Vol. 131, No. 2 October, 1966

THE

BIOLOGICAL BULLETIN

PUBLISHED BY THE MARINE BIOLOGICAL LABORATORY

DISTRIBUTION OF URCEOLARIA SPINICOLA (CILIATA, PERITRICHIDA) ON THE SPINES OF THE SEA URCHIN STRONGYLOCENTROTUS DROEBACHIENSIS

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Most of the described species of *Urceolaria* occur epizoically on various fresh-water and marine invertebrates (Hirshfield, 1949). Probably *U. patellae,* from the ctenidia of the European limpet *Patella vulgata,* and *U. mitra,* from the external surface of fresh-water triclads, are the best known, owing to the ecological studies of Brouardel (1941, 1947) and Reynoldson (1950, 1955). The only species known at present from echinoids is *U. spinicola* Beers, 1964, which occurs in abundance on the spines and pedicellariae of *Strongylocentrotus droebachiensis,* at least in the waters adjoining Mount Desert Island, Maine. Since the ciliate appears to be obligately epizoic on the urchin, its geographic range is probably coextensive with that of the host. In general, *U. spinicola* has the form of a short cylinder, which measures about 60 μ in diameter and 25 μ in height. By means of its specialized basal disc, it adheres firmly to the spines and pedicellariae, although it is capable of limited locomotion, either by sliding along the substratum or, less commonly, by swimming freely in the medium.

The preceding study (Beers, 1964) was concerned chiefly with the structure and identification of the ciliate and with its actual occurrence on the urchins of Mount Desert Island. Its distribution on the spines received only incidental mention, although it presented some remarkable features. The evidence indicated, for example, that short spines had many more urceolarias per spine than long ones, and that the ciliates attached to long spines were concentrated on the proximal halves of the spines. The reference to long and short spines does not mean primary and secondary ones. The spines of any specimen of *S. droebachiensis* differ greatly in length, but the intergrades between the extremes are practically countless. Thus, the spines cannot be separated into two categories (Hyman, 1955, p. 424). In view of the fundamental similarity of the spines, any differential distribution of *U. spinicola* on their surfaces assumes added interest. Therefore, a more thorough study of the distribution was undertaken in the summer of 1965, again on the urchins of Mount Desert Island. The results are presented in the present paper, which deals mainly with the following aspects of the urchin-ciliate association: (1) the occurrence of the ciliate on spines from different regions of the urchin test; (2) the density of the ciliate population (intensity of epifaunation) on urchins of different sizes; (3) the occurrence of the ciliate on spines of different lengths; and (4) its distribution on individual spines. Once the distribution on the spines is definitely established, an analysis of the factors responsible for such distribution can be attempted, but this aspect of the study is deferred for the present. Any consideration of the distribution of the urceolarias on the pedicellariae is likewise deferred.

Material and Methods

From June 15 to August 25, 1965, specimens of *S. droebachiensis* were collected as needed from the inshore waters of Mount Desert Island. They were taken from three localities: Laboratory Point, Bartlett Narrows and Long Ledge. Laboratory Point means the waters of Frenchman Bay adjacent to the Laboratory area. In the summer the Bay is relatively calm and littoral urchins are subjected to the minimum of wave action. Thus, their spines show very little weathering at the tips. Although the mean tidal range of the Bay amounts to 3.25 m., the amount of organic matter in the water and the bacterial count were evidently high in 1965, since much of the Bay was closed to the taking of mussels and clams for table use. In general, the waters of Bartlett Narrows, a strait in Blue Hill Bay, are likewise free of turbulence and in 1965 they were relatively uncontaminated. Long Ledge, well removed from Laboratory Point and Bartlett Narrows, presents a somewhat different habitat. The waters are quite uncontaminated, the Ledge is exposed to the winds, and a surf is constantly present. Thus, the long spines of inshore urchins are much eroded distally.

Counts of the urceolarias were made on detached fresh spines. A small piece of the test was excised from a recently collected urchin and removed to a watch glass of sea water under the dissecting binocular, with the spines uppermost. The piece was held down by a blunt needle, the tip of a small scalpel was brought against the base of a spine, and the spine was detached by a quick movement of the scalpel. When a sample of several contiguous spines was desired, the spines were detached in turn, beginning at the margin of the piece. The number of urceolarias dislodged by the procedure was negligible.

It is practically impossible to count the urceolarias *in situ* on a spine, largely because of its opacity. In order to count them, the detached spines were transferred in groups of five or ten to a watch glass of distilled water. When a fresh spine is immersed in distilled water, any urceolarias on it are immediately immobilized and after 3–5 min. they become detached. If the spine is shaken gently with forceps, they drop to the bottom of the watch glass, where they can be counted accurately.

With reference to the distribution of *U. spinicola* on the urchin, the following three regions of the test were distinguished: a circumoral region, meaning the somewhat flattened surface which is normally in contact with the substratum; an ambital or circumferential region; and an aboral region, meaning the expanse between the ambitus and the periproct.

The ages of certain of the urchins were estimated from the diameter of the test, following the data summarized by Swan (1961, Table IV). In the presentation of the results, comparisons will be made occasionally between the numbers of urceolarias in two groups. If the larger number exceeds the smaller by one-third or more, the difference is judged to be significant. Minor comments on methods will be supplied as needed.

RESULTS

1. *Occurrence of U. spinicola on spines from different regions of the urchin test; intensity of epifaunation on urchins of different sizes*

Urchins of various sizes (measured by the diameter of the test) were examined from each of the three localities. Their respective sizes are listed in column 1 of Table I and their corresponding ages in column 2, in so far as estimates of age are available. Most of the sizes represent recognized year-classes, but some urchins of undetermined age are also included. Five urchins of each of nine sizes were examined from Laboratory Point. Unfortunately, urchins 9–18 mm. in diameter were unavailable at Bartlett Narrows and Long Ledge, but five of each of the

TABLE I

Occurrence of U. spinicola on urchins (S. droebachiensis) of different sizes from three localities on Mount Desert Island, Maine (Laboratory Point, Bartlett Narrows and Long Ledge). Summer 1965

Diameter of test in mm.	Age in years from time of settling	Locality	Average number of urceolarias per spine			
			Circumoral region	Ambital region	Aboral region	Entire urchin
9–10	1	Lab. Point	1.3	1.0	0.5	0.9
12–14	?	Lab. Point	2.3	1.7	0.7	1.6
16–18	?	Lab. Point	18.4	19.1	10.1	15.9
24–26	2	Lab. Point	20.9	23.7	12.6	19.1
30–38	?	Lab. Point	28.2	32.4	13.9	24.8
40–42	3	Lab. Point	37.8	35.1	26.4	33.1
46–54	4	Lab. Point	43.1	41.6	24.3	36.3
55–60	5	Lab. Point	22.9	26.8	16.2	22.0
62–74	6+	Lab. Point	2.7	3.4	2.8	3.0
24–26	2	Bart. Nar.	9.8	8.2	4.5	7.5
30–38	?	Bart. Nar.	22.1	25.8	9.6	19.2
40–42	3	Bart. Nar.	11.0	9.2	3.6	7.9
46–54	4	Bart. Nar.	10.5	8.2	4.1	7.6
55–60	5	Bart. Nar.	1.8	1.2	0.6	1.2
62–70	6+	Bart. Nar.	0.8	0.6	0.6	0.7
24–26	2	Long Ledge	4.7	5.2	4.6	4.8
30–38	?	Long Ledge	4.0	2.9	2.2	3.0
40–42	3	Long Ledge	2.1	1.9	0.7	1.6
46–54	4	Long Ledge	2.3	2.3	1.4	2.0
55–60	5	Long Ledge	2.6	2.4	1.0	2.0
62–72	6+	Long Ledge	0.8	0.5	0.4	0.6

remaining sizes were examined from these areas. The average number of urceolarias per spine was determined from a spine-sample taken from each of the three regions of each urchin. Such a sample consisted of any ten contiguous spines from an excised piece of test. Thus, each entry in columns 4, 5 and 6 of Table I represents an average based on 50 spines. It is understood that the spines of any sample varied considerably in length (usual range, 1.0–15.0 mm., but reduced to 0.5–5.0 mm. in samples from small urchins).

Turning to Table I, consider the average number of urceolarias per spine on different regions of the test, beginning with the urchins from Laboratory Point. In any of the nine size-classes, the average number of ciliates per spine was approximately the same on the circumoral and ambital regions (columns 4 and 5). For example, in size-class 24–26 mm. the average numbers were 20.9 and 23.7, respectively (no significant difference). On the other hand, the average number on the aboral spines (column 6) was decidedly smaller in all the size-classes, with one exception—the class consisting of the largest urchins (62–74 mm.), which had very few ciliates per spine, regardless of the region. In general, the foregoing comments also apply to the urchins from Bartlett Narrows, although the average number of ciliates per spine was smaller without exception. With reference to the Long Ledge urchins, the ciliate populations were extremely sparse and the average number of urceolarias per spine was therefore much reduced. Indeed, the ciliate counts were so small that comparisons between the respective regions of the test are scarcely practicable. Nevertheless, the general features of the distribution were in agreement with those already described.

Referring again to Table I, consider the average number of urceolarias per spine on urchins of different sizes; that is, the intensity of epifaunation of the entire urchin (column 7, each entry of which is based on a total of 150 spines). With reference to the urchins from Laboratory Point, the average number of ciliates per spine increased with the size of the urchin, until a diameter of 46–54 mm. (or an age of about 4 years) was attained. On urchins larger than these, the number decreased abruptly. The scarcity of urceolarias on urchins 62 mm. or larger in diameter (presumed to be at least 6 years of age) was remarkable. Indeed, on many urchins of this size it was impossible to find any urceolarias, either on the spines or pedicellariae. In general, the foregoing remarks also apply to the urchins from Bartlett Narrows, although the average number of ciliates per spine was consistently smaller and the maximal number occurred on urchins 30–38 mm. in diameter, some of which were probably 3 years of age. On the Long Ledge urchins the average number of urceolarias per spine was small, and comparisons between successive sizes are therefore less meaningful. Nevertheless, the trend in the intensity of epifaunation agreed with that already mentioned.

Spine-samples from the ambulacral and interambulacral areas of certain urchins were also examined comparatively, although the results are not presented in tabular form. Without exception, the average number of urceolarias per spine was essentially the same on the two areas. For example, on a 41-mm. urchin from Laboratory Point, the average number per spine was 27.3 on an ambulacral area and 26.7 on an adjacent interambulacral area, based on a sample of 50 spines removed at random from each area. Evidently the presence of the tube feet does not affect the occurrence of the ciliate.

In summary, the results show (1) that *U. spinicola* is more abundant on the circumoral and ambital spines than on the aboral ones; (2) that it occurs in equivalent numbers on the ambulacral and interambulacral areas; (3) that the density of the ciliate population increases gradually as the urchin grows and attains its maximum on urchins 40–54 mm. in diameter; and (4) that the density decreases markedly on urchins 62–74 mm. in diameter, many of which bear no urceolarias whatsoever.

2. Occurrence of U. spinicola on spines of different lengths from three regions of the urchin test

Considerable numbers of spines were detached from each of the three regions of five urchins (diameter, 40–42 mm.) from Laboratory Point, and the number of urceolarias per spine was recorded. These records supplied numerous counts for

TABLE II

Occurrence of U. spinicola on spines of different lengths from three regions of the urchin test. Number of urchins, 5. Diameter of test, 40–42 mm. Spine-sample, 10; namely, 2 spines of each length from each region of each urchin

Spine length in mm.	Average number of urceolarias per spine			
	Circumoral region	Ambital region	Aboral region	Entire urchin
0.6–0.9	8.8	7.4	10.2	8.8
1.0–1.9	29.5	31.3	21.0	27.3
2.0–2.9	28.9	32.4	18.4	26.6
3.0–3.9	42.9	30.3	14.9	29.4
4.0–4.9	28.8	21.5	10.1	21.5
5.0–5.9	14.6	13.4	7.1	11.7
6.0–6.9	8.0	6.4	3.8	6.1
7.0–7.9	6.3	4.6	4.5	5.1
8.0–8.9	5.8	3.9	1.6	3.8
9.0–9.9	3.1	2.5	0.6	2.1
10.0–10.9	*	2.7	1.8	2.3
11.0–16.0	*	2.8	1.2	2.0

* None of this length present.

spines of many different lengths. Representative data on the relation of the number of urceolarias to the length of the spine are presented in Table II. For descriptive purposes, most of the spines will be treated as "short" and "long" ones. Although these terms are relative, they are nonetheless useful. Spines 1.0–4.9 mm. in length, which comprise about 80% of the spines on urchins 24 mm. or more in diameter, will be called short spines, whereas spines 5.0 mm. or more in length, which comprise about 15%, will be called long spines. Spines shorter than 1.0 mm., which make up the remainder, are therefore uncommon on such urchins.

Reference to Table II shows that the smallest spines (length, 0.6–0.9 mm.) of all three regions had relatively few ciliates per spine. The average number varied from 7.4 to 10.2, and the average for the entire urchin (based on 30 spines) was 8.8. Presumably most of these spines were immature ones which had not acquired their full complement of urceolarias. Spines 1.0–4.9 mm. in length, on the other hand, had the largest numbers of ciliates per spine; for example, the average number on the circumoral spines varied from 28.8 to 42.9. Then, spines 5.0 mm. or more in length had decreasing numbers of ciliates, and in general the average number per spine varied inversely with the length of the spine. In agreement with the data of Table I, spines from the circumoral and ambital regions had approximately equal (and maximal) numbers of ciliates, whereas those from the aboral region had fewer, although certain exceptions appear in Table II.

In general, the distribution of urceolarias shown in Table II was typical of urchins 24–60 mm. in diameter from Laboratory Point. For example, 50 short spines detached at random from five 25-mm. urchins had an average of 17.2 urceolarias per spine whereas 50 long ones had only 4.4 per spine. Similarly, 50 short spines from five urchins 55–58 mm. in diameter had 29.4 ciliates per spine, and 50 long ones had only 4.8. Thus, the results show conclusively that the short spines of urchins 24–60 mm. in diameter bear many more urceolarias per spine than the long ones.

Some further aspects of the urchin-ciliate association can be mentioned at this point. With respect to any individual urchin, the number of urceolarias on the spines of a particular length is extremely variable. For example, on ten ambital spines of length 2.0–2.9 mm. from a 50-mm. urchin, the number varied from 12 to 57; on ten spines of length 6.0–6.9 mm., from 1 to 15; and on ten of length 10.0–16.0 mm., from 0 to 9. It is evident, furthermore, that the number will vary with the intensity of epifaunation of the host. The largest number of urceolarias found on any spine in the entire study was 157 on an ambital spine 3.2 mm. long from a 31-mm. urchin. If an urchin bears a somewhat dense urceolaria population (of the degree indicated in Table II), ciliates will be found on practically every short spine, including those of the periproct, but their occurrence on long spines is unpredictable. It is a remarkable fact, which is at present unexplained, that urceolarias are absent on many of the longest spines (length, 10.0–16.0 mm.), even though the urchin as a whole harbors a dense population.

3. *Distribution of U. spinicola on individual spines of different lengths*

It has been shown that short spines bear significantly more urceolarias per spine than long ones, but there is a further peculiarity in the distribution. Briefly, the ciliates are not always distributed uniformly along the spine; on long spines they are concentrated on the basal (proximal) half. The regional distribution on individual spines was studied by cutting detached spines in half transversely and counting the urceolarias on the respective halves. A 45-mm. urchin from Laboratory Point was selected for special examination, since such urchins usually had undamaged spines and substantial epifaunations.

The counts compiled from various spine-samples from this urchin are summarized in Table III. From this Table it is seen that spines 0.6–0.9 mm. in length from any of the three regions had approximately equal numbers of urceolarias on the basal and distal halves. Likewise, spines 1.0–1.9 and 2.0–2.9 mm. in length had equivalent numbers on their respective halves. Spines 3.0–3.9 mm. in length, on the contrary, had approximately three times as many on the basal half as on the distal, and spines 4.0–4.9 mm. in length showed a still greater difference in numbers between the halves. Finally, spines 5.0 mm. or more in length had on the basal half many times the number on the distal half. The spines of two additional urchins, a 34-mm. specimen from Bartlett Narrows and a 31-mm. one from a lobster trap in 11 m. of water in Frenchman Bay, were subjected to a similar analysis with results in full agreement with those of Table III.

With reference to the long spines, the data as presented in Table III are inadequate to show the true distribution on them. For example, on spines 5.0–6.9 mm. in length, most of the urceolarias of the basal half were actually restricted to the basal third, and on spines 7.0 mm. or greater in length, to the basal fourth or even the fifth. Unfortunately, lack of time prevented me from cutting such spines into four parts and counting the ciliates on the respective quarters. Thus, the

TABLE III

Distribution of U. spinicola on individual spines (basal and distal halves, respectively) from a 45-mm. urchin. Spine-sample: 5 of each length from each region

Spine length in mm.	Average number of urceolarias on circumoral spines		Average number of urceolarias on ambital spines		Average number of urceolarias on aboral spines	
	Basal half	Distal half	Basal half	Distal half	Basal half	Distal half
0.6–0.9	8.2	6.8	8.8	10.2	9.0	7.6
1.0–1.9	11.4	12.2	16.8	18.8	12.6	11.4
2.0–2.9	21.2	20.4	22.4	18.0	12.4	11.2
3.0–3.9	34.0	11.2	35.8	9.6	7.6	2.6
4.0–4.9	27.2	7.8	21.4	6.2	4.6	0.0
5.0–5.9	10.8	0.2	9.0	0.0	5.8	0.4
6.0–6.9	5.0	0.2	6.6	0.2	3.0	0.2
7.0–7.9	4.4	0.4	2.2	0.0	1.4	0.0
10.0–15.0	*	*	0.8	0.0	0.4	0.0

* None of this length present.

statement is based merely on an inspection of the spines and not on actual counts, but I believe that it is nonetheless correct.

In summary, the data of Table III permit the following generalization: on spines 3.0 mm. or less in length, the urceolarias are distributed uniformly along the length of the spine; on spines longer than 3.0 mm., they are largely restricted to the basal half of the spine.

4. *Consideration of some factors affecting the distribution of U. spinicola on individual spines*

With reference to such factors, various possibilities suggest themselves. For example, does the distribution coincide with the ciliation of the spines? Hyman (1955, p. 438) points out that in echinoids the epidermis of the spines is "more or less ciliated" and that "the ciliation tends to disappear with age except around the spine base. . . ." In my experience with the spines of *S. droebachiensis*, however, carmine particles are swept energetically toward the distal ends of all the spines regardless of their length, indicating that much, if not all, of the spine surface is ciliated. Thus, the evidence indicates that the absence of urceolarias on the distal portions of long spines does not result from the absence of cilia. Furthermore, specimens of *U. spinicola* which have been gently brushed off the spines are capable of adhering firmly to various non-ciliated surfaces, such as glass, metal and granite. Although these observations are not extensive, they show at least that a ciliated surface is not necessary for the firm attachment of *U. spinicola.*

A second possibility affecting distribution relates to the constant movements of the pedicellariae and spines; that is, does contact of the pedicellariae with the long spines or contact of such spines with one another limit the distribution of urceolarias to the basal portions? The movements of the pedicellariae, spines and attached ciliates can be readily observed on an excised piece of test. The stalks of the pedicellariae, especially those of the triphyllous and tridentate ones, vary considerably in length, and in their movements the outer surfaces of the jaws commonly rub against spines of various lengths. Indeed, the jaws of the shorter pedicellariae frequently come in contact with the ciliates on spines 2.0–3.0 mm. long. When touched, the urceolarias move away from the area of contact, but they quickly resume their former distribution. In view of their abundance on such spines, it is evident that their distribution is not adversely affected by contact with the pedicellariae. Spines may likewise touch the ciliates on other spines, but with little more than a temporary disturbance of the distribution. It is unusual for the jaws of a pedicellaria actually to seize a spine and thereby injure the ciliates.

If it is assumed, nevertheless, that mechanical contact affects the distribution unfavorably, one might expect the ciliates on the bases of long spines to distribute themselves uniformly when the spines are detached and thereby isolated from one another. To ascertain whether the distribution changes under such conditions, 12 spines 3.6–4.8 mm. in length, which had urceolarias on their basal halves only, were detached from a 35-mm. urchin and tranferred to two Syracuse watch glasses of filtered sea water (six spines in 8 ml. in each watch glass; water changed daily; normal temperature of 14° C. maintained). The average number of ciliates per spine (counted at the end of the experiment) was 32. The general distribution of the ciliates on the respective quarters of each spine was recorded daily. In such an experiment it is difficult to compile quantitative data, since it is impossible to count accurately the number of urceolarias on any part of a relatively opaque spine. Fortunately, such data were not needed, for the changes in the original distribution were almost negligible. For example, after 3 days conditions in the watch glasses were as follows: cilia still active on the spines (epidermis living); urceolarias firmly attached (none swimming freely), moving slightly on the spine surface (normal behavior); two urceolarias on the penultimate quarter of each of two spines; none on the distal quarters; the remainder on the basal halves as originally. The experiment was discontinued 2 days later, when conditions were as follows: 29 ciliates detached and motionless near their respective spines; one swimming freely; 14 on the penultimate and distal quarters of certain spines; the remainder, totaling 340, still attached to the basal halves.

The experiment was repeated, using 12 spines 4.6–6.4 mm. in length from a 42-mm. urchin which carried an especially heavy epifaunation. The average number of urceolarias per spine was 31. On eight of the spines, the ciliates were restricted to the basal quarter; on the remaining four, to the basal half. After 4 days the original distribution was unchanged, except for four ciliates on the penultimate quarter of one spine. Two days later, when the ciliates were beginning to die and detach, this distribution still prevailed. It is evident, therefore, that when spines are detached and isolated from contact with other spines or pedicellariae, the distribution of the urceolarias undergoes no significant change.

Discussion

Since the presence of *U. spinicola* on its host was demonstrated somewhat recently, there has been little opportunity for an intensive study of the host-ciliate relationship. Nevertheless, certain features can be discussed briefly.

Transmission from host to host. In *U. patellae,* Brouardel (1947) observed that a very small percentage of the urceolarias left the limpet spontaneously from time to time and swam freely. Somewhat larger numbers detached when the host was in an unhealthy or moribund condition, and agitation of the medium facilitated detachment. Some of the free-swimming urceolarias survived for 6–8 hr. in sea water, and urceolaria-free limpets acquired ciliates when immersed in the water. Reynoldson (1950) concluded that *U. mitra* was dispersed when small populations occasionally assumed a free-swimming habit.

My efforts to induce *U. spinicola* to leave its host and disperse in the medium were notably unsuccessful. Its persistent adhesion to detached spines has been mentioned. Its behavior was also studied from day to day on excised pieces of test and on eviscerated whole tests. A few of the ciliates detached and swam briefly, but the number was insignificant, and the remainder perished *in situ.* Agitation of the medium, whether by vigorous stirring or by directing a stream of sea water on the urchin, was also ineffective. When a strong stream of water from a small glass nozzle was directed on a spine, the urceolarias merely retreated to the opposite side of the spine.

Probably the natural method of dispersal can be determined only by studying the association throughout the entire year. In *U. patellae,* Brouardel (1941) observed well-defined seasonal variations in the density of population, which was minimal in April and maximal in September and October. He found that dividing individuals were relatively numerous in May, but very scarce in January. In *U. spinicola,* the population appears to be relatively stable in the summer months. Dividing individuals are scarce—a fact reported earlier (Beers, 1964) and confirmed in the present study—and the population density, judged by counts per spine, seems to be as high in mid-June as in late August. Evidently *U. spinicola* in summer is physiologically specialized for continued adhesion to the host and not for dispersal. Presumably dispersal to new hosts occurs at other times of the year.

Population density in relation to habitat of the host. In *U. mitra,* Reynoldson (1955) found that fluctuations in the ciliate population were directly correlated with changes in the bacterial population of the water. Since *U. spinicola* feeds primarily on bacteria, its high incidence on the urchins of Frenchman Bay is attributed to an abundance of bacterial food. Similarly, its low incidence on the littoral urchins of Long Ledge is attributed largely to a scarcity of food, although the abrasive action of the surf, which erodes the spines, probably reduces the ciliate population through mechanical injury. Presumably the waters of Bartlett Narrows are intermediate with respect to the availability of food.

For the present I am unable to explain why *U. spinicola* is less abundant on the aboral surface of the host than elsewhere. My earlier statement (1964) to the effect that "it is found very sparingly on the spines and pedicellariae of the equator" is incorrect; evidently it resulted from the examination of inadequate samples.

Distribution on individual spines. Probably the most remarkable feature of the distribution of *U. spinicola* concerns its abundance on short spines, its scarcity or absence on long spines, and its concentration on the basal portions of such spines, when it is present. Attempts to correlate the distribution with the ciliation of the spines or with certain mechanical factors, such as contact with other spines, were unsuccessful, as has been said. It may be argued that the distribution results from an avoidance of strong water currents which sweep across the surface of the urchin in its natural habitat. Actually, such currents are absent at Laboratory Point and elsewhere in Frenchman Bay, except in restricted channels of strong tidal flow. Furthermore, urchins may be kept in good health for many days in an aquarium containing gently running sea water, provided they are supplied with suitable food, such as *Laminaria*. In the absence of strong water currents, these urchins retain their urceolarias in abundant numbers for at least 10 days, and the distribution on the spines undergoes no observable change. Finally, large urchins (diameter, 62–74 mm.) occupy the same natural habitat as smaller ones. Yet *U. spinicola* is very scarce or even absent on the spines and pedicellariae of large urchins. It is evident, therefore, that its distribution cannot be related to water currents.

The availability of bacterial food on the surface of the urchin remains to be considered. It may be argued that suitable food is more plentiful near the surface of the urchin than at the free extremities of the long spines. If the correctness of this proposition is conceded, it still does not explain the distribution on the spines. For example, a long spine is usually surrounded by a group of short spines. Yet *U. spinicola* is abundant on the short spines, but scarce or absent on the base of the adjacent long spine. In this connection the scarcity or absence of the ciliate on large urchins must be mentioned again. Presumably bacterial food is quite as abundant on the surface of these urchins as on smaller ones.

It is evident that an explanation of the distribution must be sought in factors other than those already mentioned. For the present I am disposed to conclude that the distribution is related to certain intrinsic properties of the spines themselves, perhaps to the histological structure of the spine epidermis. The conclusion implies that the spine surface is not a uniform substratum. Although ciliated columnar cells predominate in the epidermis of echinoids, various types of gland cells are also present, as Hyman (1955, p. 438) indicates. It is possible that the distribution of *U. spinicola* is correlated with the presence of certain gland cells, and it is hoped that this point can be investigated.

I am indebted to my colleague, Dr. Alan E. Stiven, for useful suggestions and advice relative to the plan of the investigation. The study was further aided by a grant from the Research Council of the University of North Carolina.

Summary

1. At Mount Desert Island, Maine, *Urceolaria spinicola* is of general occurrence on the spines of *Strongylocentrotus droebachiensis*. Two aspects of the urchin-

ciliate relationship were studied, largely on urchins from Frenchman Bay: the occurrence of the ciliate on urchins of different sizes and its distribution on spines of different lengths.

2. The density of the urceolaria population was highest on urchins measuring 24–60 mm. in diameter (test only), assumed to be 2–5 years of age (average number of ciliates per spine, 27). Smaller and therefore younger urchins (diameter, 9–18 mm.) had fewer per spine (average number, 9). On the largest urchins (62–74 mm.), assumed to be at least 6 years of age, urceolarias were extremely scarce (average number per spine, 3). Indeed, many urchins of this size had no ciliates whatsoever.

3. The distribution on spines of different lengths was studied with special care on 41-mm. urchins. The smallest spines (length, 0.6–0.9 mm.) had relatively few urceolarias per spine (average number, 9), whereas spines measuring 1.0–4.9 mm. in length had the largest number per spine (average, 36). The remaining spines (length, 5.0–16.0 mm.) were seriated according to length. On all the sizes, the average number of urceolarias per spine was well below the maximum of 36 and the number decreased as the length of the spine increased. Thus, many of the longest spines lacked ciliates. On spines measuring 0.6 to about 3.0 mm. in length, the urceolarias were distributed uniformly along the length of the spine; on spines longer than 3.0 mm., they were concentrated on the basal half of the spine.

4. The distribution of *U. spinicola* on the spines could not be related convincingly to any of the following factors: degree of ciliation of the spines, contact of the spines with one another, presence of water currents in the environment or availability of bacterial food on the surface of the urchin. Therefore, it is concluded tentatively that the distribution is related to the intrinsic properties of the spine epidermis, perhaps to the distribution of gland cells in it.

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