10.—ON THE INFLUENCE OF LIGHT ON THE PERIODICAL DEPTH-MIGRATIONS OF PELAGIC ANIMALS.

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As is now well known, the animal life in the ocean and of fresh-water lakes is confined chiefly to two regions, one extending from the surface of the sea to a depth of about 400 meters, the other being the ground region of the ocean. We know, moreover, that a good many of the surface animals migrate periodically in a vertical direction, coming up to the surface during the night and going downward during the daytime, but not deeper than 400 meters. For the physiologist the question arises what determines this peculiar vertical distribution and periodical migration of marine animals. My investigations concerning the effects of light on the motion and orientation of animals made it certain that this periodical depth migration of sea animals is determined to a certain extent at least by the light. In order to make this clear I must give a short sketch of the way in which the light determines the orientation and motion of animals.

You all know that many animals, like the moth, for instance, go towards the light. It was believed that this was due to an attraction of the animals by the light, or at any rate that these animals liked the light; other animals show the opposite reaction, they go away from the light, and it was generally believed that these animals were fond of the dark. My experiments, however, showed that these reactions are the outcome of a purely mechanical effect of the light upon the animal, and that the animal, as a rule, is neither fond of the light nor of the dark. The light forces the animal to orientate itself in such a way that its symmetry axis or symmetry plane falls into the direction of the rays of light, and consequently all symmetrical elements of the surface of the animal are met by the rays of light at the same angle. There remain two possibilities: The animal in this orientation can turn either its oral pole or its aboral pole toward the source of light. In the former case I have called it positively, and in the latter case negatively heliotropic.

In the case of animals which are fixed to the ground, like hydroids, for instance, the only effect of the light consists in this orientation of the animals. But in the case of animals which are free-moving, like insects or copepods, the animal is orientated by the light, and is forced to move in this orientation. The consequence is that if the animal is positively heliotropic it must necessarily move straight toward the light. If the animal is negatively heliotropic it must move straight in the opposite direction. That the motion of the animal is determined by the direction of the rays of light, and not by the differences in the intensity of the light, can be very easily shown. Positively heliotropic animals, like plant lice, move towards the source of light even then, if by certain experimental arrangements their path goes from lighter to darker places; and negatively heliotropic animals go from the light even then, if measures are taken so that their way leads them from the dark to the light. But in both cases the animal migrates in the direction of the rays of light. An illustration will show this influence of the direction of the rays of light better than a long theoretical explanation.

Spirographis spallanzani, a marine annelid, lives in a tube which it fastens to the ground. The tube is not transparent and only the tentacles of the animal, which project from the tube, are exposed to the light. The tentacles are arranged in a circle. If we put these animals into an aquarium in which the light falls in from only one side the animal bends its tube in such a way that the symmetry axis of the circle of tentacles is parallel to the direction of the rays of light. As long as we do not change anything in the direction of the rays of light which strike the animal, it does not change its orientation, but as soon as we cause the light to fall into the aquarium from another direction the *Spirographis* changes the direction of its tube so that the symmetry axis of its tentacles is again parallel to the rays of light. Whether the intensity of the light is great or small, whether we use direct sunlight or diffused daylight, the result remains the same.

The larvæ of *Limulus* at a certain period of their life are negatively heliotropic If we put such larvæ into a glass dish and place it near a window through which the rays of sunlight fall in obliquely, the *Limuli* migrate with mathematical exactness in the direction of the sunlight away from the window as far as the sides of the dish allow them to go, and then they remain at rest. If, however, we turn the dish 180 degrees around its vertical axis the animals move again in the direction of the rays of light going away from the window. It is not possible to give you here a full account of the experiments by which it can be proved that the direction of the rays of light alone determine the direction of the motions of the animals, nor is it possible for me to give you here the theory of animal heliotropism. For both I must refer you to my former publications. I only wish to show how this heliotropism determines the periodical depth migrations of pelagic animals.

It is known that the nauplii of *Balanus* appear at the surface of the sea at night and go down during daytime to a depth of 60 fathoms and more. Groom and I found that the nauplii of *Balanus perforatus* show a very peculiar heliotropism. They are positively heliotropic when the light is very weak; but when they are exposed to strong light they very soon become negatively heliotropic. This explains the periodical migration. In the evening, and very often during the night, the light which is reflected from the sky is very weak, and in this light the nauplii are positively heliotropic. As only the vertical components of the rays of light can take effect, the horizontal ones annihilating each other, the animal is forced to move vertically upwards to the surface. At daybreak, as soon as the light becomes sufficiently intense, the animal, by the influence of the light itself, becomes negatively heliotropic and must go vertically downwards. But why does it not go to the bottom of the sea? You know that the water absorbs light and the deeper we go downwards into the ocean the less the intensity of the light becomes.

Investigations of Forel and others have shown that at a depth of about 400 meters below the surface the intensity of the light is already so small that on a bright day it hardly affects longer the most sensitive photographic plate. Thus the nauplii which, under the influence of intense light, have become negatively heliotropic on their migration downwards, very soon must reach a depth where the light is so weak that they become positively heliotropic again, and necessarily must begin to move upward. But as soon as they come back into stronger light they become negatively heliotropic, and must go downward again, and so on. So it happens that these animals, by the influence of the light, have to migrate periodically—during the night toward the surface, during daytime downward, but no deeper than 400 meters below the surface.

Later on, at Woods Holl, I tried to find out whether it was not possible to make other pelagic animals at desire positively and negatively heliotropic. I found that this could be done easily in copepods and larvæ of *Polygordius* in different ways; for instance, by the influence of the light itself. Direct sunlight made positively heliotropic larvæ of *Polygordius* negatively heliotropic within one or two minutes, but only as long as the temperature was above 10° C. In these experiments great care was taken to keep the temperature of the animals constant. But when the temperature of the water in which the animals were kept was brought down to 7 degrees or less the most intense sunlight was not more able to make the animals negatively heliotropic. On the other side, at a temperature of about 30 degrees, the animals remained permanently negatively heliotropic, even in the weakest light. I found similar phenomena in copepods. These facts, it seems to me, must have some bearing upon the depth migration of sea animals. At the surface of the Mediterranean, for instance, the temperature rises to a considerable height in summer. The consequence is that animals of a similar heliotropism, like the larvæ of *Polygordius* or copepods, can not more come to the surface even at night, for the high temperature at the surface makes them negatively heliotropic even toward weak light, which in winter time would make them move towards the surface. But on the other side it is clear that these animals can not go down to the bottom of the sea. The temperature of the water decreases with increasing depth, and as soon as these animals on their migration downward come to water which is sufficiently cool they become positively heliotropic again and now have to go upward; but this brings them back to warmer water, where they become negatively heliotropic again, etc. The investigations made at the zoölogical station at Naples have shown, indeed, that certain pelagic animals which in winter come up to the surface during the night, in summer always remain at a certain depth below the surface. These few examples may suffice to show how the light can determine the periodical depth migrations of pelagic animals.

It is unnecessary to say that it is impossible to exhaust this subject in so short a time. But in order to prevent misunderstandings I must mention that I do not believe that light is the only physical influence which determines depth migrations of sea animals.

As I have shown in former papers, gravitation, for instance, coöperates with light to bring about these periodical depth movements of pelagic animals as well as the constant distribution of sea animals.

It has been found that the jelly-fish which had been carried by the Gulf Stream from our latitude to the region of the midnight sun, continued to migrate to and from the surface in the same periodicity as they did in their former home. In this case I believe the periodical depth migration is due to periodical changes in the amount of water contained in the animal. These changes are due to metabolic processes which, however, are influenced in their periods by the change of day and night. Thus these metabolic changes adapt themselves in their periodicity to the change of day and night and this periodicity remains the same even if the animal later on is carried to the region of the midnight sun.