

Covering Response of the Echinoid *Evechinus chloroticus* (Val.)¹

TREVOR G. DIX²

ABSTRACT: Field and laboratory observations suggest that the covering response of *Evechinus chloroticus* is not significantly related to light avoidance. A positive response of the podia to contact stimuli elicits covering which may be important for the capture of food, particularly algal debris.

MANY ECHINOIDS cover, "decorate," or "mask" themselves with various substances, mainly pieces of algae, shells, and pebbles. Harvey (1956), Hyman (1955), and Reese (1966) summarize the literature. Two major functions have been suggested: to conceal or camouflage the urchin or to protect it from light; of these the latter has received most support (Lewis, 1958; Millot, 1956; and reviews by Millot, 1966; Nichols, 1964; and Yoshida, 1966).

Evechinus chloroticus, the common New Zealand sea urchin, covers itself in both intertidal and subtidal populations (Fig. 1). The following field observations, however, suggest that the habit may not be a simple light-avoidance response. *Evechinus* is often found covered in situations where light intensities are low (for example, among small pebbles beneath fairly large rocks, in up to 30 meters of dirty water, in caves and underhanging crevices). In groups of urchins exposed to similar light intensities some may be covered, and others may not; furthermore, only a small portion of an urchin may be covered (Fig. 1; Dix, 1969, fig. 1). Frequent observations on populations of *Evechinus* show that the extent of covering depends mainly on the availability of covering material. Thus after rough seas, when large amounts of algal debris drift about, more urchins become covered. This observation was also noted for *Paracentrotus lividus* by Gamble (1966). Further, dense aggregations of *Evechinus* often locally denude the substrate of algae. After calm seas when only small amounts of drift algae are present, urchins in the center of these clumps are often without cover while

those around the edges, where algae are growing, are extensively covered.

To gain a general understanding of the covering process and to test the suggestion that covering is not simply a light avoidance response in *Evechinus*, investigations into the mechanisms and stimuli involved in the covering process were carried out, and a series of experiments testing the following hypotheses was designed. If covering is a light avoidance response it would be expected that *Evechinus* would (a) not cover when placed in the dark or cover very little when placed in near-dark conditions, (b) show a physiological adaptation so that, when placed in the light, animals which had been kept in darkness would cover more rapidly and more extensively than animals kept for the same period in light, and (c) cover less at night than during the day.

MATERIAL

Experiments were performed with subtidal (shallower than 10 meters) and intertidal *Evechinus* from Kaikoura (42°25'S, 173°42'E), and subtidal urchins (shallower than 3 meters) from Kaiteriteri (42°02'S, 173°01'E). Prior to the experiments they were generally kept for several days in running-seawater tanks. For the sake of continuity, methods used in the various experiments will be discussed below.

METHODS, RESULTS, AND DISCUSSION

Mechanisms and Stimuli Involved in the Covering Process

Two broad categories of covering material are utilized by *Evechinus*: material which is likely to drift onto the surface of an urchin

¹ Manuscript received July 7, 1969.

² Department of Zoology, University of Canterbury, Christchurch 1, New Zealand.



FIG. 1. *Evechinus chloroticus* with drift algal cover in 7 meters depth, Kaikoura, New Zealand.

(mainly algal debris, Fig. 1), and material which is actively taken from the substrate (shells, pebbles). The mechanisms involved in moving materials over, and holding them against the urchin are similar to those described for *Lytechinus variegatus* by Millot (1956). Tube feet and spines move the material which is then held by tube feet.

In an investigation of the stimuli involved in the capture of floating material, Millot (1956) found that the tube feet of *Lytechinus* extended and attached to opaque cover slips floating above the illuminated aboral surface; they did not respond to clear cover slips. He concluded that tactile stimuli were "not significantly involved," but that a change in light intensity was important. When similar experiments were performed with *Evechinus* it was found that tube feet responded to neither opaque nor clear cover slips. However, single extended tube feet touched by a cover slip or other solid material

almost always attached. After several seconds other tube feet in the area of contact were extended to attach and then hold the material to the urchin. Touching the spines of *Evechinus* initiated a rapid response. Spines around the area of contact pointed toward the point of contact and after several seconds, if the material remained in touch, tube feet extended to attach and then hold the material to the urchin. The rapid spine response often held material against the urchin until the tube feet attached. Thus, in contrast to *Lytechinus*, tactile stimuli are most significant in the capture of floating material by *Evechinus*.

Further experiments showed that the tube feet of *Evechinus* are less responsive to changes in light intensity than those of *Lytechinus variegatus* (Millot, 1956) or of *Tripneustes esculentus* (Lewis, 1958). Resting *Evechinus* subjected to changes in light intensity either by shading natural or artificial light or by shining

light on shaded specimens, showed no recognizable tube feet response. In contrast, Millot (1956) found definite responses to both increases and decreases in light intensity, the responses to shadows being the most striking. "In either case tube feet are quickly withdrawn and then, after a varying interval, slowly extended . . ."

That tactile rather than photic stimuli are also involved in the capture and movement of material actively taken from the substrate by *Evechinus* is indicated by the observation that such materials are often captured for cover despite the fact that they do not cast any shadow on the urchin. This observation is reinforced by the results of an experiment in which an urchin was placed in a 25 × 22 cm tray containing equal numbers of 25-mm clear and black squares of 1.3 mm thick perspex arranged in checkerboard fashion over the bottom. The number of squares of each type utilized as cover was noted at intervals from 0930 to 1630 hours; throughout this period the urchin was generally exposed to window light in the laboratory. This experiment was repeated 60 times using different urchins, and the numbers of clear and black squares utilized as cover at 0.5, 2.5, 5.5, and 7.5 hours after the start of experiments are shown in Table 1. Observations were also made at 1.0, 1.5, 2.0, 6.0, 6.5, and 7.0 hours, but those shown are representative.

At 0.5 hours the number of black squares utilized as cover did not differ significantly from the number of clear squares. Therefore, squares were utilized irrespective of color, suggesting that tactile stimuli were involved in the initial covering response. At subsequent intervals, however, after rearrangement and further uptake of squares, significantly greater numbers of black squares were utilized, suggesting that the urchin

can distinguish between the two types. Although this might suggest that the urchins finally used the squares as shade, the small numbers of squares used (Table 1) were insufficient to shade effectively the 6–8-cm urchins. Essentially similar experiments performed by Dubois (1914) with *Strongylocentrotus lividus* gave similar results. Dubois concluded that light played a role in the orientation of objects but that it was not a necessary factor in initiating the act of lifting.

In summary, it is concluded that the stimuli involved in the capture and initial uptake of both floating material and that taken from the bottom are tactile and not photic. As with *Lytechinus* (Millot, 1956) the tube feet of *Evechinus* show variable activity under conditions of uniform illumination or darkness, but *Evechinus* individuals, particularly those in moving water, generally have at least a few tube feet extended and waving about. It is when these tube feet, or when spines, come into contact with covering material that the covering response is initiated. It is notable that Gamble (1966) suggested that covering in *Paracentrotus lividus* might not be an active shading response but "could be due to a local reflex on the part of the tube feet initiated by contact with any suitable surface."

Effects of Light on Covering

(a) COVERING UNDER LIGHT AND DARK CONDITIONS: To test the effects of light intensity on the rate of covering and on the amount of cover adopted, five similar-sized *Evechinus* collected intertidally at Kaikoura were placed in each of two 22 × 27 cm trays containing fresh seawater at 17.3°C. One tray was blacked out and the other was white and exposed to natural light (incident illumination

TABLE 1
NUMBER OF CLEAR AND BLACK SQUARES UTILIZED AS COVER BY *Evechinus*

TIME (HRS)	NUMBER OF SQUARES		χ^2	P	MEAN NUMBER PER URCHIN	
	CLEAR	BLACK			CLEAR	BLACK
0.5	108	128	1.69	.25 > P > .10	1.8	2.1
2.5	120	160	5.71	.025 > P > .001	2.0	2.7
5.5	132	170	4.78	.05 > P > .025	2.2	2.8
7.5	116	160	7.09	.01 > P > .005	1.9	2.7

ca. 10 Lux). For covering material 2.7-cm discs of the brown alga *Lessonia variegata* were evenly spread in contiguous rows over the bottom of each tray. Immediately after being placed in the trays the urchins began covering. The percentage of the surface covered was estimated at 2-minute intervals for 10 minutes and then after 20 minutes, by which time the urchins had settled down. Five such runs were performed using different urchins, all runs giving the trend shown in Figure 2, where mean percentages for all runs are plotted.

Since urchins in the blacked-out as well as the lighted tray covered at a similar rate and finally adopted similar amounts of cover (for the last observation $t = 0.76$ giving $0.5 > P > 0.4$) a tactile rather than light-avoidance response is suggested. Those in the lighted tray did, however, cover a little more rapidly suggesting that the response is affected by light.

(b) ADAPTATION TO LIGHT AND DARK: Mil-lot (1956) demonstrated a physiological adaptation in *Lytechinus*. When uncovered in strong light for a long period urchins ceased to show the covering response, but this reappeared after a sojourn in darkness. To test whether light and dark adaptation occurred in the covering process of *Evechinus*, 10 urchins were kept in each of two running-seawater trays, one blacked out and the other lit by natural light supplemented by continuous light from an overhead 40-watt tungsten filament lamp 30 cm above the tray. This gave incident illumination of ca. 23 Lux during the day and 4 Lux at night. Different groups of urchins were thus exposed for periods of 2 days or 1 week. At the end of the period the rate of covering of both light- and dark-adapted urchins was investigated in lighted trays at 10°C with incident illumination of ca. 23 Lux, as described for the previous experiment.

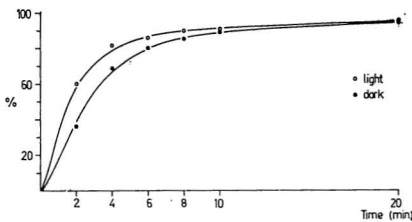


FIG. 2. Rate of covering of *Evechinus* in light and dark conditions. For further explanation see text.

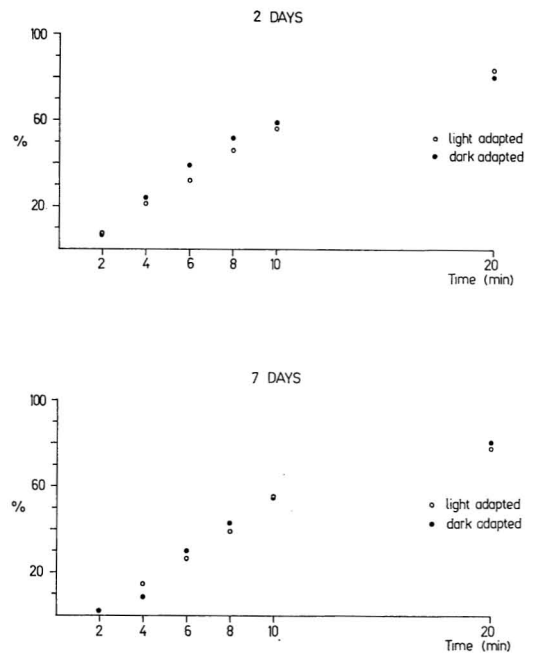


FIG. 3. Rate of covering of dark- and light-adapted *Evechinus*. Urchins were exposed for 2 or 7 days.

The mean covering rates of 70 light- and 70 dark-adapted urchins (exposed for 2 days) and those of 40 light- and 40 dark-adapted urchins (exposed for one week) are shown in Figure 3. There were no marked differences between the covering rates and amount of cover finally adopted of light- and dark-adapted urchins, after adaptation periods of either 2 days or 1 week. This suggests that physiological adaptation to light or dark does not affect the covering process of *Evechinus*.

Adaptation to light and dark can occur in *Evechinus*, however, as indicated from investigation of the phototactic response of animals as a whole. Half of a sample of 10 urchins, light adapted for 1 week as above, were placed without covering material in the zero position of a 95×15 cm trough containing fresh seawater at 9 to 10°C (Fig. 4). An equal number of dark-adapted urchins was placed in an identical trough. The troughs were half covered with a black screen and had a clear end in the uncovered portion, this end facing a window and also being lit by a 40-watt tungsten filament lamp 10 cm from the end of the trough. Positions of the urchins were then scored as shown

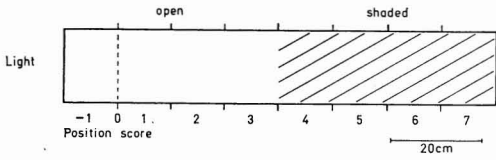


FIG. 4. Plan of apparatus used to test response to light of *Evechinus*. Positions of the urchins were scored as shown. Thus, in Figure 6 the mean position score for Run 1, no cover, 30 minutes is $0.1 (2 \times 2 + 3 + 4 + 3 \times 6 + 3 \times 7) = 5.0$.

in Figure 4 at 15, 30, 60, and 90 minutes. The experiments were then repeated with the other halves of the samples in the opposite troughs to minimize possible bias, and these runs were later repeated with different urchins. Under the scoring system used, photonegative responses were positive, increasing toward the darkened end of the troughs and photopositive responses were negative. Mean scores for 65 light- and 65 dark-adapted urchins (Table 2) indicate that the dark-adapted urchins were more photonegative than the light-adapted urchins, higher percentages moving away from the lighted end, with the result that, at $t = 90$ minutes, significantly more dark- than light-adapted urchins had scores greater than one ($\chi^2 = 3.9, 0.05 > P > 0.025$).

(c) COVERING AND DIURNAL CHANGES IN LIGHT INTENSITY: Two samples of *Evechinus* (18 from intertidal Kaikoura and 20 from subtidal Kaiteriteri), maintained in running-seawater tanks with abundant algae for food and cover for 2 weeks, were observed over a

TABLE 2

PHOTOTACTIC RESPONSE OF LIGHT- AND DARK-ADAPTED *Evechinus*
(Higher Scores Indicate a More Photonegative Response)

TIME (MIN)	MEAN SCORES		PERCENTAGE MOVING FROM THE LIGHTED END	
	LIGHT-ADAPTED	DARK-ADAPTED	LIGHT-ADAPTED	DARK-ADAPTED
15	1.18	1.49	70.8	75.4
30	1.75	2.12	78.5	81.5
60	2.18	2.85	76.9	86.2
90	2.26	3.23	73.8	87.7

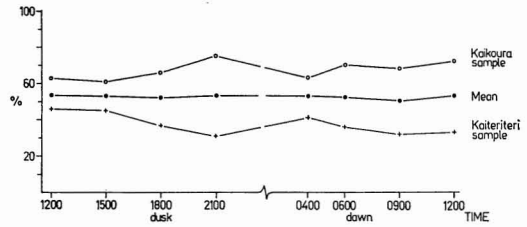


FIG. 5. Mean percentages of test covered with algae during 24 hours in a naturally lit laboratory.

24-hour period at the following times: 2 May 1968, 1200, 1500, 1800, 2100; 3 May, 0400, 0600, 0900, 1200. During this time the tanks were illuminated naturally. At each observation the percentage of the surface of each urchin covered by algae was noted. Mean percentages for each sample and means for both samples combined are shown in Figure 5.

The urchins showed no tendency to drop cover during darkness and assume it again in light. This behavior contrasts with that observed in a natural population of *Lytechinus variegatus* by Millot (1956) and in aquarium-kept specimens of the same species (Sharp and Gray, 1962), where the extent of covering was related to diurnal light changes.

GENERAL DISCUSSION

In contrast with the covering behavior of *Lytechinus variegatus* and *Tripneustes ventricosus* (Millot, 1956; Lewis, 1958) that of *Evechinus* seems very little related directly to light or to light avoidance. The stimuli involved in the capture and initial uptake of covering material are tactile and not photic. Cover is taken up in both light and dark and, although the rate is slightly faster in the former, the final amount of cover adopted does not differ between the two. The covering process (both rate and final amount of cover) is not affected by adapting the urchin to light and dark conditions, and the extent of covering does not show diurnal changes. Field observations cited in the introduction reinforce this conclusion.

It appears that the covering reaction in *Evechinus* is related to the positive reaction of the podia to contact, and is not an active shading response (see also Gamble, 1966, and Reese, 1966). What adaptive functions could this tactile response serve?

That the habit may result indirectly in light avoidance is shown by the movements of 10 *Evechinus* individuals placed in each of two half-shaded and half-lit troughs (Figs. 4 and 6), those in one trough having abundant mixed algal cover and those in the other being without cover. There was much more movement of urchins without algal cover into the shaded part of the trough than of those with cover (Fig. 6).

This function may be more important in intertidal than in subtidal populations. Intertidal urchins, if not concealed, are likely to be subjected to stronger light intensities than subtidal urchins. Field observations suggested that intertidal urchins typically had more cover (often of shells or stones) or were more concealed than subtidal urchins; they also appeared to cover faster and more extensively in laboratory experiments.

As has been suggested for other species of urchins (see references cited in the introductory paragraph), the tactile covering response in *Evechinus* could serve to camouflage small individuals which may be eaten by some fish. However, it is doubtful that covering serves this

purpose in large *Evechinus*, since they are generally covered far less completely than small specimens, and are often found in the open without cover (Dix, 1969, fig. 1). Further, all known and possible predators of large *Evechinus* are invertebrates which could not rely on image perception for capture of prey.

Diving and other field observations suggest that the covering response in *Evechinus* may be mainly related to the capture of food:

(a) The covering material of 100 *Evechinus* at Kaiteriteri and 80 at Kaikoura examined in February 1968 during diving observations on feeding is shown in Table 3. All substances utilized as cover were found to be also utilized as food (Dix, in preparation), and at Kaiteriteri, where a wider variety of cover was found, the brown alga *Carpophyllum* and shell, the two most frequent covering materials, were also the most frequent sources of macroscopic food. At Kaikoura, where cover consisted entirely of algae, food consisted mainly of the same algae.

TABLE 3

MATERIALS USED AS COVER BY *Evechinus* AT KAIKOURA AND KAITERITERI*

KAIKOURA		KAITERITERI	
COVERING MATERIAL	PER-CENTAGE	COVERING MATERIAL	PER-CENTAGE
Brown algae	30.0	<i>Carpophyllum</i>	9.0
Red algae	16.4	Shell	6.0
Red and brown algae	22.4	Leaf	4.0
None	31.2	Stick	4.0
		<i>Carpophyllum</i> and <i>Hormosira</i>	3.0
		<i>Carpophyllum</i> and shell	1.0
		<i>Carpophyllum</i> and leaf	1.0
		Shell and stone	1.0
		Shell and leaf	1.0
		Leaf and stone	1.0
		Stick and leaf	1.0
		Stone	1.0
		None	67.0

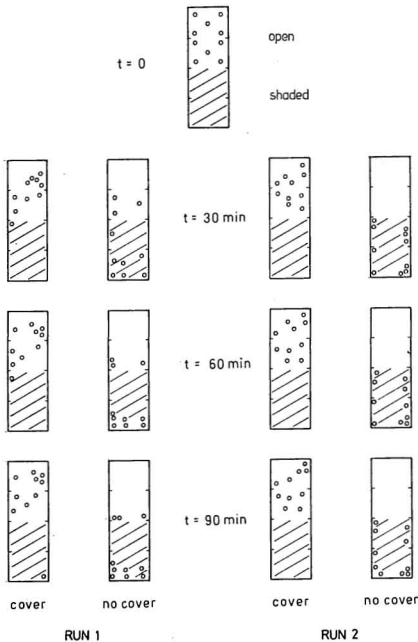


FIG. 6. Movements of *Evechinus* (circles) with and without algal cover in the apparatus of Figure 4.

* Based on samples of 80 urchins at Kaikoura and 100 at Kaiteriteri in February 1968.

(b) Both in nature and in aquaria, *Evechinus* was often found with a piece of alga wrapped around the test, this being cover on top and food underneath.

(c) During January 1969, at least 30 *Evechinus* were collected every 3 days from a population occupying a localized barren area. During most of this period seas were calm; *Evechinus* were little covered, few were observed feeding, and the gut of animals examined contained little algal food but considerable amounts of bottom material. Toward the end of the sampling period, rough seas produced large amounts of drift algae. The urchins became extensively covered and all were observed to be actively feeding in the field.

Drifting algal debris must form a significant food source for *Evechinus*, particularly if it is captured in the quantities shown in Figure 1, and especially for populations living in localized barren areas. P. K. Dayton (personal communication) independently suggested that the covering response in *Strongylocentrotus purpuratus* is maintained as a feeding device, for this animal appears often to derive most of its food from drift algae. Ebert (1968) also suggested that the algae held on the spines and tube feet of *S. purpuratus* were utilized for food. Otter (1932) suggested for urchins in general that "algae and other food may be carried by wave action on to the tube feet around the anal pole . . . and handed by them to the mouth below." G. C. B. Poore (personal communication) has also indicated that much of the food of the abalone (paua), *Haliotis iris*, is derived from drift algae. Possibly drifting, rather than growing, algae are a significant food source for a considerable number of marine algivores.

A further and interesting function is served by covering in the Antarctic urchin *Sterechinus neumayeri* (Dayton, Robilliard, and Paine, 1968). This urchin is preyed upon by the actinarian *Urticinopsis antarctica*. Twenty in situ experiments showed that when an urchin covered with a mat of hydroids comes into contact with an anemone "the anemone places its tentacles over the potential prey, touches the hydroids and then often retracts its tentacles, thereby releasing the urchin." Release occurred in 80 percent of the experiments, but uncovered

urchins induced to crawl against the same anemones were always captured and consumed.

The evidence indicates that the nature of the covering response differs between urchin species and that the response may not be concerned primarily with light avoidance in some species.

SUMMARY

1. Field observations suggested that the covering response in *Evechinus* is not a simple light avoidance response but is related to the positive reaction of the podia to contact. The following laboratory observations support this suggestion: (a) The stimuli involved in the capture and initial uptake of covering material were tactile and not photic; (b) cover was taken up at a similar rate in both light and dark conditions; (c) the covering response did not show adaptation to light or to dark, in contrast to the phototactic response; and (d) the extent of covering did not show marked diurnal changes.

2. Although the covering response may indirectly serve in light avoidance in some situations, more likely functions are camouflage in small urchins and capture of food (particularly algal debris) in both small and large urchins.

ACKNOWLEDGMENTS

This work was supported by a New Zealand postgraduate scholarship. My supervisors, Professor G. A. Knox and Dr. H. B. Wisely, gave helpful criticism.

LITERATURE CITED

- DAYTON, P. K., G. A. ROBILLIARD, and R. T. PAINE. 1968. Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. Paper presented SCAR Symposium on Antarctic ecology, Cambridge, England, July–August 1968.
- DIX, T. G. 1969. Aggregating in the echinoid *Evechinus chloroticus*. *Pacific Science*, vol. 23, no. 1, pp. 123–124.
- DUBOIS, R. 1914. Action de la lumière sur les Echinodermes. *Compte Rendu, Congrès International de Zoologie* 9 (1913), pp. 148–151.

- EBERT, T. A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology*, vol. 49, no. 6, pp. 1062-1074.
- GAMBLE, J. C. 1966. Some observations on the behaviour of two regular echinoids. Symposium of the Underwater Association for Malta, 1965, pp. 47-50.
- HARVEY, E. B. 1956. The American *Arbacia* and other sea urchins. Princeton University Press, New Jersey.
- HYMAN, L. H. 1955. The invertebrates. Vol. IV, Echinodermata, the coelomate Bilateria. McGraw-Hill, New York.
- LEWIS, J. B. 1958. The biology of the tropical sea urchin *Tripneustes esculentus* Leske in Barbados, British West Indies. *Canadian Journal of Zoology*, vol. 36, pp. 607-621.
- MILLOT, N. 1956. The covering reaction of sea urchins. I. A preliminary account of covering in the tropical echinoid *Lytechinus variegatus* (Lamarck), and its relation to light. *Journal of Experimental Biology*, vol. 33, pp. 508-523.
- 1966. Coordination of spine movement in echinoids. In: R. A. Boolootian, ed., *Physiology of Echinodermata*, pp. 465-486. John Wiley and Sons, New York.
- NICHOLS, D. 1964. Echinoderms: experimental and ecological. *Oceanography and Marine Biology, an Annual Review*, vol. 2, pp. 393-423.
- OTTER, G. W. 1932. Rock-burrowing echinoids. *Biological Reviews*, vol. 7, pp. 89-107.
- REESE, E. S. 1966. The complex behaviour of echinoderms. In: R. A. Boolootian, ed., *Physiology of Echinodermata*, pp. 157-218. John Wiley and Sons, New York.
- SHARP, D. T., and I. E. GRAY. 1962. Studies on factors affecting the local distribution of two sea urchins, *Arbacia punctulata* and *Lytechinus variegatus*. *Ecology*, vol. 43, pp. 309-313.
- YOSHIDA, M. 1966. Photosensitivity. In: R. A. Boolootian, ed., *Physiology of Echinodermata*, pp. 435-464. John Wiley and Sons, New York.