A Study of the Muscular Anatomy and Swimming Behaviour of the Sea Anemone, *Stomphia coccinea*

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SUMMARY

The sea anemone *Stomphia coccinea*, when touched by certain starfishes, frees itself from the substratum, and by a series of waving motions propels itself through the water. This locomotion has been studied by means of direct observation and by analysis of time-lapse, and normal-speed motion-picture films.

Ecological observations and stimulation tests made in the natural environment of the anemone are described and discussed.

The musculature of the anemone is described, and the function of the various muscles is discussed with regard to their participation in swimming. The muscles that play the most important part in the animal's movement through the water are the parieto-basilar and the circular muscle-sheet. The other muscles are involved in the overall reaction, but act only as aids in maintenance of the form of the anemone during actual swimming.

Experiments involving the ability of several species of starfish to elicit swimming are described. It has been established that, of those asteroids tested, only *Dermasterias imbricata* and *Hippasteria spinosa* are consistently effective in causing *Stomphia* to swim.

The possibility that swimming serves as a means of escape from starfish predators is considered. Observations and simple experiments indicate that predation may not be a factor in this relationship between starfishes and the anemone.

Observations of the anemones in their natural environment suggested that swimming might be a means to remove debris settling on the oral disk and eventually burying the animal. Experimentally, this could not be substantiated; silt is removed by the cilia of the oral end of the anemone.

That the starfish release some chemical which serves as a stimulant to the anemone is considered; but experiments indicate that if such a substance is present it probably is not water-soluble.

It was discovered that swimming could be brought about by electrical stimulation. The response is facilitated and can be controlled, to a certain degree, by giving stimuli of proper intensity and frequency for varying periods of time (e.g. 6 volts at 1-sec intervals over a period of 2 to 8 sec).

Possible uses for the swimming reaction in nature are considered, but this question still remains open to further speculation and experimentation.

INTRODUCTION

SPECIMENS of the sea anemone, *Stomphia coccinea*, dredged in the waters of the San Juan Archipelago and Puget Sound, have recently been shown to behave in a very striking and characteristic manner (Yentsch and Pierce, 1955). This anemone, when touched by certain starfishes, frees itself from the substratum, and by a series of waving motions propels itself through the water. T. A. Stephenson (1935) mentioned similar activity in *S. coccinea*, and...
recorded his observations that a specimen 'jumped' when kept under adverse conditions. It is probable that the 'jumping' which Stephenson described and the 'swimming' behaviour recorded by Yentsch and Pierce are the same. Since the animals do actually move through the water, the term 'swimming' is used to refer to this activity.

The locomotion of *S. coccinea* has been studied by direct observation and by analysis of motion-picture films, both normal speed (16 frames per sec), and time lapse (4, 8, and 16 frames per min). By means of gross dissection and histological sections, the arrangement of the muscles has been studied in relation to their function in swimming. Yentsch and Pierce showed that the response is elicited only by contact with a small number of species of asteroids. Further studies have been made of this specificity. Entire animals, isolated parts of the body, and homogenates of various starfish tissues were tested. The distribution of the anemone and the ecological conditions in which it lives have also been studied by diving with aqua-lungs in an attempt to determine whether there is in the normal environment any possible advantage from swimming activities.

**Methods and Materials**

Most of the specimens used in this study were obtained by dredging in various parts of Puget Sound and the San Juan Archipelago. The type of bottom in the collecting areas is sandy mud with scattered shells and rocks. The greater number of *Stomphia* were taken from depths of 20 to 105 fathoms. They were found attached to the shells of *Modiolus modiolus*, *Pododesmus macrochisma*, *Pecten hindsii*, and *P. hericius*, and to rocks of various sizes and compositions. *Modiolus modiolus* is the only live animal on which *Stomphia* were found. One specimen was collected on the south side of Bainbridge Island, lat. 47° 34' N., long. 122° 30' W., at a depth of 55 ft. It was found attached to an empty mussel shell. *S. coccinea* is particularly abundant in San Juan Channel, lat. 48° 40' N., long. 123° 03' W., at depths of 20 to 60 fathoms, and in President Channel, lat. 48° 40' N., long. 123° 01' W., at an average depth of 105 fathoms. Both of these areas yielded many specimens, most of which were attached to *Modiolus modiolus*. Approximately 75 specimens were collected from these two locations during the summer of 1955.

Material collected during the summer and autumn of 1955 was brought to the laboratory at the Friday Harbor Laboratories of the University of Washington and kept in tanks supplied with running sea-water. During the rest of the year the animals were maintained in the tanks in the Oceanography Building, University of Washington, where there is a refrigerated, recirculating sea-water system. Other species of animals used in the study were either dredged, collected in the intertidal zone, or obtained by diving in various areas of Puget Sound and the San Juan Archipelago.

In fixing *Stomphia* for histological study, the usual difficulties of contraction and subsequent shrinkage could easily be avoided because the anemones are unresponsive to most mechanical and chemical stimuli immediately after the
swimming reaction. During this refractory period the anemones were transferred to small dishes to which MgCl₂ isotonic with sea-water was added. The concentration of MgCl₂ was gradually increased until, after approximately 30 min to 1 h, the animals were relaxed and fixatives could be added.

Several fixatives were tried, but the one that gave the best results for this study proved to be Allen's 'B' solution. A small quantity of this solution was first added to the mixture of MgCl₂ and sea-water containing the relaxed anemones. A few ml of the fixative were then introduced into the coelenteron by inserting the needle of a hypodermic syringe through the mouth of the anemone. After a short time the anemones were transferred to vessels containing Allen's 'B' solution and fixed for a period of 3 to 4 h.

After fixation the animals were dehydrated by passage through a series of ethanol tertiary butyl alcohol solutions. After dehydration and infiltration, the specimens were embedded in paraffin for sectioning on a rotary microtome. Sections were cut at 8 and 10 µ and serially affixed to glass slides with Mayer's albumin. The sections were either stained with Mann's methyl blue / eosin and Orange-G, or iron hematoxylin and eosin.

The motion pictures, both time-lapse and standard silent film speed of 16 frames per sec, were taken with an Eastman Kodak Ciné Special II 16-mm camera. Cine-Kodak Super-X film was used exclusively and gave excellent results. The time-lapse mechanism used is manufactured by the Electro Mechanical Development Co., Houston, Texas, U.S.A. Most of the time-lapse pictures were taken at a rate of 16 frames per min, but other speeds (noted above) were also used. A copy of the time-lapse film, Behaviour of the sea anemone, Metridium senile, prepared by Dr. E. J. Batham and Mr. P. M. B. Walker, kindly given to the investigator by Dr. C. F. A. Pantin, was also useful for comparative study of the action of the muscular system of the anemones. Copies of these films are available at the Department of Zoology, University of Washington.

**FIELD OBSERVATIONS**

At North Pass, lat. 48° 37' N., long. 123° 01' W. in the San Juan Archipelago, the animals occur at depths of 80 to 135 ft. Here the bottom consists of sandy mud with scattered shells and rocks. *Stomphia* lives attached to these and the anemones were usually situated so that the lower one-half to two-thirds of the column was buried in the soft bottom debris. The anemones were neither crowded nor numerous; an average of six could be seen by swimming over the area for a distance of approximately 100 m in any given direction. Other species of animals noted in the area were Fusitriton oregonensis, Mya truncata, Schizobranchia insignis, Pseudopotamilla ocellata, Strongylocentrotus franciscanus, Modiolus modiolus, Pycnopodia helianthoides, Mediaster aequalis, Crossaster papossus, Dermasterias imbricata, Psaster brevispinus, Ascidia paratropa, Cerianthus borealis, Metridium senile, Psolus chitinoides, Psolidium bullatum, Pecten hindsii, P. hericius, Pagurus spp. (in Polynices shells), and Aglaophenia sp.
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The only species in the above list that is able regularly to elicit the swimming reaction in *S. coccinea* is *Dermasterias imbricata*. During the study of the area, a single specimen of this asteroid was found approximately 15 ft from the nearest *Stomphia*. At the time that the specimen was seen it became necessary to come to the surface and it was therefore impossible to test the capacity of this animal to stimulate any *Stomphia* in the region. In the laboratory, however, it proved to be an effective stimulator.

During later dives, other species of animals encountered at North Pass were gathered and their effect on *Stomphia* was tested. In all trials the result of stimulation was negative. The *Dermasterias* specimen previously collected during a dive at North Pass was brought along on one such occasion and was used to stimulate a *Stomphia*. The anemone released its hold on the rock to which it had been attached and swam actively for several seconds. The anemone swam, or was carried (the tides of this area cause currents up to 3 or 4 knots), a distance of about 1½ m before it was collected and brought to the surface for transport to the laboratory.

**Swimming Response: Description**

The following sequence of events can be distinguished in the swimming reaction:

1. Upon stimulation the expanded animal contracts, withdrawing the tentacles and oral disk. The normal response of *Stomphia* to tactile stimulation is contraction in typical anemone fashion.

2. The anemone then slowly expands, elongates to an unusual extent, and becomes very turgid. The sphincter muscle may still be contracted enough to keep some or all of the tentacles withdrawn during this and the two following stages, or the oral disk may expand widely.

3. Frequently, but not invariably, a writhing or waving movement occurs in which the anemone whips the oral disk from side to side by flexure of the column.

4. The animal then releases its hold on the substratum and, by movements similar to those described in 3, actively propels itself through the water.

5. After swimming for periods of time lasting from only a few sec to several min, the animal settles to the bottom and comes to rest on its side. Retaining the exceptionally expanded condition, the anemone is now almost inexcitable, not responding to stimuli, either mechanical or chemical, unless of extraordinary severity. Recovery takes place within 1 or 2 min and the anemone re-establishes its hold on the substratum and regains its normal upright posture.

The series of drawings in figs. 1 and 2 show specimens of *Stomphia* in representative positions of the activities described below.

**Muscular System: Description**

In *Stomphia*, as in any actinian, the musculature and mesogloea together with the fluid contents constitute a hydrodynamic system (Batham and Pantin,
FIG. 1. A, normal appearance of *S. coecinea*. B, specimen responding to stimulation by starfish. Oral disk is partly retracted and sphincter is contracting. C, extension of column after contraction of column. Oral disk is beginning to expand. Both actions due to contraction of circular muscle sheet of column. D, lateral bending movement caused by rapid contraction of limited area of parieto-basilar muscles. E, lateral bending toward observer. Note folds of gullet protruding through mouth as result of increased internal pressure. F, lateral bending. Note raised edge of pedal disk. G, swimming. Specimen is free from substratum and is actively swimming. H, I, and J illustrate the side-to-side bending movements. H, swimming. I, swimming. Note conical shape of pedal disk. J, anemone during period of inactivity after swimming. Note that the oral end of the animal is supported by the turgid oral disk and tentacles.
1950, 1951), since the muscles work against the fluid in the coelenteron. In each of the three functional regions of the anemone—column, basal disk, and oral disk—the muscles are capable of independent activity, but under certain circumstances may work synergistically. Through the contraction of the circular muscles and the tonus of the longitudinal muscles, the anemone is maintained in columnar form. Superimposed on this activity are the co-ordinated contractions of the various muscles which are responsible for the changes in shape. The muscles are here listed.

COLUMN

Body-wall musculature

Circular muscles. In the column there are two antagonistic muscular components, circular and longitudinal, arranged at right angles to each other. A circular sheet of muscle surrounds the column, lying just medial to the mesogloea (fig. 3, A). This sheet of fibres is fundamentally continuous, but is interrupted wherever the mesogloea protrudes into the septa. Contraction of the circular muscles causes elongation of the column and, if the sphincter is contracted, an increase of turgidity.
**Sphincter muscle.** Derived from and included in the circular muscular system is the sphincter muscle (fig. 4, A, B). In *Stomphia* it is of the diffuse mesogloeaal type, which is defined by Hyman (1940) as ‘... composed of bundles of muscle fibers or cavities lined by muscle fibers embedded in a great thickness of mesogloeae’. Functionally it is very different from the rest of the circular system, and therefore might be considered as physiologically separate. Its contraction closes the top of the column after the oral disk and tentacles have been retracted.

**Septal musculature**

**Parietal muscles.** The longitudinal muscles of the column are the parietal muscles. These are not a part of the column wall proper, but lie along both sides of all the septa near their bases. The parietal fibres lying on the endocoelic face are inserted radially into the basal disk of the anemone. Owing to the fibre arrangement (fig. 5), contraction of the parietals causes the vertical
stress in the column, resulting from contraction of circular muscles, to be distributed on to the pedal disk.

The fact that these two components of the column musculature are not superimposed upon one another, but are separated in space, conveys a definite mechanical advantage. Since the circular layer is essentially continuous and

external to the longitudinal fibres which are arranged in separate bands, the probability of the two 'buckling' (Batham and Pantin, 1951) at right angles to each other, thereby raising serious mechanical difficulties, is eliminated.

Muscles of the perfect septa

Retractor muscles. Three types of septa are present in Stomphia, as in other actinians. The perfect septa, those that connect the body-wall to the pharynx, bear well-developed longitudinal muscle-bands, the retractor muscle, on the endocoelic face. The fibres fan out above on to the oral disk, and below on to the pedal disk, thereby connecting the oral and aboral extremities of the anemones. Upon rapid contraction the retractors pull the edge of the oral disk inward and downward. At the same time the radial muscles of the oral disk contract. After retraction of the disk, the sphincter also contracts, closing over it. The retractors aid the parietals in maintaining the shape of the column.

Radial muscles. On the exocoelic face, the perfect septa bear a relatively weak group of muscle-bands, the radials (transverse muscles of some workers), the function of which is to open the pharynx, and thus help to control the

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amount of fluid in the coelenteron. These are less extensive on the directives, where the retractors are exocoelic.

**Parieto-basilar muscles.** The rest of the exocoelic face contains the stronger parieto-basilar muscles. These fibres originate on the pedal disk and have their insertion on the lower two-thirds of the body-wall. This muscle is relatively thick and bears a fold at its inside edge, similar to the edge of the retractor on the opposite face (fig. 5, A). Contraction of portions of this system produces bending of the column.

**Muscles of the imperfect septa**

The imperfect septa that bear a retractor muscle are similar to the perfect series in the muscles they support and in their functions. The primary morphological difference is that they do not join the body-wall to the pharynx, and thus the radial elements do not have the function of their counterparts on the perfect septa. The radials of these imperfect septa (figs. 5, F, G) are possibly utilized in controlling the volume and surface area of the coelenteron.

**Muscles of the microcnemes**

The microcnemes are small, imperfect septa bearing no retractor muscle, but with a parietal muscle developed in proportion to the size and age of the microcneme. It will be remembered that the other types of septa also have parietal muscles; but in the younger septa these are of greater importance, since other muscle elements are not yet developed. In spite of their small dimensions, the many cycles of these septa supply the body-wall with its effective longitudinal muscular system.

**Pedal Disk**

The muscular components of the pedal disk include a sheet of gastrodermal circular fibres continuous with that of the column; radial fibres lying on each side of the attachment of the septa contributing them; parieto-basilar muscles, and fibres derived from the retractors.

The foot is the organ of adhesion. Contact with the substratum is maintained by the parieto-basilars and the basal elements of the endocoelic longitudinal fibres, which produce a tonus in opposition to the pressure of the coelenteron. Time-lapse motion-pictures of detached animals and of animals undergoing reattachment, show clearly the action of these muscles. In conjunction with relaxation of the basilars, contraction of the endocoelic longitudinal fibres causes an inward arching of the pedal disk that will necessarily develop suction. Maintenance of attachment is also aided by the epidermal cells of the pedal disk (Batham and Pantin, 1950, 1951), which secrete a cuticle-like substance.

Release from the substratum is accomplished by contraction of the radial muscles of the pedal disk, the basilars. The contractile state of the circular muscles also affects the suction below the pedal disk. Other movements
associated with swimming cause the anemone to move from its place of attachment.

**Oral Disk**

The third region of the anemone, the tentacles and oral disk, also contains a circular sheet of muscle continuous with that of the rest of the animal, and a radial set of muscle-fibres, also medial to the mesogloea. The muscles of the disk and tentacles are important in feeding activities, but their role in swimming is only passive. They play some part in aiding the retractors, sphincter, and circular layer of the column in the retraction stage, and in maintaining the turgidity of the column.

**Muscular System: Function in Swimming**

When suitably stimulated, the anemone contracts and withdraws the oral disk and tentacles. This action is a very common response in actinians and results from contraction of the parietal and retractor groups of muscles. As soon as these muscles have withdrawn the disk and tentacles, the sphincter contracts, covering the entire oral end of the anemone. During this overall contraction it sometimes may be necessary to release some of the fluid contained in the coelenteron. This is done by the radial muscles of the septa contracting to open the pharynx.

After overall retraction of the oral disk and shortening of the column, the animals elongate and often expand the disk. This is accomplished by the circular muscle sheet of the column acting against the coelenteric fluid.

In these movements, the functional integrity of the animal as well as the activity of its three morphological regions are well illustrated. The circular muscles in all parts are essentially continuous, but in this case can readily be seen to act quite independently; the two disks at opposite ends of the column are inactive while the column elements contract strongly.

The waving motion that often occurs at this point in the reaction is the result of a co-ordinated contraction of fibres of the parieto-basilar system. To produce the lateral bending on first one side and then the other relatively small areas are involved at any one moment.

The release from the bottom is accomplished principally by contraction of the basilar muscles of the pedal disk. The circular muscles undoubtedly play an important part in this action also. Their relaxation would reduce the suction exerted under the foot, thus facilitating the release.

In released animals the pedal disk often has a definite conical shape. This is due to the contraction of the longitudinal fibres and the parieto-basilar muscles of the septa. These fibres are probably still in the contracted state that aided in the release of the anemone from the substratum. The swimming itself is done by the action of the parieto-basilars in the manner discussed in the section describing the waving motion. Possibly a localized relaxation of the circular sheet at the point of bending aids in these movements. The re-establishment of turgidity which results from the recovery of tonus in the
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circular muscles accounts for the extension of the column that occurs between
each of the bending movements. During the latter parts of the reaction the
general body tonus is maintained by the action of the circular and parietal
muscles and the longitudinal elements of the septa.

When swimming ceases, the animal becomes inactive; and as stated above,
it is usually unresponsive to stimulation during this time. The animals will,
nevertheless, soon recover and, bending the column, place a portion of the
foot against the substratum. Then, by localized contraction of the parieto-
basilars and the basal parts of the longitudinal endocoelic fibres, the pedal
disk once more slowly becomes attached to the bottom and the anemone lifts
itself into an upright position. The action of these muscles is preceded and
aided by the relaxation of the basilar muscles of the foot.

EXPERIMENTAL PROCEDURES

Since Stomphia was first seen to swim as the result of contact with star-
fishes, several species of these were tested to determine their effect upon the
anemone’s behaviour. In preliminary tests it was established that (for those

<table>
<thead>
<tr>
<th>Name of starfish used as stimulus</th>
<th>Number of positive responses</th>
<th>Number of negative responses</th>
<th>Number of trials</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crossaster papposus</td>
<td>1</td>
<td>69</td>
<td>70</td>
</tr>
<tr>
<td>Pteraster tesselatus</td>
<td>0</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Hippasteria spinosa</td>
<td>several hundred</td>
<td>0</td>
<td>several hundred</td>
</tr>
<tr>
<td>Henricia leviuscula</td>
<td>0</td>
<td>53</td>
<td>53</td>
</tr>
<tr>
<td>Leptasterias hexactis</td>
<td>0</td>
<td>23</td>
<td>23</td>
</tr>
<tr>
<td>Orthasterias koehleri</td>
<td>0</td>
<td>48</td>
<td>48</td>
</tr>
<tr>
<td>Solaster stimpsoni</td>
<td>2</td>
<td>46</td>
<td>46</td>
</tr>
<tr>
<td>Evasterias trochelii</td>
<td>0</td>
<td>47</td>
<td>47</td>
</tr>
<tr>
<td>Pisaster ochraceus</td>
<td>0</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Pisaster brevispinus</td>
<td>0</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td>Dermasterias imbricata</td>
<td>several hundred</td>
<td>few</td>
<td>several hundred</td>
</tr>
</tbody>
</table>

starfishes that cause a positive response) any part of the entire starfish brought
into contact with any part of the anemone would usually elicit the same
response. Therefore, in the tests in which entire starfish were used, no effort
was made to limit the parts, e.g. the tube feet, epidermis, &c., used to stimulate
the anemone. Table 1 summarizes a series of tests made in an attempt
to determine whether the reaction is specific for particular species. Many
more tests than actually appear in the table were made in preliminary
studies; none of these gave results in disagreement with the following data.
To be classified as ‘positive’ the anemone had to release from the substratum
and swim.

As is clear from table 1, whereas negative responses were obtained from
experiments with a majority of the starfishes tested, positive responses greatly
exceeded negative responses in the cases of two species, *Dermasterias imbricata* and *Hippasteria spinosa*.

At first, the swimming of the anemones seemed to be an avoiding reaction elicited by certain starfishes. The possibility that the behaviour serves as a defence mechanism against predators was therefore considered. To test this, specimens of the anemone and various starfishes were placed together in a confined area. The space was limited to increase the possibility of their coming into contact with one another. The starfishes tested included *Dermasterias imbricata*, *Hippasteria spinosa*, *Crossaster papposus*, *Solaster stimpsoni*, *Pisaster ochraceus*, *Henricia leviuscula*, *Evasterias troschelli*, and *Leptasterias hexactis*.

In all tests, except those involving the first two species listed above, the results were negative. In some of these tests the starfishes were seen to crawl over the anemones; except in the instances involving *Dermasterias* and *Hippasteria*, this usually did not disturb the anemones enough even to cause retraction. On contact with either of these two starfishes the anemones usually swam. Since swimming anemones have no control over the direction of movement, they often swim in such a manner that the activity repeatedly brings them into contact with the starfish. This was not entirely due to the confined area, because the phenomenon was noticed quite often in other tests involving much more space for movement. Also, the movements of the starfish were completely random and they never appeared to seek out the anemones. Even though the space available was only approximately 1 1/2 cu. ft., the time required by a starfish of 8 to 10 in. in diameter to come into contact with a *Stomphia* was often more than a week.

The possibility that swimming is used as a means of getting rid of bottom debris in the event that anemones become covered by mud and silt was tested experimentally by allowing them to become attached to the inside of battery jars filled with sea-water, and then adding enough mud collected from their normal habitat to cover them partially. The mud was then stirred up by shaking the container or introducing a fast stream of water, thus partly burying the anemones. In no test were complete or even partial swimming movements noted. Mud particles were removed from the upper part of the column and from the oral area by ciliary action. By extending and contracting the column a few times, the anemones succeeded in establishing themselves in a condition not unlike that observed in their natural surroundings.

The possibility that the starfishes give off a substance that causes the anemones to swim was considered. That a water-insoluble substance on the surface of the asteroids elicits the response was suggested by the fact that *Stomphia* swam when touched by the experimenter’s fingers after a *Dermasterias* had been handled. This starfish produces a slimy substance which is easily transferred to other objects that come in contact with the asteroid. A series of tests (table 2) showed that positive responses could be obtained if sterile gauze wrapped on the end of a clean glass rod was first rubbed on a ‘leather-star’ (*Dermasterias*) and then used to touch the anemones. As a con-
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trol, the gauze was similarly applied without being first rubbed on a Derma-sterias. Similar tests with other starfishes proved negative.

It may also be noted here that Pteraster tesselatus, which produced copious amounts of slime, as well as Stichopus californicus, which has a very slimy epidermis, were completely ineffective in causing Stomphia to swim.

TABLE 2

<table>
<thead>
<tr>
<th>Stimulant</th>
<th>Number of positive responses</th>
<th>Number of negative responses</th>
<th>Number of trials</th>
</tr>
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<tbody>
<tr>
<td>Control</td>
<td>0</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>Gauze rubbed on Derma-sterias</td>
<td>14</td>
<td>16</td>
<td>30</td>
</tr>
</tbody>
</table>

It seemed possible that some water-soluble secreted substance might cause swimming. To test this, Dermasterias, Crossaster, Hippasteria, and Pisaster ochraceus were placed in clean, dry, porcelain pans and allowed to drain. The resulting liquid was collected and tested by application to Stomphia in two ways: by dipping a gauze-wrapped rod in the fluid and applying it to the anemone, and by using a pipette to squirt the fluid on to the oral disk of the animal. Both techniques gave negative results in more than 100 trials.

Experiments were undertaken to determine if the substance that might cause the reaction is slowly released by the starfish into the surrounding medium. To test this hypothesis, specimens of Dermasterias, Crossaster, and Hippasteria were placed in battery jars partially filled with sea-water. These were then wrapped in several layers of cloth that served as bumpers and floated in the large sea-water tank to be kept at nearly the same temperature as that of ordinary laboratory conditions. After remaining for from 3 days to a week under these conditions, the starfish were periodically removed and set aside. Specimens of Stomphia, previously attached to 15-cm square glass plates, were then transferred into the battery jars. The anemones retracted the oral disk and contracted the column in some instances, but gave no indication of the swimming reaction.

The water from the battery jars was also tested by the gauze and pipette methods described above, again with negative results.

To test further the hypothesis that a chemical is the stimulating substance, entire starfishes and isolated parts from Dermasterias and Hippasteria were homogenized in a Waring blender and applied to the anemones in the same way as the slime from Dermasterias. These trials were negative, except for two instances which can possibly be attributed to small particles from the homogenate which dropped on the anemones. The blended material was too viscous to filter; therefore it was likely that some small bits would be drawn into the pipette, possibly supplying a necessary mechanical stimulus to give a positive reaction. Results of similar tests with homogenate of Crossaster were also negative.

Since starfishes were handled in order to stimulate the anemones, it seemed
possible that this treatment might cause the secretion of a material that initiates the swimming activity. Tests were therefore made in which the anemones were brought into contact with the starfish (the starfish thus being the passive individual). This was accomplished by using *Stomphia* attached to glass plates and placing a starfish in the same tank in such a position that the anemones could be brought into contact with it by moving the glass plates. In this manner neither of the animals involved was handled directly. The results of these tests is shown in table 3.

**Table 3**

<table>
<thead>
<tr>
<th>Starfish used</th>
<th>Positive</th>
<th>Negative</th>
<th>Number of trials</th>
</tr>
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<tbody>
<tr>
<td><em>Dermasterias</em></td>
<td>5</td>
<td>6</td>
<td>11</td>
</tr>
<tr>
<td><em>Hippasteria</em></td>
<td>5</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td><em>Crossaster</em></td>
<td>0</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td><em>Evasterias</em></td>
<td>0</td>
<td>6</td>
<td>6</td>
</tr>
</tbody>
</table>

It has been previously stated that all parts of the anemones are receptive to stimulation by the proper starfish. This was further tested experimentally by stimulating different regions of anemones in contracted and in relaxed conditions. All other experiments recorded were done with the anemones in a state of normal extension, and the starfish used as a ‘stimulator’ was touched to the tentacles and/or the oral disk. However, a series of trials was also run in which the stimulus was applied to the column.

Several specimens of *Stomphia* were caused to contract completely and then were stimulated with starfishes known to induce the reaction in relaxed individuals. Specimens in states of partial contraction were also tested. Starfish were brought into contact both with the column and with the few tentacles exposed (fig. 1, b). The results of one series of these tests are shown in table 4. In some instances a specimen would begin to respond but the animal did not release; these are noted as ‘partial response’ wherever they occur.

The results suggest differences in the responsiveness of various regions of the anemone to stimulation by *Dermasterias*. Such differences may be attributed to the relatively fewer nerve-fibres in the column as compared to those of the oral disk and tentacles (Pantin, 1935b); or they may be attributed to a scarcity
of receptors, rather than a more diffuse organization of the nerve net of the column.

It is of some interest that release often occurred and the animal swam without the oral disk being expanded. This was due to the fact that the sphincter still was in a state of contraction, but it was also true of some individuals that had been stimulated while in the relaxed and expanded state. In the extension stage of the reaction such animals elongated but did not expose the oral disk. This did not seem to alter the reaction beyond changing the appearance of the anemone.

In experiments involving electrical stimulation of *S. coccinea*, the animals were stimulated by non-polarizable electrodes placed in contact with the base of the column. This enabled repeated stimuli to be given without the animal withdrawing from contact with the electrodes. The threshold was determined to be between 2 and 3 volts. All the stimuli were given at 6 volts for 50 ms at various frequencies, controlled by means of a Grass stimulator. The responses to these stimuli were recorded on a slow-moving kymograph drum by an isotonic lever attached to the oral disk of the specimens by means of a cotton thread and glass hook. Thus it is primarily the actions of the longitudinal muscles of the septa that are recorded in fig. 6.

Facilitation (Pantin, 1935a, b, c; Hall and Pantin, 1937; Ross and Pantin, 1940; Ross, 1946a, b, 1952, 1955; and Pantin and Passano, 1954) was exhibited when a series of stimuli was given at 1-sec intervals. The first stimulus produced no response, but each succeeding stimulus caused an increase in contraction up to the point at which the animal was maximally contracted.

It was found that the various stages of the swimming reaction could be demonstrated with suitable electrical stimulation. Stimulated with impulses of 6-volt intensity at a frequency of 1 per sec, the following reactions were observed:

2 shocks: incomplete contraction.
4 shocks: all but the tips of a few tentacles retracted.
6 shocks: complete contraction followed by extension and a few waving movements. A long interval occurred between each of the latter, whereas in the normal reaction to starfishes they usually follow one another immediately.
8 shocks: full contraction, extension, release, with or without the waving
activity, and the animals swam actively. They also remained unresponsive for a short time at the termination of swimming.

In order to determine if the stimuli given in the experiments described above were the number required to produce the swimming response, the frequency was increased to 8 per sec, and a series of tests was run at 1- to 8-sec periods of stimulation. The results of this increased frequency were no different from experiments in which shocks at 1 per sec were applied to the column of *S. coccinea*; except that in one case, of the total of 6, the anemones swam after 9, instead of 8, sec of stimulation.

**Analysis of Time-Lapse Motion-Pictures**

The animals photographed for this part of the study were placed in a large glass-walled aquarium supplied with running sea-water. The lighting was constant for the 3 to 4 h required for the photographic procedure, so that the only conditions that were varied were those noted in the experiments described below.

The time-lapse motion-pictures proved a valuable aid in studying the muscular activity of *Stomphia*. They demonstrate that the animals are in constant motion. The actions of undisturbed actinians, too slow to be otherwise detectable, involve continuous movement of the body-wall and tentacles and, every now and then, a retraction of the oral disk and/or contraction of the column.

Portions of two reels of time-lapse pictures showed especially interesting activities that were provoked by appropriate stimulation. In one case, the anemone being photographed was subjected to excessive heat caused by the arrangement of the lamps used in photography. As the temperature of the water rose, the activity of the animal increased greatly. This increase in activity took the form of convulsive contractions of the circular muscular system, lateral waving due to parieto-basilar activity, and repeated retraction and extension of the oral area, for which the retractors and sphincter muscle are responsible. The edge of the pedal disk was soon raised from the substratum and the animal moved away from its original place of attachment. It finally re-attached itself some 60 cm distant, out of the direct rays of the lamps. The time required for this movement was 3 to 3½ h.

In another case, one of the two anemones being photographed was fed with a bit of mussel. Feeding took place after the animals had been photographed in an undisturbed condition for about 1,500 frames at the speed of 16 frames per min. From this moment on, the activity of the circular muscle system in the fed anemone increased. This activity was very similar to peristaltic movement, and it might be so termed. The parieto-basilar muscles and the longitudinal muscles of the septa were also activated. The overall activity was not so intense as that elicited by excessive heat, nor were the individual movements so rapid. The unfed anemone was not affected by the activity of its neighbour. It remained in the expanded condition; the only movements noted were the
constant waving of the tentacles and a slight contraction of the column from
time to time.

**DISCUSSION AND CONCLUSIONS**

The waving motions by which *S. coccinea* swims involve at a given moment
the contraction of relatively small areas of the parieto-basilar muscle-system.
Contraction of these muscles may also cause a whirling of the oral area about
the oral-aboral axis of the anemone. This action appears to be the result of a
wave of contraction proceeding around the column. The side-to-side motions
are probably produced similarly. The difference in the two resulting activities
is possibly due to an interruption of the impulse as it proceeds around the
column, or to the fact that some of the muscular elements may be in a refrac-
tory state.

That the slime produced by *Dermasterias imbricata* will elicit swimming in
*Stomphia* suggests that this starfish may secrete some substance into the water,
or on to the anemone upon contact with it. As the experiments indicate, this
could not be demonstrated. Since none of the substances that could be ob-
tained by homogenizing the material had any consistent effect on the behaviour
of *Stomphia*, it can only be concluded that the reaction is not due solely to
such stimulation. Further, there was no evidence that *Hippasteria* produces
a substance which can be transferred to the anemone and elicit swimming.

In the experiments in which starfishes were kept in battery jars, the fact
that the anemones contracted may have been due to the necessity of their
being exposed to air for a short time during their transfer from the tank into
the battery jars. None of them contracted during this transfer, and all appeared
normal upon immersion into the water which had contained the starfish. The
contraction may also have been caused by something in the water, or might
have been due to the stagnant state of the water that resulted from its not
being changed in the attempt to allow a sufficient quantity of the hypothetical
substance to diffuse into it from the starfishes.

The experiment in which the anemones were the active and the starfish the
passive participants, indicates that any substance released by the starfish that
might stimulate the anemone is not released as the result of the handling and
consequent disturbance of the animals. Considering the small number of these
tests, the high number of negative results may indicate some important factor
of the anemone-starfish association that is not evident at the present time.
Further studies will have to be made before this question can be answered.

The experiments in this study seem to indicate that the time-interval over
which the stimuli are given is the main factor in eliciting a swimming response,
although many more experiments involving electrical stimulation of *Stomphia*
should be done before definite conclusions are drawn. This tentative con-
clusion is substantiated by the fact that stimulation by starfish usually requires
a period of similar duration. Positive results from electrical stimulation experi-
ments also illustrate the fact that a chemical substance is not necessarily
involved in the stimulation of swimming by *S. coccinea*. 
From the time-lapse motion-pictures it can readily be seen that anemones are constantly in some state of activity. With proper stimulation, e.g. temperature increase or feeding, the activity takes the form of a definite pattern of movements that seem to be quite well co-ordinated. The best example of such co-ordination revealed by these studies is the case of temperature increase, where the anemone co-ordinated its muscular activity to enable it to 'walk away' from the area of most severe heat to a spot where the environmental conditions were more suitable. It should be stressed that *Stomphia* walked away, but did not swim, as the result of this severe stimulation.

The slow activities described above for *Stomphia* (as seen in time-lapse motion-pictures) closely parallel those of *Metridium* as described by Batham and Pantin (1950a, b). The similarity is very striking when the time-lapse film prepared by Batham and Walker and the films used in this study are compared. In the former, the responses of *M. senile* to food and the locomotion of the animal in response to certain stimuli are illustrated (Batham and Pantin, 1950a).

*Metridium* is known to 'walk' without any apparent cause; but Batham and Pantin say, 'Occasionally locomotion in *Metridium* seems directly initiated in response to a prolonged adverse stimulus . . . an anemone subjected to repeated electrical or mechanical stimulation or to prolonged very powerful illumination or to the sewing-in of a recording thread would begin walking during the following night.' The anemones move over the substratum by extending one side of the pedal disk to an advanced position, attach this area of the foot to the bottom, and move the rest of the foot to the new position. The motions by which the foot is raised and advanced seem to be random; but the attachment and consequent locomotion occur only in one direction. The mechanism influencing the direction in which the anemones proceed is not understood. A complete comparative study of the locomotion of *Stomphia* and *Metridium* is lacking; but the slight differences (observed in time-lapse films) in the manner in which the two anemones move can probably be attributed to the variation in the musculature of the two species (Batham and Pantin, 1951a, b).

The response to solid food is similar in the two species. Both anemones, when given a bit of food, engulf the particle and greatly increase the activity of the circular muscle-sheet of the column (peristalsis). One apparent difference in the feeding motions of the two animals is that unfed specimens of *Stomphia* adjacent to a fed individual are unaffected by the activities of the fed animal. *Metridium*, in similar circumstances, appears to make searching movements, and peristaltic contractions are often noted in the unfed animal. A possible explanation of this variation in the activities of the two species may be the differences in the ability of the sphincter muscle in *Stomphia* more effectively to close the coelenteron and thus not allow the food juices to diffuse into the surrounding medium. Batham and Pantin illustrate an increase in the activities of *Metridium* in response to the presence of soluble food materials in the water.
Study of the musculature, and the observations of the behaviour of *Stomphia* and *Metridium*, indicate that actinians are capable of only a limited number of different kinds of movements. But as is shown in these studies, the order in which these various individual movements take place may form a definite behaviour pattern which is determined by the stimulus. In the case of swimming, the muscles that are used and the way in which they contract are similar to those in the slow, and apparently unco-ordinated, actions of the anemone 'at rest'. But in swimming the muscular contractions are powerful, rapid, and co-ordinated. How that co-ordination is accomplished, and through what mechanism co-ordination is achieved, remains a problem to be explored.

Throughout this investigation the most intriguing questions have concerned the adaptive significance of such an activity as swimming. It is true that certain starfish are predators of anemones (Milligan, 1916); and if *Stomphia* is preyed upon, its ability to swim certainly must be considered an effective means of escape. For, even though anemones may again come into contact with the starfish during swimming, their activities help to prevent their being grasped and held by the slow-moving asteroids. But all experiments designed to test whether predation is a factor in this starfish–anemone relationship have been consistently negative.

Another possible use for the reaction was suggested by the fact that the anemones were observed in nature to have one-half to two-thirds of the column covered by the sandy mud of the bottom. It was therefore postulated that in the event of stormy seas or violent currents the anemones could conceivably become covered by settling debris. In such cases some method of getting uncovered, such as the writhing movements of the swimming reaction, would be useful. In laboratory experiments the anemones uncover themselves simply by the action of the epidermal cilia; this hypothesis, then, does not account for the swimming behaviour. Therefore, for the present, the question of the value of the swimming response still stands unanswered and open to further speculation and testing.

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