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MODIFIABILITY IN THE BEHAVIOR OF THE CALIFORNIA SHORE-ANEMONE *CRIBRINA XANTHOGRAMMICA* BRANDT

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INTRODUCTION

No feature of the behavior of sea-anemones has received more consideration from biological investigators than have the feeding reactions of these interesting animals. Yet there are few parts of their répertoire of responses about which there is more uncertainty existing than about the real explanation of their modified behavior in relation to food. It was with the idea of throwing additional light on this matter that the researches reported in this paper were begun. In the main, they were conducted in the zoological laboratories of the University of California. Many valuable observations were made during a two weeks stay at the Hopkins Sea Side Laboratory of Leland Stanford Jr. University.

The writer wishes to express here his thanks to Professor S. J. Holmes for the suggestion of the problem and for the kindly help and interest which he has contributed to the work. To Professor Harold Heath of Stanford University he acknowledges many courtesies during his brief stay at the Hopkins Sea Side Laboratory. For the identification of the material used he acknowledges his indebtedness to Professor H. B. Torrey of Reed College.

HABITAT AND HABITS

Cribrina xanthogrammica Brandt is the common shore anemone of the Pacific Coast of North America, and its recorded dis-

tribution ranges from Sitka, Alaska, to as far south as Panama. It commonly occurs in great masses, entirely covering the sides of rocks, and thus affording a great abundance of easily obtainable material. This species is relatively easily kept in good condition in the laboratory provided the sea water in the dishes is frequently changed and the animals kept in a cool room. The size of the individuals varies considerably, depending largely upon the age of the anemone. Individuals from a few millimetres diameter to several centimetres can be secured, though those about five centimetres in diameter were found most suitable for the greater part of the work presented in this paper.

At low tide, the thousands of *Cribrina* exposed on the rocks are in a contracted condition, retaining sufficient water to keep the body tissues in good shape in spite of the desiccation to which they are subjected. When the anemones are strongly stimulated, much of this water is expelled, finding its way out through the mouth opening, the tips of the tentacles, or of the tubercles with which the column and the edge of the disk are covered. Pickering has called attention to this habit in *Bunodactis artemisia* and Verrill has noted the same thing in *B. Dowii*. Torrey (1906) has observed this reaction in *Cribrina xanthogrammica*, and considers that "permanent openings probably exist, although difficult to find in sections." This response must occur quite frequently in the life of the animal, since any agency which causes a close contraction of the body must necessarily cause the discharge of the surplus water contained in the gastrovascular cavity. The expulsion occurs at the points of least resistance in the body, and it appears to me that the openings at these points represent temporary ruptures which in the economy of the individual are soon repaired.

The masses of this species of anemone when exposed on the rocks blend to a quite marked extent with the sand and gravel scattered around them. This is largely due to the habit which *Cribrina* has of attaching the tips of the tubercles distributed over the column of its body to small gravel, pieces of shell, spines of sea-urchins or any similar material with which they chance to come in contact. The concealing effect is often so great as to cause one to quite overlook large masses of material in the search for anemones. After the specimens have been

kept in the laboratory for a few days, these particles of foreign material are almost all shed. In the tide-pools, specimens in an expanded condition were injected with substances such as potassium chloride and beef juice, and in many cases, immediately dropped the attached pieces of debris. These facts would seem to indicate that a certain tonus of these tubercles is necessary for them to continue to hold the covering with which they have decked themselves. That there is a changed responsiveness in animals removed to the laboratory for a few days as contrasted with those remaining in the normal habitat is a fact too obvious to escape the notice of any one who has experimented with anemones. Bohn (1907) has made this fact clear in his discussion of the diverse factors influencing general responsiveness in several species of anemones on which he worked.

In tide-pools, numbers of anemones may be found expanded during the day, thus indicating that this species of anemone remains open under the influence of strong sunlight. This conclusion is further substantiated by the experiments on the light reactions of specimens kept in the laboratory.

FOOD

Many times the attempt was made to have specimens kept in the laboratory to accept stones and perfectly clean pieces of filter paper handled with clean forceps. The tentacles in many cases would adhere to the objects and incline towards the mouth opening, but not with any considerable vigor of response, and in every case, the proffered objects were eventually refused. No difficulty was experienced, however, in having the anemone take in pieces of filter paper soaked in oyster or clam juice.

When specimens in an expanded condition in the pockets among the rocks along the shore were given apparently clean stones loosened in the sea water around them, in dozens of cases, they grasped them with their tentacles and took them into the gastrovascular cavity. One large anemone accepted a stone as large as a pigeon's egg, and apparently perfectly clean. Fair sized crabs were taken in entire by the larger anemones, as well as detached chelae of adult specimens of the rock crab, *Cancer antennarius*, and kelp crab, *Epialtus pro-*

ductus. Limpets were rapidly taken in and constitute one of the possible if not common foods of the anemone. Small marine gasteropods were also readily accepted, even though the mollusc had retracted and shut its shell with the operculum. Nereid worms and other marine annelids were in many cases held successfully by the tentacles and taken into the gastrovascular cavity. Even pieces of the foot and column of other anemones were accepted by members of the same species. In fact *Cribrina xanthogrammica*, when in its normal habitat seems to be not at all discriminating in regard to its food. The normal condition of the anemone in the tide-pools examined seems to be always that of hunger. That from the ingestion of inert bodies, such as stones, the anemone is likely to receive a certain amount of nutriment from the encrusting plant growths and minute animals has been suggested by Torrey (1904) in his paper on *Sagartia*, and my observations lead me to extend his suggestion to *Cribrina*.

In the material extruded from the gastrovascular cavity of specimens of *Cribrina* after being brought into the laboratory is to be found a variety of remains. This material from more than a dozen specimens was carefully examined, as well as the contents of the cavity of a couple of dozens of dissected specimens. The contents of the digestive cavity are usually to be found enveloped in the midst of a copious matrix of mucus. The extruded material is always surrounded by mucus, and usually is in the form of a somewhat spherical mass. Spines of sea-urchins, small gravel, chelae of crabs, remains of various of the smaller crustaceans, such as amphipods, isopods, and *Hippolyte*, and numerous small mollusc shells tell the story of a general wholesale engulfing on the part of the anemone when the waves were washing over it. To what extent some of this engulfed material affords nutriment is a doubtful matter and involves the question of the digestive abilities of the sea anemone, a subject which has not formed a part of this investigation. On breaking apart several of the detached chelae of the crabs which were taken in the extruded material the only content was found to be a small quantity of mucus. Whether these chelae contained upon being ingested the muscles which they have normally is a matter which would have to be tested by digestion experiments.

REACTIONS TO LIGHT

The literature on the reactions of sea anemones to light indicates that by far the greater bulk of these forms remain contracted during the major portion of the day, expanding only under the influence of darkness or during the hours of early dawn and twilight. Hargitt (1907) has called attention to the few observations which have been made on the sea anemones in relation to light. According to the Hertwig brothers (1879), Quatrefages (1842) working on the species of *Edwardsia* found that rays of light from a lamp concentrated upon the specimens produced partial retraction. Haime (1854) observed in species of *Cerianthus* that bright sunlight produced a contraction into their tubes, expansion occurring when the light became less intense. It was the experience of the Hertwigs (1879) that from their observations on the deep-sea form, *Cladactis costae* this species was more or less contracted during full daylight, and expanded as the light became less intense. Jourdan (1889) records a similar condition in a species of *Peractis* upon which he experimented.

Hargitt (1907) found in *Eloactis producta* that: "It only required a few observations to determine beyond doubt that only in a light of low intensity, such as twilight, or in the aquarium under the rather dim light of an incandescent lamp at some distance, did the specimens protrude their oral portions and tentacles and show any degree of activity." The same worker found a like condition to hold in the case of *Sagartia leucolena*. *Metridium* he records as rather indifferent in its responsiveness to changes in light intensity.

Jennings (1905) records *Aiptasia annulata* as "very sensitive to light, expanding in darkness, but contracting after a few seconds when exposed to strong light."

Bohn (1907) discusses the light reactions of several species of sea anemones and finds them very variable, dependent upon many conditions. In some of them he finds a persistence of an impressed diurnal rhythm for three or four days after removal from the sea.

In specimens of *Cribrina xanthogrammica* the writer observed that upon coming into the laboratory in the evening about seven o'clock, the bulk of some fifty or more specimens kept in aquaria were contracted. During the day they had been noted to be

persistently open. Some manifestations of individual idiosyncrasies were observed among the specimens, since a few of them were closed sometimes, even in spite of the daylight. However, these cases were so rare in occurrence as to make them of negligible significance. Even the most closely contracted specimen, however, could be opened under the influence of a light intensity of 32 candle power. This was tried upon a whole dish of a couple of dozens of specimens which had contracted from the effects of darkness, and by shifting the light every individual was caused to expand fully, some of the more persistently closed ones requiring from a half-hour to an hour of exposure.

This species of anemone is brightly colored; the disk may be a greenish white to green, or even a brown or pink, the tentacles partaking of much the same color. Torrey (1906) says in regard to this color: "The characteristic green color of the species is found only in individuals exposed to the sun. It is due to the presence of a unicellular alga in the endoderm of the column wall, mesenteries and tentacles. Where sunlight does not penetrate, as under wharves (Calkins), or in caves, the algae, though present, do not develop so luxuriantly as in the more exposed situations, and the polyps are correspondingly pale." It may be that in the relations of the alga to the anemone we have the explanation of its apparently exceptional behavior to light.

In order to test the possible persistence of rhythms, both tidal and diurnal, a half dozen specimens were kept for five days under both constant dark and constant light. A second series of experiments was conducted with this same end in view, and these two dozen specimens showed so far as I was able to determine, no impressed rhythmical behavior. Observations were made at intervals of three or four hours usually, and from eight o'clock in the morning to eleven o'clock in the evening. Under constant darkness, in the first experiment made, except for the expansion of an occasional specimen for a few hours, the individuals remained persistently closed for over a week. After this time there were decidedly irregular periods of contraction and expansion. Specimens kept under constant light showed a uniform continuation of the expanded condition, contracting only on the sixth day, and then as the result of an in-

crease in temperature in the water rather than from the influence of light. The first series of experiments was conducted on specimens which had been kept in the laboratory for about a week, in order that they might have time to become acclimated somewhat to laboratory conditions. The second series was, however, carried out on specimens allowed only one day in the laboratory in order that they might become attached and normally expanded. The uniformly closed condition under the influence of darkness was even more completely shown in these individuals fresher from the sea-side. The specimens kept under constant light remained persistently expanded both night and day. Control experiments of individuals taken from the same lots were carried on in each case, the conditions for these being that of normal day and night illumination. These showed the specimens to remain in each case expanded during the day, and contracted during the night.

The following record shows the results in total darkness for the first two days of the second series of experiments mentioned above. The results for the succeeding three days of the experiment being the same as given for the second day, that is, all closed, it is unnecessary to include these.

November 11th.

- 1:00 P. M. All six fully expanded (experiment begun).
 2:30 " One partially contracted.
 6:00 " Four well closed, one partially open, one completely open.
 9:30 " Five well closed, one open.
 11:00 " Two partially open, four closed.

November 12th.

- 8:00 A. M. All specimens closed.
 2:00 P. M. " " "
 5:00 " " " "
 7:00 " " " "
 9:30 " " " "
 11:00 " " " "

Thus in *Cribrina xanthogrammica* the evidence seems to point towards the contraction and expansion as resulting very largely

from the direct action of the light rays. There seems to be indicated no persistence of rhythm in this species, either tidal or diurnal. The specimens from which these data were derived, however, were secured from Baker's Beach, San Francisco Bay, and while this location is only a short distance removed from the Golden Gate and the open sea, still the specimens here do not get the full effects of the tides as experienced along the unprotected ocean front. For this reason the evidence may be insufficient to state positively that tidal rhythms are not established in *Cribrina* as was found by Bohn (1907) in his work on several species of anemones. However, the evidence does lead one to the conclusion that the contraction and expansion in this species is largely the result of the direct action of the sun's rays, due perhaps to the symbiotic relation of the algae contained in the cells of the body of this species of anemone. The higher temperatures, desiccation, toxic solutions of sea water, and such factors are effective also in producing contraction, as was found by Bohn in his experiments on sea anemones.

FEEDING REACTIONS

Parker (1896) found in *Metridium* by feeding alternate pieces of meat and filter paper soaked in meat juice to the tentacles of one side of the disk, after a few times, the filter paper was refused, though the meat continued to be accepted. Finally, the tentacles of that side of the disk refused the meat also, but when this was offered to the tentacles of the opposite side, they accepted both the meat and soaked filter paper like the side first fed. In accounting for this behavior, Parker (1896) says: "The successive application of a very weak stimulus is accompanied, not by the summation of the effects of stimulation, but by a gradual decline in these effects till finally the response fails entirely."

Jennings (1905) found in *Aiptasia* that refusal of the filter paper was caused more rapidly by feeding meat alone for several times than by feeding successively filter paper alone or alternately filter paper and meat. He fed specimens of this genus several pieces of crab meat in succession to the tentacles of the left side only. When these tentacles became irresponsive, the meat was offered to the tentacles of the right side and these immediately accepted it. After a short period, meat was again

slowly accepted by the tentacles of the side first fed. However, these tentacles soon became irresponsive, and the food was offered again to the tentacles of the right side, which had reacted only once and that fifteen minutes before. These were found to react just as did those of the left side, hanging back from the disk along the column. Jennings concludes as the result of this behavior "that the animal is a unit so far as hunger and satiety are concerned. If the satiety has arisen through the activity of the tentacles of one side, the tentacles of the other side are equally affected by it. It is the general progress of metabolism that is the chief factor in determining the reactions to food." In discussing the comparative responses of the hungry and well individuals he says: "The well fed animal reacts less readily and strongly to simple mechanical shock. If touched with a needle, the well fed individual either does not react at all, or contracts very slightly while the hungry specimen reacts suddenly and powerfully. A slight disturbance in the water has no effect on the well fed individual while the hungry one contracts strongly. To chemical stimuli the same relations apply."

Allabach (1905) in working on *Metridium* tried feeding alternately pieces of meat and soaked filter paper, not allowing the filter paper to be swallowed. Refusal of the filter paper occurred just as in the cases where it had been swallowed. Thus the effect of the paper after it reaches the digestive cavity cannot be the cause of its rejection. Filter paper was also refused after the tentacles of the same region of the disk had several times accepted meat. "This result was likewise reached if the animal was not allowed to complete the swallowing of the meat, the latter being removed after it has passed into the oesophagus. This of course shows conclusively that the loss of hunger is not the cause of the change of reaction towards the paper." In a succeeding portion of the paper Allabach says: "It appears evident therefore that it is the reaction of the animal, not the precise character of the stimulus that causes the fatigue. This is perhaps what should be expected when the nature of the food reactions is taken into consideration. In taking food the region in contact with the food produces a very large quantity of mucus, enveloping the food body. It is not surprising that successive immediate repetitions of this excessive production of

mucus gradually exhausts the region. As is usual in fatigue, strong stimuli may produce reaction for some time after weak ones have failed. The fatigue thus caused usually lasts only two to five minutes. After this period has elapsed the fatigued region is frequently as ready to take food as before—provided the animal is still hungry.”

FEEDING REACTIONS OF *CRIBRINA XANTHOGRAMMICA*

The responses involved in food taking in *Cribrina* are much the same as those so excellently described by Jennings for *Stoichactis helianthus*. If a piece of fresh oyster is given the tentacles of a hungry *Cribrina* these immediately adhere to the meat, and bending over with it, hold it tightly against the surface of the disk. A depression of the disk takes place in the region of the food, and in this way the mouth opening is brought nearer to the piece of oyster. This opening in the meanwhile has become enlarged and the bladdery lobes of the stomodaeum are extruded towards and around the food. The tentacles release their hold, and the food is taken into the gastrovascular cavity by the muscular action of the stomodaeum. Depending very largely upon the size of the piece of meat, either a part or the whole of the disk and tentacles may contract during the feeding reaction. For a small piece, usually only a portion of the disk is involved in the food taking if the anemone is of fair sized proportions.

It occurred to the writer that there might be some way of securing the same effect on the metabolism of the anemone as is produced by the food without the muscular effort incident to food taking. Thus the factor of muscular fatigue as such could be eliminated. Wyeth's beef juice, for which the manufacturers claim “that it contains all the albuminous principles of beef in an active and soluble form” was the first substance used. A dilution of this, two parts of beef juice to eight parts of sea water, was forced by means of a pipette into the gastrovascular cavities of several anemones. It was found impossible to prevent an ejection of this material to a certain extent by the contraction of the anemone, and the consequence was a diffusion of the beef juice over the tentacles, with an immediate

copious secretion of mucus from the surface of the tentacles and also from the gastrovascular cavity. The anemone contracted strongly as the result of the stimulus, but in a short time expanded. The tentacles were coated with mucus, some of them tending to remain in bunches as a result. Application of contact stimulus showed that they were practically insensitive to stimulation of this character. Many of the tentacles hung flaccidly over the edge of the disk.

As far as possible, the mucus was removed entirely from the disk and tentacles, and the animals placed in a dish of fresh sea water. Pieces of oyster given to the tentacles were persistently refused, though when placed over the mouth opening they were slowly accepted. In a few hours the tentacles were observed to again become responsive to contact stimuli. After a varying period of from one to three days, all of the specimens had so far become recuperated as to readily accept food given to the tentacles.

Next a rather strong solution of peptonoids was forced into the gastrovascular cavity of several specimens with much the same results as were secured in the case of beef juice. A concentrated oyster extract obtained from macerating fresh oysters was tried, the tentacles in this case showing the same flaccidity and excessive mucus secretion as in the case of the beef extract, though to a less degree. This lessened degree of secretion was evidenced in the relative quantity of mucus secreted as the result of injection, as well as by the earlier recovery of the individuals so treated. After a period of about one day, provided the animals were kept in a cool room, the tentacles of most of the specimens had become thoroughly responsive and would accept food offered them.

Parker (1905) in his work on the reversal of ciliary action in *Metridium* records that a copious secretion of mucus was one of the results produced by the application of a potassium chloride solution of sufficient strength to cause reversal of ciliary movement in the region of the mouth of the anemone. This suggested the idea that there might be a number of chemicals producing a similar effect, and the results of an investigation into the effects of several solutions of varying strengths and composition are given below.

METHODS EMPLOYED

In the succeeding experiments, the animals were placed each in a separate dish, twelve centimetres in diameter. Here they were allowed to remain for two or three days so as to become thoroughly acclimatized and normally responsive. Each individual was tested to see that it accepted food before the injection of the chemical was made, and if it failed to do so, the animal was not used in the experiment.

With a thoroughly clean pipette, consisting of a glass tube drawn out to a sufficiently small point, each substance was forced through the mouth opening into the gastrovascular cavity of the animal, or over the surface of the disk and tentacles according to which was desired. As soon as the injection was made, the water was removed from the dish, the specimen thoroughly rinsed with uncontaminated sea water, and a quantity of sea water equal to the original amount in the dish placed over the anemone. The experiments were performed in the strong diffuse light of the laboratory, in order to have the animals expand as soon as possible after treatment. The mechanical part of the operation could in no way injure the body of the specimen, since the point of the pipette was not left irregular but was melted down to a perfectly smooth glass edge.

RESULTS OF INJECTION EXPERIMENTS

Pure sea water.—Some of the solutions were made up in sea water, and in order to determine what effect the mechanical part of the operation might have a dozen anemones were injected with clean sea water. Contraction was of course produced as the result of the contact stimulus, but the anemones almost immediately began to expand. Upon expansion their reactions to food, mechanical stimuli, etc., appear entirely normal. A similar result was secured upon the injection of fresh water. Thus there seems no complicating factor in this regard.

Sodium chloride.—(Normal solution in sea water and $3/8$ normal in distilled water.) Immediately upon expanding after injection, the tentacles showed normal responsiveness. No mucus appears to have been secreted. The tentacles accepted food readily upon its being given to them. A $5/8$ M NaCl + $1/3$ M NaCl was injected also but with the same result.

Potassium chloride.—(Normal solution in sea water and $3/8$ normal in distilled water.) Thorough injection produced a copious mucus secretion. At end of two hours specimens had not expanded, but the tentacles were almost totally irresponsive. When a piece of oyster is placed over the mouth, the bladdery lobes of the stomodaeum were extended and the food taken in. The following morning the tentacles had recovered almost normal responsiveness to contact stimulation, but still refused food given to them. At four o'clock of the same day the tentacles slowly accepted food offered them. The second day after the experiment, the anemones in many cases accepted food quickly, and the most of them seemed in every way, so far as discernible, entirely normal in responsiveness.

In the case of the $3/8$ M KCl in distilled water, a solution practically isotonic with sea water, the anemone in three cases out of six slowly accepted food after injection and subsequent expansion. The mucus secretion upon treatment with this strength of solution was not nearly so copious as in the case of the normal solution. Consequently I am led to believe that the number of potassic ions present was not sufficiently an excess to produce an exhaustion of the mucus secretion of the tentacles adequate to prevent the acceptance of food by these through their lowered responsiveness. This view is strengthened by the fact that $5/8$ M KCl + $1/3$ M KCl did produce a condition to all effects the same as that produced by the normal solution of potassium chloride used. This solution of potassium chloride contained a larger number of potassium ions than did the solution isotonic with sea water. The fact that it is a solution hypertonic to sea water is not of significance, I believe, since a solution of sodium chloride of the same strength effects no change in food response. This is also an indication that the potassium ions are the factor producing the secretion of mucus and not the chlorine ions.

Mercuric chloride.—(0.2 per cent solution in sea water.) A thorough injection produced a very marked secretion of mucus apparently from all of the surfaces of the body. The individual was killed as the result of this injection, even though the sea water was changed immediately. Where a partial injection was secured into the gastrovascular cavity at fifteen minutes past nine in the morning, at noon response of the tentacles was

practically as sluggish as immediately after the anemone had expanded. At half past one o'clock of the same day, the tentacles had recovered somewhat in their responsiveness to contact stimulation, but did not show any response to food. When pieces of oyster were placed over the mouth of the animal they were slowly accepted.

In another case, the solution was forced over only the disk and the tentacles. This was done at twenty minutes past nine in the morning and at noon the specimen had not expanded. At one o'clock, however, the specimen was open, but the tentacles persistently refused food, and hung entirely irresponsive over the edge of the disk. The bladdery lobes of the stomodaeum were extruded around a piece of oyster placed over the mouth opening and this food was taken into the gastrovascular cavity.

The specimens treated with mercuric chloride recovered most slowly of all of the anemones experimented upon. The applications were made one Friday morning, and it was a week from the following Monday before many of the specimens injected would accept food given to them. On the third and fourth days after injection, a heavy film of mucus was shed from the entire surface of the body. Pavlov (1910) from his work on mucus secretion in the stomach of the dog has the following to say in regard to the excessive secretion of mucus in relation to the economy of the organism: "When potent reagents such as absolute alcohol, a 0.2 per cent sublimate solution, a ten per cent solution of nitrate of silver, or a strong emulsion of oil of mustard, were introduced for a few minutes into the small stomach they produced a more or less copious, indeed in many cases enormous secretion of mucus. * * * The contrast between the intensity of the phenomenon and its short duration is really striking. One cannot help thinking that in these cases a morbid condition has not as yet been established, but rather that the pathogenic influence, had been successfully encountered and conquered before one's eyes." He suggests that in this behavior the true function of the surface epithelium has been revealed. Its copious secretions dilute the noxious substance, or form chemical combinations with it and at the same time expel it from the stomach wall.

Calcium chloride.—(Saturated solution in sea water, and $3/8$ normal in distilled water.) With the saturated solution in sea water at the time of injection, forty minutes past nine in the morning, a medium secretion of mucus was produced and a semi-responsive condition immediately upon expanding. At noon the animal was almost normally responsive to contact stimulation. While in the afternoon, the tentacles of the animal had recovered normal responsiveness to contact stimulation, food given them was not accepted. The next day, however, food was slowly accepted in the afternoon, and the succeeding day, the tentacles responded entirely normally when given food. Of the four specimens tested with $3/8$ M CaCl in distilled water, two showed a greater mucus secretion than the others and accepted food several hours after; the other two accepted food immediately upon expanding.

Lithium chloride.—(Normal solution in sea water and $3/8$ normal in distilled water.) Comparatively little secretion of mucus was produced upon injection. The anemones appeared entirely normal upon expansion, and gave immediate and vigorous response to food given to the tentacles. The same effect was produced in the case of the specimens treated with a $3/8$ M solution in distilled water.

Magnesium sulphate.—(Normal solution and $3/8$ normal in distilled water.) A number of anemones injected with magnesium sulphate in considerably greater volumes than were used in the preceding experiments showed practically no secretion of mucus, but almost all of them practically total irresponsiveness to contact stimulation. The tentacles presented a more rigid condition than was the case with the other substances producing a lowered degree of tonus. This is perhaps to be attributed to a partial paralysis of the muscles coupled with a condition of anesthesia in the body of the animal. The experiment was begun at ten o'clock in the morning and by two o'clock that afternoon the tentacles contracted after several successive stimulations with a glass rod. At four o'clock in the afternoon of the same day, the tentacles had so far recovered as to become almost normally responsive to contact stimulation, but persistently refused food given to them. Food placed upon the mouth was taken into the gastrovascular cavity. Three

days after treatment the tentacles slowly accepted food, however, not in an entirely normal manner. Inclining with the piece of oyster, they dropped it over on to the disk to be accepted by the mouth.

In the case of the $\frac{3}{8}$ M Mg SO₄, the individuals showed considerable variability. Three of the five specimens treated showed a similar though less intense effect to that produced by the normal solution; the other two accepted food upon expanding a few minutes subsequent to their treatment.

With regard to the action of magnesium salts Cushny (1910) says: "The magnesium salts have recently been shown by Meltzer to have a very powerful action when injected hypodermically or intravenously. The most characteristic effect is complete anesthesia, resembling that induced by the chloroform group and ending in fatal cases in paralysis of the respiratory centre."

The effect of magnesium sulphate upon anemones is known to all who have ever preserved specimens of these forms. The condition of anesthesia produced in the animal prevents its contraction upon the addition of the preserving fluid, and the specimen is secured in an expanded fixed condition. Thus the irresponsiveness of the *Cribrina* in these experiments is to be attributed to the anesthesia produced as the result of these injections. There seems to be produced also a paralysis of the muscular fibrils of the cells of the body.

EXPERIMENTS ON THE NORMAL FEEDING REACTIONS OF *CRIBRINA*

The experiments of Parker (1896) on *Metridium* were repeated on *Cribrina* and it was found that the tentacles of the left side accepted pieces of oyster given it for eight successive times. The oyster was then given to the right side and was immediately accepted. For the two succeeding times food was taken by them, but subsequent tests gave a refusal in this region. This is to be accounted for, I believe, as the effect of the diffusion of the food juices in the water causing the production of mucus in addition to that caused by the actual contact with the food. No doubt what von Uexküll would term a "withdrawal of tonus" from the tentacles to the region of the mesenteries also takes place due to the secretion of digestive

juices incident to the digestion of the food already taken in by the action of the tentacles of the other side.

As previously stated, depending upon the size of the piece of food taken in, either a part or the whole of the disk and tentacles is involved in the feeding reaction. In order to determine what effect this factor might have in the relative responsiveness of the two sides, two specimens were fed large pieces of oyster, thus causing the greater portion of the tentacles of the anemone to come in contact with them during the feeding response. The oyster was given to the tentacles of the right side, which in one anemone accepted five times successively, in the other anemone seven times. Then the oyster was offered to the tentacles of the left side of each anemone. In one case, the tentacles slowly accepted one piece of oyster; in the other, the meat was refused entirely.

An anemone which was previously tested and found to accept food quickly upon its being given opportunity to do so, was made to contract for a dozen successive times as the result of mechanical stimulation with a sterile glass rod. Oyster was then given to its tentacles, and was accepted for eight times, as many times as the average individual of those experimented upon would accept food without having been previously stimulated mechanically. This would seem to indicate that the factor of muscular fatigue is not a significant one in the modifiability in response to food, except as it is perhaps incident to a depression from mucus secretion. This experiment was several times repeated with a similar result.

The matter of giving the tentacles food and allowing them to carry it to the oesophagus and then removing it before it was swallowed was also tested. It was found that after about the normal number of times for the acceptance of food, the tentacles would fail to respond, seeming to indicate that refusal of the food material is very largely if not entirely a matter of the responsiveness of the tentacles, especially since the mouth is always, even under the most adverse circumstances ready enough to accept food given to it. Allabach (1905) has found that *Metridium* will accept food placed over its mouth until the body of the animal is gorged, and ejecting this accumulated amount, the mouth will again accept food placed over it. The same worker has tested the matter of feeding the animal but

not allowing the food to be swallowed, and says with regard to her experiments: "The fatigue thus caused usually lasts only two to five minutes. After this period has elapsed the fatigued region is *frequently** as ready to take food as before—provided the animal is *still hungry*."* My experience was, however, that in some cases, as many as seven hours were required for the animal to recover responsiveness sufficient to accept food given to the tentacles. In no case where the animal had been thoroughly fed until it refused to accept food with the tentacles of any part of the disk did I succeed in getting animals to accept food more than twice after a period of five to ten minutes, and these cases were comparatively rare. The fact that the anemone will accept food after this short period of rest is what might be expected to be the case, since the juices of the food are not sufficiently strong to entirely exhaust the tentacles through mucus secretion as the stronger substances have been shown to do. One or more partial recoveries before complete exhaustion is what might be looked for even in the matter of mucus secretion. This being the case, I think that there is no necessity for the belief that this reaction is due to the fact that the animal is "still hungry," but rather that it is due to the rallying power of the tentacles before complete exhaustion.

FEEDING REACTIONS IN NORMAL HABITAT

A two weeks' stay at the Hopkins Sea Side Laboratory, Pacific Grove, California during a period when the tides were exceptionally favorable permitted not only observations on the normal food habits of the anemones recorded in a previous portion of this paper, but also an opportunity to try the effects of injecting the specimens in the tide-pools with certain of the substances used in the laboratory experiments.

After injecting specimens in an expanded condition in the pockets among the rocks at low tide with the same strength of beef juice previously used, there was noted the same excessive secretion of mucus, almost total irresponsiveness to stimulation, and total neglect of food on the part of the tentacles as was found in the specimens kept in the laboratory. Potassium chloride gave even more marked results of depression than the

* Italics mine.

beef juice. Injection with a strong sodium chloride solution seemed to alter in no way the normal responsiveness of the animal either to food or to contact. The animals used in these experiments were first tested to see that they would take food before the experiment was performed, with the result that they immediately availed themselves of the opportunity. In fact, I have yet to see an anemone of this species in an expanded normal condition in their native habitat refuse to accept food; for they all appear to be in a condition of quick responsiveness to stimuli of the various kinds.

RÔLE OF MUCUS SECRETION

Duerden (1906) in a most interesting paper on the rôle of mucus in corals has shown that it serves two general functions. (1) The protection of the polypal surface from foreign objects and in keeping it clean, and (2) the entanglement and ingestion of prey and food substances. He notes that nutritive substances and extractives placed upon the polyp increase the amount of mucus exuded. The same result is secured, though to a less degree, by mechanical stimulation. He says: "Not only does the mucus serve as a protection to the polyp under adverse circumstances and assist in getting rid of foreign substances which may fall upon it, but it is of much importance in the process of nutrition, by serving as a vehicle or means of conveyance of nutritive substances to the mouth and down the gullet."

Perhaps the rôle of mucus in the actinian polyp is not essentially different to that played by it in the corals. The idea of Pavlov (1910) quoted in a preceding paragraph to the effect that the secretion of mucus in the stomach of the dog upon the application of potent reagents is protective in that it dilutes or neutralizes the noxious substance is certainly suggestive in its application to the results secured in *Cribrina*. We must conclude, I believe, that the copious exudation of mucus upon the application of such substances as potassium chloride and mercuric chloride serves in a decidedly protective manner. I have too little evidence to say to what extent the mucus acts as a food securing factor. In the extruded material of the anemones examined, many smaller organisms were found, and it is quite possible that these might accumulate in the mucus film always over the surface of the anemone until they had acquired a

sufficient nutritive strength to cause the reversal of ciliary action and the consequent ingestion of the mucus material. Certainly the conditions under which an anemone is fed in the laboratory are most unusual, and it may be that there are substances in the oyster, crab, or other meat employed in the feeding experiments, which are more or less injurious in nature to the anemone, and that these substances produce the copious mucus secretion. There does seem to exist some relation between the reversal of the beat of cilia and the secretion of mucus, since substances producing the one, usually produce the other.

DISCUSSION OF RESULTS

Removal of the mucus.—One possible explanation of the phenomena described in the preceding experiments might be thought to be that the mucus forms a coating over the tentacles and that this acts as a mask to lower the responsiveness by covering the sensory cells. That this is not the case can be quite easily demonstrated by removing all of the mucus with a camel's hair brush from several tentacles and then stimulating these. They will be found to be as irresponsive as the tentacles about them on which the mucus still remains. Also, even upon very strong contact stimulation immediately after expansion, the tentacles remain perfectly flaccid, in many cases, a condition which would not hold true were the insensitiveness due solely to the masking effect of the coat of mucus.

Muscular fatigue.—That the loss of responsiveness on the part of the tentacles after much food has been taken in is not due to fatigue resulting from the activity of taking in food on the part of the muscular fibrils has been shown by Allabach in the following experiment. An anemone was fed on one side of the disk till the tentacles of that region refused to accept food. Meat given to the opposite side was not taken at all, though these had not been active in food taking. A clearer indication of the fact that muscular fatigue alone as the result of food taking plays but a negligible part in the decrease of response is shown by the experiment described in an earlier portion of this paper. Anemones made to contract as the result of contact stimulation with a sterile glass rod for as many times as they normally accept food showed no decrease from the average of times other anemones had been found normally to

accept food. Upon watching an anemone in its normal habitat one observes the dozens of times that it partially contracts and expands under the stimulation of the waves and it is perhaps due to this type of response enforced upon the animal by the conditions of its very existence that the muscular fibrils do not become so easily fatigued. Certainly also a single injection of beef juice causing the animal to contract only once cannot cause the muscles to become fatigued solely through the power of a single contraction. There seems to be some other more fundamental reason involved, though no doubt the marked contraction following such a treatment may to a certain extent be an accessory factor.

Diminution of responsiveness from mucus secretion.—Parker's conclusion from his experiments on the feeding reactions of anemones is "that the successive application of a very weak stimulus is accompanied, not by the summation of the effects of stimulation, but by a gradual decline in these effects till finally the response fails entirely." Jennings concludes in regard to the modifiability in *Stoichactis helianthus* and *Aiptasia annulata* that "it is clear that the animal is a unit so far as hunger and satiety are concerned." In case the satiety has arisen through the efforts of the tentacles of one side, the tentacles of the other side are equally affected by it. The chief factor in determining the reaction to food is the general progress of metabolism.

Allabach (1905) observes in her paper on *Metridium* that in taking food the region in contact with the food produces a very large quantity of mucus enveloping the food body. Holmes (1911) in discussing the claims of Fleure and Walton (1907) for the power of associative memory in the sea anemone says: "It is possible that the seat of the change of behavior is in the tentacles alone. Allabach has shown that after the tentacles of *Metridium* have responded to a stimulus a few times their production of mucus becomes much diminished and this probably affects their subsequent activity. If this factor would modify the irritability of the tentacles for some time it might explain the change of behavior."

There can be no doubt that the reaction accompanying the excessive secretions of mucus as the result of beef juice and potassium chloride does alter the irritability of the tentacles.

Just how the mucus secretion affects the responsiveness of the muscular fibrils has not been determined in the present work. There seems to be a disturbance of the balance of nutrition in the cell and the muscular fibrils of that cell suffer as a consequence. An important agency in effecting the lowered tonus would seem to be a withdrawal of nutritive materials from the muscular elements and the tentacles hang flaccidly along the edge of the disk. The relation of the neurofibrillar system of the anemone to the secretion of mucus is scarcely possible of determination. There is a possibility that the changed responsiveness in the anemone may be due to the effects produced in the neurofibrillar system by the chemicals employed. There may be even a condition similar to anesthesia produced.

It would certainly seem to the writer that from the data presented in this paper, there is no valid ground for stating that the modified behavior in relation to food is due, as Jennings (1905) contends, to the animal's acting as a unit in "satiety." If the general condition of satiety affects the organism as a "unit" why should it be that even after being gorged with food, the gastrovascular cavity ejecting the material through the mouth opening, the mouth continues to accept food? And why is it that the tentacles of the animal can be made irresponsive to food without any of this food entering the gastrovascular cavity? Then, too, Parker (1896) has found and Jennings (1905), in certain cases, as well as Allabach (1905) and the present writer that upon the tentacles of one side being fed to refusal, the tentacles of the opposite side of the disk will accept food. The view that the seat of the modified responsiveness lies very largely in the individual tentacles is more clearly in accord with what is known of the structural organization of the sea anemone than that the animal acts as a unit. The successive applications of pieces of food, through the accompanying mucus secretion serves to lower the responsiveness of the tentacles, and a gradual decline in this responsiveness is produced till finally the feeding response fails entirely on the part of the tentacles.

SUMMARY

The species of anemone studied, *Cribrina xanthogrammica* Brandt usually remains expanded during the day and contracted during the night. It is suggested that the presence of numerous

algal cells in the endoderm of the column wall, mesenteries, and tentacles probably tends to make such behavior adaptive in character.

There seems to be no impressed diurnal or tidal rhythm in specimens of *Cribrina* removed to the laboratory; for when placed under uniform illumination this species remains expanded for several days continuously, and when subjected to darkness, contracts and remain contracted for a like period.

In their native environment, all of the anemones examined appeared to be hungry, and in many cases, quite readily swallowed apparently clean objects such as stones. The food of *Cribrina* was found to be very varied in its kind.

The introduction of a solution, two parts of beef juice to eight parts of sea water, into the gastrovascular cavity of the anemone produced a copious secretion of mucus, accompanied by a lowered responsiveness of the organism. Food offered to the tentacles of an anemone so treated was rejected.

Much the same reaction, though to a less degree, was secured upon the application of a concentrated extract of fresh oyster. A quite marked mucus secretion and a proportionate degree of depression was produced upon treatment with both potassium chloride and mercuric chloride.

Solutions of sodium chloride and lithium chloride isotonic with the potassium chloride were found to produce only negligible effects upon the anemones treated. The tentacles of these accepted food immediately upon the expansion of the anemone.

Muscular fatigue seems to be of little importance in the modified responsiveness to food.

It was found possible to produce a condition of irresponsiveness to food on the part of the tentacles by feeding these large pieces of oyster successively and not allowing this meat to be swallowed.

The altered behavior in relation to food on the part of the tentacles seems to be due to the lowered responsiveness accompanying mucus secretion. This depression is perhaps caused by the disturbance of the balance of nutrition in the cell; perhaps as the direct effect of the substance employed on the neurofibrillar system of the anemone.

The evidence seems to warrant the conclusion that the modified behavior in relation to food is due rather to a gradual decline

in the responsiveness of the tentacles to food than to the animal's acting as a "unit" in hunger and satiety.

BIBLIOGRAPHY

- ALLABACH, L. F. Some points regarding the behavior of *Metridium*. Biol. Bull., 1905. 10, 35-43.
- BOHN, G. Introduction a la psychologie des animaux a symetrie rayonnee. Bull. de l'Institut Gen. Psychol., 7, 1-87.
- CUSHNY, A. R. Pharmacology and therapeutics. 10th ed. 744 pp. Philadelphia. 1910.
- DUERDEN, J. E. The role of mucus in corals. Quart. Journ. Micr. Sci., 49, 591-614. 1906.
- FLEURE, H. J. and WALTON, C. L. Notes on the habits of some sea anemones. 1907. Zool. Anz., 31, p. 212.
- HARGITT, C. W. Notes on the behavior of sea anemones. Biol. Bull., 12, 274-284. 1907.
- HOLMES, S. J. The evolution of animal intelligence. Henry Holt and Co., pp. 1911. 296.
- JENNINGS, H. S. Modifiability in behavior. I. Behavior of sea anemones. Journ. Exp. Zool., 2, 447-472. 1905.
- JOURDAIN, E. Les sens chez les animaux inferieurs. Paris. 1889.
- LOEB, J. Studies in general physiology. Univ. of Chicago, Decennial Publ., vol. 1905. 15,, part II, pp. 440-449.
- PARKER, G. H. The reactions of *Metridium* to food and other substances. Bull. Mus. Comp. Zool. at Harvard Col., 29, 107-119. 1896.
1905. (a) The reversal of ciliary movement in metazoans. Amer. Journ. Physiol., 13, 1-16.
- (b) The reversal of the effective stroke of the labial cilia of sea anemones by organic substances. *Ibid.*, 14, 1-6.
- PAVLOV, I. P. The work of the digestive glands. 2nd Eng. ed., London. pp. 1910. 238.
- TORREY, H. B. On the habits and reactions of *Sagartia davisii*. Biol. Bull., 6, 1904. 203-216.
1906. The California shore-anemone, *Bunodactis xanthogrammica*. Univ. of Cal. Publ. in Zool., vol. 3, no. 3, pp. 41-45.