THE RHYTHMICAL MOVEMENTS OF LITORINA LITOREA SYNCHRONOUS WITH OCEAN TIDES.[1]

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INTRODUCTION.

Through the kindness of Dr. Sumner, the writer was given an opportunity to work in the laboratory of the Bureau of Fisheries at Woods Hole, Mass., during the summer of 1907. He is indebted to Dr. Sumner for many valuable suggestions.

The purpose of the present paper is to show that the movements of *Litorina litorea*, which are synchronous with ocean tides, are not due, directly, to either geotropism or phototaxis but to the action of the film of water on the more or less exposed snails. In arriving at this conclusion many experiments were performed not only in the laboratory but also under natural conditions. In addition, the exact habitats of three species of *Litorina* were studied in detail. Such observations are necessary when the natural oscillations of *Litorina*, which correspond to the rise and the fall of the tides, are to be considered.

Lastly the writer will attempt to show that *Litorina litorea* does not retain a rhythm, which is synchronous with the tides, either in quiet aquaria or in nature when the effects of films of water have been removed by keeping the snails permanently submerged.

I. THE HABITAT OF *Litorina*.

(*a*) Individuals of *Litorina rudis* are as a rule found on rocks which lie between the tidal marks, but occasionally an individual occurs on rock weeds and even on the muddy shore. This species was abundant everywhere in the region of Woods Hole, excepting in Grape and Tashmo ponds, both of which are brackish.

(*b*) Individuals of *Litorina palliata* live as a rule on rock weeds which grow between the tidal marks. This species was not encountered at Nobska Point or in Grape, Lagoon and Tashmo

[1] The final preparation of this paper has been delayed on account of the writer's long trip in South America for the Carnegie Museum. Only the more important results are stated and many of the details have been omitted.

ponds. It is always more abundant along protected coasts and hence its absence from Nobska Point, which is exposed to the open sea, was to be expected.

(*c*) Individuals of *Litorina litorea* (said to have been imported to the American coast from Europe) usually live on rocky surfaces which lie between the high-tide mark and one foot below the low-tide mark. The species was not found in Tashmo Pond but a few young individuals were seen in Grape Pond living on transplanted oysters. This observation, taken in connection with others described below, indicates that the absence of *Litorina* from these brackish ponds was not due, directly, to the lower specific gravity that exists there.

In order to explain the restricted distribution of *Litorina* the following observations and experiments were made:

A. *Food.*—*Litorina palliata* is nearly always found on two common species of rock weeds, and its supply of food is doubtless associated with these plants, while *Litorina rudis* and *litorea* eat small green algæ which grow more abundantly on the rocks which are situated between the tidal marks.

When individuals of *Litorina litorea* were placed in shallow aquaria, which contained rocks from the sea shore, from Lagoon Pond or from the street and contained also pieces of glass and fish they came to nest for the most part on the rocks taken from normal sea water. The snails, which were taken from the entrance to Lagoon Pond with their accompanying rocks, also settled on the sea rocks.

B. *Salinity.*—When individuals of *Litorina litorea* were placed in a mixture of equal parts of fresh and sea water, they were able to crawl about; but when they were placed into a mixture of two parts fresh and one part sea water, all died within eight days. When they were placed in sea water, to which as much as fourteen grams of sun evaporated sea salt had been added to each 800 c.c. of sea water, all died within eight days. The specific gravity of the various test solutions indicated that *Litorina* could live in water which has a lower specific gravity than was observed in Grape and Tashmo ponds.

C. *Temperature.*—The variation in the temperature along the coast did not appear to affect the distribution of *Litorina*. Snails

were subjected to much greater changes of temperature than occur along the coast and no observable effects were detected.

D. *Pressure.*—Several individuals of *Litorina litorea* were submerged in cages, which contained sea shore rocks, to a depth of 8, 18 and 30 feet of water. Two weeks later the snails appeared to be perfectly normal.

E. *Aeration.*—*Litorina litorea* is very sensitive to slight changes in aëration and consequently it is very difficult to arrange the condition in an aquarium so that they behave normally.

F. No direct effects of light on the distribution of *Litorina* could be detected either by experiment or direct observations made in nature.

G. *Waves.*—When individuals of *Litorina litorea* are violently splashed by waves, they become quiescent.

H. *Character of the Surface.*—Individuals of *Litorina litorea* are rarely found on either sand or mud, due in part to the absence of food in such places and in part to the difficulty encountered in crawling over such surfaces. This is especially true when the waves constantly change the position of the same and hence tumble the snails about at random.

I. *Moisture.*— *Litorina litorea* does not crawl on dry surfaces.

II. Factors which Determine the Movements of *Litorina*.

It appears evident from the preceding data that the character of the surface, moisture and food are the chief factors which determine the litoral distribution of these snails. But as I hope to demonstrate in the following pages, these three factors produce random movements of the snails and should not be confounded with the factors which directly produce rhythmical movements corresponding to the rise and fall of the tides.

The following experiments and observations will, I think, determine what the "directive force" of rhythmical movements is.[1]

1. The snails which are located on flat horizontal surfaces between the tidal marks do not show rhythmical movements which correspond to those of the tide. The snails which are located or placed below the low-tide mark on either a vertical or a horizontal surface do not show rhythmical movements.

[1] The majority of the experiments are easily performed along the seashore by marking the snails and the stones.

But the snails which are located on any more or less vertical surface between the tidal marks do exhibit rhythmical movements which correspond to those of the tides.

2. When a stone, which has snails crawling on a flat surface below the low-tide mark, is raised and lowered in the sea, the snails do not show rhythmical movements which correspond with those of the stone, *i. e.*, their movements were not directive. The same results are obtained when, with the flat surface horizontal, the stone is raised out of and lowered into the sea. But when, with the surface vertical, the stone is raised out of and lowered into the sea, the snails at once showed rhythmical movements which correspond to those of the stone. These same snails were known (from observations made on snails placed between the tidal marks and below the low-tide mark) to have shown in some cases and not to have shown in other cases rhythmical movements during several days previous to the experiments. Therefore any alleged retained rhythm has nothing to do with the above results.

Even more interesting is the fact that when, with a vertical surface, a stone, upon which snails were crawling at random, was raised out of the sea, the snails always followed the vanishing film of water even when the vertical surface was rotated through an angle of 180°. In this case the rotation of the vertical surface would reverse the direction of motion of the film of water and the snails would at once turn around and follow it. But if most of the water was previously removed from the surface of the stone, in order that the film might entirely disappear before the snails (which were crawling downward in the direction of the vanishing film) had reached the lower surface, and if, as the film was drying up, the vertical surface was rotated through an angle of 180°, the snails continued to crawl for some time in the direction in which they had started. In other words, the snails crawled upward instead of downward. They continued to crawl thus until the rough surface, food and moisture either deflected or stopped their movements. In the above experiment, the mere turning of the moist but filmless surface through an angle of 180° does not seem adequate to reverse at once the reaction to gravity and light, if either of these have a direct influence on the rhythmical movements of *Litorina*.

3. When the eyes of *Litorina litorea* are destroyed, they still show rhythmical movements, on vertical surfaces between the tidal marks. Individuals of *Litorina litorea* also oscillate with the tides during dark nights.

4. During the months of July and August, the writer could not detect any relative change in the position of snails on large boulders. If phototaxis is an important factor, a marked change would be expected because the daily lagging of the tides as well as the diurnal and monthly changes of the relative solar position of the earth, constantly change the relative angle of the rays of light.

5. When it rains on exposed snails, they become quiescent just as they do when splashed by the water. Therefore during stormy as compared with fair days, a considerable difference in the amount of oscillations of *Litorina litorea* was noted.

6. Submerged snails could be only slightly or not at all directed by currents of water. The currents were produced artificially and also by moving stones with snails through the water. Hence the behavior of *Litorina* on vertical surface between the tidal marks is not of a rheotropic nature.

7. When individuals are left high and dry on vertical surfaces during low tide, they come to rest "directed upward," *i. e.*, with their head end toward the sky. This is true for all sides of the stones and is obviously due to the shape of the aperture of the shells which makes it far easier for exposed individuals to cling thus to vertical surfaces.

8. Individuals of *Litorina litorea* are on an average found slightly higher on the north side of large boulders than on the south side. This appears to be due to greater moisture and a higher growth of both algæ and barnacles over which snails crawl with difficulty.

9. Some bottles partly filled with water and air plus hydrogen and others partly filled with carbon dioxid were used to test the effect of crawling out of the water into a gaseous medium and vice versa. No differences were detected from that of crawling out of water into the atmosphere unless so much hydrogen and carbon dioxid were used that the snails were asphyxiated.

10. Thin films of olive oil and kerosene were placed on water

in aquaria to test the effect of surface tension. Under these conditions the snails had considerable difficulty in breaking the surface film and always hesitated at the surface pushing themselves to the right and to the left until their bodies were elevated sufficiently to break the surface tension. Their behavior under the above condition showed that the hesitation on entering and leaving the surface was due to the surface film and not to phototaxis, hydrotaxis or chemotaxis.

11. When individuals of *Litorina litorea*, *rudis* and *palliata* were placed in a small round aquarium equal areas of which were painted brown, yellow and dark olive, they as a rule came to rest on the dark olive sector, rarely stopped on the brown sector and still more rarely on the yellow sector. When the same snails were placed in a similar unpainted aquarium before a window, about one half of them came to rest on the lighter side and half on the darker side. The position of the aquaria were interchanged and the same results were obtained. Various shading experiments were tried and neither positive or negative phototaxis could be detected. In nature one sees snails crawling at random from lighter areas into shaded areas and vice versa.

The writer was unable to detect why the snails stopped on the dark olive sector, but inasmuch as such conditions are not met on vertical surfaces of stones between the tidal mark, the results appear to have nothing to do with the rhythmical movements of *Litorina*.

12. Many snails were placed in quiet aquaria and aquaria in which running water was kept at a constant level and they never exhibited any signs of oscillations which corresponded to those of the tides. In these experiments, snails which were known to have been previously oscillating with the tides were used. I also placed snails, which had been oscillating with the tides, on vertical surfaces below the low tide mark and an average of many counts did not show rhythmical movements which corresponded to those of the tides.[1] Only when the snails are touched by the surface film of water are directive movements called forth.

[1] Morse has recently obtained a similar result.

Discussion.

Mitsukuri ('01) found that the roughness of the surface scatters the snails and that they never crawl on dry surfaces. He also stated that *Litorina exigua* hesitated on entering the water and concluded that their oscillations with the tides were due to phototaxis. In this connection the writer found that the snails hesitated as much on leaving the water as they did on entering it. This fact, taken in connection with several of my experiments and especially those on surface tension, show that the observed hesitation was due to the effect of the surface-film of water and not to phototaxis.

Bohn ('05) also concludes that phototaxis is the important factor which determines the oscillatory movements of *Litorina*. He states that *Litorina rudis*, *obtusata* and *litorea* have for all their lives been desiccated again and again, and when placed in quiet aquaria, all three species retained a period of rhythm synchronous with the tides and lasting from thirteen hours to fourteen days. My observations show that *Litorina litorea* does not have such an established rhythm.

The behavior of *Litorina* in experiment 2 is sufficient to show that the "directive force" in their rhythmical movements synchronous with the tides is the film of water and not phototaxis. Also the fact, that only snails on vertical surfaces between the tidal marks have oscillatory movements, shows that the directive force is not phototaxis because many snails on flat horizontal surfaces could crawl to the edge of the surface and descend to the base of the stone. Especially the observations made during dark nights as well as many other experiments already cited indicate that Bohn's view is untenable.

Conclusion.

In conclusion, then, it appears that submerged individuals of *Litorina litorea* crawl about on large stones at random, perhaps in search of food. They never crawl on dry surfaces and consequently are not found above the high-tide mark. When the tide rises, the environment is temporarily enlarged and consequently many submerged snails on more or less vertical surfaces by mere chance will crawl up higher.

The individuals which were previously left high and dry are already directed upward and hence follow the rising tide. Before maximum high tide is reached, the unevenness of the surface along with the presence and absence of food scatter the snails at random because the rapidly rising tide soon submerges them and then there is no "specific directive force."

When the tide begins to fall some of the snails are already crawling downward and those that are not will be directed thus by the surface film. During a falling tide, some snails are crawling down beneath the surface, some with the surface, and some above the surface. As the tide falls lower and lower, many snails lag behind more and more until they are finally left on filmless surfaces under which conditions there is no specific directive force and such snails are left exposed. This lagging appears to be due to feeding, rough surfaces, rough sea, rapid fall of the tide and the more rapid desiccation on certain days. As a result of all these factors the amount of oscillation varies from day to day.

The snails on either flat horizontal surfaces between the tidal marks or on any kind of a surface below the low-tide mark have no "specific directive force" and consequently do not exhibit oscillatory movements synchronous with the ocean tides.

Summary.

1. *Litorina rudis*, *palliata* and *litorea* are found in definite zones.

2. Individuals of *Litorina litorea*, located on vertical surfaces between the tidal marks, exhibit oscillatory movements which correspond to those of the tides but they do not exhibit such movements when they are located either on flat horizontal surfaces between the tidal marks or on any kind of a surface below the low-tide mark.

3. The primary directive force for rhythmical movements is the surface film of water. The secondary directive forces are the quiescent position of desiccated individuals, character of the surfaces, moisture and food.

4. *Litorina litorea* has no established rhythm in the absence of tidal changes.

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