EFFECTS OF LIGHT, TIME OF DAY, AND SURGE ON THE COVERING RESPONSE OF TRIPNEUSTES VENTRICOSUS

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ABSTRACT (DKS & DML)

Tripneustes ventricosus is one of many sea urchin species that has the tendency to cover its aboral surface with various materials by holding them in place with its tube feet. It has been proposed that this covering behavior could reduce the harmful effects of high light or wave action. We expected that percent cover would increase with increased light and surge, and would vary with changes in light and surge through the day. In the field, we found some correlation over the course of a day between a decrease in light and a decrease in percent cover, as well as between constant light levels and constant percent cover. However, we found no relationship between surge levels and percent cover.

In outdoor tanks, T. ventricosus individuals kept in the complete absence of light for 24 hrs. had a constant, low percent cover, while those allowed to experience ambient light levels had higher percent cover during daylight hours than at night. These results suggest that T. ventricosus uses light as a cue to cover, either to avoid predation, or to escape the deleterious effects of UV irradiation.

Key Words: Tripneustes ventricosus, covering response

INTRODUCTION (DKS)

Several sea urchin species exhibit covering behavior, which is the movement of pieces of vegetation and debris to the aboral surface and holding them in place with the tube feet. Very little is known about the stimuli or functional basis for this covering response. Lees and Carter (1972) showed that exposure to ultraviolet irradiation, direct sunlight, and surge in the laboratory can cause covering by Lytechinus. Mechanical and photic stimuli could induce covering directly, by providing a cue that conditions are unfavorable, or indirectly, by triggering increased activity and therefore also increased activity of the tube feet (Lawrence, 1976).

Tripneustes ventricosus and Lytechinus variegatus have a higher percent cover in exposed habitats than in non-exposed habitats, suggesting that these animals can facultatively cover based on their visibility to predators and exposure to light and surge (Sakowitz, 1987 FSP). We decided to investigate whether there is a relationship in the field between time of day, surge levels, and light levels, and the degree to which T. ventricosus covers. We expected to see higher percent cover as surge and light increased , both within a day and across days.

The second part of our study consisted of an outdoor tank experiment in which urchins were monitored over a 24hr period to compare variations in percent cover in a tank that was covered to exclude sunlight, and one that was left uncovered and exposed to daily light fluctuations. We predicted that the absence of light during daylight hours would lead to a lower percent cover relative to the urchins in the control tank.

METHODS (LCB)

We observed Tripneustes ventricosus on 2-4 March, 1994 in the west back reef of Discovery Bay, Jamaica. Three simultaneous surveys of 25 urchins each were made in three adjacent areas parallel to the reef crest at 07:45, 11:30, 15:30, and 18:00 each of the three days. Surge and light were categorized as high or low for each time period and percent cover (0, 20, 40, 60, 80, or 100%) was recorded for each urchin.

The laboratory experiment was conducted from 10:00 on 6 March to 09:00 on 7 March, in two outdoor tanks with circulating seawater behind the Discovery Bay Marine Laboratory. In each tank, we placed ten urchins and 17 metal skewers each with 25 Thalassia blades. One tank was covered with metal sheets for the entire 23 hours to prevent light from entering the tank. Percent cover of each urchin was recorded every hour from 10:00 to 19:00 on 6 March and 05:00 to 09:00 on 7 March and every other hour from 19:00 6 March to 05:00 7 March.

The effect of date, time period, and plot on percent of the aboral surface of the urchin covered for both field and laboratory were analyzed using a fully functional repeated measures ANOVA. For the laboratory experiment mean percent cover of the open and closed treatments for each time period were compared using student's t-tests.

RESULTS (DML)

On Day 1 of our field experiment, urchin percent cover was greatest at 07:45 and then tended to decrease through the day. Light was low at both 07:45 and 18:00, but high during the two midday observation periods. Surge was high at all observation times except 18:00 .(Figure 1).

Percent cover remained fairly constant throughout Day 2. Light and surge levels were low during all observation periods except at 18:00 when surge was high (Figure 2).

On Day 3, urchin percent cover stayed relatively constant until late in the afternoon when it decreased. Surge levels were high throughout the day. Light was low at the early morning and evening observation times, but high at the two midday observation times (Figure 3).

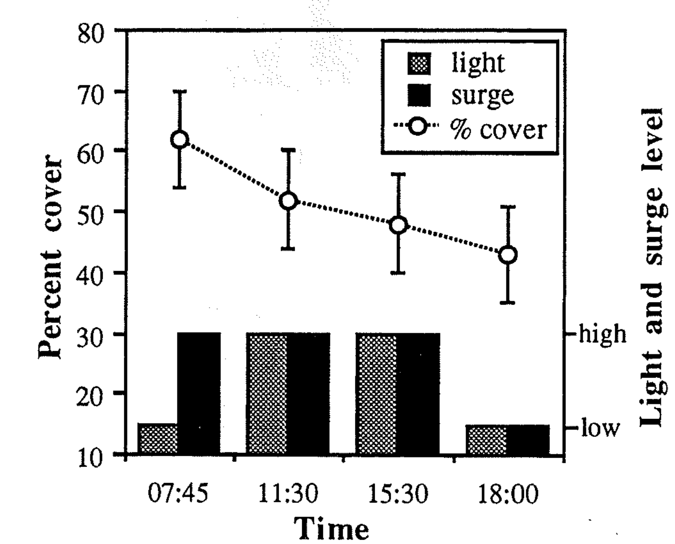

Figure 1. Changes in light, surge, and urchin cover with time during Day 1.

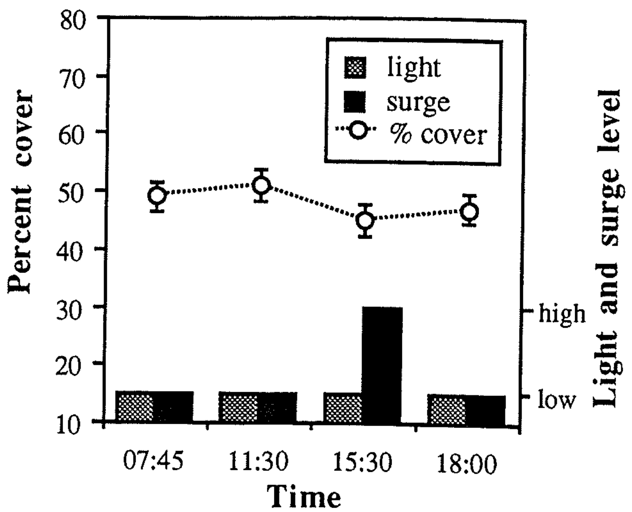

Figure 2. Changes in light, surge, and urchin cover with time on Day 2.

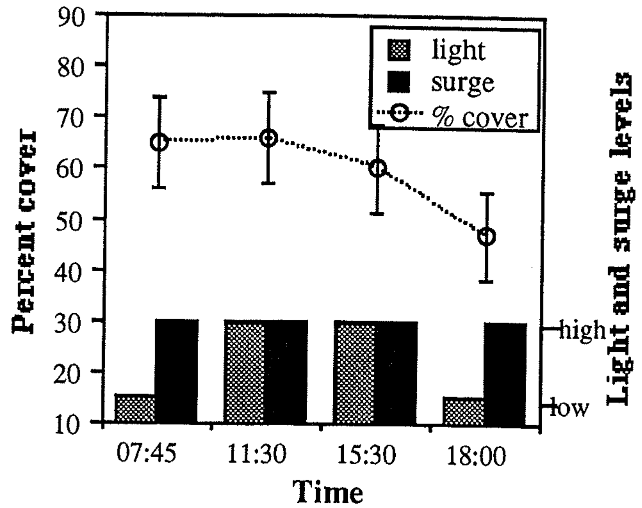

Figure 3. Changes in light, surge, and urchin cover with time on Day 3.

The effect of time of day on urchin percent cover was significant and differed for each

Table 1: Results of ANOVA looking at effects of day and plot on percent cover.

	df	f	p
Day	2	12.108	0.000
Plot	2	5.619	0.004
Day * Plot	4	2.737	0.030

of the three days ($p < 0.001$ and $p = 0.015$ respectively; Table 2). We were unable to statistically analyze the effects of either light or surge on urchin percent cover, however, Figures 1-3 show a possible relationship between light level and percent cover. Percent cover tended to decrease with decreasing light on Days 1 and 3 and remain constant with constant light level on Day 2. No relationship between surge level and urchin percent cover was shown in the figures.

Our field experiment also showed urchin percent cover to be highly variable in nature differing significantly both between days and between plots ($p < 0.001$ and $p = 0.004$ respectively; Table 1).

In our laboratory experiment, urchin percent cover differed significantly between treatments ($p < 0.001$; Table 3). It remained at a fairly constant low level in the closed tank over the 24h period. In the open tank, percent cover tended to increase during the morning and early afternoon, peaking at 15:00, and then decrease in the late afternoon and evening to a relatively constant low level overnight. The effect of time of day on percent cover in the outdoor tanks was significant and differed for each of the two treatments ($p = 0.008$ and $p = 0.005$ respectively; Table 4).

Table 2: Results of repeated measures ANOVA looking at the effect of time of day on percent cover.

	df	f	p
Time	3	12.707	0.000
Time * Day	6	2.645	0.015
Time * Plot	6	0.731	0.624
Time * Day * Plot	12	1.421	0.151

Table 3: Results of ANOVA looking at effects of open and closed tank treatments on percent cover over 24h.

	df	f	p
Treatment	1	23.682	0.000

Urchin percent cover was significantly higher in the open tank than in the closed tank during the day between 10:00 and 16:00 and at 18:00, but did not differ significantly between treatments at night (Figure 4). We observed that the majority of the urchins in the open tank stayed in shaded areas during the daylight hours. We also noticed that urchin percent cover tended to be lower on average in the outdoor tank than it had been in the field.

DISCUSSION (LCB)

Our hypothesis that urchin percent cover would change with time of day was supported

Table 4: Results of repeated measures ANOVA looking at the effect of time of day on percent cover in open vs. closed tank treatments.

	df	f	p
Time	18	2.037	0.008
Time * Treatment	18	2.117	0.005

in the field experiment. However, there did not seem to be a trend that covering increased with increasing surge, indicating that surge is probably not the main cause of diurnal changes in covering response. The trend of decreased covering over the course of Days 1 and 3 was not consistent with the rise and then decline in light levels over those days; however, the relatively constant low levels of light over the course of Day 2 was consistent with the constant covering of urchins throughout the day.

The high variation in percent cover across days, time periods, and plots maybe in part due to environmental variation. The type of microhabitat in which an urchin was found and the

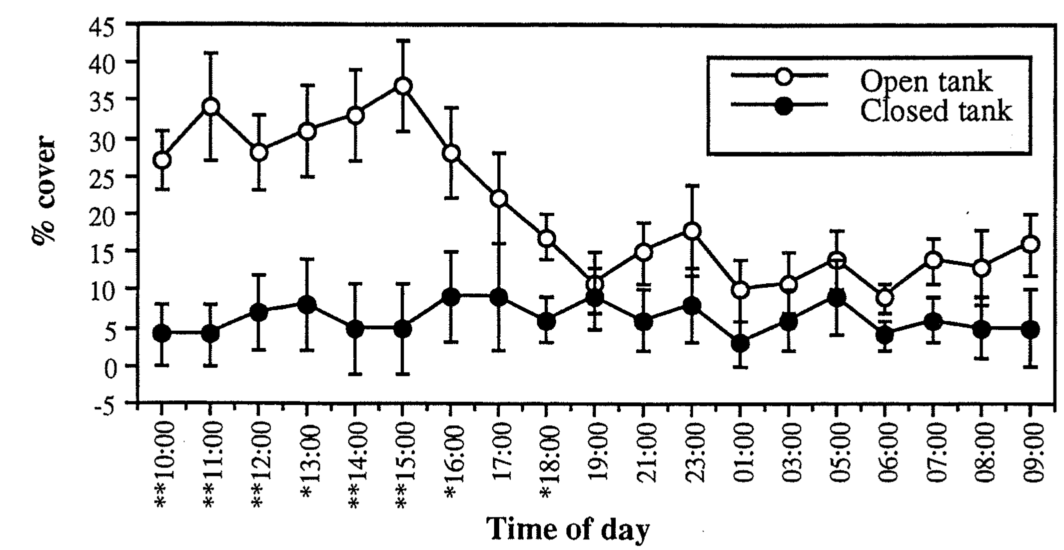

Figure 4. Changes in percent cover of urchins in lab with time of day over a period of 24h. (* = $p < 0.05$; ** = $p < 0.01$)

complexity of the habitat and abundance of covering materials in that habitat may have affected the percent cover of an urchin. In addition, behaviors of urchins like clumping may serve to reduce the need for covering through increased protection from predators or surge.

In the outdoor tank experiment, the absence of diel changes in covering response in the closed treatment indicates that the covering response is triggered by an external, not an internal, stimulus. Light seems to be this external stimulus since the diurnal changes in covering in the open tank occurred in the absence of surge.

The delayed peak in percent cover in the illuminated tank as compared to the field experiment could have been a result of additional stimuli, like surge, in the field or decreased light in the laboratory due to shading of the tank by trees and cement walls. The lower overall covering by urchins in the tank experiment may have been due to a lack of available material in the tank.

Three main functional explanations for the sea urchin covering response have been suggested: 1) increased stability to withstand surge; 2) creating a physical barrier to prevent ultraviolet radiation damage; and 3) camouflage to avoid visual predators. Surge does not seem to be the primary stimulus as high surge was not consistently associated with high percent cover (field) and urchins demonstrated a covering response in the absence of surge (outdoor tank). Light appears to be a stimulus, however, both the UV and predation hypotheses are reliant upon light as a stimulus. That sea urchins tended to prefer the shaded part of the open tank favors the UV hypothesis. Yet, the high degree of individual variation in field covering responses does not allow us to disregard the predation hypothesis. If covering response is genetically controlled, the reduced predation pressure in recent years on this reef may have allowed the survival of genotypes that cover to a lesser degree, increasing the variation in covering response within the species.

Further studies could investigate the covering of urchins just before dawn and the relation to light and other stimuli. Similar habitats that have consistently high or low surge could be compared. Light and surge should be better quantified. Additionally, it would be interesting to see if covering does increase in response to surge in the absence of light in the field. Finally, individual urchins could be followed over time to investigate individual diurnal variation in covering.

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