitions.

shallow area, they would, in the course of a few minutes, be stranded on the dry bottom. Ten fourth-stage lobsters were first used for experiment and the results, ascertained by counts made as in all other cases, were as follows: (The arrow shows the direction of the light coming through the end window of the box, while the numbers at the top of the columns represent the division areas of the box):

TEST.	→ *1.*	*2.*	*3.*	*4.*	NUMBER STRANDED.	TIME (after).
1	1	1	3	5	4	5 minutes
2	1	2	1	6	3	10 minutes
3	0	1	1	8	6	20 minutes
4	1	1	3	5	5	50 minutes
Totals.....	3	5	8	24	18	

The results of this experiment and of several others similar to it, show, that out of a total of twenty-four larvæ which gathered in the area farthest from the light, eighteen allowed themselves to be stranded rather than to retrace their course into deeper water, and in so doing to approach the light.[4]

Case 2. Fifth-stage lobsters—When the same experiment involved the fifth-stage lobsters, the results were similar. The only difference that could be observed was that the intensity of the reaction was greater for the fifth-stage than for the fourth. The result of twelve tests, each with ten lobsters showed the distribution to be as follows: Area 1, nine; area 2, ten; area 3, twenty-one; area 4, eighty, of which seventy were "stranded." These last would have perished, had they not been returned to the water at the end of each successive test.

(*C.*) *Conclusions concerning the reactions to light of fifth-stage lobsters*—The results of the foregoing experiments on the reactions of fifth-stage lobsters, demonstrate the following points: (1) Like the fourth-stage lobsters, the fifth-stage lobsters are negatively phototactic from the beginning of the stage to the end of it, and this holds good for all intensities of light which cause any reaction whatever. (2) Unlike the early fourth-stage but much like the late fourth-stage lobsters, the fifth-stage lobsters are negatively photopathic from the beginning of the stage to the end. (3) This negative photopathic reaction, unlike the photopathic reactions of the earlier stages (in which case the photopathic reaction was entirely subservient to the phototactic), has itself become a well grounded tendency, and, although it can be modified, it can not be entirely obliterated (so far as its value in causing a certain orientation is concerned) by the tendency to react to the directive influence of the light rays. (4) The intensity and energy with which the late fourth-stage, but especially the fifth-stage, lobsters manifest a negative phototactic reaction may lead to results fatal to the lobsters themselves.

(*D.*) *Contact-irritability versus reaction to light*—In the preceding section the phototactic and the photopathic reactions, together with some points of their inter-relation, have been considered. We shall now examine that response of lobsters to solid portions of their immediate physical environment which may be ascribed to contact-irritability or thigmotaxis.

It frequently happens that single types of reaction (phototaxis, chemotaxis, geotaxis, and the like) may be studied to best advan-

[4] It should be noted, however, that the water in no case receded more than 5 to 10 mm. as measured horizontally on the bottom of the box.

tage only when another stimulus of known effect is present and operative. For instance, if the two conditions of stimulation which respectively bring about a photopathic and a phototactic reaction are so arranged as to oppose one another (i. e., by determining opposite reactions in the larvæ), and if the constant effect of one set of conditions is known, then it is possible to form an estimate of the persistency of the reaction determined by the opposed set of conditions. For example, if light rays of low intensity coming through the end of box *B*, resulted in driving the enclosed larvæ, which had just previously given a negative photopathic reaction, to the opposite end of the box, and at the same time forced them from a region of low into a region of high intensity, we should say that the negative photopathic reaction of these larvæ was of slight importance as compared with the phototatic. If, on the other hand, it was learned by experiment that the rays entering the end window of box *B* would not force the negatively photopathic larvæ from the dark into the brightly illuminated end of the box, but resulted in their gathering in the middle of the box (for instance, in the green or orange area) then it might be inferred that the negative photopathic reaction had a greater influence in determining the final reaction of the larvæ, although it was in this case directly and strongly opposed by the tendency to manifest a phototactic reaction. In the following experiments, made to discover the value of contact-irritability in determining the reaction of the larvæ, the principle mentioned above was made use of, and in this instance a combination was made between experimental conditions which would allow the demonstration of contact-irritability, and those which would insure the manifestation of negative phototaxis if no other modifying conditions (such as contact-irritability) were present. But before going farther with the description of the technique of the experiments, a few observations on the behavior of the lobster larvæ under natural circumstances may be considered. This may form a better basis for the consideration of experiments dealing with contact-irritability versus reaction to light under the especially devised conditions to be described.

It might reasonably be imagined that the loss of the swimming branches (exopodites) of the thoracic appendages, which takes place with the entrance to the fourth stage, would at once determine a very radical change in the habits of lobster larvæ. We should surmise that the larvæ would immediately abandon their pelagic manner of existence and enter upon a more sedentary life among the rocks and weeds of the sea bottom. But this is by no means the case, for never in the life history of the lobster do we find surface swimming more strongly manifested than in the fourth stage, and just after the loss of those accessories without which swimming would have been impossible in any of the earlier stages. The energetic surface-swimming of the fourth-stage lobsters was evident from many observations, made under both natural and experimental conditions. It was observable not only in the large hatching bags but also in the quiet water surrounding the bags and hatching apparatus. One case is especially noteworthy. In July a steam launch, of which the captain lost control, rammed one of the floats which suspended six large hatching bags containing lobsters in various stages. As a result many fourth-stage lobsters were suddenly liberated in the water about the hatchery. When order had been restored, an attempt was made to recover the lost lobsters, and over five hundred of the fourth-stage which were swimming actively at the surface of the water were picked up with scrim nets. A far different phenomenon obtains in the behavior of fifth-stage lobsters under natural conditions. This is illustrated by an interesting sequence of changes in the swimming habits. When the majority of the lobsters in the bags were in the fourth-stage, they usually swam near the surface. As the larvæ moulted into the fifth stage, fewer lobsters were to be seen. The reason for this was ascertainable if one poked with a stick about the mass of weeds and algæ adhering to the sides and bottom of the bag. Here could be found, carefully hidden, a large number of fifth-stage lobsters. By the time all the individuals in the bag had passed to the fifth-stage, scarcely one could be discovered swimming freely. Whenever a number of fifth-stage larvæ were liberated in the open water, it was an interesting sight to observe them swim for a moment, then turning head down, disappear for good in the deeper water—a great contrast to the behavior of the fourth-stage lobsters under similar conditions.

Another set of observations refers to the burrowing instinct of the young animals. When early fourth-stage lobsters were transferred to glass dishes, on the bottom of which was a layer of sand, gravel and a few broken shells, they at first paid no heed to these conditions, but for several days continued to swim as persistently as ever. Finally, however (usually within two or three days after having been placed in the dish), the lobsters began to plough through the sand of the bottom, especially near the rim of the container, and to construct burrows beneath shells, stones or other objects in the sand. Yet, even after these burrows were completed, the fourth-stage lobsters seldom remained in them, but came out and crawled rapidly over the bottom or swam more or less actively near the surface of the water. When, on the other hand, fifth-stage lobsters were introduced into the dishes containing sand, gravel, and shells they commenced burrowing at once and when the burrows were completed they showed a much greater tendency to remain therein than did the late fourth-stage larvæ. Although the fifth-stage lobsters came out for food, free swimming was seldom indulged in during such sorties. The question now arises as to what conditions or factors cause the energetic surface-swimming of the early fourth-stage lobsters and the bottom-seeking and burrowing habit of the late fourth and the fifth stage. Are these reactions to be explained as phototropic, geotropic, or thigmotropic reactions? Or do all three of these, and perhaps still other factors, unite in determining the final result? While we are not yet prepared to venture an answer to these queries, the records of a few simple experiments which were undertaken to ascertain the value of the part played by contact-irritability in determining the orientation of the fourth and fifth stage lobsters, under certain known conditions, will be presented.

Experiment 29. Fourth-stage lobsters—The technique employed in the present experiment was as follows: One-half of the bottom of box *B*, was sprinkled with sand to the depth of five mm., the box was filled with salt water to a depth of 3 cm., ten early fourth-stage lobsters were introduced, and the box covered. The aim was to learn whether, in the total absence of light, the larvæ would "choose" either the sanded or the clear area. The result of a typical test is presented below. The readings were taken every five minutes, and after each reading the lobsters were caused to distribute themselves about the box:

Sanded area.		Clear area.	
1.	*2.*	*3.*	*4.*
4	3	2	1
2	2	3	3
3	2	2	3
1	1	4	4
10	8	11	11
18		22	

These and other tests were made, but in no case was it apparent that the early fourth-stage lobsters showed any preference for the sanded area. When, in another series of four trials involving ten lobsters each, the window at the sanded end of the box, was opened so as to allow the rays to stream through, every lobster but one was driven to the compartment farthest from the light. When this experiment was tried with late fourth-stage lobsters, it appeared that a greater number remained on the sanded area, even in the presence of the light conditions mentioned above. The results of a typical experiment of this sort involving five trials of ten lobsters showed that, while thirty were driven to the clear space, ten remained on the sanded area.

Experiment 30. Case 1. Fifth-stage lobsters—In this instance ten fifth-stage lobsters were placed in box *B* as arranged for the previous experiment, no light being admitted at the end of the box. The record of seven trials separated by a period of from five to ten minutes, showed a decided preference for the sanded areas; while forty remained on the sanded region, only twenty gathered on the clear area.

Case 2—In the next instance the end window at the sanded end of the box was opened to the light, but with a red glass so interposed that the intensity of light in this region was not great. A period of from ten to forty-five minutes was allowed for each orientation. Although the influence of the light tended to drive the lobsters off the sanded area the results of six trials (ten lobsters each) showed that thirty-seven fifth-stage lobsters remained in contact with the sand, while twenty-three moved to the clear area.

Case 3—In the next series of six trials (ten lobsters each) the intensity of light was modified by substituting an orange glass before the end window. The results showed twenty-five on the sanded area, thirty-five on the clear.

Case 4—In the last series of six trials (ten lobsters in each) the conditions were still further modified by removing the orange glass and thereby greatly increasing the intensity of the light which entered the end window of the box. This demonstrated that a light of great intensity would drive the fifth-stage lobsters off the sanded area. At the end of the experiment only thirteen lobsters remained on the sanded area, while forty-seven remained in the clear region. Finally, the sand was removed from the box, and the reaction of these lobsters was tested with unobstructed light entering the end window. The resulting reaction was invariably and definitely negative; and this with light of all the intensities used in the previous cases.

Conclusions from experiments on contact-irritability versus reaction to light—Although these experiments can hardly be called critical, they demonstrate that the presence of the sanded area in the box did modify the reactions of the fifth-stage lobster. That there was manifested a tendency to remain in contact with the sand, to burrow in it, and not to be dislodged by such intensities of light as would normally rout the entire group of lobsters and send them to the end of the box farthest from the light. These facts, moreover, cannot be said to hold true for the fourth-stage lobsters that were used in the foregoing experiments, and which showed no well defined preference for the sanded area, at least in the early part of the stage-period.

VI. MECHANICS OF ORIENTATION.

The aim of the present section is to report the results of a series of observations which were made in order to answer the following question: By what movements of the lobster larvæ are the reactions to light accomplished? In our effort to answer this question we shall, for the present, attempt to avoid so far as possible considerations which deal directly with the ultimate causes of orientatation; in other words, we shall limit ourselves to the observation of the actual movement of the body, or of certain parts of the body, of individual larvæ; and attempt to show what relation exists between these movements and the external factors which appear to determine them. First, however, it is necessary to establish some points regarding the natural behavior of the larvæ when the influence of external stimuli is at the minimum.

1. The normal behavior of the larvæ—In view of the fact that swimming constitutes the chief activity of the larval lobsters, our question resolves itself into the following: What is the nature of the normal swimming? When one first observes the behavior of individual larvæ amidst the thousands contained in the large hatching bags no difference is evident in the swimming of the first three stages. In all instances the back of the larva is, for the most part, uppermost, the abdomen bent under and downward at an angle of about 60° from the longitudinal axis of the cephalo-thorax, which in turn is inclined about 30° from the horizontal plane. In daylight this position may be maintained without modification for several minutes, but the equilibrium is often interrupted by other body-movements which, upon superficial examination, appear to be of a most diverse and ill-ordered nature. There are leanings, turnings, fallings, somersaults, revolutions and rotations which follow each other in no apparently definite sequence, and which disturb the general equilibrium greatly or slightly as the case may be.

Whether the balanced equilibrium, the devious rotations or other activities are present, the exopodites or swimming attachments of the thoracic appendages beat the water more or less constantly with short vibratory strokes, sometimes lifting the larvæ high toward the surface, and again allowing them to sink to the bottom, where they frequently lie for some moments almost motionless, only again to resume their varied activity. Now they swim forward, now backward, now lurch to the side, now to the rear, always maintaining more or less energetically these apparently aimless movements. Such is the nature of the swimming in daylight or other brilliant illumination; but for our purpose it cannot be called the normal swimming of the lobster larvæ. It is only under special conditions that the latter may be observed; and, in view of the fact that it is the conditions of light which influence more strongly than any other factors the behavior of the larvæ, it is only when they are under certain light-conditions that we may expect to find manifested what we may call the characteristic or normal swimming.

The twilight or nocturnal swimming of the larval lobsters invariably gives us the fairest example of natural behavior. At such times alone (or when the larvæ are submitted to artificially produced twilight) variations in temperature and the multiplicity of conflicting cross-light influences are eliminated. Frequently when the twilight was so dim that observation was rendered difficult, the swimming was delicate and regular, and the young larvæ would mount up, bird-like, to the surface of the water, hover many seconds in a single position, or swim backward or forward with equal ease. In such a case, when a lighted match was brought near the side of the jar in which the larvæ were confined, the same restless and uncertain swimming, characteristic of the diurnal activities, was again manifested, together with the accompanying leanings and rotations. From these facts it may be assumed that the twilight swimming of the larvæ probably represents the natural behavior or at least the behavior that arises purely from the internal states themselves; and that the peculiar antics characteristic of the daylight swimming represent a type of behavior chiefly due to the action of external stimuli.

The question now naturally arises—Do the various turnings, rotations, leanings, and fallings which constitute the apparently haphazard behavior of the larval lobsters when swimming in daylight or other brilliant illumination, give any indication of method ? Observations have given a suggestion as to the means whereby we may attempt to ascertain the value of certain light-conditions in determining these peculiar forms of behavior.[5]

If larval lobsters of any of the first three stages are subjected to the influence of light which comes from one direction only, as from the side, the first fact observable is that the larvæ undergo a certain body-orientation; they turn away from the light and place the long axis of the body parallel to the direction of the rays. The second fact which may be noticed is that the larvæ move in the direction of the light rays either toward or from the source of illumination. A third fact, which is of prime importance and which involves those stated above, is that no matter whether the progressive movement of the larvæ be toward or away from the source of light, the orientation of the body (head away from the source of light) remains unchanged. To state the matter briefly we may say that, whatever the nature of the progressive orientation of the larvæ, *the body-orientation is at all times, and under all conditions, negative.* BOHN (1905, p. 8) has clearly pointed out this fact for the larvæ of the European lobster. In this regard he says: "En général, les larves de homard se placent dans le sens négatif; même, dans les premières heures après l'éclosion, alors qu'elles se groupent vis-à-vis des lamps, leur tête se tourne du côté opposé, et les larves s'approchent de la lumière en regardant l'obscurité, c'est-à-dire en reculant. Ainsi, après l'éclosion, l'orientation a lieu dans le sens nègatif, mais le déplacement se fait dans le sens positif. Dans le suite, si le sens de l'orientation

[5] Many of the observations which follow were made previous to the writer's knowledge of the excellent work of GEORGES BOHN (1905) along similar lines, upon the larvæ of the European lobster, Homarus vulgaris. The writer would acknowledge, however, his great indebtedness to this investigator, whose work has proved suggestive in the highest degree, and whose observations on the mechanics of behavior the writer has been able, in the majority of instances, to verify as well as supplement.

reste le même, le sens du déplacement peut changer." LYON (1906) has recorded a similar observation for several larval stages of Palemon. This condition of affairs is rather at variance with the majority of observations on the phototactic reactions of animals and it is contrary to the condition of body-orientation which we find in the fourth stage of the lobster itself, for in this stage (at least in some of the assumed phototactic reactions) the body-orientation brings the head toward the source of illumination instead of away from it as is invariably the case in the first three stages.

The question has already arisen as to what we may mean by a positive phototactic reaction, for in this case it is clear that we may very frequently have a negative body-orientation coupled with a positive progressive orientation. Until we know more regarding the differences between body-orientation and progressive orientation, it may be considered safe to say that the *direction of the progressive movement*, with respect to the source of illumination, may be held as the surest criterion of the sign of the phototactic response of animals. On the other hand the point has been made clear by some writers, that in the body-orientation of organisms the definite relation of the body-axis to the lines of active force is the primary consideration for all problems of progressive orientation. However this may be, we have before us at least one instance wherein, although the relation of the body-axis to the lines of force is an important consideration, the body-orientation *per se* has little or nothing to do with the question of the positive or negative progressive orientation of the organism; for as we have already observed, conditions which invariably determine a negative body-orientation may determine either a positive or a negative progressive orientation, as other circumstances demand. We may, therefore, first concern ourselves with the *mechanics of progressive orientation* and then turn with better understanding to the *mechanics of body-orientation*, for these two reactions apparently depend upon quite different circumstances.

2. *The mechanics of progressive orientation*—The only means of locomotion possessed by the larvæ of the first three stages are the exopodites of the thoracic appendages and the strong, flexible abdomen with its broad terminal fan (Fig. 1). It is but seldom, however, that the latter is used, and never when it is a question of progressive orientation to light. We are then confronted with the problem: How, by the motion of the thoracic exopodites

alone, is the larval lobster able to execute those movements which determine his progress either toward the source of illumination or away from it?

If the larval lobsters in any of the first three stages be put in a glass jar which is surrounded by black paper and placed in subdued daylight, the short vibratory strokes of the exopodites can be readily observed. At one time, certain individuals may be seen to swim rapidly backward, and again forward, with no apparent change in the position of the body or in the direction of the stroke of the exopodites. If, however, the thoracic appendages themselves be carefully watched, one can observe that, from time to time, these limbs undergo either a forward shifting (extension) as shown in Fig. 8, or a backward shifting (contraction) as shown in Fig. 9. This change from the "anterior" position to the "pos-

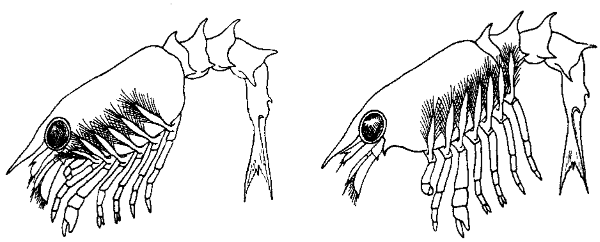

FIG. 8. FIG. 9.

FIG. 8 shows a larval lobster with the thoracic appendages in the extended or 'anterior" position; the resulting movement is forward and upward.

FIG. 9 represents the appendages in the contracted or "posterior" position; the resulting movement is backward and upward.

terior" position may occur at short intervals, each position may persist for some seconds, or there may be a successive alteration with periods of longer duration in either one position or the other. It may be observed further, that when the thoracic appendages take the "anterior" position, the direction of the strokes of the exopodites becomes somewhat forward as well as downward, and the *resulting motion of the larvæ becomes backward and upward.* When, on the other hand, the thoracic appendages assume the "posterior" position, the stroke of the exopodites becomes backward and downward; and *the resulting motion of the larvæ becomes forward and upward.* During a great part of the time, the upward movement of the larvæ, as a result of the outward and downward stroke of the exopodites, does little more than compensate for the natural tendency to sink toward the bottom. For this reason the progress of the larvæ may often be directly forward or directly backward with but slight deviation from the horizontal plane; while at other times, when the stroke of the exopodites is directly outward and downward (exclusive of either the "forward" or "backward" factor), the larvæ may mount to the surface in nearly vertical lines.

It thus becomes evident that the progression of the larvæ, backward or forward, upward or downward, is largely determined by the position (state of extension or contraction) of the thoracic appendages. In other words, if for the greater part of the time these appendages are in the "anterior" position the phototactic reaction of the larva is positive; but on the contrary, if the thoracic appendages are more frequently in the "posterior" position, then the consequent reaction of the larvæ is negative. Naturally the next important question which arises is: What conditions determine the "anterior" or the "posterior" position of the thoracic appendages? It cannot be questioned that these changes are directly due to certain variations in the intensity of the illumination and are modified by the "physiological state" of the larvæ themselves; and that, furthermore, the state of extension or contraction of the thoracic appendages, and the stroke of the exopodites, are regulated to a great degree through the mediation of the eyes and the nervous system of the larvæ. But further consideration of this subject must be postponed until later. In the meantime we may turn our attention to the mechanics of body-orientation.

3. The mechanics of body-orientation—Under the present heading we shall consider the nature of those peculiar movements which the lobster larvæ undergo when they are under diverse and changing conditions of stimulation, in order to explain the cause of these actions and to show their relation to certain definite laws which may be said to regulate to a great degree the body-orientation of the larvæ. As we have observed, it is the influence of light which is most active in determining the behavior of the larvæ; furthermore, it is in the absence of such influences as diverse and changing conditions of illumination afford that the most realistic picture of the normal behavior of the larvæ is obtained. It will then prove the most practical method of approaching this problem, first, to obtain conditions of light which allow natural behavior (normal swimming); and then, by gradually modifying these conditions, to observe the effects upon the behavior of the larvæ.

A. The Effects of Direct Lighting and Shading. *Technique and Methods of Observation*—This section deals more especially with the directive influence of light rays so introduced as to strike the larvæ from different directions; from before, from behind, from the side, from above, from below, or obliquely to the body-axis. These conditions were obtained, for the most part, in two ways. The larvæ were placed either in a cylindrical glass jar, or in an especially constructed rectangular glass box (similar, perhaps, to the révélateur used by Bohn), three inches wide, six inches long, and two and a half inches deep, all sides and the bottom being of glass. Either of these receptacles might be placed in the dark box already described. To regulate the intensity, slides of colored glass were used as in the earlier experiments,

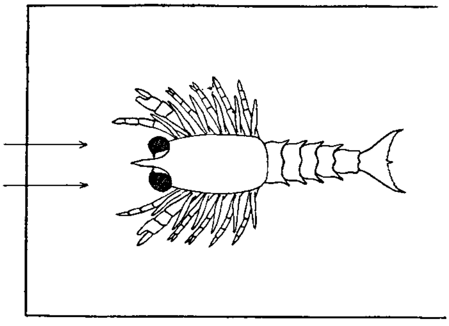

Fig. 10.

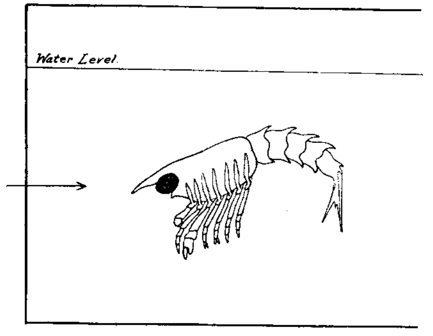

Fig. 11.

Fig. 10 represents a dorsal view, Fig. 11 a lateral view, of a larval lobster in the glass container. For description, see Case 1, p. 265.

while to change the direction of the rays a series of mirrors was employed. In certain instances, when light from the bottom was required, the receptacle containing the larvæ was placed upon a glass plate raised a certain distance above the bottom of the box, and the mirror was placed below. In still other instances the direction or the intensity of the light was modified by the use of light-absorbing (black) or light-scattering (white) backgrounds. These were used more frequently when the observations were made in diffuse daylight, and the subdued light came to the glass containers from several different directions. From the experiments it appears very probable that in determining the orientation of the organisms, the backgrounds were instrumental only in regulating the amount and the general direction of the light which they reflected or absorbed. First, however, we shall consider the effects of suddenly throwing the light from a certain direction upon larvæ oriented in various positions.

Case 1. Illumination from before—In the first instance the behavior of a single larva was studied (the stage does not matter). It was oriented in the rectangular container, in the dark box with its head toward the three by one inch window, which was closed (Fig. 10), but in such relation to the glass box that its longitudinal axis was parallel to the direction of the rays of light coming from this window when it was opened. While the larva was so oriented, the screen was drawn aside and light from the small window was allowed to strike the larva "head-on." Under these conditions, one of two reactions resulted. The larva underwent either a forward or a backward somersault, or rotation, which brought the back below with the head directed away from the source of illumination. Whether the rotation was backward or forward made no difference in the resulting orientation and which one occurred depended upon the direction of the rays of light which struck the eyes of the larva. In normal swimming the body of the larva in any of the first three stages is bent about 30° from the horizontal. Now if the rays of light had the direction of *A* or *B* (Fig. 12) the rotation was usually forward, while if the light came from below, direction *C*, the rotation often was backward. After this first orientation the larva (position *B′*) frequently performed a rotation on its long axis, either to the left or right, which brought the back again uppermost, and it then progressed in the direction of the rays, either toward or away from the source of illumination.

Corollary 1—If the rays striking the eyes of the larva had the slightly oblique direction shown in Fig. 13, *a* or *c*, but were in direction or plane *B* (Fig. 12), then the larva pivoted at the middle of its own longitudinal axis and swung to one side or the other, always keeping the back uppermost.

If the rays of light took the direction designated $a^1 — a^4$ or $c^1 — c^4$, the result was the same; the larva swung until the longitudinal body-axis was parallel with the incident rays, and the head was directed away from the source of illumination.

Corollary 2—If the rays striking the eyes of the larva had the oblique direction, $a^1 — a^4$ or $c^1 — c^4$ (Fig. 13) in plane *A* of Fig. 12, then the resulting movement was a combination of the forward rotation and the side swing (Cor. 1). In other words, the larva performed a side-somersault, and ended with the back directed below and to the side. Whether it turned to the left or to the right depended upon the direction of the rays in either the *a* or the *c* series. At the end of this reaction the larva usually became righted again with the back above and the head away from the light, and continued its progressive orientation in one direction or the other according as the reaction was positive or negative.

Corollary 3—If the rays striking the eyes of the larva had the oblique direction $a^1 — a^4$ or $c^1 — c^4$, and were in plane *C* of Fig. 12, the resulting reaction was a combination of the backward rota-

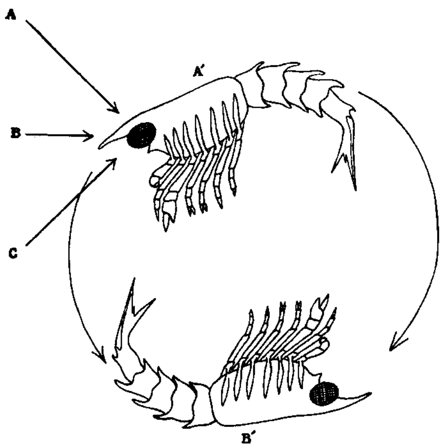

FIG. 12. For description, see Case 1, Cor. 1.

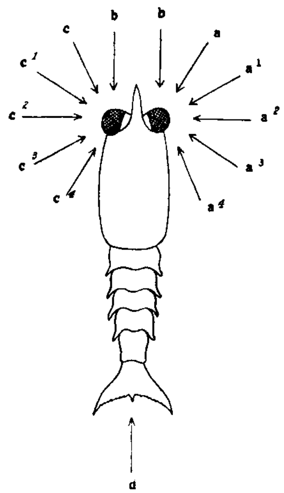

FIG. 13. For description see Case 1, Cor. 2.

tion and the side swing (Cor. 1). That is to say, the larva performed a backward side-somersault, became oriented as in Corollary 1 and 2, again turned the back uppermost, with the eyes directed away from the source of light, and continued its progressive orientation, in one sense or the other.

Case 2. Larva lying with back downward; head toward light—In these instances, the larva was oriented head toward the (closed) window, and back downward. The rays were introduced from before, as in Case 1. It may be said that this orientation was difficult to obtain. Often it was necessary to wait fifteen minutes or more before it occurred, then at the proper moment the light was admitted and the consequent reaction observed. On the other hand, it was common to find the larvæ on their backs and oriented obliquely to the rays of light. When the larva was oriented in this manner and the light was admitted, there usually occurred either a forward or a backward rotation (Fig. 14), but the forward rotation was most common. Whichever one occurred, however, the final orientation was the same: the back of the larva was again brought uppermost, and the head was directed away from the source of light.

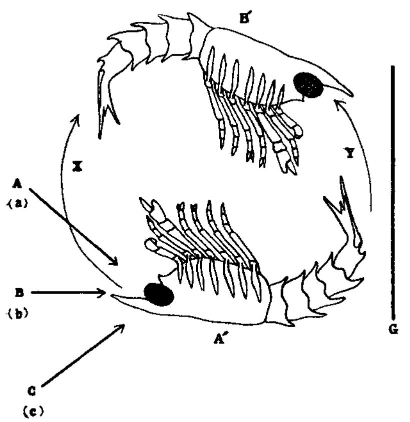

FIG. 14. For description, see Case 2.

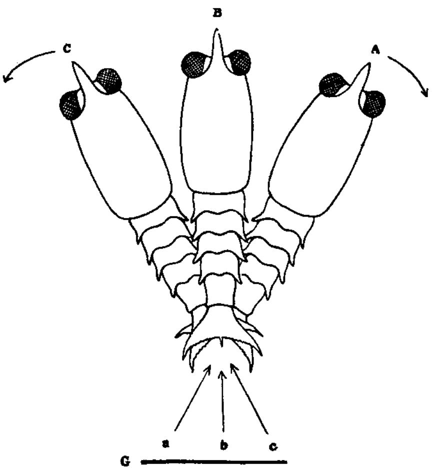

FIG. 15. For description, see Case 4.

Corollary 1—If the larva was oriented with the back below, the head toward the closed window, and the body-axis oblique to the direction of the incident rays, the resulting orientation was a combination of the upward and forward rotation and a swing of the body, pivoted on the middle of its long axis, away from the incident rays (this last reaction was similar to Case 1, Cor. 1, except that in the former instance the larva oriented back below). The final orientation was as in Case 2 (Fig. 14, *B′*). Whether the incident rays were in plane *A*, *B*, or *C* did not appear to make as much difference in the manner of orientation when the lobster was lying back below. It was observed that rays coming from above (plane *A*) more frequently determined the backward rotation; and that rays coming from below (plane *C*)more often determined a forward rotation.

Case 3. Larva lying with the side downward; head toward light—In this case, the larva was oriented with one side uppermost and the head turned toward the source of light. The conditions may be represented by Fig. 14, if it be imagined that for the present case the larvæ are lying in a horizontal plane rather than in the vertical as originally intended in this figure. The arrows *A*, *B* and *C* represent rays in the same vertical plane, while (*a*), (*b*) and (*c*) represent them in a horizontal plane. When the light was admitted to a larva so oriented, the reaction was similar to that described under Case 2. In the present instance, however, when the rays had the direction (*a*), the backward rotation was more likely to occur than when the rays had the direction *A* as in Case 2. Rays in the direction (*b*) or (*c*) almost invariably determined a forward rotation, in which, if the larva was fatigued, it would merely turn through 180° in the same plane, and become oriented, still lying on the side, but with its head away from the source of light. If, however, the larva was fresh and active at the end of the rotation of 180° in the arc of a circle (*A'*), it would rotate through 90° on its longitudinal axis and come into the normal swimming position with the back uppermost and the head directed away from the source of light.

Case 4. Larva oriented with back above; head directed away from the source of light—When the larva was thus oriented and the light was so introduced that the rays streamed in a direction parallel to the longitudinal axis of the larva, no change in the body-orientation took place. The progressive orientation, however, might continue as either positive or negative. In case, however, the light came from the sides *a* or *c* (Fig. 15) the larva reacted by swinging (pivoted on the middle or end of its longitudinal axis) to either one side or the other, and it might then undergo positive or negative progressive orientation. If the direction of the rays changed through the series, *a*, *b*. *c*, the larva could likewise be made to swing as regularly as a pendulum and for long periods of time, according as the light came from one side or the other. Indeed the animal was quite at the mercy of the influence of light.

In case the light came somewhat from above as shown in Fig. 16, *A*, the larva would incline itself farther forward, the number of degrees of rotation depending upon the degree of the angle formed by *A* with the horizontal. When the angle was slight the forward rotation of the larva was but a few degrees, and it continued to swim in this body-position, and might undergo a positive or negative progressive orientation, as ordinarily. When, however, the angle between *A* and the horizontal was greater, the degree of rotation of the larva was proportionately greater, and in certain cases it might undergo a rotation of 180° and fall to the bottom.

When, on the other hand, the incident rays struck the larva in the direction of *C* (Fig. 16), then the larva underwent a backward rotation whose degree was dependent upon the breadth of the

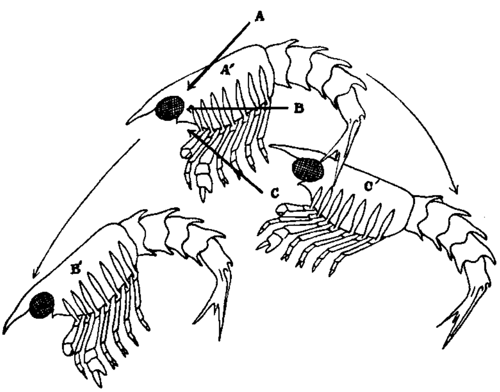

FIG. 16. For description, see Case 4.

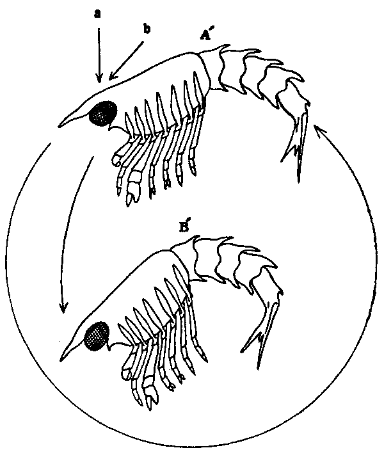

FIG. 17. For description, see Case 6.

angle between *C* and the horizontal. If the angle thus formed was slight, the backward rotation of the larva was correspondingly slight, and it would continue to swim in the position designated *C* (Fig. 16), undergoing positive or negative progressive orientation as other conditions of light might determine. If the angle formed between *C* and the horizontal was great, the degree of backward rotation of the larva was proportionately greater, and a fall to the bottom, tail downward, might result.

Corollary 1—When the direction of the rays was determined by compounding the vertical series of light factors (*A*, *B*, *C*, Fig. 12) with the horizontal series (*a*, *b*, *c*, Fig. 15), the resulting reaction was a combination of the two types of behavior described above.

Case 5. Larva oriented with back above and longitudinal body-axis at right angles to direction of light rays—When the larva was oriented as above and the rays were introduced at right angles to the longitudinal axis (Fig. 13, a^2, c^2) the behavior was similar to some phases of Case 1, Cor. 1. The larva swung directly away from the source of light until its longitudinal axis was parallel to the light rays, with the head directed away from the source of light. Obviously the swing might cover from 1° to 90° and either positive or negative progressive orientation might follow.

If the larva was lying with the back below, but otherwise oriented as in the previous instance to the directive influence of the rays, the reaction was the same; namely, a swing to one side. This resulted in placing the longitudinal axis parallel to the rays of light. Frequently, in such case, the larva would undergo a rotation on its own axis, so that it assumed a position with the back uppermost and the head directed away from the source of light. Whether or not this "righting reaction" occurred, appeared to depend largely upon the degree of freshness. Individuals which had undergone fatigue more frequently refused to rise from the bottom. It was at no time possible, however, to fatigue the larvæ to such an extent that they would not give the "swinging-reaction" into line with the light rays. By alternately changing through an arc of 30° the direction of the light which struck the larvæ from behind (Fig. 15, *a*, *b*, *c*), they could be made to swing, pivoted on the middle or end of their longitudinal axis, in an arc of equal degree. This pendulum-like activity in answer to the change in direction of the light-stimulus was extremely constant and in no case was it observable that the reaction was diminished by fatigue in spite of long periods of such alternate directive stimulation. It may be added here that prolonged direct stimulation from behind never produced a change in the body-orientation of the larva. The progressive orientation, however, might take place in either the positive or the negative sense.

Case 6. Larva oriented with back above; light enters from above—Under the conditions mentioned above, the larva was forced to give one or two reactions, depending upon the degree of intensity and the suddenness of introduction of the light:

(1) In some instances (especially when the light had the direction, *b*, Fig. 17), the larva first rotated through an arc of greater or less curvature and finally assumed a new swimming position

with the longitudinal axis of the body bent at a greater angle from the horizontal plane (Fig. 17, *B′*). This new swimming position was usually maintained so long as the conditions of light remained the same, but was sometimes replaced by the second form of reaction, which usually occurred when the light had the direction *a*, and which was merely an exaggerated form of the first.

(2) In this second type of reaction the rotation of the larvæ was not limited to an arc of a few degrees, but was extended into a forward "somersault." This in turn took place in one of two ways: (*a*) the larva might accomplish a rotation of 360° and return to its original position with the back above, but since the stimulation from above remained the same, it would not rest in this position, but would continue for a time to perform complete rotations without pause, after which it would come to rest as shown in Fig. 17, *B′*. This new swimming position was sometimes maintained as long as the conditions of light remained unchanged, though it might give place to further rotations; (*b*) the larva might, as a result of the forward rotation, come to rest with the back directed below, but this orientation was only momentary, because the influence of the light from above immediately determined a backward rotation. This last reaction might culminate when the larva had gained the new position shown in Fig. 9, *B′*, or it might be continued into one or more backward rotations through 360° and culminate after a greater or less number of such rotations, by coming into the new swimming position mentioned above. This orientation would be maintained as long as the same conditions of light were in effect; or it might be interrupted from time to time by rotations in arcs of varying degrees, and in either of the directions mentioned above.

Corollary 1—If, when the larva was oriented as in Case 6, the light was introduced from both sides and above, the resulting reaction was a combination of the forward rotation and the side swing. If the light came from above and behind (Fig. 17, *b*, then the direct assumption of the new swimming position *B′* more frequently resulted without the variable number of rotations through 180° or 360°.

Case 7. Larva oriented with back below; light enters from above—Under the above conditions of orientation (Fig. 18) there was usually one constant form of reaction. The larva would undergo a backward rotation through about 120°, and come into a new swimming position with the axis of the body bent downward several degrees from the normal swimming position (perhaps 45° from the horizontal), the exact amount appearing to be dependent upon the intensity of the light. This new swimming position was usually maintained as long as the conditions of light remained unchanged. It might sometimes be interrupted by backward rotations through 360°. These rotations invariably culminated in the assumption of the new swimming position (Fig. 18, *B*). In case the direction of the rays was both from the side and from above the resultant reaction was a combination of the reaction described above and the direct side swing.

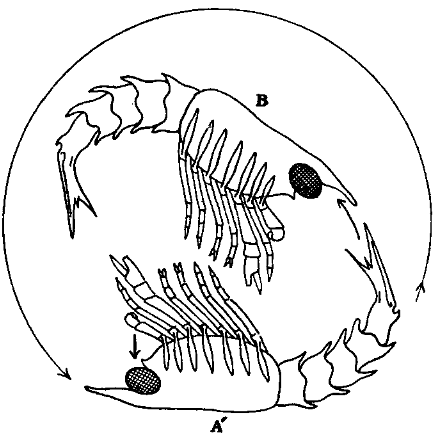

FIG. 18. For description, see Case 7.

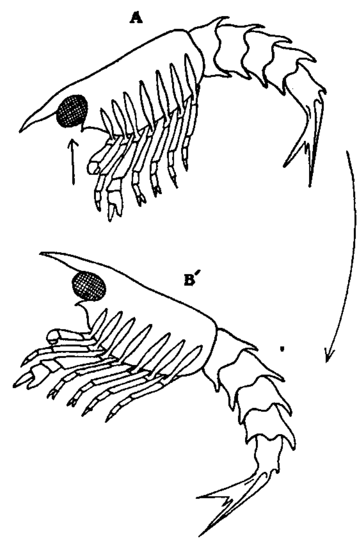

FIG. 19. For description, see Case 8.

Case 8. Larva oriented with back above; light enters from below—Under these conditions of orientation, the nature of the reaction was similar to that described in Case 6. Usually there resulted a direct backward rotation through a few degrees, which produced a new swimming position, Fig. 19, *B'*. This was usually constant while the conditions of light remained the same, but it was sometimes interrupted by backward rotations through an arc of greater extent, or even by a variable number of complete backward rotations through 360°. At the end of these, however, the new swimming position *B'* was invariably assumed. Combinations of the directions of the light (as both from the side and from above) produced modification in the reaction, but these could at any time be predicted if the individual constituents of the light were known.

Case 9. Larva oriented with back below; light enters from below —Under the conditions of orientation stated above the resulting reaction was similar to that described under Cases 6 and 8, but reversed. As in these instances, one of two results usually occurred: (1) The larva would undergo a forward rotation through a variable number of degrees, and assume directly a new "swimming-position" as shown in Fig. 20, *B′*. It was readily observed that the head was directed upward and away from the

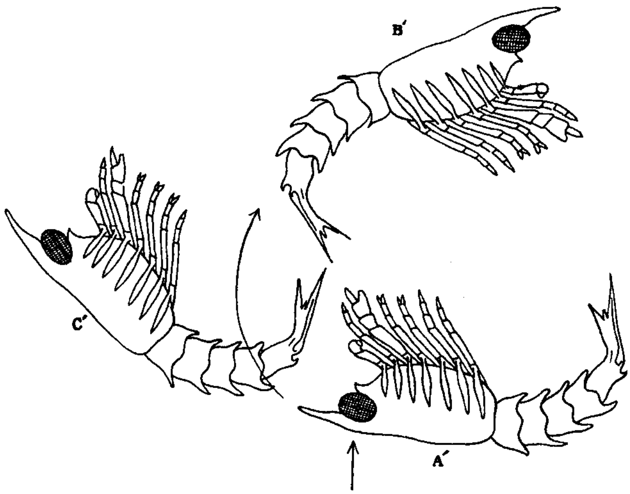

FIG. 20. For description, see Case 9.

light, not downward at an angle of about 30° from the horizontal, as in the normal swimming position; (2) it might happen, however, that instead of assuming this orientation the larva would merely come to an orientation with the back below and with the head directed upward as a slight angle as shown in Fig. 20, *C′*. It might, again, undergo one or more complete rotations forward, through 360° and then assume the new position shown in Fig. 20, *B′*, which position might be retained as long as the light conditions remained unchanged. The definiteness in these two reactions could be modified, as a result of changing slightly the direction of the light.

In addition to the facts regarding the effect of direct lighting upon body-orientation, which have been presented in the form of these nine cases, several other conditions might be mentioned:

1. If the longitudinal axis of the larva was parallel to the direction of the incident light rays, and the head away from the light, then the introduction of light produced no change in the body-orientation, but it might cause a positive or a negative progressive orientation.

2. In order that the unmodified forward or backward rotation might occur, it was learned that the light rays must strike both eyes with equal intensity, and consequently in a direction exactly perpendicular to any transverse body-axis of the larva.

3. In case the incident rays came from a direction that was not exactly perpendicular to the transverse axis of the larva, be the angle of difference ever so slight, the perfect backward and forward rotation would not occur, but would be greatly modified by swingings of, and revolutions on, the longitudinal axis of the body.

4. This type of behavior could not be observed unless the conditions of light were reduced to a single directive influence, and this factor handled with very great precision.

The effect of blocking the illumination—In the previous section we have examined the reactions which were brought about by suddenly introducing rays of light in directions which maintained a certain definite and specified relation to the longitudinal or transverse axis of the larval lobsters. In the present instance, however, we are to consider the nature of the reactions which are produced as a result of suddenly excluding or blocking the principal source of light by which the larvæ have just previously been stimulated. The "cut-off" was made by closing the window through which the light came, and thus leaving the larvæ in the subdued and diffuse light which entered the dark box from the room. Since the body-orientation of the larvæ to the directive influence of the light is always the same, obviously there could not be many different varieties of orientation caused by the change in the conditions of light. Such as were possible, however, may be described as follows:

Case 10. Larva oriented with the back above and the longitudinal body-axis exactly parallel to the incident rays—In case the larva was oriented as described above, when the light was shut off there usually resulted a forward rotation through 180°. This reaction caused the larva to become oriented (often on the bottom) with the back below and the head toward the previously existing source of light. This position was not maintained, but was succeeded by a "righting reaction," usually a revolution on the longitudinal axis, which brought the back again uppermost. After this response the larva might swim in diverse directions.

Case 11. Larva oriented with the back above and the head away from the light, which comes slightly from the side—If, when the larva was oriented as described above, the light was suddenly cut off, there resulted a swing of the long body-axis so that the larva was brought more or less nearly to face in the opposite direction; i. e., in the direction from which the light had previously come. This orientation, however, was not permanent, but other consequent reactions occurred and the larva might swim in one of several directions.

Case 12. Larva oriented as in Fig. 17, B′—If the direction of the light was from above, and the orientation of the larvæ as in Fig. 17, *B′*, when the light was cut off, the head of the larvæ would swing upward to face the direction from which the rays had previously come. Consequently, however, the orientation became that of the normal swimming position.

Case 13. Larva oriented as in Fig. 20, B′—When, as the result of light stimulation from below (as in Case 9), the larva was oriented with the head directed upward, and the illumination was suddenly cut off, the head of the larva would swing downward to face the direction from which the light had previously come; sometimes the larva would perform a rotation in an arc of greater or less extent and fall to the bottom. The body-orientation with head downward was not maintained, however, but was at once superseded by the normal swimming position.

It thus appears from these cases that there was usually an excessive movement to produce the new body-orientation; but that these movements invariably ended in the assumption of the normal swimming position.

Résumé of experiments on the effects of direct lighting and shading—(A) The effect of suddenly submitting the larval lobsters to a light which has a directive influence is to cause the larvæ to orient themselves in such a manner that the longitudinal axis of the body finally assumes a definite relation to the direction of the light rays. This orientation is a position with the long axis of the body parallel to the light rays, and with the head turned away from the source of light. (B) The effect of suddenly blocking the light to which the larvæ are reacting phototactically is to cause a new body-orientation by which the head is usually brought to face the direction from which the light had previously come. In either of the cases mentioned above the body-orientation is brought about by a single motor reflex or by a longer or shorter series of motor reflexes, some of which are "over-produced" movements. These movements include the following types:

1. *Forward or backward rotations,*[6] *or somersaults*—These were rotations in an arc, of a few degrees, which directly determined a new swimming position with the head raised or lowered, depending upon the direction from which the light or shadow had been introduced. In other cases these rotations took the form of a variable number of complete rotations through 360°, either backward or forward, in which the body of the larva formed a constant part of the circumference.

2. *Revolutions on the longitudinal axis of the body or rollings*—The revolutions or rollings took place either to the right or left, but usually in such direction that the back of the larva became directed more or less toward the light. They might be through a few degrees, or they might exceed 90°, in which case the larva fell to the bottom. In the case of larvæ one of whose eyes had been injured this revolution took place very rapidly, oftne at the rate of one hundred and fifty per minute, and always in a determined direction, the normal eye over, the injured eye under (HADLEY 1907b).

3. *Swingings of the longitudinal axis of the body*—These reactions were swingings in such a direction that the head was brought by the shortest path to face the dark, and the tail to point toward the light.

[6]Three similar types of movement are described by BOHN (1905, p. 4) as follows:

1° *Mouvement de manège*—l'animal décrit un cercle de plus ou moins grand rayon, l'axe du corps, courbé en arc, faisant partie constamment de la circonférence; la rotation se fait tantôt dans le sens des aiguilles d'une montre, tantôt dans le sens inverse. Parfois, au lieu de décrire un mouvement de manége pur, l'animal décrit des courbes de rayon variable qui constituent une sorte de spirale.

2° *Mouvement de rotation en rayon de roue*—l'axe du corps ne dévie pas; il est une des parties d'un des rayons du cercle décrit, et non une partie de la circumférence du cercle: la tête peut se trouver a la circonférence ou au centre.

3° *Mouvement de rotation sur l'axe, ou roulement:* l'animal tourne autour d'un axe longitudinal qui traverserait le corps dans sa longeur; la rotation commence par une inclinaison de l'animal d'un côté, et le sens de la rotation se trouve ainsi determiné. Le roulement peut s'accompagner d'un mouvement de translation et devient un mouvement en pas de vis.

4. *Rotations in the radii of a circle*—In these the longitudinal axis of the larva formed a radius, and with either the head or the tail at the center the animal rotated about a fixed point. These reactions were uncommon and, as yet, unexplained.

These four types of movement seldom occurred separately, except under especially devised experimental conditions. Under natural conditions, they were usually combined to form a composite action. To the previously mentioned simple components, however, all the more complex movements of the larval lobsters could be reduced.

B. THE EFFECT OF SCREENS AND BACKGROUNDS—It is probable that the reactions which are brought about through the use of backgrounds, are, generally speaking, dependent upon the same factors and conditions of illumination which are effective when light-absorbing or light-scattering screens are used. The term "screening" has been employed by BOHN (1905) to designate his method of submitting organisms to the influence of surfaces of light and shade. This investigator made use of screens of black and white of such size that he could readily bring them close to the sides of the glass containers in which the organisms under observation were placed. He has made a special study of the reactions of Crustacea to the influence of such screens, and in several instances the observations of the writer upon the larvæ of Homarus americanus merely confirm certain points in BOHN's earlier work. In many instances, however, new facts have been added.

The influence of white screens—The lobster larvæ were confined in a cylindrical jar, crystallization dishes, or in a rectangular glass container. The latter was used most frequently. The larvæ were then placed in the dark box and this was illuminated in such a manner that a general twilight was produced and the directive influence of light was at a minimum. While making observations it was even found necessary that the writer should wear a black mask over his face and collar, and, often, darken his hands in order not to modify the uniform light. For white screens pieces of white cardboard were employed, and brought over, under, or beside the receptacle containing the larvæ, as the case might require. Sometimes the screen was brought gradually toward the container, sometimes abruptly; but in all cases the results were definite and agreed with great uniformity. In order to secure the best results with the white screen, it was found best to reduce the intensity of light within the dark box below the degree used in the case of the black screens. The results of the series of experiments with white screens may be summarized as follows:

Case 14—When the larva was oriented with back above and the screen, held vertically, was so introduced from before that its plane was at right angles to the longitudinal axis, and parallel to any transverse axis of the larva, there resulted a rotation through 180° with, perhaps, a fall to the bottom. After this, and as a result of a revolution on the body-axis, a "righting reaction" usually occurred and the back would again be brought above. Now, with the head directed away from the white screen, the larva might either approach or depart from it, according as the progressive orientation was positive or negative. Sometimes, instead of producing a rotation through an arc of 180°, the larva underwent a series of rotations, its body forming a constant part of the circumference. The final orientation mentioned above would, however, invariably succeed. In case the screen was not held squarely before the larva, but somewhat at an angle to any transverse axis, the consequent reaction was a direct side swing away from the screen in order to place the longitudinal body-axis perpendicular to, and the head away from, the screen. In other cases there resulted a combination of the side swing and the forward rotation, so that the larva performed a sort of "half-somersault," and eventually assumed the normal swimming position, with the head directed away from the screen, as pointed out above.

Case 15—When the larva was oriented with the back above and the screen, held vertically, was made to approach the posterior end of the larva, no change in the body-orientation resulted. There might occur, however, either a positive or a negative progressive orientation.

Case 16—In this case the larvæ were swimming promiscuously about the container. When the screen was made to approach larvæ which held a position with the back above and one side turned toward the screen, these larvæ experienced a swing of their longitudinal axis so that the head came to be directed away from the screen and the longitudinal body-axis at right angles to the plane of the screen.

Case 17—When the screen, held horizontally, was made to approach, from below, a larva which held the normal swimming position, one of two reactions(which probably represent different degrees of the same reaction) resulted: (1) The larva would swing the head upward as shown in Fig. 20, *B′*, and maintain this swimming position so long as the light condition remained unchanged, or (2) it might, on the other hand, experience this same reaction in an exaggerated form, i. e., there might result a backward, rotation through 180°, which reaction would cause the larva to fall to the bottom and to assume a position with the back below and with the head directed upward at a slight angle as shown in Fig. 20, *C′*, Usually, however, this form of orientation resulted only when the light was of greater intensity, such as that secured in cases of direct illumination.

Case 18—When the larva was oriented in the normal swimming position and the white screen was made to approach from above, the reaction was similar to that described for Case 6, p. 270. The one difference was that while the direct lighting often caused a number of complete rotations through 360° before the final body-orientation was assumed, the white screen, on the other hand, usually acted by changing the swimming position directly to that of Fig. 17, *B′*. This difference in response was probably due to the difference in the intensity of light (direct or reflected) coming from above.

The black screen—The method of conducting the experiments with the black screen was almost the same as that for the white screen. There was one point of difference. It was found that, in order that the black screen should determine any reaction of the larvæ, it was necessary to have a slightly greater illumination within the dark box. The following report of cases shows the result of making the screen to approach, from various directions, the larvæ diversely oriented.

Case 19—When the larva was in the normal swimming position and the back screen was presented opposite the head, and at right angles to the longitudinal axis, the orientation was not changed, but was retained constantly so long as the screen remained in position.

Case 20—When the larva was in the normal swimming position and the screen was made to approach from behind, so that its plane was parallel to a vertical plane passing through both eyes of the larva, there usually resulted a forward rotation of 180° in the arc of a circle. This reaction brought the back of the larva below, and the head toward the black screen. This position was at once further modified by a revolution of 160° on the long body-axis, either to the left or right (determined by the nature of the lateral or secondary illumination), and the larva again assumed the normal swimming position, but with the head directed toward the black screen. In case the plane of the screen was not exactly parallel with the vertical plane passing through the eyes of the larva, the reaction was not represented by the simple forward rotation, but was modified by side movements.

Case 21—When the larva was in the normal swimming position and the black screen approached from the side, several reactions might occur. Most commonly the larva underwent a swing of its longitudinal axis so that the head was brought to face the screen. Another reaction sometimes observed was a rolling, or revolution, on the long body-axis, in such a manner that the back moved away from the screen. At the same time there occurred a swing of the longitudinal axis which caused the head to be directed toward the screen. These two reactions might occur simultaneously, and the resulting reaction be a blending of the two components mentioned above. The rolling on the longitudinal body-axis was seldom over 90° from normal (back above), usually less. Yet in cases where the illumination in the dark box was greater, or when the screen was introduced suddenly, the rolling motion might exceed 90°, and the larva fall to the bottom of the container.

Case 22—In this instance the larva oriented in the normal swimming position and the screen was made to approach from above. This combination produced several forms of reaction. In cases where the general illumination in the container was not great, the larva merely experienced a slight change in the direction of the longitudinal body-axis; the head assumed a superior position, so that the long axis of the body was nearly horizontal, or even directed upward at a small angle, rather than bent downward at an angle of 30° from horizontal, as in the normal swimming position. On the other hand, if the illumination was greater, the larva might undergo a rotation on its own longitudinal axis through 180° and fall, back downward, to the bottom. Whatever reaction occurred, it could be explained as an effort of the larva to turn the head toward the black screen, and the degree to which this was attained depended very much upon the intensity of illumination throughout the container. The type of reaction mentioned above was demonstrated to better advantage in the following experiment. A large tube containing a number of larvæ was placed in an upright position on the laboratory table, and the upper half covered with a roll of black paper. The larvæ gathered in the more brightly illumined end of the tube, which was below. So long as they swam in the lower part of the illuminated area, they assumed the normal swimming position, but whenever they came into the upper regions, and approached the edge of the black paper, the direction of the longitudinal body-axis was changed from 30° below horizontal to 30° or even more above the horizontal plane.

Case 23—In the following case the larva was oriented in the normal swimming position and the screen was made to approach from below. As a result the larva usually reacted by a slight forward rotation, the head passing through an arc of a few degrees, and producing a still greater angle between the longitudinal axis and the horizontal plane. This new swimming position was seldom subject to further modifications so long as the light conditions remained unchanged. Regarding the reactions of the larvæ of Homarus vulgaris under similar experimental conditions, BOHN (1905, p. 11) remarks: "Si la larve nage le dos dirigé le haut, il y a roulement de 90° ou de 180°, la par suite la larve dévie lateralement ou tombe."

Such a result as the above was not observed by the writer. On the other hand, it was observed that, whatever the body-orientation of a group of larvæ might be previous to the approach of the black screen from below, its presence usually determined a rise of the larvæ from the bottom of the container to the upper waters, where normal swimming was manifested so long as the screen beneath remained in place. When it was removed, however, or replaced by a white screen, the consequent reaction was, as we have already seen, characterized by rotations and revolutions through 90° or 180°. These reactions in turn resulted in bringing the larvæ again toward the bottom, and in determining a consequent absence of larvæ in the regions near the surface of the water.

Case 24—In this instance the larvæ were oriented with back below, and the black screen was made to approach from behind in such a manner that the plane of the screen was parallel with a vertical plane passing through both eyes of the larva. Under these conditions (see Fig. 14, *A′*) the reactions were as follows. When the black screen, *G*, was introduced, the larva, *A′*, underwent a forward rotation through an arc of 180°, and assumed the normal swimming position, *B′*, with the back uppermost and the head facing the screen. This orientation was maintained with a greater or less degree of constancy so long as the conditions of light remained the same. If, on the other hand, the screen was so placed, or the larva had such a position, that the plane of the screen was not exactly parallel to the vertical plane passing through the two eyes of the larva, a different reaction was experienced. In this instance the first response was a revolution on the longitudinal axis, usually through 180°. This resulted in bringing the back of the larva uppermost, and was usually followed by a swinging of the longitudinal axis, which brought the head to face the screen. The direction of this side swing (to the left or the right) was determined by the angle which the longitudinal axis of the larva made with the screen. For instance in Fig. 15, the larva designated *A′* would swing to the right, while the larva designated *C′* would swing to the left, each in the direction indicated by the arrows. In other words we may say that the larva would swing in that direction which brought the head, by the shortest course, to face the screen. But the two reactions mentioned above might, as in previous cases, be blended to form a composite reaction, which differed from either of its simple components.

Case 25—In the present instance the larva was oriented lying on its back and the screen was introduced from before. Under these conditions, as in Case 19, there was no modification in the body-position. In certain instances the larva underwent a revolution through 180° on its longitudinal axis and assumed a position with back above and head still directed toward the black screen; but in the great number of cases the orientation remained unchanged.

Case 26—In case the larva was oriented with the back below and the screen was made to approach from the side the reactions were as follows. The larva experienced a rolling or revolution on its longitudinal axis, in consequence of which the back moved away from the screen through an angle of 90°, occasionally more. At the same time there was a swinging of the longitudinal axis, itself, so that the larva came face to face with the screen, eventually with the back uppermost. During this reaction the larva often departed from the screen. As in Case 21, mentioned above, these two reactions might occur at the same time, and then the resulting reaction was a composite.

Case 27—In the present case the larva was oriented with back below and the black screen was introduced from above. Under these conditions it usually underwent a slight forward rotation with a consequent rise from the bottom, and came into a new swimming position with the longitudinal axis directed somewhat upward as shown in Fig. 20, *B'*.

Case 28—In this instance the larva was oriented with back below and the black screen was introduced from beneath. The reactions were usually as follows. The larvæ underwent a revolution of about 180° on its longitudinal axis, and assumed practically the normal swimming position, with the back uppermost and the head bent downward at an angle of about 30°. In other cases, however, this new position was brought about by a different sort of reaction; namely, a backward rotation through an arc of 180°. This resulted in throwing the larva again into the normal swimming position.

Generally speaking, we may say that, when black or white screens were made to approach larvæ of any one of the first three stages, diversely oriented, the larvæ manifested two forms of response. First, a motor reflex, which tended to place the longitudinal axis in a certain relation to the plane of the screen; secondly, and subsequent to the first response, a progressive orientation, toward or away from the screen, as the luminosity of the screen, the physiological state of the larvæ, and other conditions of the case, determined. When the white screen was used, the larvæ commonly became oriented with the head directed away from the screen. In the case of black screens, on the contrary, the head was directed toward the screen and the back more or less away. These reactions occurred whether the screens were made to approach from above, below, behind, or the side. After body-orientation had taken place, the larvæ might approach or recede from the black or the white screen, according as they were reacting positively or negatively.

The mechanics of reaction upon which orientation to the screens was found to depend, agree, for the greater part, with the types of reaction to black screens reported by BOHN (1905), who has made a careful study of the effects of causing a black screen to approach the larvæ of Homarus vulgaris, diversely oriented. There are, however, certain disagreements. First, it is certainly true that bringing the black screen parallel to the longitudinal axis of the larva frequently determined a rolling of the larva on its own longitudinal axis, whatever the original orientation may have been. But in Case 21, certain orientations of the larva were noted in which these rollings did not occur. It is true, moreover, that the progressive orientation often took place in that direction in which the back was directed. But several instances were observed wherein the orientation to the black screen resulted merely from a swinging of the longitudinal axis of the larvæ so that the head was directed toward the screen and where consequent progressive orientation was either a movement backward or forward, head foremost or tail foremost, as in positive or negative phototaxis.

We have now examined somewhat in detail the effects of sudden illumination and of sudden shading, the effects of white screens and of black. If we now compare the detailed results of these studies, we note that the effects produced by introducing a white screen are comparable with those obtained by suddenly admitting illumination, while the results brought about by black screens are comparable to those determined by suddenly cutting off the light. In other words, the larvæ appear to respond to the influence of screens of black and white by reactions which are dependent upon the same simple forms of response observed under the conditions of direct lighting and shading.

In view of this correspondence in the nature of reaction to direct lighting and to screens of black and white, it may be considered probable that the screens and backgrounds are instrumental in determining the behavior of the larvæ, only in so far as they are themselves the source of (reflected) illumination. Thus, when the black background causes a swing of the larva, as a result of which it comes to face the screen, we cannot say that the primary factor is the blackness of the screen; but rather that the small amount of light reflected from the screen permits rays of light from other directions to become effective, The larva "heads" to the black screen because his eyes encounter no light rays coming from this direction; and he turns away from the white screen because his eyes encounter stronger reflected light from this than from any other direction.

The effect of backgrounds—The question of the influence of backgrounds in determining the orientation of crustacean larvæ has been brought forward by KEEBLE and GAMBLE (1904). Aside from the effects of screening, the more general problem of backgrounds did not receive especial attention in the course of the present investigation, but, as we shall see, the question of screening which we have discussed in the preceding section is probably only a single phase of the problem of backgrounds. The following experiments which were performed more or less at random in connection with other experiments, but which deal with the question of backgrounds, may, however, be presented.

By the term background, as it is used in the present case, is meant the permanent color-tone of the surrounding walls (as a whole or in part) which confined the young larvæ. This condition was somewhat different from that determined by the use of screens which were movable and could be placed at any angle with reference to the body-axis of the larvæ. Backgrounds were employed in several different ways. They were sometimes represented by the black or white lining of the reaction boxes; again, by the ground upon which the glass dishes or tubes rested, and in still other cases by the outer covering of these dishes, or tubes. The subject may be considered under two heads: (1) the effect of backgrounds in connection with the purely photopathic response; (2) their effect in determining the "choice" of a particular region of light-intensity when phototaxis also is operative. In view of the fact that the investigation of the first phase of this problem was not undertaken in the present work, we may pass directly to the consideration of the second point stated above.

The effects of backgrounds in connection with both the phototactic and the photopathic response—Under this head we may consider those conditions of experiment, which, although they be chiefly productive of reactions to the directive influence of the light, nevertheless were modified by response to the intensity of the light. These conditions were secured by the use of Y-tubes. The following experiments serve to show why, in the case of the larval lobsters, the tendency to gather in the brighter areas (assumed positive photopathy) is often associated with positive phototaxis; and why a tendency to gather in the darker areas (assumed negative photopathy) may be associated with negative phototaxis. In the diagrams of Fig. 21 are represented the Y-tubes as set up for experiment. Those whose arms are above were arranged for experiment with larvæ having positive phototactic reaction; those whose arms are at the bottom, for larvæ having a negative phtototactic reaction. In tubes *A* and *B* one side of one arm was fitted with a band of black paper which extended half over the circumference of the arm and a very short distance down each stem. In tubes *C* and *D* the same arrangement existed, save that white instead of black paper was used. In every case the light rays came from the window in the direction of the arrows. In all cases of larvæ manifesting a negative reaction, the start was made at the end of the tube (lying horizontally on the table) nearer the window. In the case of positively reacting larvæ, the start was made from the end of the tube farthest from the window. The end marked *a* in every instance was the end *from which* the larvæ moved, the purpose of the test being to determine in which arm of the tube the larvæ would eventually gather.

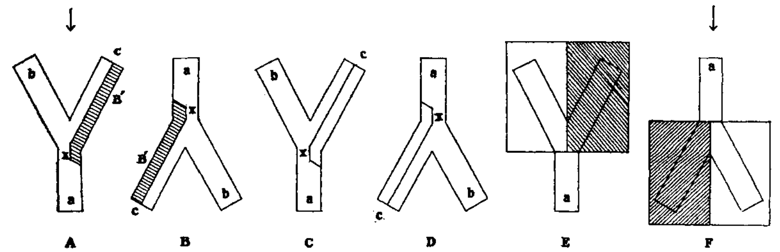

Fig. 21. Showing the Y-tubes set up for experiment. In every case the light came from above in the direction of the arrows. The tubes whose arms are above were set up for positively reacting lobsters; those whose stems are above, for negatively reacting lobsters. In tubes *A* and *B* the cross-hatched areas represent the part covered with black paper. In tubes *C* and *D* the clear area was covered with white paper. Tubes *E* and *F* are shown equipped with the glass plates placed over the arm. In every instance the larvæ were started from the end of the tube designated *a*. For further explanation, see Cases 29–33 inc., pp. 286-289.

Case 29—The tube was arranged as in Fig. 21, *A*. Ten positively-reacting, first-stage larvæ were placed in the Y-tube, and, by certain manipulations of the light and by virtue of their positive reaction, they were made to congregate in the stem end. Then suddenly, the direction of the light was changed so as to come in the direction of the arrows. Immediately the larvæ oriented with their heads toward the end *a*, and passed through the tube toward the light. As soon as they approached the region marked *x* they came under the influence of the dark background bounding the side of the tube. Immediately, as we have seen to be the case in previous instances, the longitudinal body-axis swung so that the head came to face, more or less obliquely, the dark background, *B'*. The directive influence of the rays, however, continued to draw the larvæ on, but since they must travel in the direction in which the tail pointed, they entered the arm *b*, and passing close to the inside continued until further progress was prevented by the end of the arm. Space will not be taken to show the numerical results of this and similar experiments. Suffice it to state that nearly all of the positively reacting larvæ, of whatever stage or age, when submitted to these conditions of experiment, reacted as has been described above. This experiment was modified by placing the Y-tube so that the uncovered arm of the tube rested upon a piece of black paper. The results were invariably the same; the majority of the larvæ progressed to the arm of the tube not overlying the black ground.

Case 30—In this case the conditions of the experiments were further modified by reversing the Y-tube so that the arms pointed away from the window. In this instance larvæ which were manifesting a negative reaction were employed, and were first placed in the end (*a*), nearer the window. When the light was admitted the larvæ at once oriented with their heads directed away from the light and began to move away from the window. When they had reached the point designated *x*, they immediately underwent a swing of the longitudinal axis, as in previous cases, so that the head was directed toward the black ground, bounding the outer surface of the arm *c*. Thus they would continue, passing close to the inner wall of the tube until the majority had gathered in this arm. In this instance, however, the larvæ would usually rest between *x* and *c*, instead of moving to the end of the arm.

Case 31—Here the black background bounding the outer side of one arm was exchanged for a white ground of the same size and having the position shown in Fig. 21 *C*. Third-stage larvæ giving a positive reaction were employed for the experiment. They were started in the end *a*. When the light was admitted, the usual body-orientation resulted, and the larvæ began their progression through the tube toward the window. When they had arrived at *x* they came under the influence of the white ground and turned their heads away from this side. Progressive orientation then continued and the larvæ eventually became grouped in arm *c*. Similar results were obtained when half of this arm of the tube was laid over a sheet of white paper.

Case 32—The previous experiment was further modified by reversing the Y-tube so that the arms were directed away from the window (Fig. 21, *D*). Larvæ which were giving a negative reaction were employed. They were placed in the end *a*, and the light was admitted. After the usual body-orientation had taken place, the progression away from the window began. When the larvæ reached the point *x*, and had come under the influence of the white ground bounding one side of the tube they would swing their heads toward the right and continue their progress until all were gathered in arm *c*. This was somewhat unexpected. It eventually transpired, however, that the white ground bordering the outer surface of the tube did not act as a reflector or intensifier of the light rays, but as an opaque shield, cutting off the rays which would otherwise have entered the arm *c*. Thus, as in Case 30, the negatively reacting larvæ had merely grouped themselves in the arm where the light was least bright. When the Y-tube was so placed that half of arm *c* rested upon a sheet of white paper the result was different. The larvæ congregated in arm *b*, which was, under these conditions, the region of least light intensity.

Case 33—The four cases mentioned above were supplemented by other experiments involving the use of colored glass plates. As described in Experiment 15, these plates were so placed over the arms of the Y-tube that a difference in the intensity of light striking one arm was caused by interposing a red, orange or yellow glass plate between that arm and the source of illumination. In these cases the positively reacting larvæ gathered in the arm where the light-intensity was the greater, while the negatively reacting larvæ grouped themselves in the arm where the light was least bright. As a rule, the larvæ of earlier stages seemed to be more susceptible than the others to slight differences in the intensity of light at the entrance to the arms.

Thus is explained the tendency for positively reacting larvæ to gather in regions of greater light-intensity, and on the other hand, the tendency of negatively reacting larvæ to congregate in regions of lesser light-intensity. This condition of affairs has, no doubt, given many investigators reason to believe that such reactions are but manifestations of a positive photopathy; and that photopathy and phototaxis are fundamentally the same. We now know, however, that the reaction just described in Case 5 is due to the combined effects of two tendencies; the one to turn the head toward the dark areas (areas of non-stimulation); the other to move in the direction of the longitudinal axis of the body either toward or from the source of light. Were we dependent upon such experiments as these for our belief in the existence of a separate response to light-intensity, regardless of directive influence of light, we might well say that the photopathic and phototactic responses are, in the end, one and the same. But the writer has adduced in the previous section other data which separate more clearly these two types of reaction.

VII. ANALYSIS.

It has for some time been the custom to state that certain organisms are positively phototactic or positively photopathic, and that other organisms are negatively so. The index of reaction for several crustaceans has been so recorded, but the observations are usually incomplete, often uncritical, and sometimes of questionable significance. It is true that, in a very general way, organisms react positively or negatively to light. For instance, it may be said that the lobster shuns the light, that Palemonetes is attracted by the light, and that the larvæ of Limulus avoid the light. The definite statement, however, that the larvæ of Limulus are negatively heliotropic, or that Palemonetes and larvæ of Homarus are positively phototactic, is as inadequate as would be a biography written on the basis of a single day's association with a human individual. It may be true that by the time the adult stage is reached, the reactions of many animals have become more or less stereotyped, so that reactions like those of the moth to the flame, are easily predictable. In the larval and adolescent stages, on the other hand, the reactions are frequently more variable. To say that the lobster of the second larval stage is positively phototactic or positively photopathic is, as has been demonstrated, by no means a correct interpretation of the facts of the case, for slight changes in the conditions of stimulation may be sufficient to reverse the index of reaction. This variability doubtless occurs in many arthropods. It thus becomes evident that, although the young lobsters may be regarded as machines upon which many different external forces act and cause certain reactions, still (except for the definite body-orientations which are invariably determined by the directive influence of the light rays) they are machines the nature of whose operations can seldom be predicted unless the age, the stage, the kind and degree of the stimulus, are accurately known. These conditions of reaction indicate the extent to which the behavior of young lobsters is determined by their physiological states; and the foregoing experiments show in what way these physiological states change, not only from one stage-period to another, but even during the same stage-period, through the influences of metabolism, development, and perhaps still other factors. The extent to which the natural behavior of animals in their natural environment can be explained on the basis of the results of laboratory experiments depends largely upon the animal and the kind of reactions involved. It is quite probable that some of the characteristics of reaction, which have been described in the present paper, determine in a large measure, the daily behavior of the larval and early adolescent lobsters when they are in their natural environment. Unfortunately, however, we know too little regarding the behavior of lobsters under natural conditions, to attach great importance to far-reaching explanations of their daily activities on the basis of laboratory experiments. A few points, however, may be noted. The reports of biological surveys make it clear that, at the surface of the ocean or of bays in which lobsters are known to live and breed, the stage most often taken in the tow-nets is the fourth; the larval stages are much less frequently found, the fifth stage seldom, and later stages never. Observations which were made on lobsters of different stages taken from the Wickford hatchery and liberated in the surrounding waters of Narragansett Bay yield similar evidence regarding the immediate natural distribution. In these cases the lobsters of the larval stages were found to swim for a brief time, then gradually disappear from the surface; the fourth stage lobsters swam actively at the surface so long as they were observed; while the fifth and all later stages plunged at once into the deeper water and were immediately lost to sight.

As the writer has already suggested, it is impracticable to attempt to explain the natural behavior of larvæ of the first three stages, on the basis of the reactions which have been discussed at some length in the present paper. The light (depending upon its intensity and directive influence; and upon the age, stage, and previous condition of the larvæ) may determine at one time a positive, at another a negative, response, so that the general reaction of groups of lobster larvæ can in no way be readily predicted. One exception to this may be stated. The first-stage larvæ, directly after hatching, would be strongly drawn to the surface of the water by virtue of both their photopathic and of their phototactic response. After the first day or two, however, begins that modification and variation in the phototactic action which, for groups of uncertain age and condition, makes any accurate prediction of their movements quite impossible.

In the case of the fourth-stage lobsters there is a better basis for the correlation of the natural and experimental types of behavior. We know that, under experimental conditions, hungry fourth-stage larvæ, when submitted to food stimuli, will rise immediately to the surface of the water and swim about excitedly for some moments; we know also that the early fourth-stage larvæ, under certain experimental conditions will leave a region of low light intensity and remain in regions of greater light intensity. We have learned, moreover, that the same fourth-stage larvæ, under different experimental conditions, will usually shun the light when it has a single directive influence, and travel in the direction of the rays away from their source. Finally, we have observed that the fourth-stage lobsters, except in the latter part of the stage-period, show a definite tendency to remain at the surface of the water.

The question now arises: What is the cause of this surface-swimming? Is it a response to the intensity of light, to the directive influence of light, to hunger, or to gravity? Although we know something of the effects of several of these factors when they act separately, it is difficult to ascertain their individual influence when they work in combination. If, however, we can discover any parallel between a certain type of reaction under experimental conditions and a certain mode of behavior under natural conditions, and find that as one is modified or lost the other is also, then, and then only, are we justified in believing that we know the determining cause of the particular type of natural behavior in question. We have such a parallel between the photopathic (and occasionally the phototactic) reactions and the surface-swimming tendency of the fourth-stage lobsters. As the former becomes modified and is eventually replaced by the negative reaction, so the latter is changed and finally gives way to the bottom-seeking tendency as the lobsters pass on through the fourth stage-period. With such a parallel before us, it cannot be doubted that there exists a certain causal relation between the positive photopathic reaction and the surface-swimming tendency on the one hand, and the negative photopathic reaction and the bottom-seeking tendency on the other. But the photopathic reaction may not alone be responsible for the surface-swimming tendency on the part of the fourth-stage lobsters. The presence of food particles in the water excites them strongly, and causes them, when in the glass jars, to swim excitedly at the surface of the water. It therefore appears quite within the bounds of possibility that chemotropism may also play a part in determining the surface-swimming of the fourth-stage lobsters.

The explanation of the behavior of the fifth and all later stages, in the light of the foregoing experiments, rests upon a more certain basis. We have observed that the fifth-stage lobsters invariably manifest both a negative phototactic and a negative photopathic reaction. In general this may be said to explain the fact that lobsters in the fifth and all later stages shun the light at all times. Little work was done on the behavior of the older lobsters, and it is hoped that future investigations may continue along this line.

In connection with the mechanics of orientation, the writer has shown that the reaction of larval lobsters to light is made up of two components—body-orientation and progressive orientation; and that the former is primary while the latter is secondary. In the earlier pages of this paper it was demonstrated that the *progressive orientation* is dependent upon a great number of conditions, and that the orientation responses are relatively complex reactions which are dependent in great measure upon the obscure, changing, internal conditions which are embraced under the general term, "physiological states." In later pages, on the other hand, attention has been directed to those conditions of light which determine the *body-orientation* alone; and the results recorded have made it clear that the movements producing the body-orientations are types of action which simulate more closely pure reflexes, direct, constant, and invariable.

As BOHN (1905a) has well said, it is impossible to take definite account of the complicated series of phenomena which take place in the nervous system of animals even as low as the arthropods, for these are dependent not alone upon complicated connections between neurons, but also upon their variable states. Yet it is apparent that this difficulty applies rather (at least in the reactions of the larval lobsters) to those movements which determine the *progressive orientation* to light, than to those which determine *body-orientation*. Even in the latter somewhat less complicated and more easily explained phenomena, however, we are still far from recognizing the underlying causes.

It is true that we can understand in a way why the "posterior position" of the thoracic appendages determines a negative response, while the "anterior position" determines a positive response. We can, moreover, understand why a more intense illumination of the eye on one side causes a greater activity of the swimmerets on that side, and a consequent swing of the larva away from that side. This phenomenon was well shown by experi-

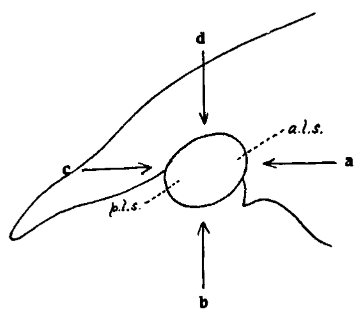

FIG. 22. Diagram showing the rostrum and one eye of a larval lobster; *a*, *b*, *c*, *d* represent direction of light striking the eye from behind, below, in front and above; *a.l.s.* represents posterior lateral surface; *p.l.s.* represents anterior lateral surface. For further explanation, see p. 297.

ments which the writer performed upon larvæ with blinded eyes (HADLEY 1908). These experiments demonstrated that, when the right eye was blinded, the direction of forward swimming was invariably to the right; in other words, the exopodites beat more vigorously upon that side of the body whose eye was most stimulated, and the larva was, in consequence, "pulled around" like a boat. These reactions are explainable on the grounds of a heterolateral stimulation and a consequent unequal action of the muscles on the two sides of the body. But we do not understand as clearly how or why the action of the light striking with equal intensity the corresponding areas of the posterior surface of the eyes (Fig. 22), for instance, brings about these "anterior" or "posterior" positions of the thoracic appendages, and the consequent positive or negative reactions. Nor do we understand why, when the larva is in one "physiological state," a certain intensity of light (striking equally the posterior lateral surface of the two eyes) causes a positive reaction, while if the same larva is in another "physiological state," the same light (striking with the same intensity the same parts of the eye-surfaces) causes the opposite reaction; or again, why when the larva is in the *same* "physiological state," one intensity of light causes a positive reaction, while light of slightly less intensity determines a negative reaction. No more do we know why the illumination of the upper surface of the eyes (Fig. 22, *d*) causes a forward rotation; or the illumination of the lower surfaces (*b*), a backward rotation; or the illumination of the anterior surface (*c*), a forward or a backward rotation. These as yet unexplainable conditions of reaction may well convince us that, however simple and mechanical some of these reactions appear to be, many of them are extremely complex, and indicate a very complex relation between the different regions of the eyes and the nervous centers. Yet, as has been stated, to such a degree as any of these reactions can be explained, those which are concerned in the processes of body-orientation are more easily interpretable on the "simple-reflex" hypothesis. In view of this fact the writer would differ from the conclusion reached by BOHN (loc. cit., p. 41): "Tous ces phénomènes (the reactions of larvæ of Homarus vulgaris) sont en relation avec des états physiologiques particuliers. Sous l'influence de l'éclairement, l'état physiologique des larves de homard ne tarde pas à changer, et les tropismes aussi." The present writer would limit the application of this theory to those reactions of the larval lobsters which are concerned with progressive orientation, excluding body-orientation.

Regarding the relation of the type of reaction found in the larval lobsters to the tropism theories, inference has already been made in the preceding paragraphs. First, to what extent does the behavior found in the larval lobsters agree with the local action theory of tropism? The primary demand of this theory is that the body of the organism should become so oriented with respect to the source of illumination that the anterior end is made to point either toward or from the source. Under these conditions the index of reaction is said to be positive or negative, according as the organism moves toward or from the light. "This orientation is produced, according to this tropism theory, by the direct action of the stimulating agent on the motor organs of that side of the body on which it impinges. A stimulus striking one side of the body causes the motor organs of that side to contract or extend or to move more or less strongly. This, of course, turns the body till the stimulus affects both sides equally; then there is no occasion for further turning and the animal is oriented" (JENNINGS 1906a, p. 266). This is also brought out by HOLT and LEE (1901, p. 479), "The light operates, naturally, on the part of the animal which it reaches." Thus, this tropism theory requires that, in order to determine the direction of movement, the stimulus must act more strongly on one side of the body than on the other. It is needless to say also that in the majority of cases the same conditions of stimulus which cause an animal to direct the head away from the source of the stimulus, also determine a movement in the same direction. Therefore, if we separate, as has been done in this paper, *body-orientation* from *progressive orientation*, we can say that, in most organisms, the index of body-orientation agrees with that of progressive orientation; the conditions of stimulation which cause the one likewise determine the other. Let us now see to what extent the behavior of the larval lobsters agrees with these requirements of the local action theory of the tropisms. In order to treat the matter concretely we must consider it under two heads. First, body-orientation; then, progressive orientation.

It has been shown in the previous pages that, whatever the sign of progressive orientation may be, the *body-orientation is invariably negative*; and that this body-position is produced as a result of diverse reactions which are attributable to the relative intensities of light which strikes the eyes of the larvæ. This body-orientation, moreover, is consta t; it is not dependent upon the age, stage, previous st mulation, hunger, "physiological state," or upon any modifications of the external stimulus, such as changes in intensity, duration of stimulation, etc. The orienting reaction always comes about in the same way, so that we here have a case where the "same-stimulus-same-reaction" principle invariably holds. In other words, the reactions by which the larval lobsters secure the characteristic body-orientation are typical and invariable motor-reflexes.

Beyond producing the body-orientation, the direct motor-reflex ceases to influence the behavior of the larval lobsters. From this moment on, a multitude of conditions appear to be brought to bear to determine the consequent *progressive orientation* of the young animals in one sense or the other. No longer can we say, "same stimulus, same reaction" (SPAULDING 1904), for there is now no constant form of reaction even to the same stimulus. The reactions appear to be no longer so dependent upon the nature of the *external* stimulus, but are more largely regulated by the "physiological states." This we might consider as the cumulative result of a long series of previously acting stimuli, to which others are constantly being added with two effects; first, of bringing about a definite reaction determined by the nature of the stimulus and by the present physiological state; second, of further modifying the physiological state itself, so that even the reapplication of the same stimulus might provoke a quite different reaction. It can not be doubted that the series of changes, which occur in the behavior of the lobster larvæ as they pass through the successive stages, is largely due to this gradual modification of the physiological condition—the cumulative effect of a long series of antecedent stimuli.

We may sum up the preceding paragraphs by saying; (1) The reactions by which the *body-orientation* of larval lobsters is produced are invariable motor reflexes, and the method of such orientation is, therefore, quite in accord with the requirements of the local action theory of tropisms. (2) The reactions by which the *progressive* orientation is produced, although appearing to be simple reflexes, are not invariable but are dependent upon many conditions of stimulation, and especially upon the physiological states.

In view of these facts, it appears that, while the body-orientation of the larval lobsters is not of primary importance in determining the index of the progressive response to the directive influence of the light rays (since the body-orientation and the progressive orientation are dependent upon quite different factors), still it is of primary importance in determining the general line along which the movement shall take place, either toward or from the source of light. It is shown by these points that this type of response is not in agreement with JENNING's theory (1906b), in which the process of orientation is of secondary importance, for neither the immediate nor the final body-orientation of lobster larvæ to light can be characterized as a "selection from among the conditions produced by varied movements" (JENNINGS 1906b, p. 452). Indeed there are no "varied movements" in the reactions by which the body-orientation to light is brought about. The only way in which the term "random movements" can be applied to the orientation of the larval lobsters is in its relation to the variable extent of the revolutions or rotations. It cannot be denied that this *degree* may be dependent upon the physiological states of the larvæ (for instance, fatigue or freshness), but, after all, this point is irrelevant to the present discussion, since it is the direction of the immediate turning and not the extent of it, which is the important consideration.

The foregoing experiments throw but little light upon the question of intensity of light versus direction of light. Indeed it is probable that the latter phase of the problem is not of great importance except in cases where the light rays are effective by passing through the body as in the case of the electric current, which, as the writer has shown elsewhere (HADLEY 1907a) causes reaction only when the direction of the current holds a certain relation to the longitudinal axis of the larvæ. It is clear, however, that the direction of the light rays does modify the reactions of the larval in two ways: (1) By determining *which of the two eyes shall be most stimulated*, thus causing a body-orientation in which the longitudinal body-axis is thrown into line with the direction of the light rays, so that the eyes shall be equally stimulated; (2) by determining *what parts of the surfaces of the two eyes shall be stimulated equally*, and thus producing a body-orientation in which the posterior lateral surface (Fig. 22, *a.l.s.*) of the eyes receives the strongest stimulation, and the anterior lateral surface (*p.l.s.*) the least. These reactions, and the consequent progressive orientations of the larvæ, the writer has called reactions to the directive influence of the light. That there may be, in addition to these responses, reactions to the intensity of light as HOLMES (1901) and others have considered possible, it is still permissible to believe, and in the earlier pages of this paper the writer has pointed out some reactions of larval lobsters, which, although not perfectly understood, may be included under the head of photopathic response.

The foregoing experiments were carried on at the Experiment Station of the Rhode Island Commission of Inland Fisheries at

Wickford, Rhode Island, where exceptional facilities were found for obtaining material of all ages and stages. The writer's thanks are especially due to Prof. A. D. MEAD of Brown University for making possible an opportunity for this line of inquiry and for material assistance; to Dr. R. M. YERKES of Harvard University, and to Dr. H. E. WALTER of Brown University for friendly criticism during the preparation of the paper; also to Mr. E. W. BARNES, Superintendent of the Wickford hatchery, for many kindnesses.

VIII. SUMMARY.

1. Larval and early adolescent lobsters present both phototactic and photopathic reactions as these responses are defined on p. 201.

2. There is no constant type of response for all larval lobsters, but a modification of reaction occurs through the metamorphosis of the larvæ.

a. First-stage larvæ, directly after hatching, give definitely positive phototactic and photopathic reactions which endure for about two days, after which the phototactic reactions change to negative, becoming positive again shortly before moulting into the second stage.

b. Both early second-stage and early third-stage larvæ manifest a negative phototactic reaction, which usually becomes positive shortly before moulting into the third and fourth stages, respectively.

c. The photopathic reaction of the first three larval stages is commonly positive from the beginning to the end of the stage.

d. The phototactic reaction of the fourth-stage lobsters is usually (i. e., except in cases where intense light is used in connection with early fourth-stage lobsters) negative throughout the stage-period, and the photopathic reaction, positive during the early fourth stage-period, eventually becomes negative.

e. During the fifth stage-period, and in all later stages, both the phototactic and the photopathic reactions are strongly negative.

3. While the photopathic reaction of the larval lobsters remains constant, the phototactic reactions are subject to modification as a result of changes in the intensity or in the direction of light.

a. During the early first stage-period no intensity of light used changes the index of the phototactic or of the photopathic response, but later an intense light may reverse the index of the phototactic reaction.

b. Throughout the second and third stage-periods, the index of the photopathic reaction is not reversible, but during the early part of these periods the negative phototactic reaction, and during the latter part the positive phototactic response, may be reversed temporarily by using light of great intensity (suddenly introduced).

c. During the fourth stage-period the negative phototactic response can not be reversed (except in such instances as are noted in Exp. 24, Cases 5 and 6), but the positive photopathic reaction of the early fourth stage-period may be reversed temporarily by using light of very great intensity.

d. None of the negative responses of the fifth-stage lobsters can be reversed by using light of any intensity whatsoever.

e. Submitting larvæ to darkness for periods of 2 to 12 hours does not change the index of reaction.

4. The reactions to light can be modified by other factors; contact-irritability is first manifested in the middle or later part of the fourth stage-period, and henceforth determines (about equally with light) the behavior of early adolescent lobsters.

5. Laboratory experiments explain some of the aspects of the behavior of the young lobsters under natural conditions of environment: (1) The positive photopathic reaction, and the positive phototactic reaction (to lights of very great intensity) together with the response to food stimuli may unite in determining the surface-swimming of the early fourth-stage lobsters. (2) The negative photopathic reaction, the negative phototactic reaction together with the response to contact-stimuli may unite in causing the late fourth, fifth and all later-stage lobsters to leave the surface water, and to burrow at the bottom of the sea.

6. The reaction of larval lobsters to light depends upon two factors; body-orientation and progressive orientation.

7. The body-orientation is invariably negative and is due to the difference in illumination of the two eyes of the larva. It is brought about by invariable reflex movements which tend to bring the longitudinal axis of the body parallel to the rays of light, with the head away from their source.

8. The progressive orientation may be either positive or nega-

tive, and is due to the position (extension or contraction) of the thoracic appendages. If these have the "anterior position," the reaction is positive; if they have the "posterior position," the reaction is negative. These positions appear to depend upon the intensity of light which strikes the posterior lateral surface of the eyes equally.

9. The larvæ orient to screens and backgrounds of black and of white by reflex movements identical with those by which they react to direct illumination and shading.

10. The reactions by which the body-orientation to light is produced, are invariable motor-reflexes, quite in accord with the local action theory of tropisms. The reactions by which the progressive orientation to light is produced, although appearing to be simple reflexes, are not invariable or constant, but dependent upon "physiological states."

11. In all the reactions to light (except the photopathic) the body-orientation is of primary importance, since progressive orientation cannot occur until the body-orientation has been established.

12. None of the reactions to light can be interpreted as "a selection from among the conditions produced by varied movements." They are not trial (and error) reactions, in the sense in which this expression is used by JENNINGS and HOLMES.

IX. LIST OF REFERENCES.

BELL, J. C.

1906a. The reactions of the crayfish to chemical stimuli. *Journ. of Comp. Neurol. and Psychol.*, vol. 16, p. 299.

1906b. Reactions of the crayfish. *Harvard Psychological Studies*, vol. 2, p. 615.

BOHN, GEORGES.

1905a. Impulsions motrices d'origine oculaire chez les Crustacés. *Bul. institut gèn. psychol.*, no. 6, p. 1–42.

1905b. Attractions et ocillations des animaux marins sous l'influence de la lumière. *Institut gèn. psychol. Memoirs*, i, p. 108.

GRABER.

1884. Grundlinien zur Erforschung des Helligkeits- und Farben-sinnes der Thiere. *Prag und Leipsig.*

HADLEY, P. B.

1906a. The relation of optical stimuli to rheotaxis in the American lobster. *Am. Journ. of Physiol.*, vol. 17, pp. 326–343.

1906b. Annual report of the Rhode Island Commission of Inland Fisheries for 1905, pp. 237-257.

1907a. Galvanotaxis in larvæ of the American lobster. *Am. Journ. of Physiol.*, vol. 19, pp. 39–51.

1907b. Annual report of the Rhode Island Commission of Inland Fisheries for 1906, pp. 181-216.

1908. Reaction of blinded lobsters to light. *Am. Journ. of Physiol.*, vol. xxi, pp. 180–199.

HERRICK, F. H.

1896. The American lobster. *U. S. Fish Commission Bull.*, vol. 15, pp. 1–252.

HOLMES, S. J.
1901. Phototaxis in Amphipods. *Am. Journ. of Physiol.*, vol. 5, p. 211.
1905. The selection of random movements as a factor in phototaxis. *Journ. of Comp. Neurol. and Psychol.*, vol. 15, p. 98.
HOLT, E. B. AND LEE, F. S.
1901. The theory of phototactic response. *Am. Journ. of Physiol.*, vol. 4, p. 460.
JENNINGS, H. S.
1906a. Behavior of the lower organisms. *The Macmillan Co., New York.*
1906b. Modifiability in behavior. II. Factors determining direction and character of movement in the earthworm. *Journ. Exper. Zoöl.*, vol. 3, pp. 435–455.
KEEBLE, F., AND GAMBLE, F. W.
1904. The color-physiology of higher Crustacea. *Philosophical Transactions of the Royal Society of London*, Series B, vol. 196, pp. 295–388.
LOEB, J.
1893. Ueber künstliche Umwandlung positiv heliotropischer Thiere in negativ und umgekehrt. *Arch. d. ges. Physiol.*, vol. 56, p. 247.
1905. Studies in General Physiology. *Decennial Publications of the University of Chicago.*
LUBBOCK, SIR JOHN.
1881. On the sense of color among some of the lower animals. *Journ. Linn. Soc.*, vol. 16, p. 121.
LYON, E. P.
1906. Note on the heliotropism of Palæmonetes larvæ. *Biol. Bull.*, vol. 12, p. 21.
MINKIEWICZ, R.
1906. Sur le chromotropisme et son inversion artificielle. *Comptes Rendus de l'académie des Sciences, Paris*, Nov. 19, 1906.
PARKER, G. H.
1902. The reactions of copepods to various stimuli and the bearing of this on daily depth migrations. *Bull. of the U. S. Fish Comm. for 1901*, pp. 103–123.
PEARL, R.
1904. On the behavior and reactions of Limulus in early stages of its development. *Journ. of Comp. Neurol. and Psychol.*, vol. 14, p. 138.
SCHOUTEDEN, H.
1902. Le phototropisme de Daphnia magna. *Annales de Société entomologique de Belgique*, vol. 46, pp. 352–362.
SPAULDING, E. G.
1904. An establishment of association in hermit crabs. *Journ. of Comp. Neurol and Psychol.*, vol. 14, pp. 49–61.
YERKES, R. M.
1899. Reactions of entomostraca to stimulation by light. *Am. Journ. of Physiol.*, vol. 3, pp. 157–182.
1903. Reactions of Daphnia pulex to light and heat. *Mark Anniversary Volume*, pp. 361–377.