BEHAVIORAL ASPECTS OF PHOTOSENSITIVITY AND SPECTRAL SENSITIVITY IN ACANTHASTER PLANCI (L.)

by

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Title: Behavioral Aspects of Photosensitivity and Spectral Sensitivity in Acanthaster planci (L.)

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The photosensitivity and spectral sensitivity of Acanthaster planci was investigated. Specimens were found to display negative phototaxis, tube foot retraction, respiratory papillae retraction, and radial flexure in response to non-filtered light and light in the spectral region between 460 and 620 mμ.

Other photosensitive responses were investigated. Excised radii and transverse sections of these radii were found to be photoresponsive. Individuals in the field were found to be sensitive to shadows. In the laboratory, intermittent light was found to be a more effective stimulus for respiratory papillae retraction than constant light.

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INTRODUCTION

The coral predator Acanthaster planci (L.) has been the subject of much recent controversy. The impact of this species on Indo-Pacific coral reefs has been the impetus for various studies including ecology (Goreau, 1963; Chesher, 1969; Pearson and Endean, 1969; Weber and Woodhead, 1970; Humes, 1970; Brown, 1971; Antonius; 1971, and Tsuda, 1971), life history (Henderson and Lucas, 1971; and Yamaguchi, 1972), pharmacology (Cullen, 1970), and feeding behavior (Barnes et al., 1970).

In general, A. planci displays nocturnal behavior. Feeding usually takes place at night and, except in "plague" conditions, specimens are cryptic during the day. Specimens are most commonly found at depths ranging between 2 and 10 meters but are also found within the shallower surge zones and at depths below 50 meters. Through a series of behavioral experiments, I investigated the photosensitivity and spectral sensitivity of the crown-of-thorns starfish Acanthaster planci.

An extensive review of invertebrate photosensitivity has been made by Hyman (1940, 1951a, 1951b, 1955, 1959, and 1967). Spectral sensitivity has also been reported in various invertebrates. From retinal potential studies the following results are noted: planarian individuals display maximum sensitivity at 508 mμ (Brown et al., 1968), the sea hare Aplysia californica is most sensitive to that region of the spectrum below 600 mμ (Waser, 1968), and the

barnacle Balanus amphitrite displays maximum sensitivity between 530 and 540 mμ (Stratten and Ogden, 1971). From phototactic studies the following results are noted: the dorid nudibranch Onchidoris fusca displays peak sensitivity to light at 500 to 505 mμ (Hughes, 1970); the scallop Pecten maximus displays two peaks of sensitivity, one peak at 475 to 480 mμ and the other at 540 mμ (Cronly-Dillon, 1966); and the pink shrimp Penaeus duorarum displays maximum sensitivity to that region of the spectrum above 508 mμ (Jachowski, 1968).

Spectral sensitivity in echinoderms has been reported by various investigators. In earlier tube foot retraction studies, an unspecified species of Asterias was reported to be sensitive to "white light" (sunlight) but insensitive to "red light" (Moore, 1921). Later tube foot retraction studies by Millott and Yoshida (1956) demonstrated the echinoid Psammechinus miliaris to be most sensitive to wavelengths between 440 and 530 mμ (Millott and Yoshida, 1957). In phototactic behavior studies, the cushion star Pteraster tesselatus displayed positive taxis to "green light," negative taxis to "blue light," and no taxis to "red light" (Guberlet, 1946). In further phototactic studies, young Asterias forbesi specimens were found most sensitive to wavelengths between 400 and 500 mμ (Rockstein and Spritzer, 1960).

The relative independence of photic responses from central nervous system influence has also been studied by various investigators. Holmes (1912) found that in the echinoid Arbacia punctulata, spine movement and tube foot retraction in response to sudden illumination

persists after the nerve ring has been "destroyed." In later studies (Millot, 1953), the photic spine response in D. antillarum was shown to exist in the absence of the circum-oesophageal nerve ring (central nervous system). It was further noted, however, that the spine response is abolished if the radial nerve is removed (Millott, 1953; and Millott and Yoshida, 1959). The nerve ring is of prime importance, however, as an integrating center for the coordinated movements of the tube feet and radii (Smith, 1950; Kerkut, 1954; and Barrington, 1967).

EXPERIMENTS

General Conditions of Experiments:

Individuals used in Experiment I were taken from an aggregating A. planci population. The total number of individuals in the aggregation was too numerous to count (plague density). Individuals used in the remaining experiments were taken from areas in which the starfish existed in sub-plague proportions (Chesher, 1969). All individuals were collected by hand and transported in separate buckets to outdoor holding tanks at the University of Guam Marine Laboratory. The general conditions of each experiment can be seen in Table I.

Experiment I. Responses to Changes in Light Intensity and Quality.

This study was of a preliminary nature and was done to demonstrate whether or not Acanthaster planci is responsive to changes in light intensity and quality.

Procedure:

The responses of A. planci specimens to light stimuli of different intensities and qualities were investigated in 10 specimens ranging in size from 18.5 cm to 35.5 cm (referred to as Group A). All experimentation was conducted outdoors in the dark after 2000 hrs.

A large wooden tank of approximately 2000-liter capacity was filled with sea water to a depth of 97 cm. Next, a rubber ball was filled with fresh water to a diameter of 34 cm and transferred to the experimental tank. The ball was bouyant, and approximately one-quarter of

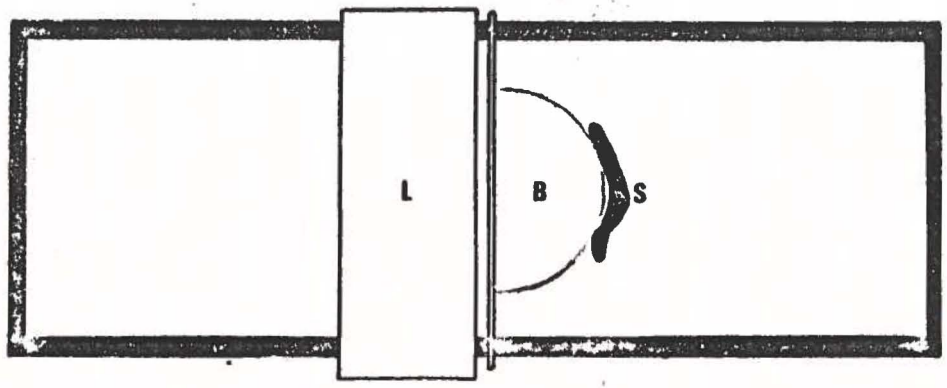
its surface was exposed to the air. This exposed portion was attached to the underside of a wooden U-shaped harness, which in turn was clamped to the inside walls (across the width) of the experimental tank approximately 3 cm above the water level (Fig 1). Specimens could thus move along the submerged surface of the ball without contacting any part of the wooden harness. A polyethylene plastic sheet divider was attached across the inside surface of the wooden harness above the water level. During an illumination period, the polyethylene divider produced a shadow over one-half of the experimental ball.

A. planci specimens kept in holding tanks outdoors for a 24-hr period were inactive during the day. However when light intensity fell below 50 ft-c (after 1800 hrs), specimens became active and moved about the tanks. With these observations in mind, I constructed a light box capable of transmitting light intensities above 50 ft-c during each illumination period. Light intensity was controlled with a Powerstat variable transformer and measured at the surface of the water with a G. E. model 213 light meter. Four sections of colored cellophane, each measuring 90.0 cm x 43.0 cm, with peak transmission values at 460, 520, 600, and 640 mμ (blue, green, yellow, and red, respectively) were independently used to produce different light qualities (Fig 2). Prior to an illumination period, a cellophane sheet was taped to a 0.64 cm thick sheet (91.0 cm x 43.0 cm) of heat absorbing window glass which was then fitted into a wooden frame across the open end of the light box.

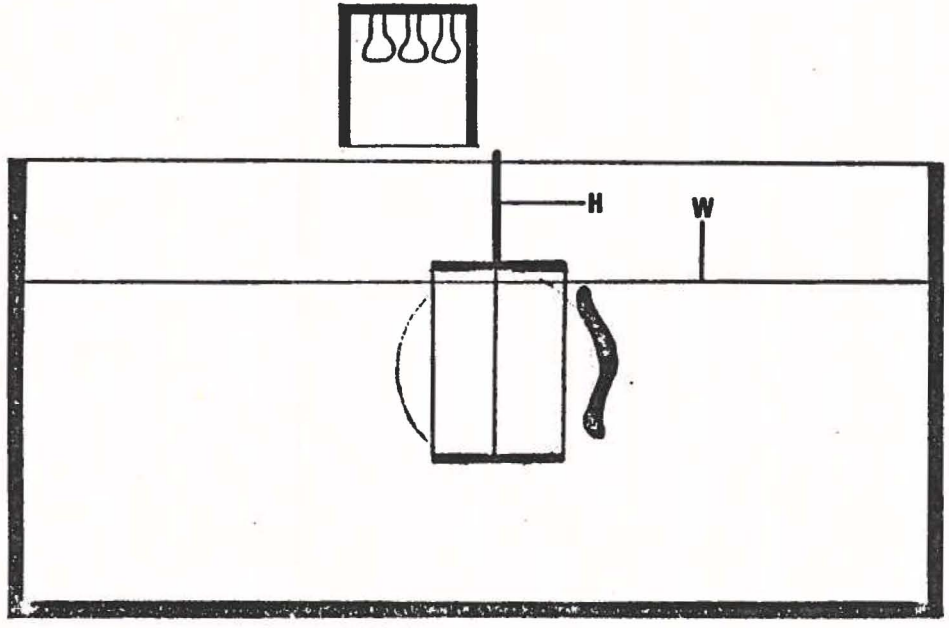
Table 1. Experimental Materials.

Description of Experiment	Experimental Apparatus	Figure	Collection Site	Specimen Group
I. Short term and Prolonged Illumination	Rubber ball, tank, light box, and G. E. type 213 light meter.	1	Catalina Point (northeast coast of Guam from a depth of approximately 10 m).	A
II. Radial Flexure Responses	Aquarium, Bausch & Lomb variable intensity microscope lamp, and Gossen Lunasix light meter.	3, 4	Piti Lagoon (southwest coast of Guam from a depth of approximately 2 m).	B
III. Respiratory Papillar Retraction	Plastic basin, B. & L. microscope lamp, 75-watt G. E. reflector flood lamp, and Gossen Lunasix light meter.	5, 6, 7	" "	C
IV. Tube Foot Retraction	Aquarium, plastic basin, plastic 1-cm mesh cradle, B. & L. microscope lamp. G. E. type 213 light meter, and Gossen Lunasix light meter.	8, 9, 10	" "	D
V. Excised Radii Responses	Culture dishes, plastic basin and B. & L. microscope lamp.	11	" "	E
VI. Phototactic Studies	Wooden trough, flood lamps, G. E. type 213 light meter, and Gossen Lunasix light meter.	12	" "	F

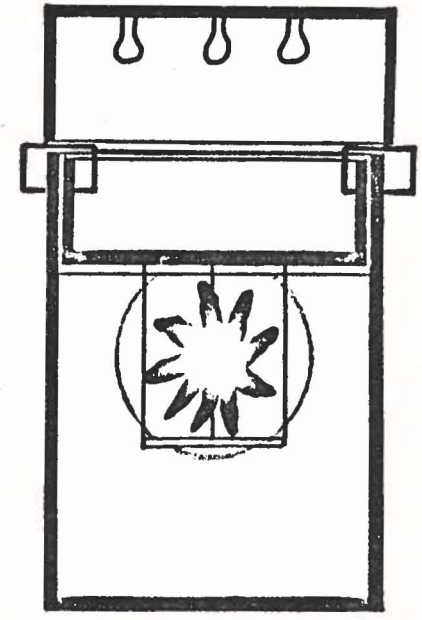
Figure 1. Experimental ball apparatus.
B, ball; H, harness; L, light box;
S, starfish; W, water level



TOP VIEW



FRONT VIEW



SIDE VIEW

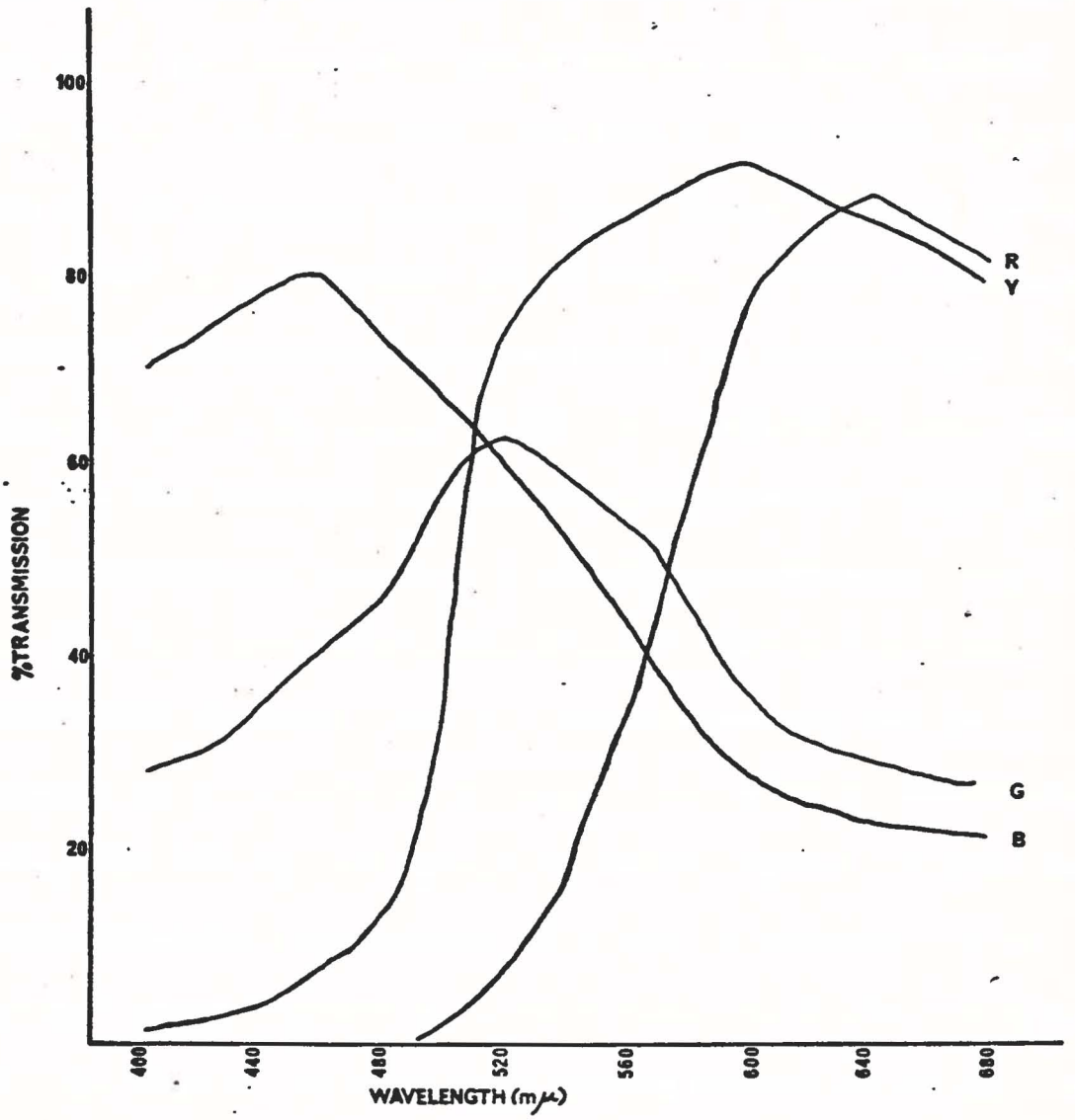
Individual response to short-term illumination was studied first. At the beginning of an experimental period, independently tested individuals were placed with their oral surfaces in contact with the experimental ball. They remained on the surface of the ball throughout the experimental period. Specimens were first subjected to an initial 30-min dark period, in which the ambient light intensity was less than 5 ft-c. At the end of the dark period the illumination intensity was increased to 225 ft-c for approximately 5 sec and then decreased to 25 ft-c. Specimens were tested at successive nutritional states: fresh from the field, starved for 60 days, and after one week of daily feeding on an exclusive diet of the coral Pocillipora damicornis (L.), under non-filtered light and at each of the filtered light qualities.

Next, individual response to prolonged illumination was studied. Specimens tested after the 60-day starvation period and again after one week of feeding were illuminated after an initial 2-hr dark period (which insured more complete dark adaption than obtained in the 30-min dark periods prior to the short-term illumination regimes) for 10 min at 225 ft-c with each light quality.

Results and Discussion:

During the initial 30-min dark periods of the short-term illumination experiments, specimens remained motionless with a few radii raised off the ball (dorsal flexure) and in contact with the surface of the water (not all radii were visible). When the illumination intensity was increased to 225 ft-c the animals lowered their radii onto the ball

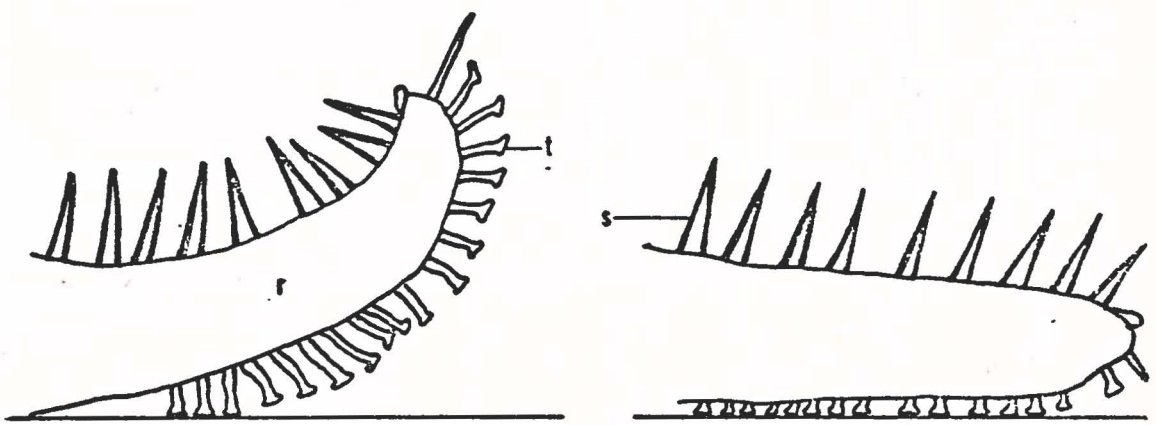
Figure 2. Light transmission of the cellophane filters used in the experimental ball studies. B, blue filter; G, green filter; Y, yellow filter; R, red filter.


100
80
60
40
20
%TRANSMISSION
R
Y
G
B
400
440
480
520
560
600
640
680
WAVELENGTH (mμ)

(ventral flexure), and when the intensity was finally lowered to 25 ft-c the specimens again displayed dorsal flexure (Fig 3).

During the initial 2-hr dark periods of the prolonged illumination experiments specimens were again motionless and again displayed dorsal flexure. When the illumination intensity was suddenly raised to 225 ft-c all individuals displayed ventral flexure. Ventral flexure was followed, after a variable amount of time, by locomotion in most individuals. Movement was directed around the circumference of the ball and parallel to the surface of the water. Individuals always moved with a few radii in contact with the surface of the water. Those which displayed locomotion showed one of the following behavioral tendencies: interface reversal behavior, primary shade-seeking behavior, or continuous movement (Table 2). Interface reversal behavior is characterized by an individual initially at rest, prior to illumination, moving from light into and through the shadow, coming to a halt when light is subsequently encountered, reversing its direction of movement 180° (without rotation of the radial disc), and finally coming to rest in the shadow. Primary shade-seeking behavior is characterized by an individual initially at rest, prior to illumination, moving from the light into the shade and there coming to rest without further movement. Continuous movement is characteristic of an individual moving continually around the ball through both shadowed and illuminated areas, throughout the illumination period.

Figure 3. Radial flexure in response to light stimuli. A, posture of a radius before illumination; B, posture of a radius during illumination; s, spine; r, radius; t, tube foot.



A
DORSAL FLEXURE

B
VENTRAL FLEXURE

Table 2. Behavioral responses (experimental ball apparatus) of starfish at different nutritional states to 10-min illumination periods of non-filtered (N. F.) and filtered light. See Figure 2 for light transmission characteristics of different filters. The sample size is 6.

Nutritional State	Filter	Number of Specimens Exhibiting Ventral Flexure	Number of Specimens Exhibiting Locomotion	Number of Specimens Exhibiting Primary Shade-Seeking Behavior	Number of Specimens Exhibiting Interface Reversal Behavior	Number of Specimens Exhibiting Continuous Movement
STARVED	N. F.	6	3	0	1	2
"	Blue	6	5	1	2	2
"	Green	6	5	1	1	3
"	Yellow	6	5	0	3	2
"	Red	6	6	1	1	4
FED	N. F.	6	4	0	1	3
"	Blue	6	5	0	3	2
"	Green	6	5	1	4	0
"	Yellow	6	4	0	3	1
"	Red	6	4	0	2	2

These two conditions (5-sec and 10-min illumination periods) indicate that the A. planci specimens tested were sensitive to changes in the illumination intensity irrespective of their nutritional state. As an index of photosensitivity, radial flexure seems to be a more sensitive response than locomotion; radial flexure occured in all cases, whereas locomotion was more variable. Radial flexure may be an "intention movement" (Heinroth, 1911), since it preceeded locomotion in all cases.

Table 3 shows that the number of specimens displaying locomotion in response to each of the light qualities increases as the duration of the light stimulus increases. This variation may be the result of stimulus response thresholds being higher in some individuals than others.

Although individuals at each nutritional state were sensitive to each light quality, it is possible that such sensitivity was limited to specific spectral regions common to all of the light qualities. Figure 2 indicates that the spectral characteristics of the light qualities are different; however, this difference is due to different degrees of transmission for the same wavelengths.

Considering these preliminary results, I designed further experiments to test for other possible responses to changes in light intensity and quality. Respiratory papillar retraction and tube foot retraction in response to light stimuli were investigated, as well as radial flexure. The preliminary results also suggested that photo-

Table 3. Locomotion response (experimental ball apparatus) of starfish at different nutritional states to 10-min illumination periods of non-filtered (N. F.) and filtered light. See Figure 2 for light transmission characteristics. The sample size is 6.

Nutritional State	Filter	Cumulative Number of Starfish Displaying Locomotion at Two Minute Intervals					Non-responsive Individuals at the End of 10 Minutes
		2	4	6	8	10	
STARVED	N. F.	1	3	3	3	3	3
"	Blue	2	3	4	5	5	1
"	Green	2	4	5	5	5	1
"	Yellow	1	3	4	5	5	1
"	Red	1	3	5	5	6	0
FED	N. F.	1	2	3	4	4	2
"	Blue	1	3	5	5	5	1
"	Green	2	4	4	5	5	1
"	Yellow	1	3	4	4	4	2
"	Red	2	2	3	3	4	2

tactic responses were possible. A series of experiments was designed to test this hypothesis as well. The light quality was varied with Kodak gelatin filters with known cutoff wavelengths. This eliminated the question of overlapping wavelengths, wavelengths common to each light quality, raised in the previous experiment.

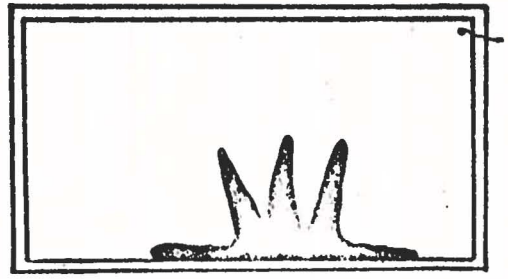
Each of the following studies were conducted in the laboratory. The ambient light intensity prior to illumination was 0.065 ft-c (measured with a Gossen Lunasix light meter). Intensity was controlled with a Powerstat variable transformer. All experimental chambers, except those used in Experiment II, were supplied with running sea water at a flow rate of 0.650 liter per min.

Experiment II. Radial Flexure Responses.

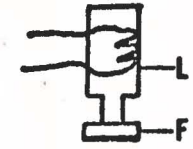
Procedure:

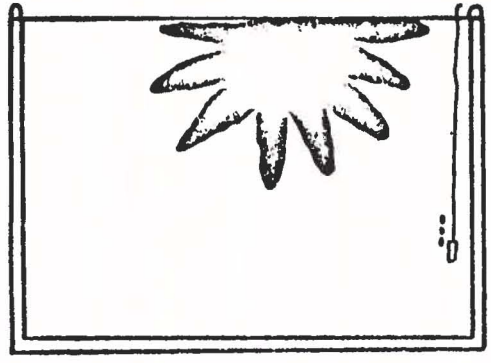
Specimens in Experiment I (Group A) displayed radial flexure in response to light stimuli; therefore, this response was selected as an index of spectral sensitivity. Each of five freshly collected specimens ranging in size from 20.0 to 32.5 cm (referred to as Group B) was placed in a separate 12-liter aquarium which was aerated with a constant air supply (Fig 4). A hand-held light source placed approximately 15 cm above each specimen was used with Kodak gelatin filters having cutoff wavelengths (shortest wavelengths transmitted) of 460, 520, 570, and 620 mμ (referred to as Series 1). To give statistical reliability to the experimental results, I subjected each specimen to

Figure 4. An aquarium used for the study of radial flexure in response to light stimuli. Specimen is shown with radii flexed along the surface of the water. S, specimen; L, light source; F, filter holder; W, surface of the water; A, aerating stone.

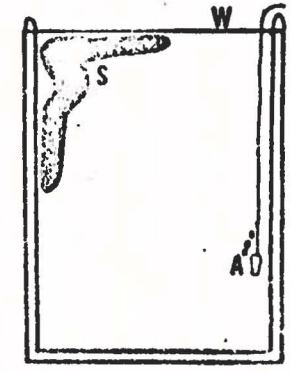


TOP VIEW





FRONT VIEW



SIDE VIEW

10 repetitive trials at each illumination quality.

Individuals ascended the walls of the aquaria and remained in a vertical position throughout the experiment. A variable number of radii were raised off the wall of each aquarium and were in contact with, and parallel to, the surface of the water. At the end of a 2-hr dark period, the oral surfaces of these radii were first illuminated with non-filtered light of varying intensities. The oral surfaces of the dorsalward flexed radii were illuminated to conform with the previous experimental ball studies. Each specimen was illuminated 10 times each at 10, 20, 40, and 80 ft-c. Each illumination trial was 30 sec and was followed by a 3-min dark period. A 10-min dark period followed the last trial at each intensity.

A standard light intensity of 80 ft-c was selected for the study of radial flexure in response to different wavelengths. Five starfish were illuminated with non-filtered light and then with filtered light using the methods previously described.

Results and Discussion:

Table 4 shows that the number of specimens which displayed radial flexure increased as the light intensity increased. Variable response thresholds to light intensity between individuals might account for this observation. During many of the trials at a given intensity, radial flexure did not occur in all radii illuminated. Each radius of each specimen might thus act as an independent photoreceptive unit. An analysis of variance of Table 4 data showed that

starfish displayed a significantly different radial flexure response to light intensities at 10 and 80 ft-c ($P \leq .05$).

Table 5 shows that, in most cases, all five specimens displayed sensitivity to wavelengths shorter than 570 mμ but longer than 460 mμ. Two specimens displayed sensitivity to wavelengths longer than 570 mμ. The one specimen which displayed flexure while being illuminated with wavelengths longer than 620 mμ was in the process of moving. In this case radial flexure may have been associated with locomotion rather than being a response to light stimuli. All other specimens illuminated were at rest. It appears that all specimens were insensitive to wavelengths longer than 620 mμ and maximally sensitive to non-filtered light and to wavelengths between 460 and 570 mμ. An analysis of variance of Table 5 data showed that there is a significant variation component for radial flexure in response to wavelength treatment ($P \leq .05$).

Experiment III. Respiratory Papillar Response to Changes in Light Intensity and Quality.

A. Response to Constant Light

The respiratory papillae of undisturbed specimens in the field and in the laboratory are normally expanded a few millimeters above the aboral epidermis. If specimens are disturbed (e. g. a physical stimulus applied), the respiratory papillae are withdrawn below the epidermis (retraction response). Respiratory papillar retraction in

Table 4. Number of specimens displaying radial ventralward flexure in response to non-filtered light stimuli of increasing intensities (laboratory aquaria experiment). The vertical arrangement of light intensities indicates the sequence of treatments. The sample size is 5.

Light Intensity (ft-c)	Trials									
	1	2	3	4	5	6	7	8	9	10
10	0	1	1	0	1	1	1	1	1	1
20	3	2	2	3	3	2	3	2	2	3
40	5	5	4	3	5	4	5	4	5	3
80	5	5	4	5	4	4	3	4	5	5

Table 5. Number of specimens displaying radial ventralward flexure in response to non-filtered (N. F.) and filtered light stimuli (laboratory aquaria experiment). The light filters are designated by their cutoff wavelengths (i.e., shortest wavelengths transmitted). The vertical arrangement of the filters indicates the sequence of treatment. All light qualities are transmitted at 80 ft-c. The sample size is 5.

Filter	Trials									
	1	2	3	4	5	6	7	8	9	10
N. F.	5	5	4	5	4	4	3	4	5	5
460	5	5	4	4	5	5	5	5	5	5
520	5	5	5	4	4	5	5	4	5	5
570	1	0	0	0	0	1	0	0	0	0
620	0	0	1	0	0	0	0	0	0	0
N. F.	5	5	5	5	5	5	5	5	5	5

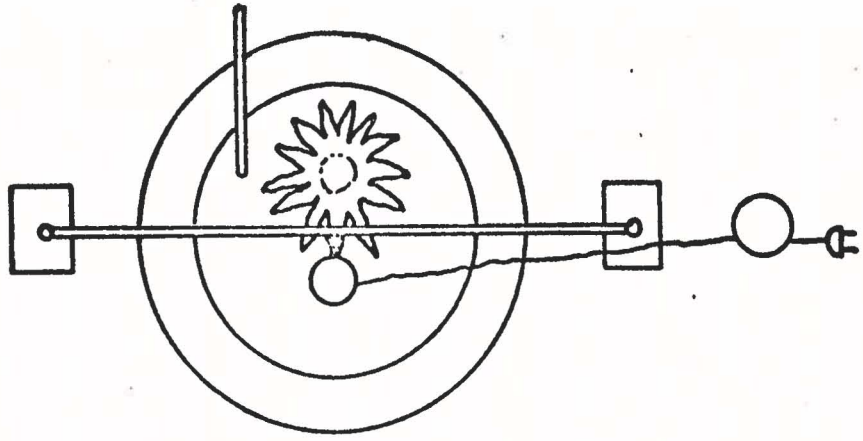
response to sudden illumination has been described by MacCurdy (1912) for the starfish Asterias forbesi.

Procedure:

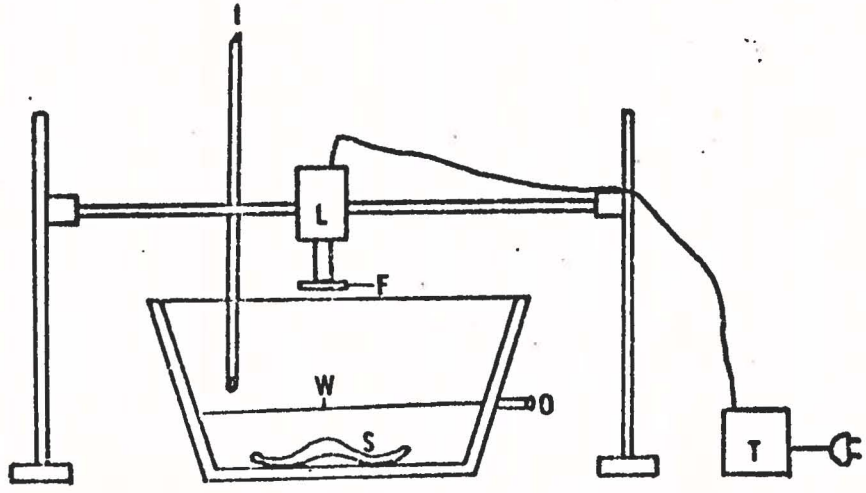
Respiratory papillar retraction in response to a sudden increase in the illumination intensity was investigated in a group of 16 A. planci ranging in size from 22.0 cm to 35.5 cm (referred to as Group C). A plastic basin with a depth of 13.5 cm and minimum diameter of 35.5 cm, holding a single specimen, served as the experimental chamber (Fig 5). A light source was positioned approximately 11 cm above the specimen. With the lamp at this distance, an illuminated area approximately 4 cm in diameter was produced on the dorsal surface of the radial disc. The starfish was restricted to the bottom of the chamber by maintaining a low water depth and by placing it under a 1-cm plastic mesh grid held directly in contact with the radial disc and parallel to the bottom of the chamber.

Specimens were first maintained for 2 hr in the dark (0.065 ft-c). Individuals were then illuminated (with non-filtered light) at 10 ft-c. If papillar retraction occurred within 10 min there was no further experimentation. Specimens which did not display retraction during the first illumination period (10 min) were subjected to additional illumination periods of increasing light intensities until a papillar retraction response occurred. Successive illumination periods were separated by 30-min dark periods, and again the maximum length of any illumination period was 10 min.

Figure 5. Experimental basin used in respiratory papillar retraction studies. F, filter holder, L, light source; S, specimen; T, transformer; W, water level; I, water inflow; O, water outflow.



TOP VIEW



FRONT VIEW

Respiratory papillar retraction in response to an increase in the illumination intensity was also used as an index of spectral sensitivity. The experimental apparatus and methods of handling were the same as used in the previous experiment. The wavelengths transmitted during an illumination period were controlled with five Kodak gelatin filters with cutoff wavelengths at 460, 510, 570, 620, and 650 mμ (referred to as Series 2). Light intensity was 10 ft-c for each light quality investigated. The time required for papillar retraction to occur was recorded with a maximum 10-min exposure period allowed for each illumination quality. Specimens were left undisturbed for 2 hr in the dark prior to the first illumination period.

Results and Discussion:

Specimens displayed papillar retraction when a beam of non-filtered light was focused on the aboral surface of their radial disc and radii (Fig 6). Only those papillae within the illuminated area retracted. As shown in Table 6, the stimulus response threshold varied from 10 to 400 ft-c for the 16 individuals tested, with 10 individuals responding at 10 ft-c and all individuals responding at 400 ft-c.

In Asterias forbesi the behavior of the respiratory papillae with respect to light was thought to be significant since "...their retraction must influence the extent of the aerating surface of the animal" (MacCurdy, 1913). In A. planci the retraction response is only temporary. After a few seconds, subsequent to the initial response,

Figure 6. A transverse section through the aboral epidermis showing the respiratory papillae before and during illumination. A, before illumination; B, during illumination; s, spine; p, respiratory papillae.

A

EXPANDED

B

RETRACTED

Table 6. The non-filtered light intensity required to stimulate respiratory papillar retraction in 16 specimens (laboratory basin experiment).

Light Intensity at Retraction (foot candles)	Cumulative Number of of Starfish Reacting Within 10 Minutes
10	10
50	11
100	13
150	13
200	13
250	14
300	15
350	15
400	16

the respiratory papillae are again extended above the epidermis, even in the continued presence of the original light stimulus. Since the retraction response is only temporary, its influence on respiration may be of only min mal significance. Respiratory papillae extension in the presence of the initial light stimulus would seem to indicate the specimen has become "habituated." In this case the light stimulus becomes biologically meaningless if it is not reinforced by a second stimulus such as physical contact.

The same 10 specimens which were responsive to non-filtered light at 10 ft-c in the previous papillar retraction study were tested for wavelength sensitivity. Table 7 shows that all specimens displayed papillar retraction in response to non-filtered light and light in the wavelength region between 460 and 510 mμ, while none of the specimens responded to wavelengths longer than 620 mμ. Three individuals responded to wavelengths between 570 and 620 mμ. These results indicate that the sensitivity of those specimens tested was limited to that region of the spectrum between 460 and 620 mμ.

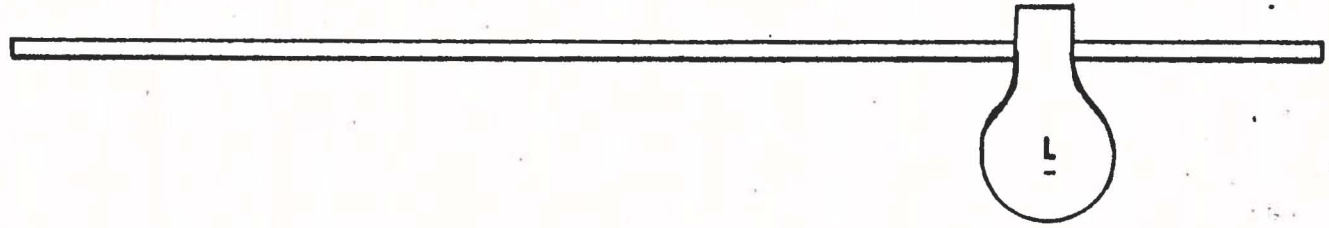
B. Response to Intermittent Light

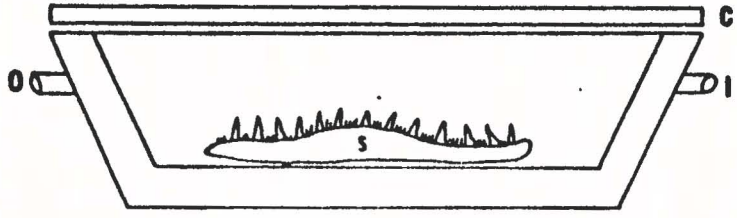
In the above laboratory studies, 10 individuals displayed papillar retraction in response to constant non-filtered light at 10 ft-c. Response times, however, varied from 20 to 325 sec. During the first few seconds of an illumination period, I made a mistake and turned the light source off. The light was quickly turned on again, at which

Table 7. Number of specimens exhibiting respiratory papillar retraction in response to non-filtered (N. F.) and filtered light stimuli (laboratory basin experiment). The light filters are designated by their cutoff wavelengths (i.e., shortest wavelengths transmitted). The vertical arrangement of the filters indicates the sequence of treatments. All light qualities are transmitted at 10 ft-c. The sample size is 10.

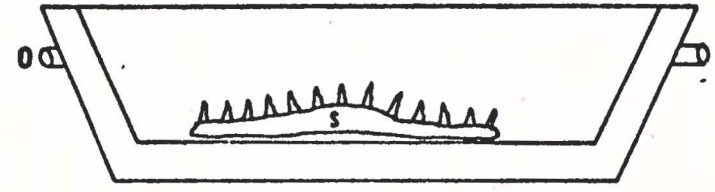
Filter	Minutes				
	2	4	6	8	10
N. F.	4	6	10	10	10
460	4	7	10	10	10
510	5	7	9	10	10
570	0	0	0	1	3
620	0	0	0	0	0
650	0	0	0	0	0

Figure 7. Plastic basins used for intermittent light studies. L, light source; C, cover; s, specimen; I, water inflow; O, water outflow.





BASIN COVERED
(specimen in dark)



BASIN OPEN
(specimen illuminated)

time an immediate respiratory papillae retraction response was noted. This response was investigated in the same group of individuals.

Procedure:

At the beginning of an experimental period two specimens were placed oral side down into two experimental chambers (Fig 7). Plywood covers were placed over each chamber and left for 2 hr. At the end of the dark period the cover of one chamber was removed and the light source turned on. Four intermittent light sequences of increasing intensity and duration were used for each starfish, with a 30-sec dark period between sequences.

The following light sequences were used for each starfish: illuminate for 2 sec at 10 ft-c, dark for 2 sec, illuminate for 2 sec at 10 ft-c; illuminate for 10 sec at 10 ft-c, dark for 2 sec, illuminate for 10 sec at 10 ft-c; illuminate for 2 sec at 70 ft-c, dark for 2 sec, illuminate for 2 sec at 70 ft-c; illuminate for 10 sec at 70 ft-c, dark for 2 sec, illuminate for 10 sec at 70 ft-c.

Results and Discussion:

As shown in Table 8, four individuals displayed papillar retraction in response to 2-sec illumination periods at 10 ft-c. When the duration of the illumination periods at 10 ft-c was increased to 10 sec all 10 individuals displayed papillar retraction. Similarly, when the intensity of the 2-sec illumination periods was increased to 70 ft-c, nine individuals displayed retraction and all 10 individuals responded

Table 8. Respiratory papillar retraction in response to intermittent illumination of variable intensity and duration (laboratory basin experiment). The sample size is 10.

Light Intensity (ft-c)	Illumination Period #1 (sec)	Duration of Darkness (sec)	Illumination Period #2 (sec)	Number of Specimens Responding
10	2	2	2	4
10	10	2	10	10
70	2	2	2	9
70	10	2	10	10

to 10-sec illumination periods.

These results indicate that intermittent light in the laboratory is a more effective stimulus than constant illumination, since total response times were shorter for intermittent light than constant illumination.

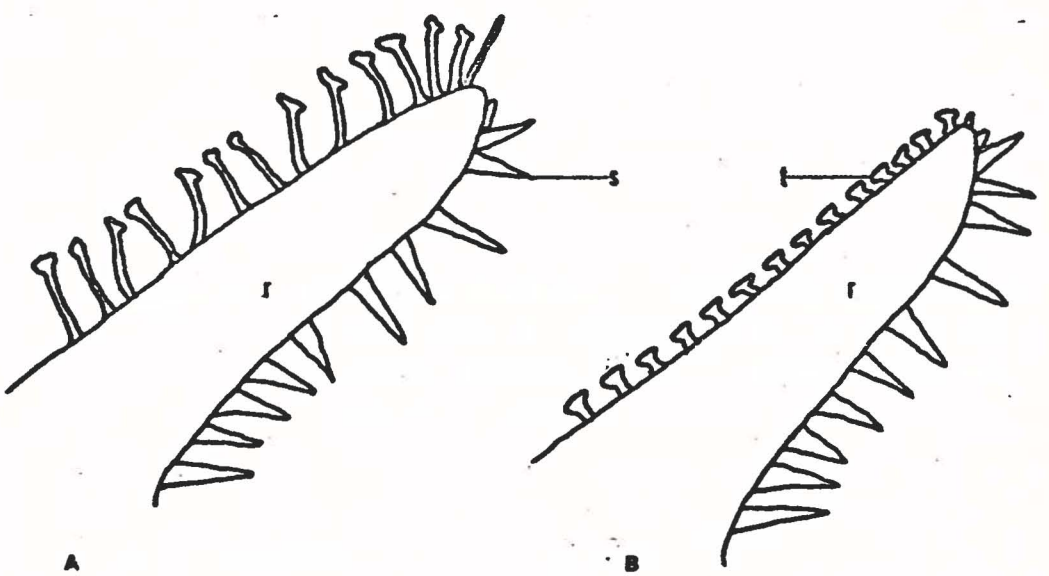
C. Response to Shadow.

In the field A. planci specimens displayed papillar retraction in response to a decrease in light intensity. Longitudinal shadows of different widths were introduced by slowly passing metal rods of increasingly larger diameters above and across the aboral surface of each specimen. As shown in Table 9, the number of specimens displaying respiratory papillar retraction increased as shadow size increased. When the width of the stimulating shadow was approximately 1 mm, two specimens displayed retraction and when shadow width was increased to 15 mm all 50 individuals responded. The adaptive significance of respiratory papillar retraction in response to shadow may be associated with a response to potential predators that may feed on the papillae; however papillar extension will occur shortly after retraction even in the continued presence of the stimulating shadow. Respiratory papillae extension in the presence of the initial stimulating shadow would seem to indicate the specimen has become habituated as postulated for previous observations on papillar extension in the presence of a continued light stimulus. In both cases a

Table 9. Respiratory papillar retraction in response to shadows of variable size (*in situ* field study). The sample size is 50.

Approximate Width of Shadow (mm.)	Number of Specimens Exhibiting Respiratory Papilla Retraction
1	2
5	16
10	35
15	50

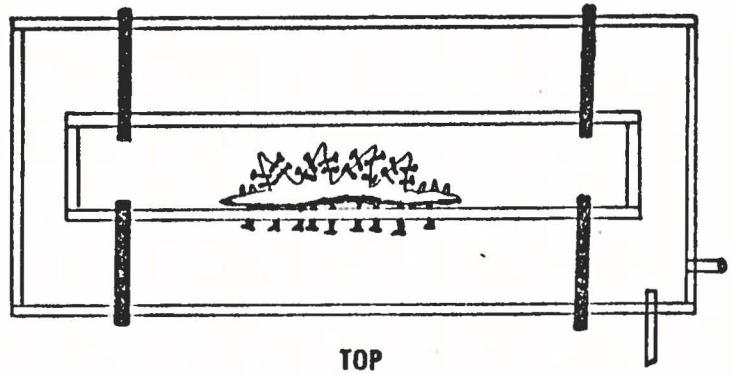
Figure 8. A longitudinal section of a radius showing the tube feet before and during illumination. A, before illumination; B, during illumination; s, spine; r, radius; t, tube foot.



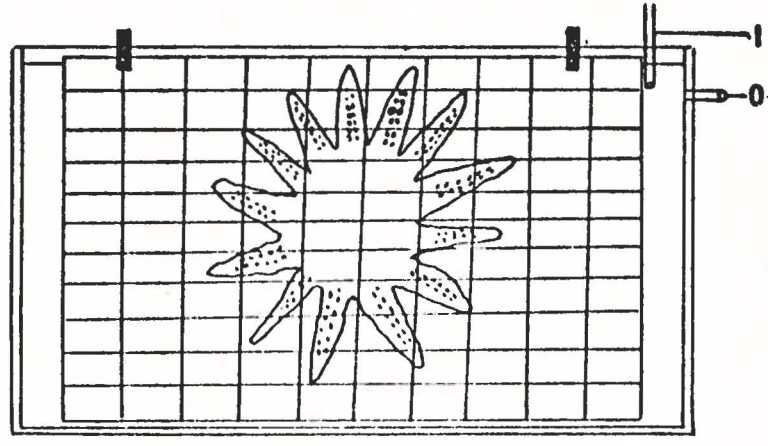
A
EXPANDED

B
RETRACTED

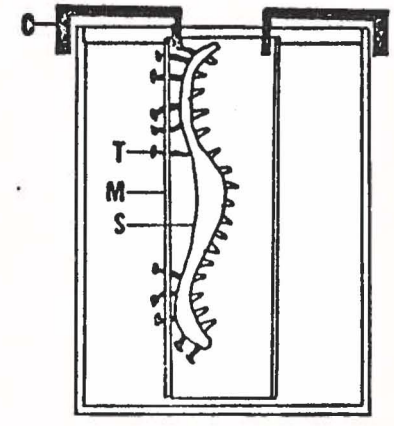
Figure 9. Aquarium used for tube foot retraction study. T, tube foot; S, specimen; M, mesh cradle; O, water exhaust valve; I, water inflow valve; C, plastic clamp.



TOP



FRONT



SIDE

reinforcing stimulus is necessary for continued respiratory papillae retraction. Individuals which are handled are found to display continuous papillar retraction. In this way, a predator which feeds on the respiratory papillae would provide the physical stimulus (contact during attempted feeding) to reinforce the initial shadow stimulus.

Experiment IV. Tube Foot Retraction Responses to Changes in Light Intensity and Quality.

Procedure:

When a beam of light is suddenly projected onto the oral surface of starfish that have been kept in the dark for extended periods of time, the tube feet retract into the ambulacral groove (Fig 8).

The 10 specimens of Group C used for the study of papillar retraction in response to light quality were also used for the study of tube foot retraction in response to light of selected wavelengths. A plastic 1-cm mesh cradle measuring 47.0 cm x 6.0 cm x 35.5 cm supported specimens in a vertical position in a 51-liter plexiglass aquarium. The cradle was held parallel to the aquarium walls with four plastic clamps (Fig 9). The light intensity at the surface of the mesh cradle was 10 ft-c for all light qualities investigated. Filter series 2 was used to vary the light quality.

Each specimen was left undisturbed for 2 hr in the dark (0.065 ft-c) prior to the first illumination period, in which the light beam at 10 ft-c was focused on the oral surface of each radius. A 30-min dark period followed each illumination period. Since tube foot re-

traction in response to light stimuli occurs almost immediately, the maximum length of any illumination trial was 3 min (one trial per quality).

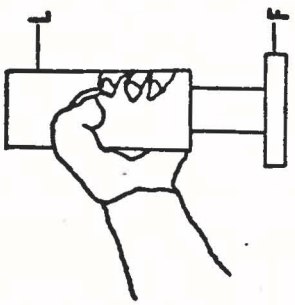
Additional repetitive trials were performed on Group B individuals. A plastic 1-cm mesh disc supported specimens in an inverted position in the plastic basin used in previous respiratory papillar retraction studies (Fig 10). After a 2-hr dark period the radii were first illuminated with non-filtered light. The spectral characteristics of the projected light beam were then varied with Kodak filters (Series 1). A 30-sec illumination period was set for all trials. Ten replicate trials with the same filter were separated by 3-min dark periods, and a 10-min dark period followed the last trials with different filters. All illumination qualities were transmitted at 10 ft-c.

Results and Discussion:

Table 10 shows that all Group C individuals displayed tube foot retraction in response to non-filtered light and light in the wavelength region between 460 and 510 mμ, while none of the individuals responded to wavelengths longer than 620 mμ. An intermediate condition was noted in which four individuals responded to wavelengths between 570 and 620 mμ.

Table 11 shows that the sensitivity of the five Group B individuals tested was limited to that region of the spectrum below 620 mμ, except for one individual which displayed tube foot retraction during the fifth illumination trial at 620 mμ. This response was followed by

Figure 10. Plastic basin used for the study of tube foot retraction in response to light stimuli. F, filter holder; L, light source; m, mesh grid; t, tube foot; s, specimen; W, water level; I, water inflow; O, water outflow.


L
F

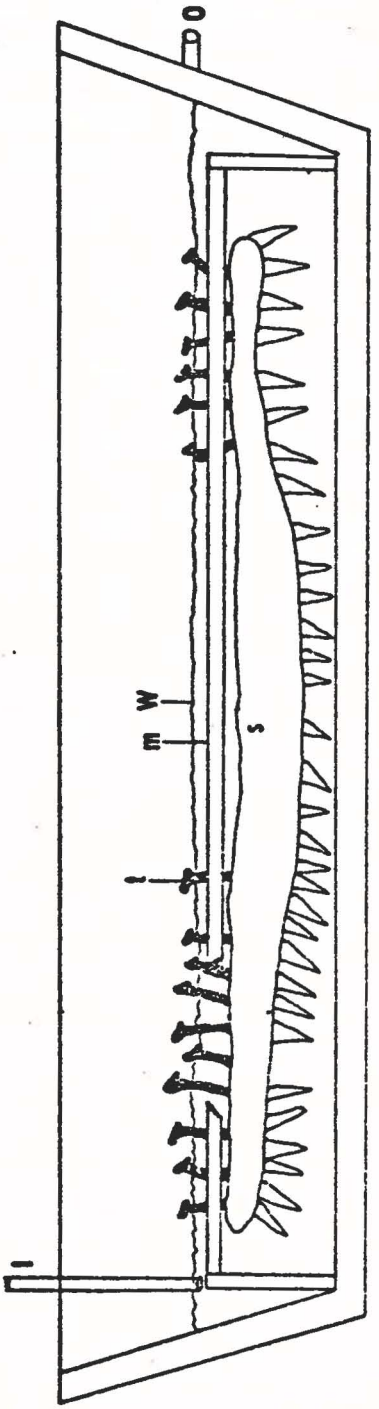

O
W
m
s
I
E
FRONT VIEW

Table 10. Number of specimens displaying tube foot retraction in response to non-filtered (N. F.) and filtered light stimuli (laboratory aquarium experiment). The light filters are designated by their cutoff wavelengths (i.e., shortest wavelengths transmitted). All light qualities are transmitted at 10 ft-c. The sample size is 10.

Filter	Number of Starfish Exhibiting Tube Foot Retraction
N. F.	10
460	10
510	10
570	4
620	0
650	0

Table 11. Number of specimens displaying tube foot retraction in response to non-filtered (N. F.) and filtered light stimuli (laboratory basin experiment). The light filters are designated by their cutoff wavelengths (i.e., shortest wavelengths transmitted). The vertical arrangement of the filters indicates the sequence of treatments. All light qualities are transmitted at 10 ft-c. The sample size is 5.

Filter	Trials									
	1	2	3	4	5	6	7	8	9	10
N. F.	5	5	5	5	5	5	4	5	5	5
460	5	5	5	5	4	4	5	5	5	5
520	5	4	5	5	5	5	5	5	5	5
570	2	2	2	2	2	2	2	2	2	2
620	0	0	0	0	1	0	0	0	0	0
N. F.	5	5	5	5	5	5	5	5	5	4

locomotion. In this case tube foot ret- ction may have been associated with locomotion rather than a response to light stimuli. An intermediate condition was again noted in which two individuals responded to wavelengths between 570 and 620 mμ. An analysis of variance of data in Table 11 reveals that there is a highly significant variation component for tube foot retraction in response to wavelength treatment ($P \leq .001$).

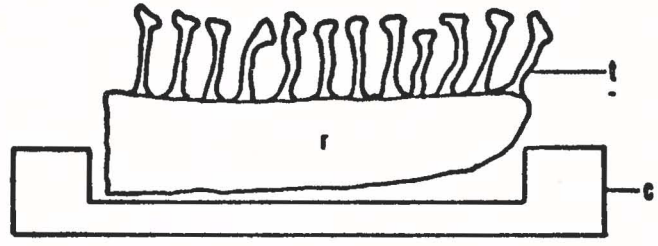
Experiment V. Excised Radii Responses to Changes in Light Intensity.

Procedure:

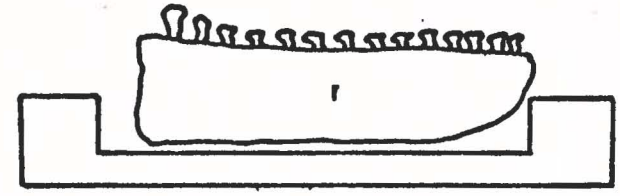
The responses of excised radii to light stimuli were investigated to test the role of the central nervous system in photoreception. A single radius was randomly selected from each of the 10 specimens in Group C which had displayed tube foot retraction and respiratory papillar retraction in response to light stimuli at 10 ft-c. Surgical scissors were used to excise radii along an imaginary line approximating the junction of the radius and radial disc and to remove all aboral spines of each excised radius. Removal of the aboral spines facilitated the stabilization of each radius oral-side-up in separate 10-cm culture dishes. The dishes were then submerged inside a larger basin and separated from each other with black plastic dividers (Fig 11). Individual radii were subjected to increasingly higher light intensities.

Immediately after the last illumination period of each group (a

Figure 11. A longitudinal section of an excised radius in an experimental culture dish, showing the position of the tube feet before and during illumination. A, before illumination; B, during illumination; r, radius; c, culture dish; t, tube foot.



A
EXPANDED



B
RETRACTED

Table 12. Responses of excised radii to increasing illumination intensities (non-filtered light; culture-dish experiment). The sample size is 10.

Light Intensity (ft-c)	Cumulative Number of Radii Exhibiting Tube Foot Retraction	Cumulative Number of Radii Exhibiting Flexure
10	10	0
40	10	5
80	10	6
120	10	9
160	10	10

Table 13. Responses of excised radii half-sections (transverse) to increasing illumination intensities (non-filtered light; culture-dish experiment). The sample size is 20.

Light Intensity (ft-c)	Cumulative Number of Radii Exhibiting Tube Foot Retraction	Cumulative Number of Radii Exhibiting Flexure
10	20	0
40	20	8
80	20	16
120	20	18
160	20	20

group consisted of five radii), all radii were cut in half along imaginary lines perpendicular to their longitudinal axes. The resulting half sections were then subjected to the same illumination intensities of the previous experimental group (entire radii sections).

At the beginning of the experimental period the individual radii were left undisturbed in the dark (0.065 ft-c) for 2 hr. Each radius was then illuminated for 30 sec at the following light intensities: 10, 40, 80, 120, and 160 ft-c. A 10-min dark period followed each illumination trial.

Results and Discussion:

Tables 12 and 13 show that excised radii and half radii sections displayed tube foot retraction and radial flexure responses to an increase in light intensity. Tube foot retraction, in these preparations, as well as in previously studied intact specimens seems to be a more sensitive response to light stimuli than radial flexure. All excised radii and half radii sections displayed tube foot retraction at 10 ft-c while radial flexure did not occur until the illumination intensity was raised to 40 ft-c. The number of radii exhibiting radial flexure increased as the light intensity increased. Sister half-sections exhibited radial flexure to the same light intensities.

A. planci specimens which are missing various portions of their radial discs, and central nervous systems, are often found living in the field (personal observation). Hence, although A. planci is soft bodied and easily mutilated, the destruction of the central nervous

system may be of little consequence with respect to the perception of changes in the ambient light intensity. Indeed, mutilated specimens found during the day display the same cryptic behavior as intact specimens (personal observation). If the cryptic behavior of A. planci is important to the survival of the species, then such behavior in regenerating specimens, possibly more susceptible to predators than intact specimens, would be of considerable value. These studies on the photosensitivity of excised radii seem to support the hypothesis that the central nervous system is not of prime importance for the perception of light in A. planci.

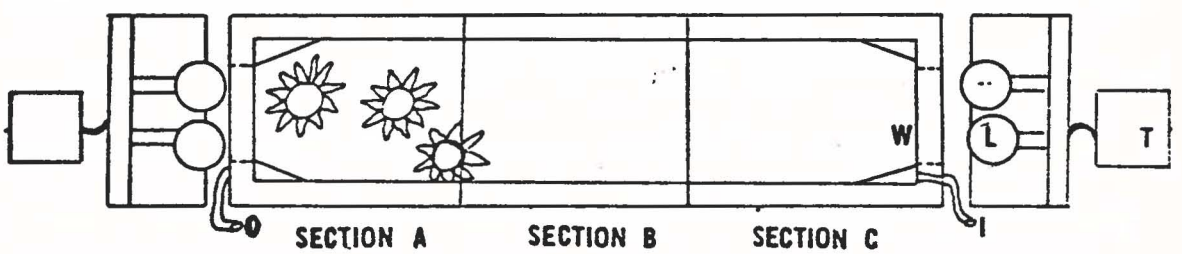
Experiment VI. Phototaxis in Response to Changes in Light Intensity and Quality.

Procedure:

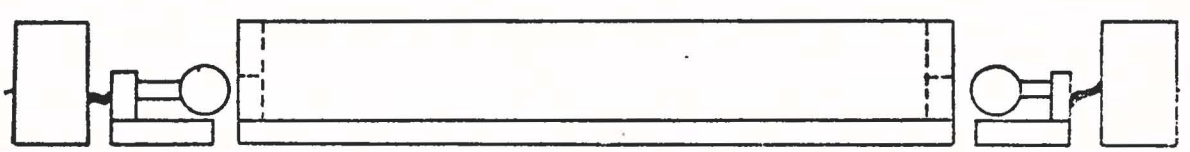
Phototaxis was investigated in a fresh group of 20 A. planci specimens (referred to as Group D) ranging in size from 9.5 cm to 18.5 cm. A wooden trough measuring 116 cm x 35.5 cm x 17.0 cm served as the experimental chamber (Fig 12). Located at each end of the trough was a 250-watt and 300-watt flood lamp. Light was transmitted into the trough through plexiglass windows (one at each end) measuring 15.0 cm x 3.5 cm. To divide the trough into three equal imaginary sections (A, B, and C), I fastened two lengths of string across its width. Water inflow and exhaust valves (one valve at each end of the trough) were installed 9.0 cm above the trough floor.

Figure 12. Experimental trough used in the study of phototaxis. L, light source; T, transformer; W, window; I, water inflow; O, water outflow.

TOP VIEW



SIDE VIEW



Groups of five specimens each wer placed into the middle section of the trough (Section B). The ambient light intensity was 0. 065 ft-c. At the end of the first dark period specimens were illuminated with 160 ft-c of non filtered light from one end of the trough. A second dark period followed the first illumination period. After the second dark period specimens were re-illuminated with non-filtered light (160 ft-c) from the opposite end of the trough. Individual distribution during each of the above 25-min light and dark periods was noted.

Results and Discussion:

The results shown in Figure 13 suggest that those specimens tested exhibited negative phototaxis to non-filtered light. During both illumination periods individuals moved away from the light source and into areas of lower light intensities towards the opposite end of the trough. Specimens were inactive during both dark periods and their distribution within the trough remained constant. These observations are consistant with field observations in which individuals are found to exhibit cryptic behavior during the day (personal observation).

The trough was further used to study spectral sensitivity in 10 of the same specimens. Specimens were treated as outlined in the previous experiment with one exception. During each illumination period, I simultaneously illuminated specimens (at 160 ft-c) with two opposing light sources of different spectra from opposite ends of the trough.

As shown in Figure 14, the results indicate that specimens exhibited negative phototaxis to wavelengths between 460 and 620 mμ.

Figure 13. The effect of sudden non-filtered illumination from one end of the experimental trough on the distribution of A. planci specimens. This is a summary of 4 experimental groups of 5 specimens each under 4 experimental conditions. Condition 1, dark; condition 2, light source at end A; condition 3, dark; condition 4, light source at end C. All light intensities are 160 ft-c.

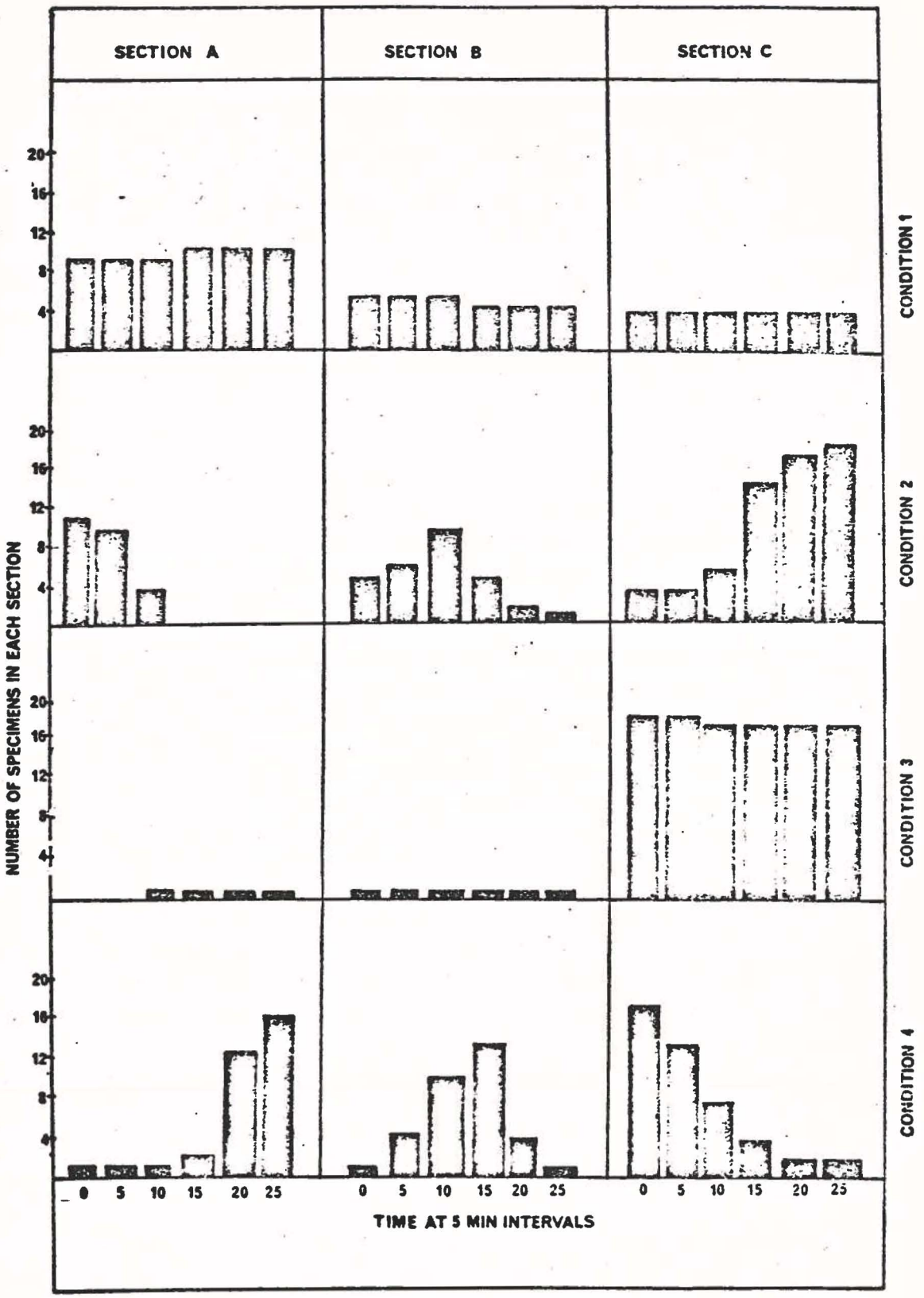

SECTION A
SECTION B
SECTION C
CONDITION 1
CONDITION 2
CONDITION 3
CONDITION 4
NUMBER OF SPECIMENS IN EACH SECTION
20
16
12
8
4
0 5 10 15 20 25
TIME AT 5 MIN INTERVALS

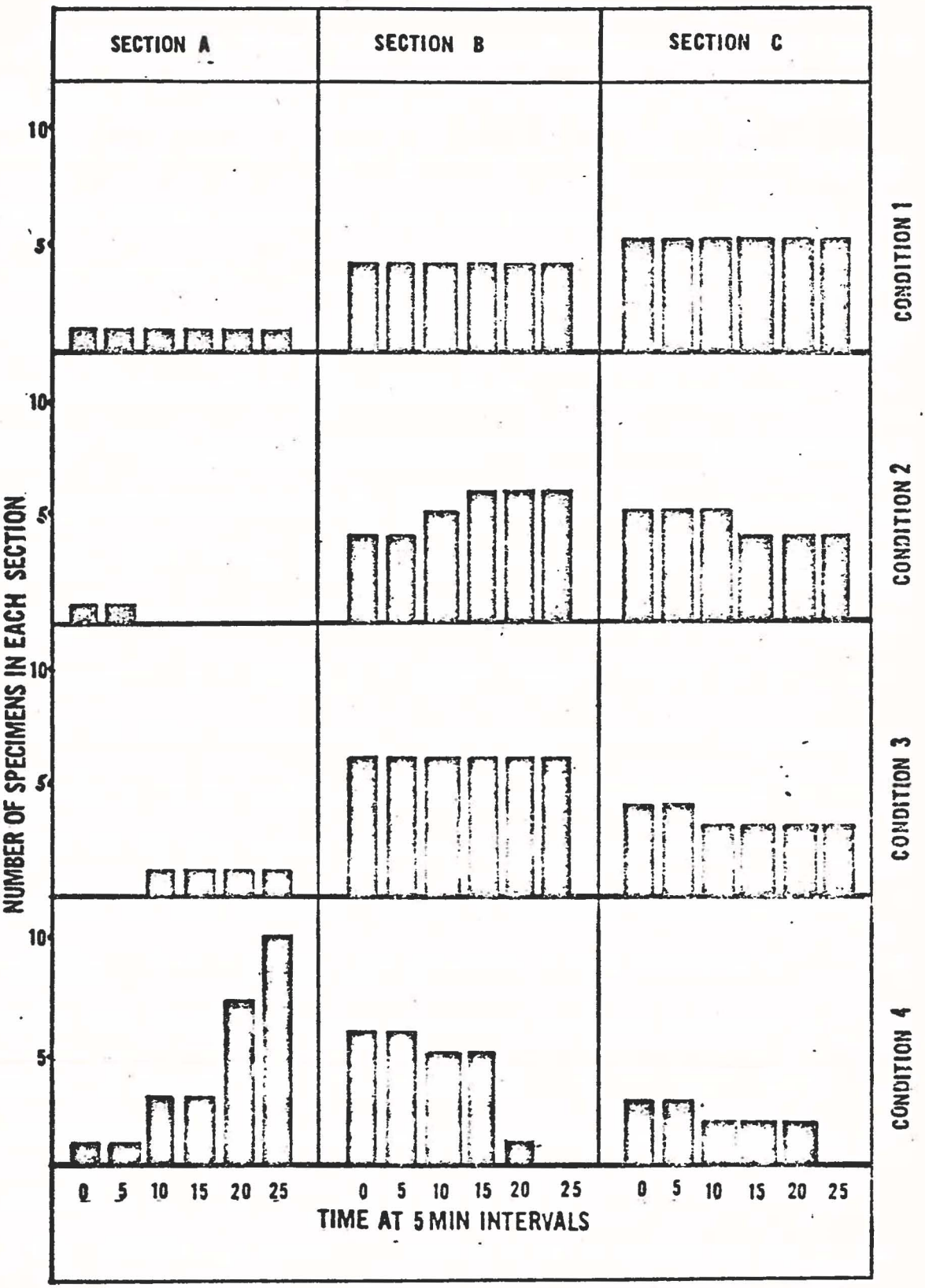
Figure 14. The effect on the distribution of A. planci as a result of simultaneously illuminating the trough from both ends with different light spectra. This is a summary of 2 experimental groups of 5 specimens each under 4 experimental conditions. Condition 1, dark; condition 2, cutoff wavelengths at Ends A and C are 460 and 620 mμ, respectively; condition 3, dark; condition 4, cutoff wavelengths at Ends A and C are 620 and 460 mμ, respectively. All light intensities are 160 ft-c.


SECTION A
SECTION B
SECTION C
CONDITION 1
CONDITION 2
CONDITION 3
CONDITION 4
NUMBER OF SPECIMENS IN EACH SECTION
10
5
0 5 10 15 20 25
0 5 10 15 20 25
0 5 10
TIME AT 5 MIN INTERVALS

In previous laboratory studies of tube foot retraction, respiratory papillar retraction, and radial flexure in response to light stimuli of selected wavelengths, specimens were found to be sensitive to non-filtered light and light in the wavelength region below 620 mμ. The trough studies have again shown that individuals are sensitive only to the region of the spectrum below 620 mμ.

The importance of eyespots in the phototactic responses of the same individuals was also investigated. Specimens were treated as outlined in the previous experiment. Prior to experimentation, however, all eyespots were removed from each individual. As shown in Figure 15, specimens again displayed negative phototaxis to wavelengths between 460 and 620 mμ, moving away from the light source transmitting wavelengths longer than 620 mμ. In earlier studies of the responses of excised radii to light stimuli, I found that radial sections without eyespots displayed the same photic responses as did sections with eyespots. The observations of "eyeless" specimens (trough studies) and on responses of radial sections to light stimuli indicate that in A. planci a non-ocellar mechanism for light reception exists.

Figure 15. The effect on the distribution of A. planci specimens without eyespots as a result of simultaneously illuminating the trough from both ends with different light spectra. This is a summary of 2 experimental groups of 5 specimens each under 4 experimental conditions. Condition 1, dark; condition 2, cutoff wavelengths at Ends A and C are 460 and 620 mμ, respectively; condition 3, dark; condition 4, cutoff wavelengths at Ends A and C are 620 and 460 mμ, respectively. All light intensities are 160 ft-c.


SECTION A
SECTION B
SECTION C
CONDITION 1
CONDITION 2
CONDITION 3
CONDITION 4
NUMBER OF SPECIMENS IN EACH SECTION
10
5
0 5 10 15 20 25
TIME AT 5 MIN INTERVALS

GENERAL DISCUSSION

In preliminary experimental ball studies, individuals were found to be sensitive to changes in light intensity. The question of spectral sensitivity, however, remained unanswered. Further studies of arm flexure, papillar retraction, tube foot retraction, and phototactic studies demonstrated that A. planci shows a selective sensitivity to wavelengths shorter than 620 mμ. These data agree with wavelength sensitivity reported in other echinoderms such as Asterias sp. (Moore, 1921); Pteraster tesselatus (Guberlet, 1946); Psammechinus miliaris (Millott and Yoshida, 1956); Diadema antillarum (Millott and Yoshida, 1957, 1960a, 1960b; and Millott, 1957, 1960); and Asterias forbesi (Rockstein and Spritzer, 1960; and Rockstein, 1962).

Specimens were observed to remain inactive during the dark periods of the above experiments. The inactivity of these specimens in the dark, however, seems to contradict the observations of Goreau (1963) and Chesher (1969). These investigators described A. planci generally as being nocturnal, hiding in crevices during the day and emerging to feed at night. The presence of food (coral) in the natural habitat may trigger nocturnal "searching behavior" observed in A. planci. The lack of food in experimental chambers might then account for the general lack of activity observed in the experimental specimens.

The spectral sensitivity of fishes as well as marine invertebrates

is described by Munz (1965) as closely conforming to the spectral distribution of the available sunlight within the species' natural habitat. In general, as depth increases, the longer wavelengths are selectively filtered out and the photosensitivity of animals living at these depths becomes increasingly restricted. At depths of (for an unspecified oceanic area) 3 m, 5 m, 12 m, 22 m, and 70 m the maximally transmitted wavelengths were found to be 590, 540, 510, 490, and 475 mμ, respectively (Munz, 1965). The insensitivity of A. planci to wavelengths longer than 620 m may be a reflection of the spectral distribution of sunlight present within the aquatic habitat of this species.

In papillar retraction studies, individuals were found to respond to increases as well as decreases in the ambient light intensity. Similar results have been reported for the echinoid Diadema antillarum where movements of the spines, pedicellariae, and tube feet are described as reflexes associated with changes (both increases and decreases) in the ambient light intensity (Millott, 1954; Millott and Yoshida, 1957). Shadows which are cast on the test of D. antillarum result in vigorous movements of the aboral spines. This response is thought to be of selective advantage since a sweeping movement of the spines over a threatened area might deter predators (Millott, 1954). The echinoid Psammechinus miliaris is noted to withdraw its podia in response to sudden shading (Millott and Yoshida,

1956). When the illumination intensity is suddenly decreased, the echinoid Lytechinus variegatus is observed to cover itself with fragments from the surrounding environment (Millott, 1956). In A. planci the adaptive significance of respiratory papilla retraction in response to shading may be a possible response to potential predators. If the response is not further reinforced by a more meaningful stimulus such as touch, extension of the papillae will occur.

The responses of "eyeless" specimens (trough studies) and excised radii without eyespots, demonstrate that, in A. planci, a non-ocellar mechanism for photoreception does exist. The hypothesis of non-ocellar mechanism in light reception has been supported by past investigators. Cowles (1911) found that in Echinaster crassipina, light reception is not confined to the eyespots at the tips of the radii but, "...a large part of the aboral surface seems sensitive to light." It has been found that in Asterias forbesi and Echinaster sp., individuals without the eyespots react "...as definitely to light as those with the pigment spots intact" (MacCurdy, 1913). In later studies of Asterias forbesi, Rockstein (1956) found that the eyespots were not essential for the general positive trophic responses of the species to light. In the starfish Asterias amurensis, Yoshida and Ohtsuki (1968) demonstrated that both ocellar and non-ocellar mechanisms function in photoreception; however, the ocelli (eyespots) were additionally found to work as directional units during locomotion.

The responses of excised radii also indicate that in A. planci the central nervous system is not necessary for photoreception and associated behavioral responses such as tube foot retraction and radial flexure.

In the laboratory, intermittent light was found to have a greater stimulus value than constant light. Intermittent light, however, seems to offer value as a tool for further research into the photosensitivity of echinoderms.

The experiments described here were preliminary investigations into the photosensitivity and spectral sensitivity of Acanthaster planci. These experiments serve as a foundation for further research into this aspect of the behavior of this species and provide additional input into behavioral studies of other echinoderms.

SUMMARY

1. An experimental ball apparatus was used to demonstrate whether or not the Acanthaster planci specimens tested were responsive to changes in light intensity and quality. Individual responses during short term (5 sec) illumination periods of variable color were investigated. Specimens were tested at successive nutritional states: fresh from the field, starved for 60 days, and after one week of daily feeding on an exclusive diet of the coral Pocillipora damicornis (L.). During the initial dark periods, all specimens remained motionless with a few radii raised off the ball (dorsal flexure). When the illumination intensity was increased to 225 ft-c for each light quality, the specimens lowered their radii onto the ball (ventral flexure) and when the intensity was finally lowered to 25 ft-c, the specimens displayed dorsal flexure.

Individual responses during prolonged (10 min) illumination periods of variable color were also investigated. Specimens were tested after the 60-day starvation period and again after one week of feeding. During the initial dark periods, all specimens remained motionless and displayed dorsal flexure. When the illumination intensity was raised to 225 ft-c, the specimens displayed ventral flexure. In most individuals, ventral flexure was followed by movement around the circumference of the ball. Three distinct movement responses were identified: primary shade seeking

behavior, specimens moved from the light into the shade and there came to rest; interface reversal behavior, specimens moved away from the light and through the shade but when light was again encountered they reversed their direction of movement 180° and came to rest in the shade; continuous movement, specimens moved continually around the ball through both the shaded and illuminated areas.

2. Ventral radial flexure in response to light stimuli was selected as an index of spectral sensitivity. Individuals were held in aquaria and the oral surfaces of dorsalward flexed radii were illuminated with non-filtered and filtered light. Illumination periods were set at 30 sec. Specimens were responsive to non-filtered light and light in the wavelength region between 460 and 620 mμ.
3. Respiratory papillar retraction in response to light stimuli was used as an index of spectral sensitivity. Individuals were held in plastic basins and the dorsal surfaces of their radial discs were illuminated with non-filtered and filtered light. The maximum length of each illumination period was 10 min. Specimens were responsive to non-filtered light and light in the wavelength region between 460 and 620 mμ.
4. The value of intermittent light as a stimulus for respiratory papillar retraction was investigated. Individuals were held in plastic basins and their dorsal surfaces were illuminated with non-

filtered intermittent light. Intermittent light periods of increasing intensity and duration were used for each specimen. Specimen response times were shorter for intermittent light than constant light.

5. Respiratory papillar retraction in response to a decrease in light intensity was investigated with all experimentation being conducted in the field. Metal rods of increasingly larger diameters were slowly passed above and across each specimen. As a result of this procedure, longitudinal shadows of increasingly larger widths were produced across the aboral surface of the specimens. The number of specimens displaying respiratory papillar retraction increased as shadow width increased.
6. Tube foot retraction in response to light stimuli was investigated in two groups of specimens. Specimens of the first group were supported in a vertical position on a plastic mesh cradle set inside a plexiglass aquarium. Specimens of the second group were supported in an inverted position on the underside of a plastic mesh disc in a plastic basin. The oral surface of each radius was illuminated with non-filtered and filtered light. Specimens were responsive to non-filtered light and light in the wavelength region between 460 and 620 mμ.
7. The responses of excised radii to light stimuli were investigated to test the role of the central nervous system in photoreception.

Individual radii were placed oral-side up in separate glass culture dishes. These radii were then illuminated with non-filtered light at increasingly higher intensities. At the end of the last illumination period, each radius was cut in half along an imaginary line perpendicular to its longitudinal axis. The half radii sections were then subjected to the same illumination intensities as were the previous whole radii sections. Excised radii and half radii sections displayed tube foot retraction and arm flexure responses to an increase in light intensity. All specimens displayed tube foot retraction at 10 ft-c while radial flexure did not occur until the illumination intensity was raised to 40 ft-c.

8. Phototaxis in response to changes in light intensity was investigated with the aid of a wooden trough which served as the experimental chamber. During light periods when the trough was illuminated from one end with non-filtered light at 160 ft-c, specimens moved away from the light source. During dark periods, specimens were inactive and their distribution within the trough remained constant.

9. The trough was used to study spectral sensitivity. Specimens were simultaneously illuminated (at 160 ft-c) with two opposing light sources of different spectra from opposite ends of the trough. Specimens moved away from the light source transmitting wavelengths longer than 460 mμ and towards the light source trans-

mitting wavelengths greater than 620 mμ.

10. The trough was again used to test spectral sensitivity in specimens from which all eyespots were removed. Specimens moved away from the light source transmitting wavelengths longer than 460 mμ and towards the light source transmitting wavelengths longer than 620 mμ.

CONCLUSIONS

1. The Acanthaster planci specimens tested were sensitive to changes in light intensity.
2. Specimens responded to light intensity changes by locomotion, retraction of respiratory papillae, retraction of the tube feet, and flexure of radii.
3. Specimens displayed a selective spectral sensitivity and were maximally sensitive to non-filtered light and light in the wavelength region between 460 and 620 mμ.
4. Specimens were not dependent on the central nervous system or eyespots for photoreception.
5. A 60-day starvation period seemed to exert no effect on the responses of specimens to light stimuli.
6. In the laboratory, intermittent light was more effective than constant light as a stimulus for photic responses.

LITERATURE CITED

Antonius, A. 1971. The Acanthaster problem in the Pacific (Echinodermata). Int. Revue ges. Hydrobiol. 56(2):283-319.

Barnes, D. J., R. W. Brauer, and M. R. Jordan. 1970. Locomotory responses of Acanthaster planci to various species of coral. Nature 228:342-343.

Barrington, E. J. W. 1967. Invertebrate structure and function. Nelson (ed.), London.

Brown, H. M., H. Ito, and T. E. Ogden. 1968. Spectral sensitivity of the planarian ocellus. J. Gen. Physiol. 51(2):255-260.

Brown, T. W. 1971. Pollution of the marine environment and the Acanthaster planci infestation of the Indo-Pacific region. Report to South Pacific Commission for presentation to the United Nations International Conference.

Chesher, R. H. 1969. Acanthaster planci. Impact on Pacific coral reefs. Final Report to U. S. Department of Interior. Westinghouse Research Laboratory No. 96-951-Ocean-R2. 152 pp.

Cowles, R. P. 1911. Reactions to light and other points in the behavior of the starfish. Mar. Biol. Lab. Tortugas. 99-111.

Cronly-Dillon, J. R. 1966. Spectral sensitivity of the scallop Pecten maximus. Science 151:345-346.

Cullen, M. 1970. Crown of Thorns toxin study. A personal communication to Dr. L. G. Eldrege, University of Guam Marine Laboratory.

Goreau, T. F. 1963. On the predation of coral by the spiny starfish Acanthaster planci (L.) in the southern Red Sea. Israel South Sea Exped. No. 2.

Guberlet, J. E. 1946. The morphology and behavior of the cushion star Pteraster tesselatus Ives. Univ. Wash. Publ. Biol. 12:12-47.

Heinroth, O. 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Verch. V. Int. Ornithol. Kongr. Berlin.

Henderson, J. A. and J. S. Lucas. 1971. Larval development and metamorphosis of Acanthaster planci (Asteroidea). Nature 232:655-657.

Holmes, S. J. 1912. Phototaxis in the sea urchin Arbacia punctulata. J. Animal Behavior 2:126-136.

Hughes, H. P. I. 1970. The spectral sensitivity and absolute threshold of Onchidoris fusca (Muller). J. Exp. Biol. 52(3): 609-618.

Humes, A. G. 1970. Stellicola acanthasteris N. sp. (Copepoda, Cyclopodia) associated with the starfish Acanthaster planci (L.) at Eniwetok atoll. Publ. Seto Mar. Biol. Lab. 17(5):329-338.

Hyman, L. H. 1940. The Invertebrates. Vol. I. McGraw-Hill, New York.

_____. 1951a. The Invertebrates. Vol. II. McGraw-Hill, New York.

_____. 1951b. The Invertebrates. Vol. III. McGraw-Hill, New York.

_____. 1955. The Invertebrates. Vol. IV. McGraw-Hill, New York.

_____. 1959. The Invertebrates. Vol. V. McGraw-Hill, New York.

_____. 1967. The Invertebrates. Vol. VI. McGraw-Hill, New York.

Jachowski, R. L. 1968. Photo-orientation of the pink shrimp, Penaeus duorarum. Bull. Mar. Sci. 18(1):191-202.

Kerkut, G. A. 1954. The mechanisms of coordination of the starfish tube feet. Behavior 6:207-231.

MacCurdy, H. 1913. Some effects of sunlight on the starfish. Science 38 (968):98-100.

Millott, N. 1953. Light emission and light perception in a species of Diadema. Nature 171:973-974.

_____. 1954. Sensitivity to light and the reactions to changes in light intensity of the echinoid Diadema antillarum Philippi. Phil. Trans. B 238:187-220.

_____. 1956. The covering reactions of sea urchins. 1. A preliminary account of covering in the tropical echinoid Lytechinus variegatus (Lamarck), and its relation to light. J. Exp. Biol. 33:508-523.

_____. 1957. Naphthaquinone pigment in the tropical sea urchin Diadema antillarum Philippi. Proc. Zool. Soc. Lond. 129: 263-272.

_____. 1960. The photosensitivity of sea urchins. In: M. B. Allen (ed.) Comparative Biochemistry of Photoreactive Systems. pp. 279-293. New York Academic Press.

Millott, N., and M. Yoshida. 1956. Reactions to shading in the sea urchin Psammechinus miliaris (Gmelin). Nature 179:1300.

_____. 1957. Spectral sensitivity of an echinoid. Nature 179:924.

_____. 1959. The photosensitivity of the sea urchin Diadema antillarum Philippi: Responses to increases in light intensity. Proc. Zool. Soc. Lond. 133:67-71.

_____. 1960a. The shadow reaction of Diadema antillarum Philippi. 1. The spine response and its relation to stimulus. J. Exp. Biol. 37:363-375.

_____. 1960b. The shadow reaction of Diadema antillarum Philippi. 2. Inhibition by light. J. Exp. Biol. 37:376-389.

Moore, A. R. 1921. Stereotrophic orientation of the tube feet of starfish (Asterias) and its inhibition by light. J. Gen. Physiol. 4:163-169.

Munz. R. W. 1965. Adaptation of visual pigments to the photic environment. Pages 27-43. In: CIBA Foundation Symposium on Physiology and Experimental Psychology. Little and Brown, Boston.

Pearson, R. G., and R. Endean. 1969. A preliminary study of the coral predator Acanthaster planci (L.) (Asteroidea) on the Great Barrier Reef. Fisheries Notes Vol. 3, No. 1. Dept. of Harbours and Marine.

Rockstein, M. 1956. Role of the terminal pigment spots of the starfish Asterias forbesi in light orientation. Nature 177:341-342.

_____. 1962. Some properties of Stellarin, the photosensitive pigment of the starfish Asterias forbesi. Biol. Bull. 123:510.

Rockstein, M., and R. Spritzer. 1960. Light orientation in the starfish Asterias forbesi. Anat. Rec. 138:379.

Smith, J. E. 1950. Some observations on the nervous mechanisms underlying the behavior of starfishes. Symp. Soc. Exp. Biol. 4:196-220.

Stratten, W. P., and T. E. Ogden. 1971. Spectral sensitivity of the barnacle Balanus amphitrite. J. Gen. Physiol. 57(4):443-447.

Tsuda, R. T. (ed.). 1971. Status of Acanthaster planci and coral reefs in the Mariana and Caroline Islands, June 1970 to May 1971. University of Guam Marine Laboratory Technical Report No. 2.

Waser, P. M. 1968. The spectral sensitivity of the eye of Aplysia californica. Comp. Biochem. Physiol. 27(1):339-347. Abstr.

Weber, J. N., and P. M. J. Woodhead. 1970. Ecological studies of the coral predator Acanthaster planci in the South Pacific. International J. on Ocean Life in Oceans and Coastal Waters 6(1):12-17.

Yamaguchi, M. Y. 1972. Life history of A. planci. In: R. T. Tsuda (compiler), Proceedings of the University of Guam - Trust Territory Acanthaster planci (Crown-of-Thorns Starfish) Workshop, March 27-29, 1972. University of Guam Marine Laboratory. Technical Report No. 3.

Yoshida, M., and H. Ohtsuki. 1968. The Phototactic Behavior of the Starfish Asterias Amurensis Lutken. Biol. Bull. Mar. Biol. Lab. Woods Hole 134:516-532.