generally eats only microscopic foods and those macroscopic algae small enough to be consumed entire or nearly so. The reasons for this are not clear, but may be related to the structure of the mouth or the preference for certain types of substrates. *Littorina scutulata* is frequently found eating macroscopic algae, especially *Cladophora, Pelvetia,* and other more easily ingested forms. The effects of this feeding are probably important in limiting the spread of new plants, and the effects on established thalli, while probably considerable in some instances, appear to vary greatly with the species of algae.

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Function of the Cephalic Tentacles in *Littorina planaxis* Philippi

(Gastropoda : Prosobranchiata)

BY

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(10 Text figures)

In Fretter & Graham (1962, p. 14), the following description is given for part of the sensory apparatus in the snail *Littorina littorea:* "Toward its posterior end the head carries a pair of laterally placed tentacles. . . . At the base of each is a cushion-like bulge. . . . This is the eye stalk, and the dark spot on it is the eye. The tentacle, which is tactile and olfactory, is thus the seat of three major senses." The snail *Littorina planaxis* (Philippi, 1847), common along the California coast, has tentacles very similar to those described for *L. littorea.* Studies have revealed that the eye definitely is a light receptor and causes the animal to respond predictably to various light stimuli (Dieter Eckert, personal communication). However, the portion of the tentacle distal to the eye has not undergone extensive investigation, and tactile and olfactory capabilities of this part of the organ are undetermined. In April and May, 1964, studies were carried out at the Hopkins Marine Station of Stanford University, Pacific Grove, California, to determine the behavior and function of that part of the tentacle extending beyond the eye in *L. planaxis.*

The two cephalic tentacles are situated at the sides and slightly back of the large blunt snout. The organs are contractile, and when contracted they fit snugly at the sides of the mouth. Upon extension, they appear as delicate finger-like structures which exhibit movement patterns that vary depending on the substrate or environmental condition the animal has encountered. They are innervated from the cerebral ganglion.

The tentacles are used by the animal as a main guide to its movements in the rocky areas which it so abundantly inhabits. The snail moves primarily during the lower temperatures at night and in the film of moisture provided by high tide and surf, with the tentacles generally remaining on the stony substrate and slowly moving from side to side. As the moisture decreases, or as obstacles are encountered, the organs begin an up and down pattern of movement, with the snail touching the substrate and immediately lifting the tentacle usually no more than one to one and a half millimeters. When the snail reaches an obstacle in its path, it undertakes a tactile survey of the impediment by extending the organs to their full tapering length and moving them about. When the animals are submerged, tentacular movement is usually restricted to a continuous motion from side to side, in contact with the substrate. In any circumstance, movements of the two tentacles may either be highly coordinated, as in horizontal swaying motions, or one tentacle may move completely independently of the other.

In order to determine more precisely the functions of the cephalic tentacles, I extirpated the organs in a group of *Littorina planaxis* and compared their responses with those in a group of normal snails under various conditions. It was necessary to anesthetize the animals prior to removing the tentacles. An aqueous solution of magnesium chloride isotonic with seawater proved to be superior to 1% propylene phenoxetol (Owen & Steedman, 1958), 1% chloral hydrate (Sivik, 1953), and 10 parts/million Sevin (Carriker & Blake, 1959) for the purposes of this investigation. Having adequately relaxed the animals, I could easily pull the head a good distance from the shell and snip off the entire tentacle distal to the eye with a pair of iridectomy scissors. The snails were then placed in normal seawater for recovery. In all instances, the operated snails exhibited activity similar to that of the normal snails. The wound appeared healed after two or three days, and operated animals placed in the field resumed normal activity and would occasionally be noted traveling three to five feet during a very moist night.

The following experiments and observations were carried out to compare the responses of normal snails with those of snails in which the tentacles had been removed.

GENERAL MOVEMENT AND RIGHTING

In the laboratory, the *Littorina planaxis* without cephalic tentacles did not exhibit striking locomotive inabilities. Glass dishes were used for all of the tests, and in practically every instance the animals that had been operated on travelled across the smooth surface at approximately the same speeds as the normal ones. When encountering obstacles, however, a definite difference in reaction was noted. A normal snail, with its tentacles exploring the substrate immediate in its path, would reach an object, touch it with the tentacles, and stop before bumping into it with the shell. On the other hand, a tentacleless snail would encounter the obstacle, bump into it with the shell, and continue for a time as if trying to push the object over. If the impediment happened to be another snail, the animals without tentacles could climb onto the shell, although observably slower than a normal animal.

To see if a lack of the tentacles produced an impairment to the ability for righting, I placed about 180 snails with tentacles and a like number without tentacles on their backs in glass bowls containing fresh seawater. They were

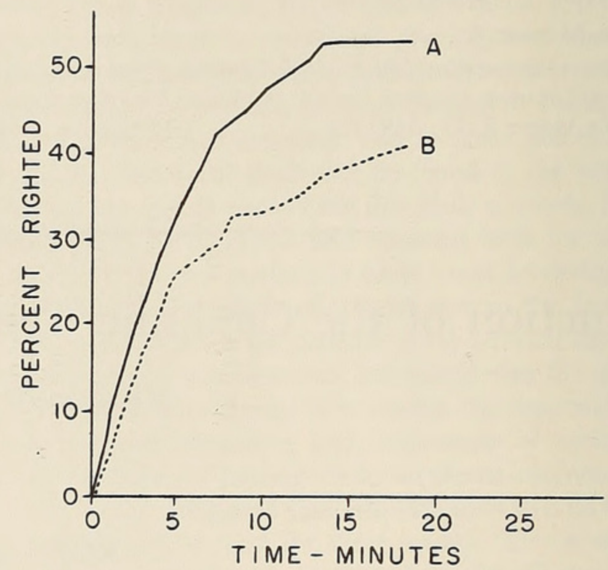

Figure 1: Rate of righting in *Littorina planaxis.*
A - normal snails (n = 180); **B** - snails with tentacles removed (n = 180).

then timed from entry into the water until righted, at one minute intervals. The results, shown in Figure 1, indicate that of the animals which did complete the maneuver, the normal *Littorina planaxis* were slightly quicker. Further corroborating evidence that the snails are tactically dependent upon the organ for righting is that a fewer number of tentacleless animals than normal ones completed righting after trying.

RESPONSE TO WATERBORNE EXTRACTS OF *Acanthina spirata*

When the predaceous inter-tidal snail *Acanthina spirata* is introduced into a dish containing normal *Littorina planaxis,* a definite evacuation from the area of the larger snail will be detected within minutes. This response to the predator is induced through the effects of a waterborne chemical stimulus that issues from the *A. spirata,* probably produced in association with its mucus (Kenneth Tittle, personal communication). To determine if the point of reception for this stimulus is the cephalic tentacle or if removal of the organ in any way affects the response, animals with and without tentacles were tested in the following manner.

From approximately the same area in the field, 100 *Littorina planaxis* were collected and the total population was anesthetized in isotonic magnesium chloride. After about an hour, the tentacles were removed from one half of the animals. After the operations, all of the snails were placed in fresh seawater for recovery. Three to four hours later the *Littorina* appeared totally recuperated and were then subjected to the tests. Two finger bowls were placed side by side, each containing 100 ml of seawater. In one bowl, five normal animals were placed and five animals lacking tentacles in the other one. Both groups were timed to determine the tendency to leave normal seawater. After 20 minutes, the snails were placed back into the center of the bowl, and 20 ml of seawater were added from a jar which had contained 30 *Acanthina spirata* in 180 ml for two days. Evacuation from the bowls was again timed and an accelerated departure from the water in both bowls was observed. To determine whether or not the animals were merely leaving the extract containing water because of having been replaced into water after

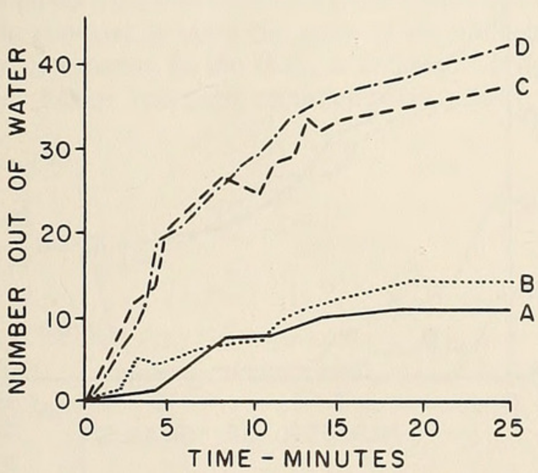

Figure 2: Response to waterborne extracts of *Acanthina spirata.* A - normal animals in untainted seawater; B - extirpated animals in untainted seawater; C - normal snails, response to *Acanthina spirata;* D - extirpated snails, response to *Acanthina spirata.* In each test n = 50

an initial departure, several tests were run with snails placed directly into the *A. spirata* water. Differences in response in the two instances were negligible. Identical runs were performed for the entire test population, using fresh seawater and *A. spirata* extract from the same jar each time.

Results of all trials are summarized in Figure 2, and show that the escape responses in normal *Littorina planaxis* and in the animals lacking tentacles were almost identical. It is therefore evident that the cephalic tentacles are not critically important as chemo-receptors in the detection of *Acanthina spirata* at a distance under water.

RESPONSE TO WATERBORNE EXTRACTS OF FEMALE *Littorina planaxis*

If water that has contained a group of female *Littorina planaxis* is added to water containing normal males of the same species, within a short period definite clustering and increased activity can be noted (Karin Rohe, personal

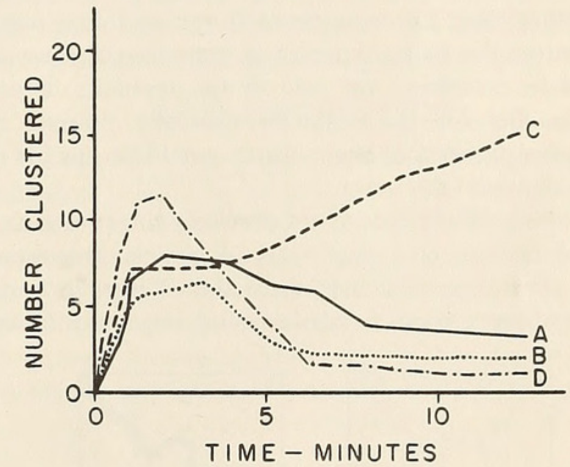

Figure 3: Response to waterborne extracts of female *Littorina planaxis;* A - normal males in untainted seawater; B - extirpated males in untainted seawater; C - normal males, response to female extract; D - extirpated males, response to female extract. In each test, n = 50.

communication). To determine if the cephalic tentacles were pertinent in detecting this waterborne molluscan aphrodisiac, tests similar to the *Acanthina spirata* experiment were set up, using the same general procedure as described. In one bowl containing normal seawater were placed five normal males; in a second bowl, also containing seawater, five males lacking tentacles were placed. At one minute intervals clustering tendencies were timed by recording the number of snails in contact with other animals, either side by side or one on top of another. Following this, 20 ml of seawater, taken from a jar containing approximately 200 ml of water in which 25 female snails had been kept for four hours, was added to each bowl. Again the number of clustered animals versus time was noted. Tests were run on 50 normal and 50 operated individuals.

Results of all tests are summarized in Figure 3. All snails, both experimentals and controls, showed some initial tendency to pair and thus form clusters. However, this tendency is short lived except in the normal males exposed to female extract. Perhaps the reason the response is not sustained in extirpated males is that once the animal has climbed onto the back of another snail, he lacks the probing equipment necessary to determine the sex of his partner or to assume the correct position. The results again suggest that the tentacles do not play a role in chemo-reception, though they appear necessary for definite sex recognition on contact.

RESPONSE TO MUCUS TRAILS

It has been observed (Allan Miyamoto, personal communication) that *Littorina planaxis* tend to follow mucus trails across the rocks. A series of experiments were developed to determine the role of the tentacles in such behavior. Because the tentacles tactically precede the animal, it appears that these organs would be apt for detection of trails.

By cutting off the foot of a *Littorina planaxis* and dabbing the structure on a glass plate, an artificial mucus path can be applied as depicted by the dotted lines in Figure 4a. Two normal male *L. planaxis* and two males lacking

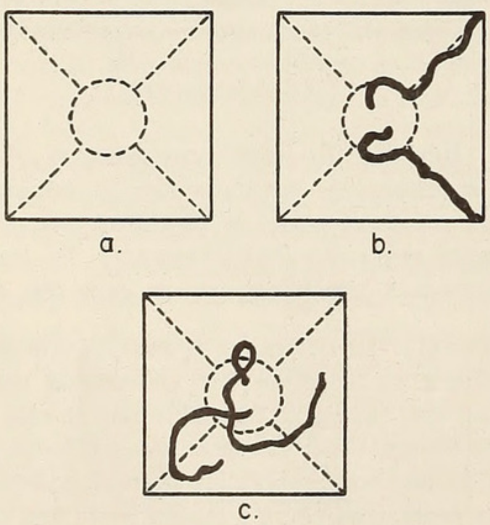

Figure 4: Response to mucus trails. a - pattern of mucus applied on all test plates. b - example of movement recorded for two normal *Littorina planaxis;* c - example of movement recorded for two *Littorina planaxis* lacking tentacles.

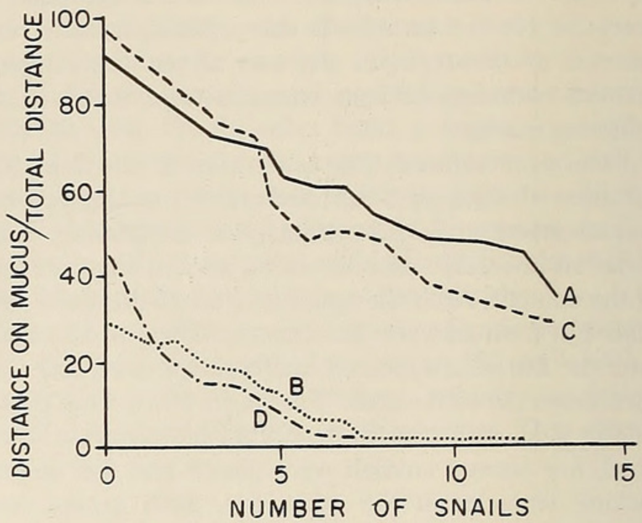

Figure 5: Relative tendency of male *Littorina planaxis* to follow mucus trails from male and female *Littorina planaxis;* A - normal male, response to female mucus; B - extirpated male, response to female mucus; C - normal male, response to male mucus; D - extirpated male, response to male mucus. In all tests, n = 10.

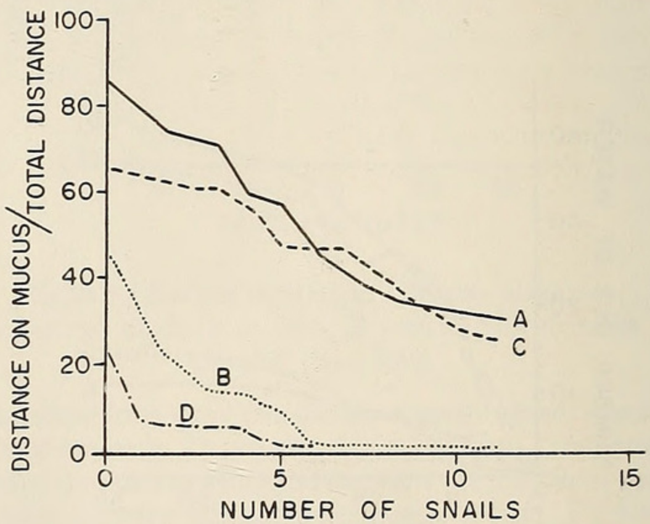

Figure 6: Relative tendency of female *Littorina planaxis* to follow mucus trails from male and female *Littorina planaxis;* A - normal female, response to male mucus (n = 8); B - extirpated female, response to male mucus (n = 8); C - normal female, response to female mucus (n = 6); D - extirpated female, response to female mucus (n = 6).

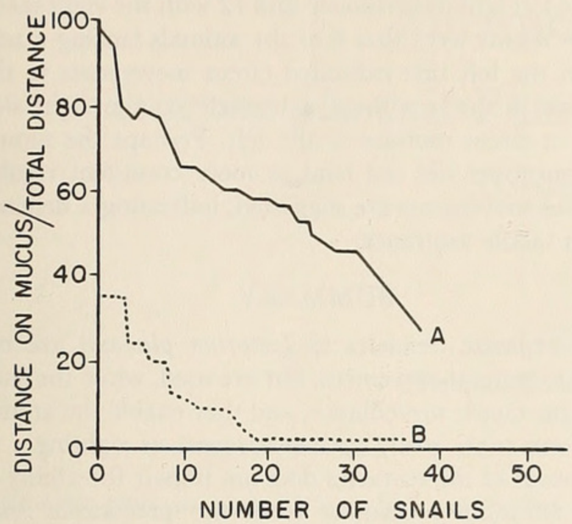

Figure 7: Tendency to follow mucus trails; composite results from Figures 5 and 6; A - normal *Littorina planaxis,* response to *Littorina planaxis* mucus; B - extirpated *Littorina planaxis,* response to *Littorina planaxis* mucus.

tentacles were placed respectively in the centers of two plates 6 by 6 inches square, each plate bearing mucus trails from female feet. The plates were then taken into a dark room and sprayed lightly and equally with seawater. After 15 minutes, the snails were removed and the glass plates were immersed in a dilute suspension of India ink in seawater to mark the paths of the animals during their movements in the dark, a technique designed by Dieter Eckert (personal communication, 1964). Experiments were carried out using each sex as a source of mucus and each sex as a test animal. Two specific examples of typical results obtained appear in Figures 4b, c.

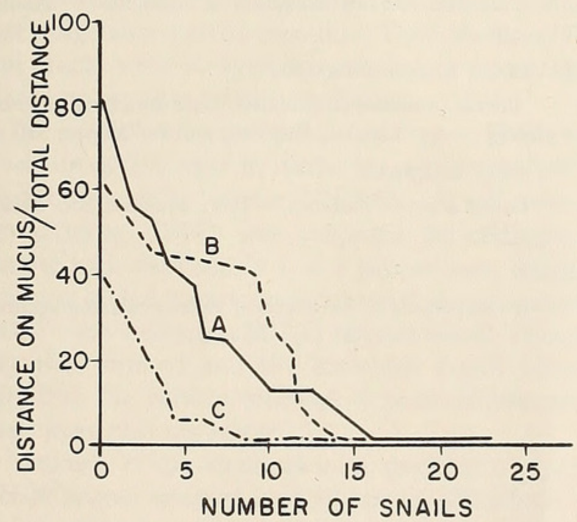

Figure 8: Relative tendency of normal *Littorina planaxis* to follow mucus trails of other inter-tidal snails; A - mucus of *Acmaea digitalis* (n = 16); B - mucus of *Acanthina spirata* (n = 12); C - mucus of *Tegula funebralis* (n = 8).

Figures 5, 6, and 7 summarize the results of all tests performed. They clearly indicate that the animals do employ their tentacles in following *Littorina planaxis* mucus trails, and that they follow trails regardless of the sex of the animal making the trail. This result suggested that perhaps the tentacles are sensitive to any mucus or material that noticeably changes the surface texture of the substrate. Therefore the mucus from several other intertidal molluscs was employed, using the same method as described. The results for this set of investigations is shown in Figure 8. In most cases it seems that the mucus from species living in close proximity to the *L. planaxis* populations exhibit properties close enough to the *Littorina* mucus to elicit at least partial following. Artificial trails made with methyl cellulose and granular mucin were tried, but neither provided positive results.

FIELD OBSERVATIONS

For observations concerning activities of both normal and tentacleless animals while in regular field conditions, 100 males and 100 females were taken from a large rock surface. All were anesthetized using magnesium chloride, the tentacles were removed from one half of the males and one half of the females, the animals were marked, and all were placed back on the rock in a large fenced area from which all other *Littorina* were removed. Reg-

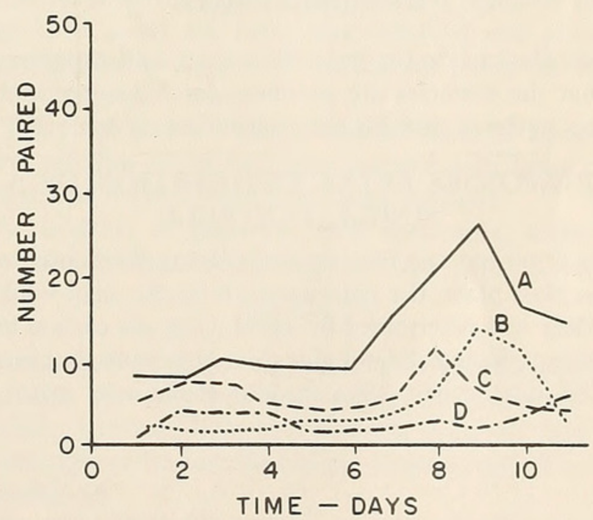

Figure 9: Pairing frequencies for all four combinations of normal males and females and males and females lacking tentacles. In the field, animals were considered paired when the male was on the back of a female; A - normal males on normal females; B - extirpated males on normal females; C - normal males on extirpated females; D - extirpated males on extirpated females.

ular daily observations were recorded pertaining to pairing, clustering, and single activity for 12 days. Figure 9 shows pairing frequencies for all four combinations of normal males and females and extirpated males and females. Field observations suggest that the males locate the females for copulation. Therefore Figure 10 shows the comparative pairing, with any type female, of normal and extirpated males. Both of these results indicate that the animals without tentacles, especially males, are less able to locate female *Littorina* for pairing. This result follows

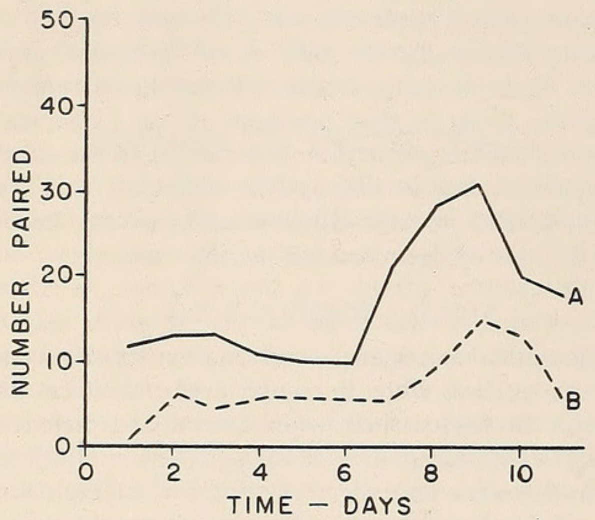

Figure 10: Pairing frequencies for normal and extirpated males, based on data of Figure 9; A - normal males; B - extirpated males.

the conclusions drawn from the mucus trail experiments, in that the tentacles are pertinent for following another mucus pathway and for sex recognition on contact.

RESPONSES AFTER EXTIRPATION OF A SINGLE TENTACLE

After removing one tentacle and placing the animal on a clean glass plate, the path assumed by the snail while in the dark was determined by again using the carbon bath. Such experiments did not give clear cut results, but merely hinted at tendencies. Twenty-four snails were tested, 12 with the left tentacle removed and 12 with the right taken off. The results were that 8 of the animals lacking a tentacle on the left side exhibited circus movements to the right, and 6 snails without a tentacle on the right side moved in circus motions to the left. Perhaps the nature of the substrate did not lend to more consistent results, but circus movements are suggested, indicating a dependency on tactile assurance.

SUMMARY

1. The cephalic tentacles of *Littorina planaxis* are not critical to general movement, but are used, while the snail moves, for tactile surveillance, and they enable the animal to perform more easily such maneuvers as righting.

2. Removal of the tentacles does not impair the ability to detect diffusible substances from the predaceous snail *Acanthina spirata* or from female *Littorina planaxis*.

3. The tentacles appear necessary for sex recognition on contact.

4. The tentacles are employed in following mucus trails on the substrate. The trails of other *Littorina planaxis* are followed more consistently than are trails laid down by other species of mollusks.

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