

A TIDAL RHYTHM IN THE GULF OF CALIFORNIA  
HERMIT CRAB, CLIBANARIUS DIGUETI (BOUVIER)

by

Elaine Kay Snyder

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SIGNED: Elaine Snyder

APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

Elisabeth A. Stull  
Elisabeth A. Stull  
Assistant Professor of  
Biological Sciences

30 Nov 72  
Date

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## ABSTRACT

In nature populations of the hermit crab Clibanarius digueti (Bouvier) aggregate at low tide and disperse at high tide. The components of aggregative behavior were assessed by studying the possible rhythm properties of oxygen consumption, gregariousness, phototaxis, and light-dark substrate color preference of the organism in the laboratory. A physiological basis for clumping was also sought by testing critical thermal maxima and minima, salinity tolerances, and resistance to desiccation.

While no rhythm of phototaxis was evident, tidal rhythms of both gregariousness and substrate color preference were demonstrated. These rhythms persisted under constant laboratory conditions for approximately two tidal cycles. Oxygen consumption data for segregated individuals failed to show this tidal rhythm. However, the rhythm may be present in aggregations.

Two possible functions of aggregation are as a means of escaping predators and to facilitate social interactions such as shell grooming, shell exchange, fighting and breeding. Aggregation in this species is not likely to serve thermal or osmoregulatory functions as this species is demonstrated to be eurythermal and euryhaline. Also, C. digueti can tolerate desiccation for lengthy periods, so clumping probably does not occur to conserve moisture.

## INTRODUCTION

Contiguous (clumped) distribution is quite common among marine invertebrates. Aggregation is known for ten species of gastropods, eight species of crustaceans, six species of insects, and six species of echinoderms in the Hawaiian Islands (MacKay, 1945). To date MacKay's study appears to be the only survey conducted of aggregations of motile invertebrates in the intertidal zone, although research on the biology of particular species has often incidentally disclosed the presence of aggregative behavior.

Several elements may be involved in aggregative behavior of motile benthic invertebrates of the intertidal zone. In some cases purely physical factors may explain clumped distribution. For example, aggregation of the sand crab Emerita analoga has been attributed to distribution effects of lateral flow within wave washes (Cubit, 1969). More often explanations have been in terms of individual responses to the environment, i.e., kineses and taxes. Kineses are undirected locomotory reactions in which the rate of movement or turning depends on the intensity of the stimulus, while taxes are directed reactions toward or away from a source of stimulation (Fraenkel and Gunn, 1961). Thus, tide levels are thought to regulate clustering and dispersal of the gastropod Cerithium Clypeomorus moniliferum by induction of changing barokinetic (pressure) and thigmotactic (touch) responses (Moulton, 1962). Aggregation of the coquina Donax variabilis is reported to result from an acoustic response to waves. Emerging from the sand when the wave shock

is of a certain magnitude, the beach clams migrate with the rising tide front (Turner and Belding, 1957). Millard (1968) suggested that wave action and tide level may play a part in the clustering of the limpet Acmaea digitalis, but did not propose a mechanism. Because sociality is often recognized to occur only in insects, higher invertebrates and vertebrates, the role of sociality in clustering behavior has been neglected. However, Dix (1969) demonstrated that it is likely an important element in the clumping of the echinoid Evechinus chloroticus. And aggregates of the spider crab Maja squinado are structured according to a social hierarchy (Štević, 1971).

Several species of Pagurid crabs have been noted to cluster, for example, Clibanarius misanthropus (Drzewina, 1907), C. zebra (MacKay, 1945), and Pagurus samuelis and P. granosimanus (Ball, 1968). A common inhabitant of northern Gulf of California intertidal areas, Clibanarius digueti (Bouvier) displays a marked year-round rhythm of clumping. Extreme tides govern the northern Gulf of California. These tides are of the irregular semidiurnal type and have a spring tide maximum range of 7 meters in the region studied. At low tide clusters with as many as 200 individuals appear primarily on dark basalt boulders both above and below water. Movements forming a clump begin during tidal ebb, but once formed, individuals tend to remain immobile until covered by the incoming wash of tidal flow. By high tide the hermit crabs are found dispersed on sand and light-colored coquina limestone (shell-hash beach rock), as well as on the boulders. Active roaming and feeding take place while the animals are dispersed.

I have attempted to explain the aggregative behavior of this hermit crab by focusing on two questions. What are some components in the mechanism of aggregation? What physiological or behavioral functions are promoted by aggregation? To answer the first question I examined rhythmicity of oxygen consumption, gregariousness, and two tactic responses - phototaxis and preference for light or dark substrate. Critical thermal maxima and minima, salinity tolerances, and resistance to desiccation were measured to see if any of these factors might account for the adaptive value of clumping behavior.

## METHODS AND MATERIALS

### Rhythm Experiments

Clumps of hermit crabs were collected at low tide from Station Beach, Puerto Peñasco, Sonora, Mexico, at La Universidad de Sonora - University of Arizona marine station. For respiration measurements hermit crabs were transported back to Tucson prior to testing and tests were not conducted immediately. In the other experiments described, tests were conducted in the Puerto Peñasco marine facilities. The acclimation period in all experimental situations was two hours, and all tests were done under constant light and temperature, using sea water collected at the same time as were the hermit crabs.

I measured oxygen consumption in a Warburg respirometer on two occasions, December 4, 1971, for two individuals seven days in captivity and February 20, 1972, for eight individuals four days in captivity, using the method of Umbreit, Burris and Stauffer (1964). Each animal was isolated in a separate flask so that individual respiration rates were obtained. These two tests ran for 25 hours and 20 hours each. In the first test I read the manometer at two hourly intervals with intermittent equilibration times of approximately 15 minutes each. In the second test readings covered hour-long periods, again allowing about 15 minutes for gas equilibration between test times. Temperature was maintained by use of a controlled water bath at  $23.1 \pm .1^{\circ}\text{C}$  and light intensity (fluorescent) was approximately 900 lux, as measured by a Gossen Luna-six exposure meter, for both tests.

I checked changes in response to light (phototaxis) by placing 20 hermit crabs in a container 20 by 30 cm. Half the area of the container was then covered with aluminum foil in such a way that the foil formed a curtain extending down to within 1 cm of the water, which was approximately 1 cm deep. Numbers of individuals occupying the lit section were counted each half hour. There were four experiments (two sets) to test this response. Test dates were September 22-23 and October 7-8, 1972. The first set of tests lasted 24 hours, with the temperature maintained at  $27.0 \pm 1.8^{\circ}\text{C}$ . The light intensity (incandescent) was approximately 525 lux during both sets of experiments.

I measured changes in light-dark substrate preference using the design shown in Figure 1. The containers used were plastic dishpans, spray painted into black and white quadrants. In each test 20 hermit crabs were placed in each pan, five per quadrant. Numbers in each quadrant were then counted every half hour. I ran six tests (three sets) on July 23-24, October 7-8, and October 20-22, 1972. On the latter two test dates sequential photographs every hour for the first 13 hours of the experiments were taken for a single test. The three tests lasted for 24, 30, and 47 hours, respectively. During the final test, there was an intermission of three hours in which no data was taken, occurring after the first 30 hours of test time. Temperatures maintained were  $29.4 \pm 1.8$ ,  $27.0 \pm 1.8$  and  $22.7 \pm 1.6^{\circ}\text{C}$  for these three test sets. Light intensities were approximately 525, 175, and 175 lux on the three dates. The water changing schedule also varied. The water was changed once after twelve hours, every three hours, and not at all on the three

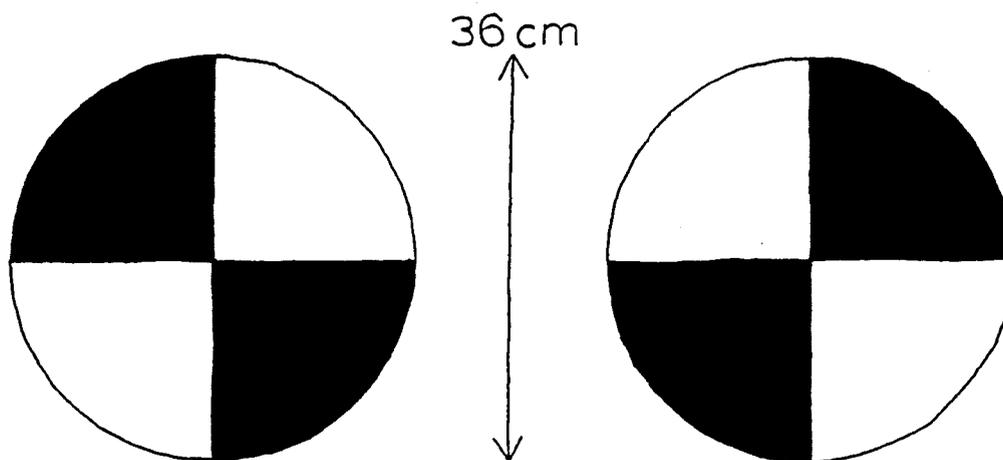


Figure 1. Design to test light-dark substrate preference.

In each set of experiments the pans were oriented so as to randomize any directional component. The light source is overhead. Numbers of individuals occupying each quadrant were ascertained every half hour for twenty four hours or more.

experimental sets, respectively. In all the tests, however, the water level maintained was 1 cm.

Changes in clumping behavior (gregariousness) of C. digueti were estimated using the design depicted in Figure 2. The dishpans were spray painted either all white or all black. In each test 20 hermit crabs were placed in each pan, two per section. Numbers in each section were then counted every half hour. I performed six tests (three sets). On October 7-8, one set using pans with white backgrounds was run. On October 20-22, sets with both the white and black backgrounds were tested. On both the first and second dates one of the clumping experiments employing the white background was photographed hourly for 13 and 14 consecutive hours respectively. Test conditions were the same as those described for the substrate preference tests. The analysis of clumping data was by calculation of the chi squares of deviation from expected randomness. Since 20 hermit crabs were placed in each test pan, which was divided into ten sections, two hermit crabs per section were defined as the random condition.

#### Physiological Tolerances

Specimens were obtained on several occasions between October and December, 1971, from Station Beach. These were kept in five gallon oxygenated aquaria in Tucson in which temperatures ranged from 18-23°C and salinities varied between 35 and 40 ‰. I determined critical thermal maxima using a one gallon oxygenated aquarium into which glass heating units were inserted. The water in these tests warmed at a rate of .5-1.5°C per minute. In two similar tests five hermit crabs were

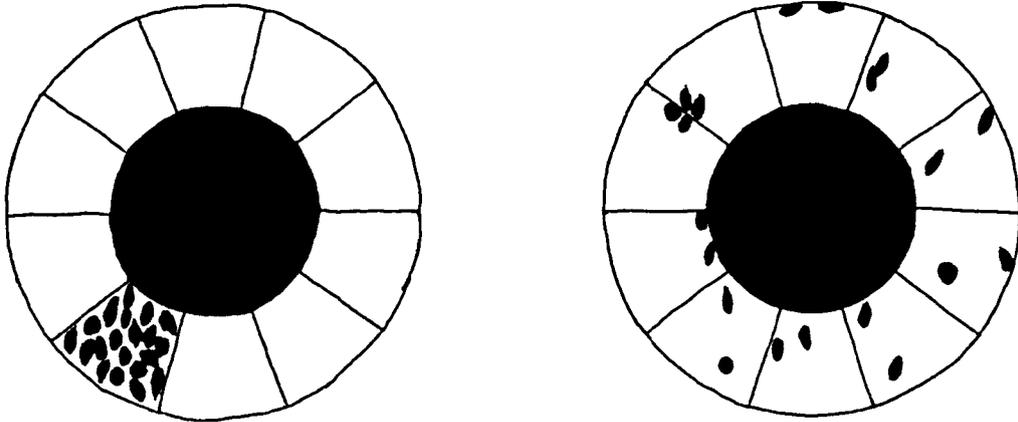


Figure 2. Design to test gregariousness.

The hermit crabs are free to move in the doughnut shaped pathway. Shown above are the theoretical states of maximum clumping ( $X^2 = 180$ ) and maximum dispersal ( $X^2 = 0$ ). Numbers occupying each of the ten sections were checked every half hour for twenty four hours or more.

placed in the tank at once and times and temperatures of death, defined as lack of movement of appendages, antennae, and maxillipeds, were recorded. I deduced critical thermal minima from two different tests involving the same hermit crabs. In the first test seven individuals were placed in a 1000 milliliter beaker and this was placed in an ice bath. The beaker cooled to 5°C at a rate of 0.4°C/min. Allowing the beaker to warm slowly, I observed the survival rate. Since all the hermit crabs survived, this beaker was then placed in a freezer unit. It chilled to 0°C at a rate of .7°C per minute. After one hour, the temperature fell to -1°C. Removed from the freezer, the beaker was left to warm and survival rate was again ascertained.

I measured salinity tolerance by placing 10 C. digueti each into sea water solutions of salinities 0, 15, 30, 45, and 60 ‰. Survival rate after 1 and 24 hours was then ascertained. Resistance to desiccation was exacted under low humidity conditions,  $38 \pm 5 \%$ , at 20°C. I placed 123 dry individuals in a tray. Every hour I removed 10 hermit crabs for the first eight hours. Then 10 hermit crabs were removed at 17 and 28 hours after the beginning of the test. Lastly, 23 hermit crabs were removed 32 hours after the test's onset. Hermit crabs removed were placed in sea water and survival was judged after one hour of immersion.

## RESULTS

As seen in Figure 3, there was no obvious tidally rhythmic component of phototaxis in this species. On both dates responses to light seem to be rather erratic and may be attributed to random action. Thus, although an exogenous phototactic response may be involved in the behavior of *C. digueti*, the response to light is not a rhythm regulated component of its aggregative behavior.

In the six experiments performed a clear tidal rhythm of light-dark substrate preference was demonstrated as seen in Figures 4, 5, and 6, and in the photographic sequences of Figures 7 and 8. At times of low tide up to 100 per cent of the hermit crabs selected a black substrate, while at times of high tide a white substrate was chosen. This rhythm remained distinct under laboratory conditions for approximately two tidal cycles.

A tidal rhythm of gregariousness also occurred in the behavior of this species as depicted in Figures 9, 10 and 11, and in the two photographic sequences of Figures 12 and 13. The data show that clumped (non-random) distribution increases at times of low tide, while dispersion (randomness) increases at times of high tide. Data on percentage of hermit crabs in physical contact with each other, derived from analyses of the photographic sequences, are shown in Figure 14. These data also reveal a rhythm pattern in gregariousness, with increased contacts during times of low tide. Like the rhythm of preference for

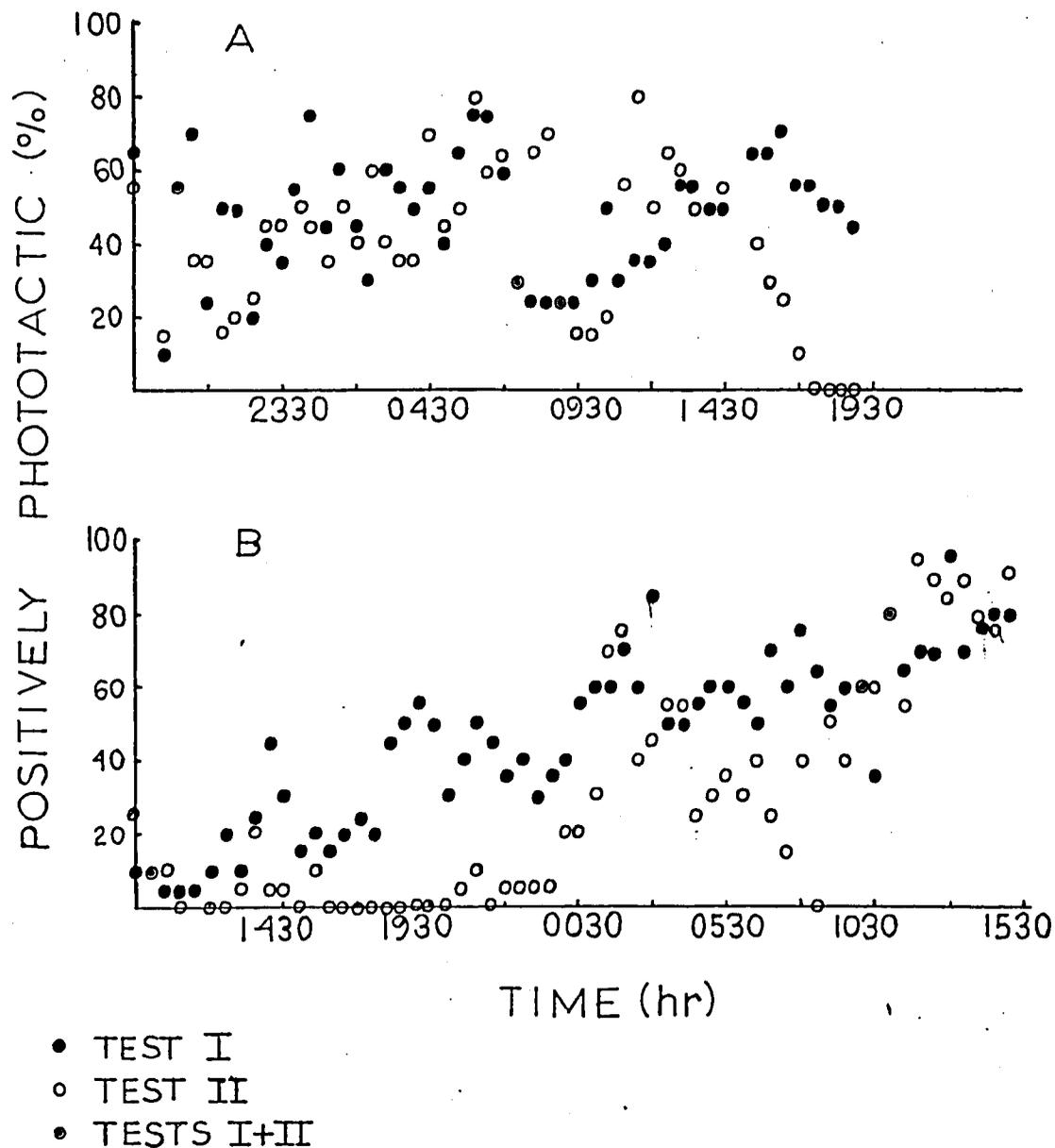


Figure 3. Phototactic response of *C. digueti* as a function of time.

A. Results of two tests, Sept. 22-23, 1972. B. Results of two identical tests, Oct. 7-8, 1972. Each dot represents percentage of hermit crabs (20) in a single test which occupied the lit as opposed to the dark test area at a certain time.

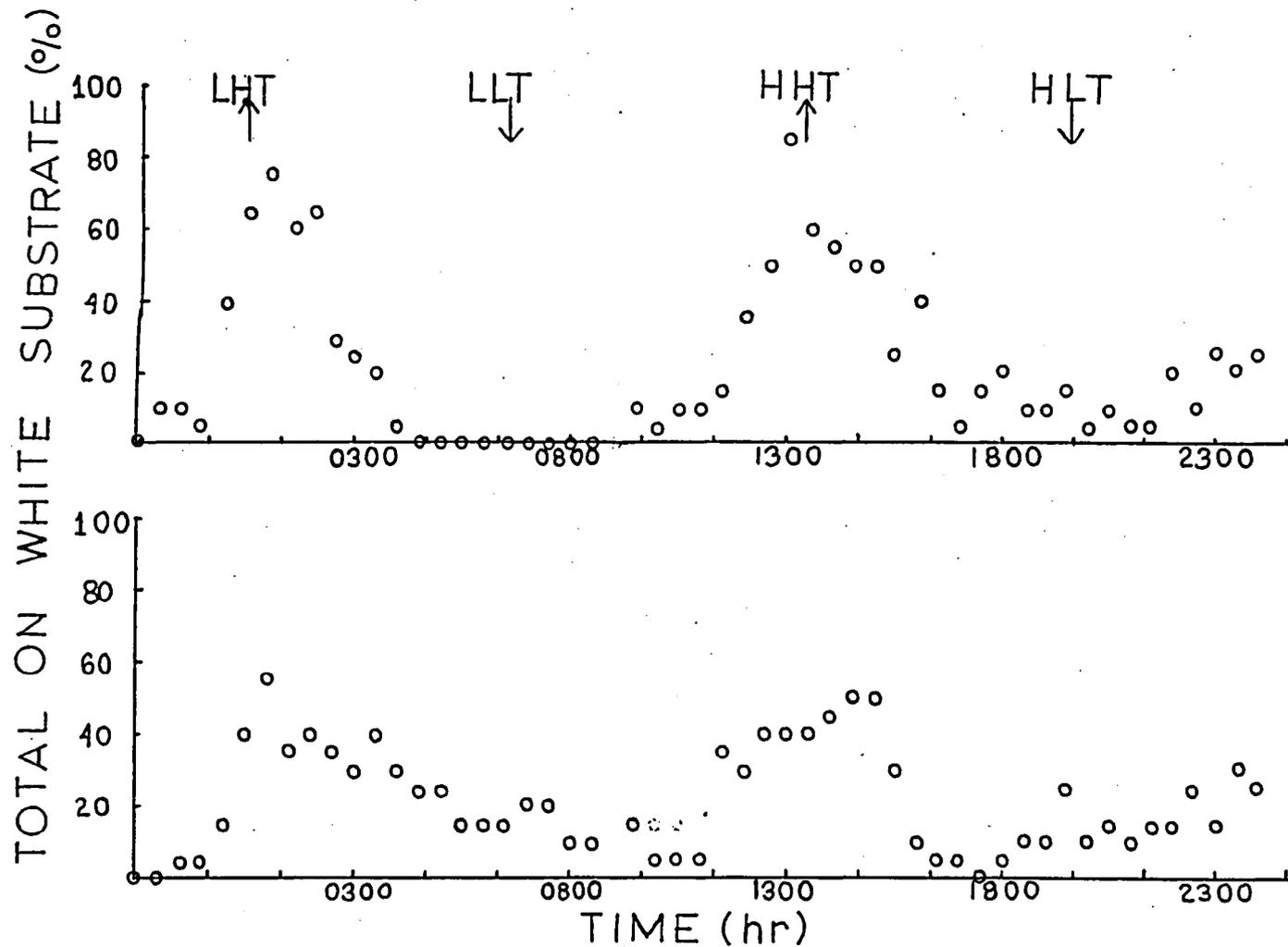


Figure 4. Tidal rhythm of preference for white versus black substrates in C. digueti, July 23-24, 1972.

In each test (n=20) the per cent of hermit crabs occupying the white substrate is shown as a function of time and tidal stage (arrows above). The tests ran for 24 hours.

Figure 5. Tidal rhythm of preference for white versus black substrates in C. digueti, Oct. 7-8, 1972.

In each test (n=20) the per cent of hermit crabs occupying the white substrate is shown as a function of time and tidal stage (arrows above). The tests ran for 30 hours.

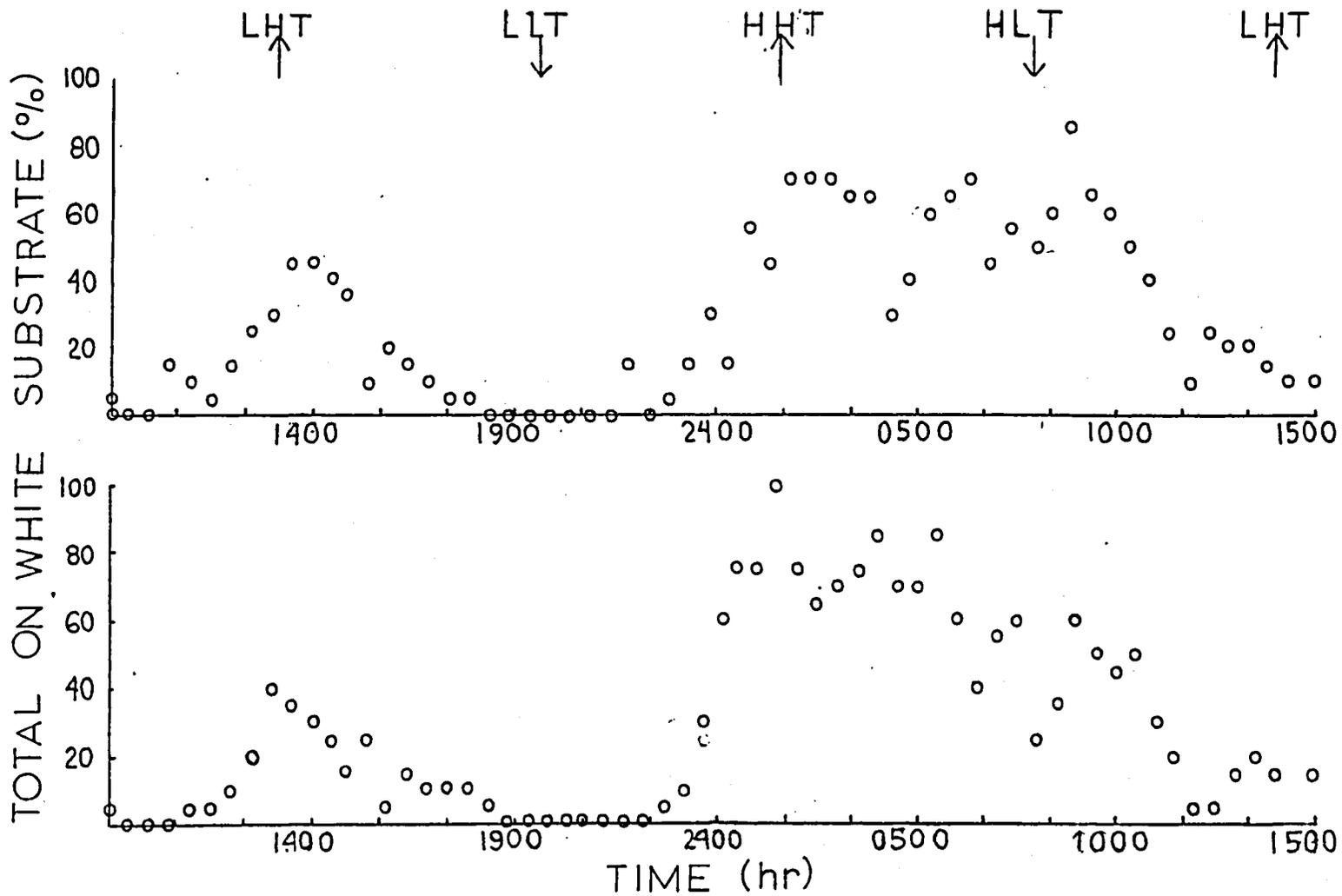


Figure 5. Tidal rhythm of preference for white versus black substrates in *C. digueti*, Oct. 7-8, 1972.

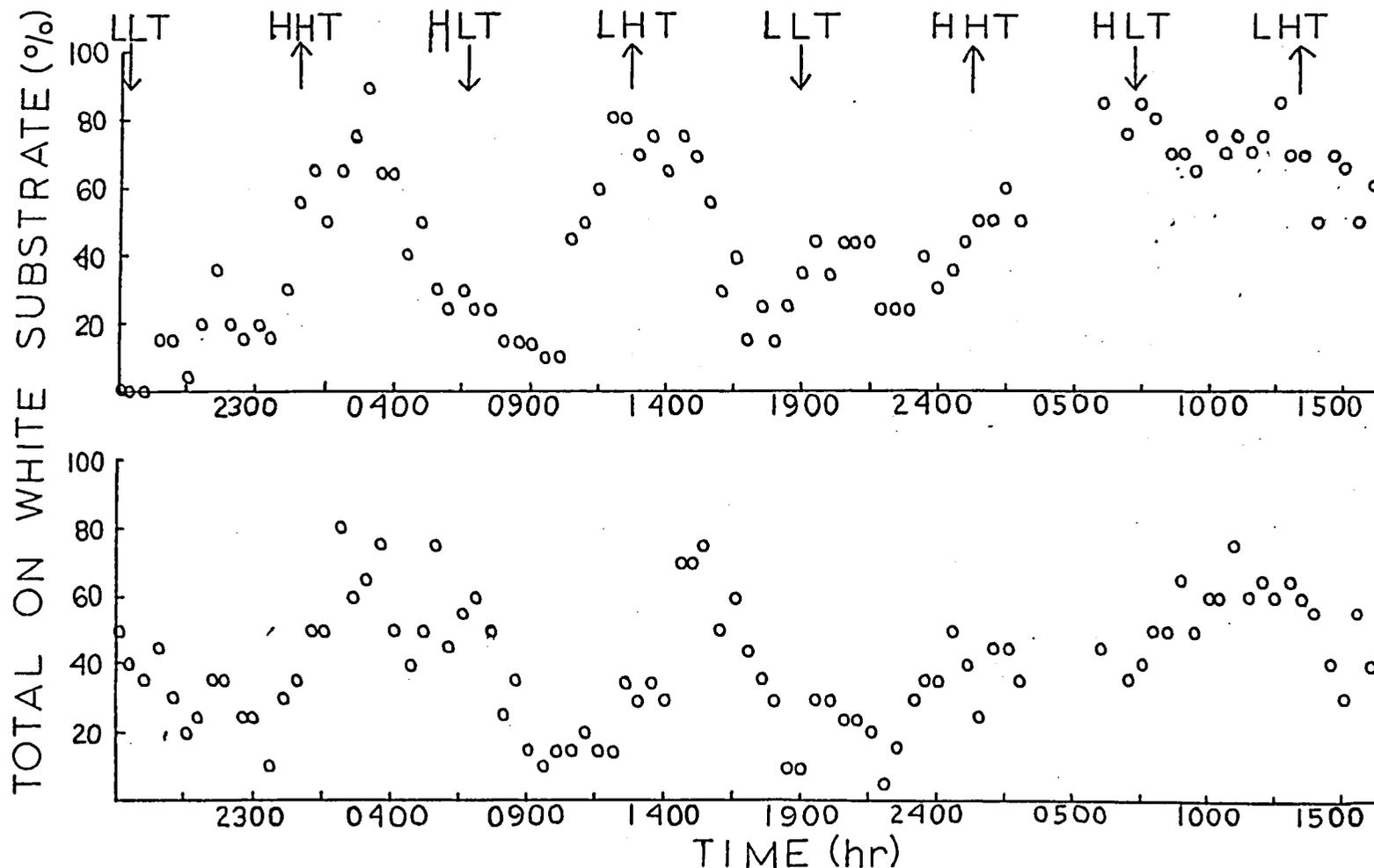


Figure 6. Tidal rhythm of preference for white versus black substrates in *C. digueti*, Oct. 20-22, 1972.

In each test (n=20) the per cent of hermit crabs occupying the white substrate is shown as a function of time and tidal stage (arrows above). The tests ran for 47 hours.

Figure 7. Photographs showing tidal rhythm of light-dark substrate preference in C. digueti, Oct. 7, 1972.

In each photograph the number of hermit crabs occupying the white substrate can be seen. The time is indicated above each photograph. The first low tide, high low tide, occurred prior to testing at 0742, followed by low high tide at 1341, low low tide at 1944.

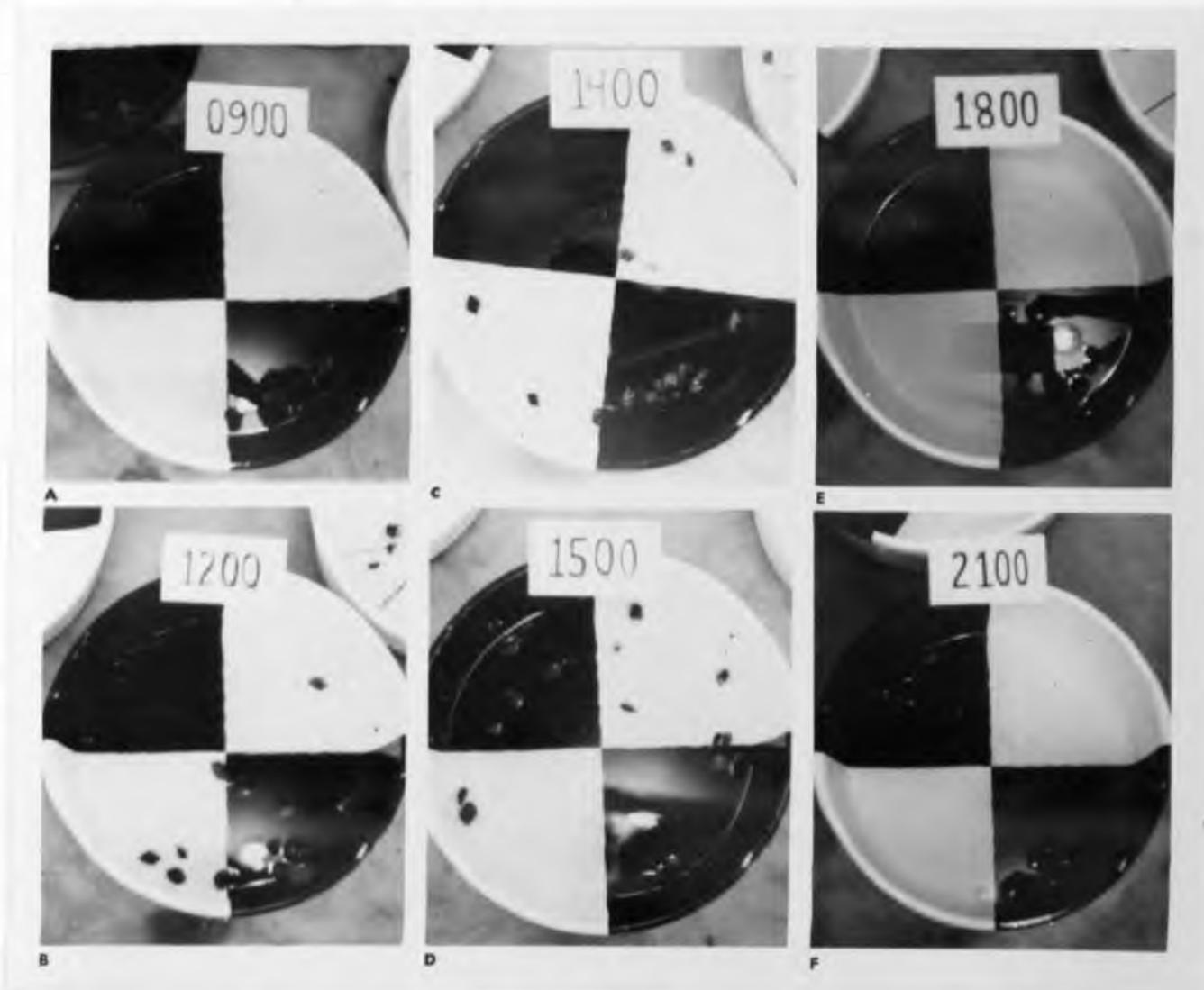


Figure 7. Photographs showing tidal rhythm of light-dark substrate preference in *C. digueti*, Oct. 7, 1972.

Figure 8. Photographs showing tidal rhythm of light-dark substrate preference in C. digueti, Oct. 20-21, 1972.

In each photograph the number of hermit crabs occupying the white substrate can be seen. The time is indicated above each photograph. The first low tide, low low tide, occurred at 1822, followed by high high tide at 0039, high low tide at 0643.

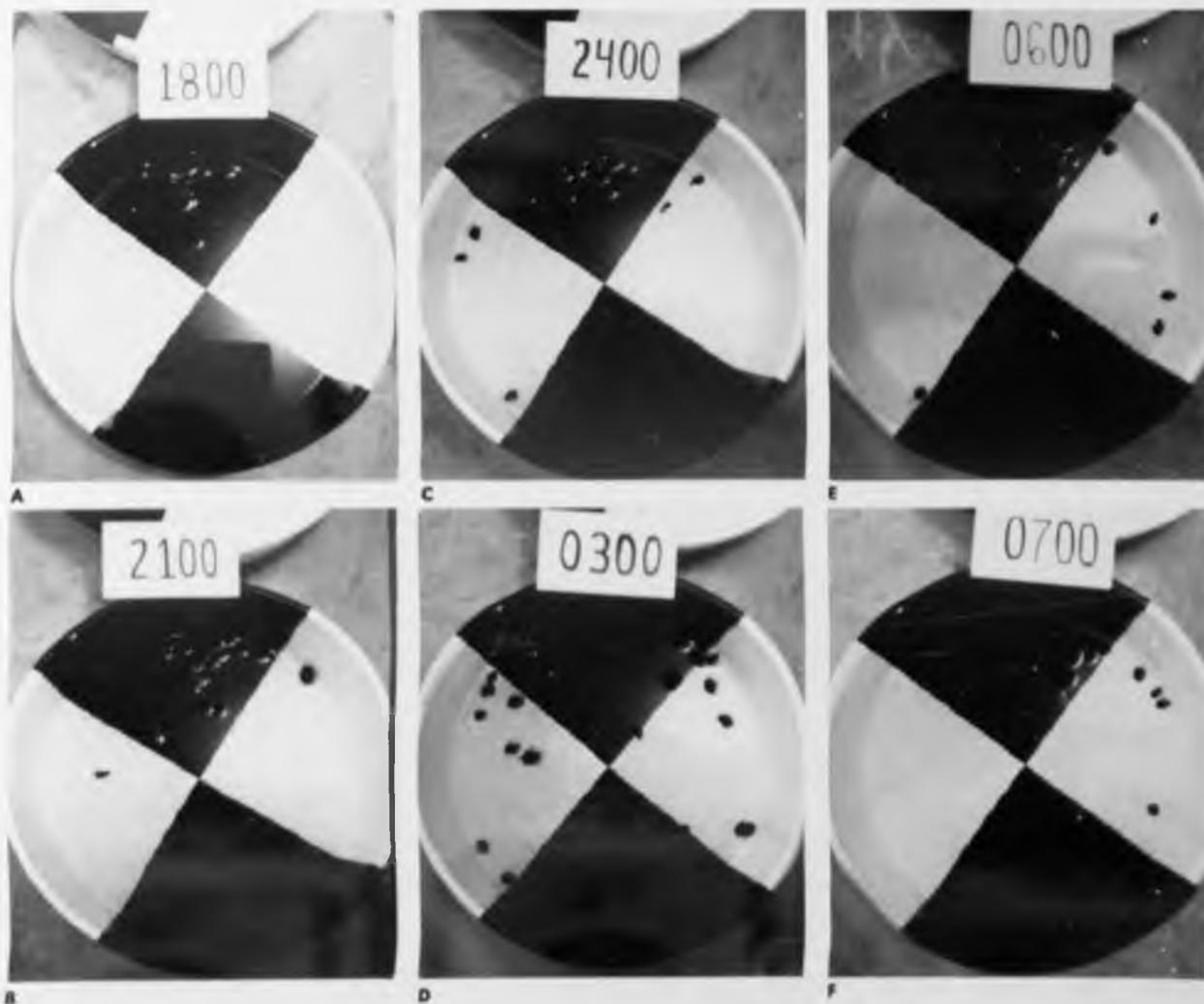


Figure 8. Photographs showing tidal rhythm of light-dark substrate preference in *C. digueti*, Oct. 20-21, 1972.

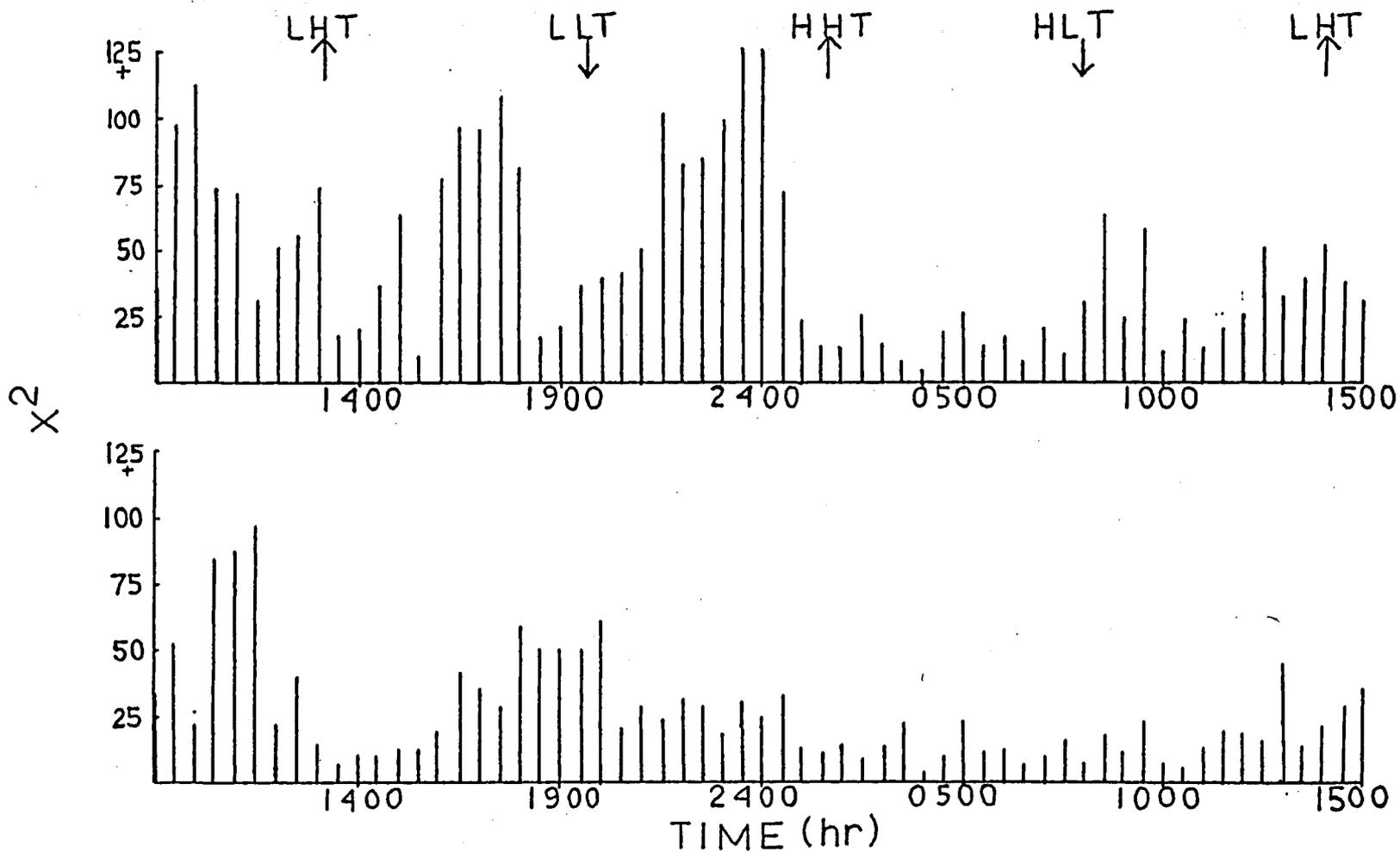


Figure 9. Tidal rhythm of gregariousness in C. digueti in tests using white substrates, Oct. 7-8, 1972.

Chi squares of deviation from expected randomness are plotted as a function of time and tidal stage (arrows above). Each test ( $n=20$ ) ran for 30 hours.

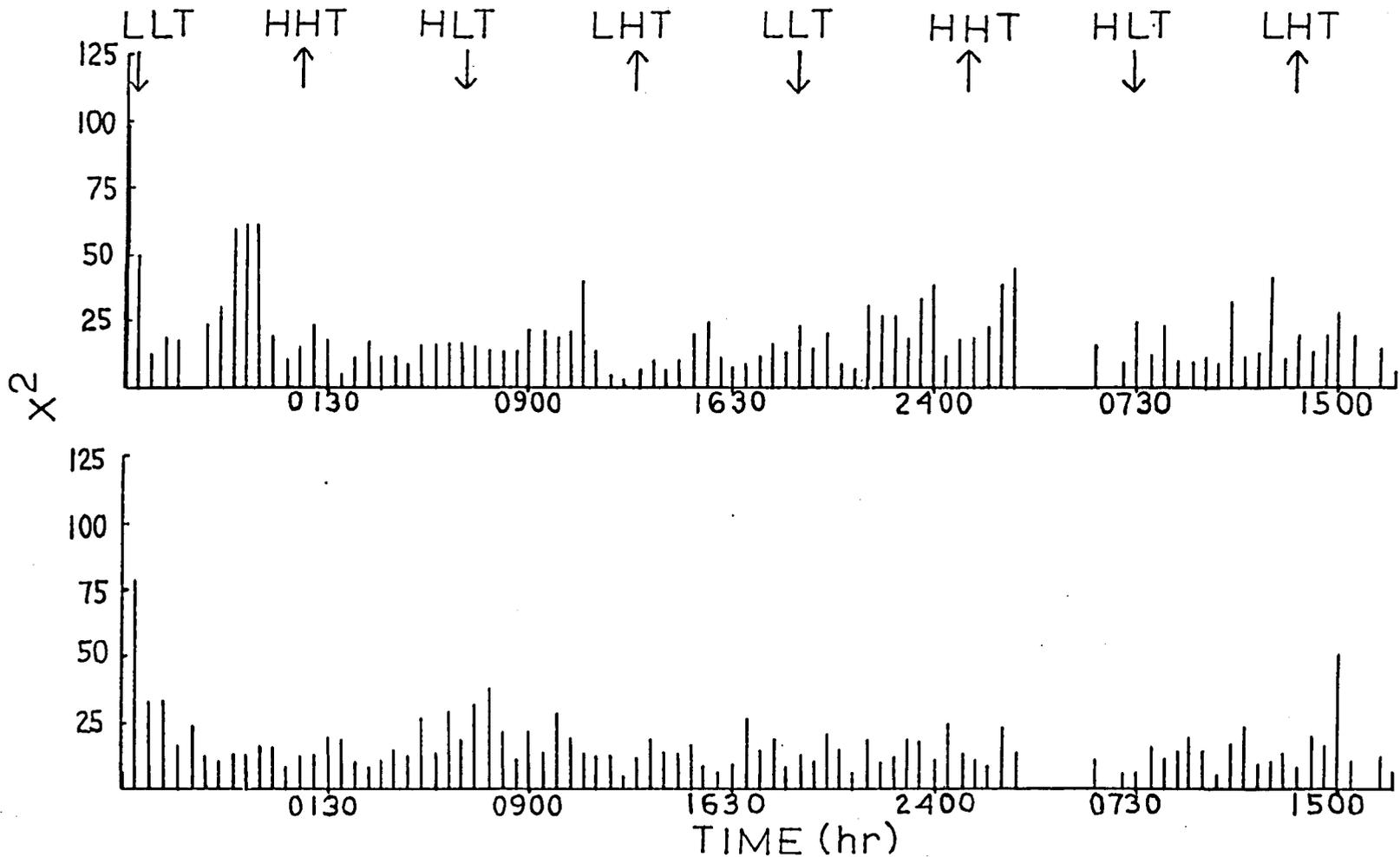


Figure 10. Tidal rhythm of gregariousness in *C. digueti* in tests using white substrates, Oct. 20-22, 1972.

Chi squares of deviation from expected randomness are plotted as a function of time and tidal stage (arrows above). Each test ( $n=20$ ) ran for 47 hours.

Figure 11. Tidal rhythm of gregariousness in C. digueti in tests using black substrates, Oct. 20-22, 1972.

Chi squares of deviation from expected randomness are plotted as a function of time and tidal stage (arrows above). Each test (n=20) ran for 47 hours.

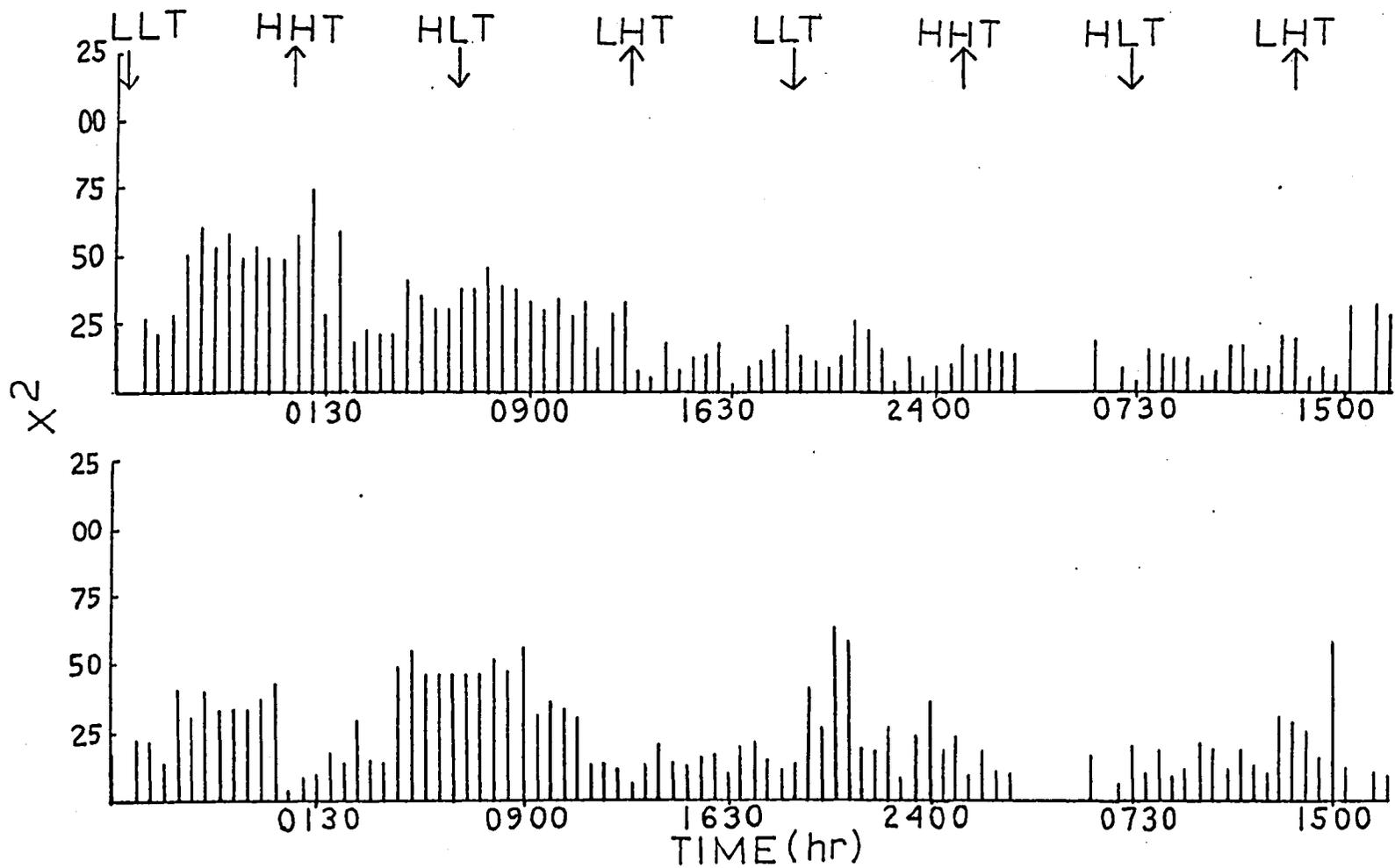


Figure 11. Tidal rhythm of gregariousness in *C. digueti* in tests using black substrates, Oct. 20-22, 1972.

Figure 12. Photographs showing tidal rhythm of clumping in C. digueti,  
Oct. 7, 1972.

In each photograph relative clumping or dispersal can be seen. The time is indicated above each photograph. The first low tide, low low tide, occurred prior to testing at 0742, followed by low high tide at 1341, low low tide at 1944.

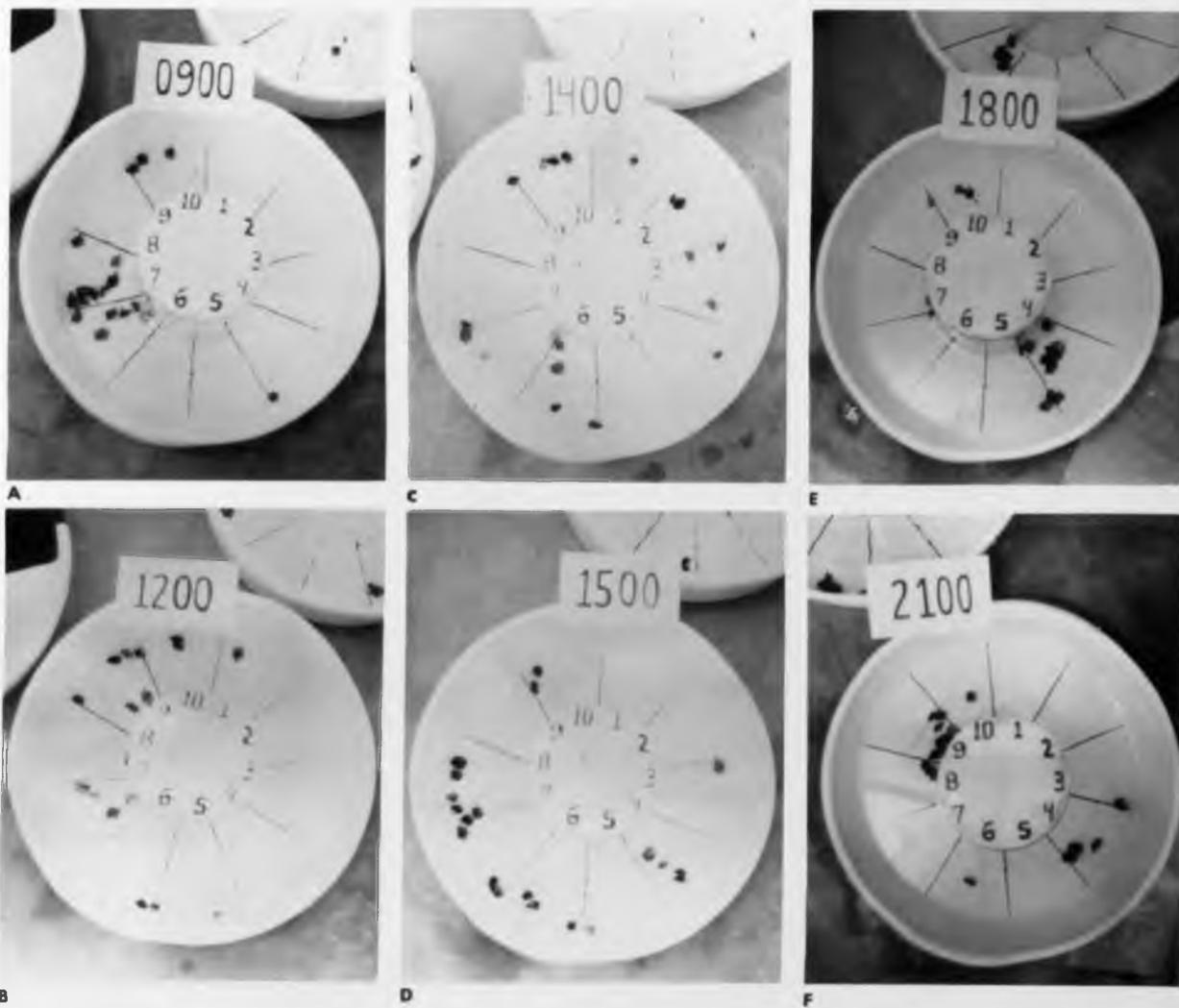


Figure 12. Photographs showing tidal rhythm of clumping in *C. digueti*, Oct. 7, 1972.

Figure 13. Photographs showing tidal rhythm of clumping in C. digueti,  
Oct. 20, 1972.

In each photograph relative clumping or dispersal can be seen. The time is indicated above each photograph. The first low tide, low low tide, occurred at 1822, followed by high high tide at 0039, and high low tide at 0643.

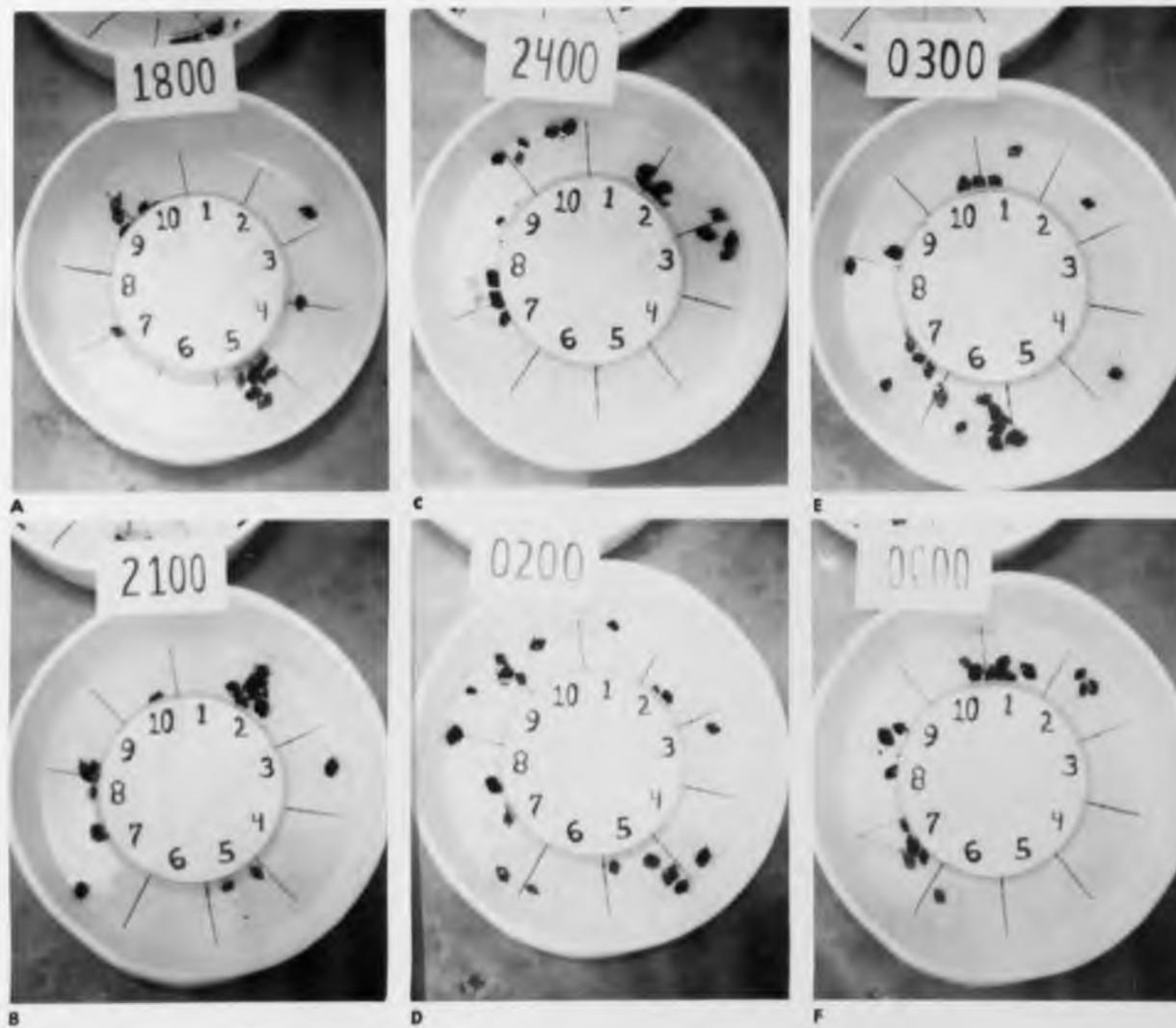


Figure 13. Photographs showing tidal rhythm of clumping in *C. digueti*, Oct. 20, 1972.

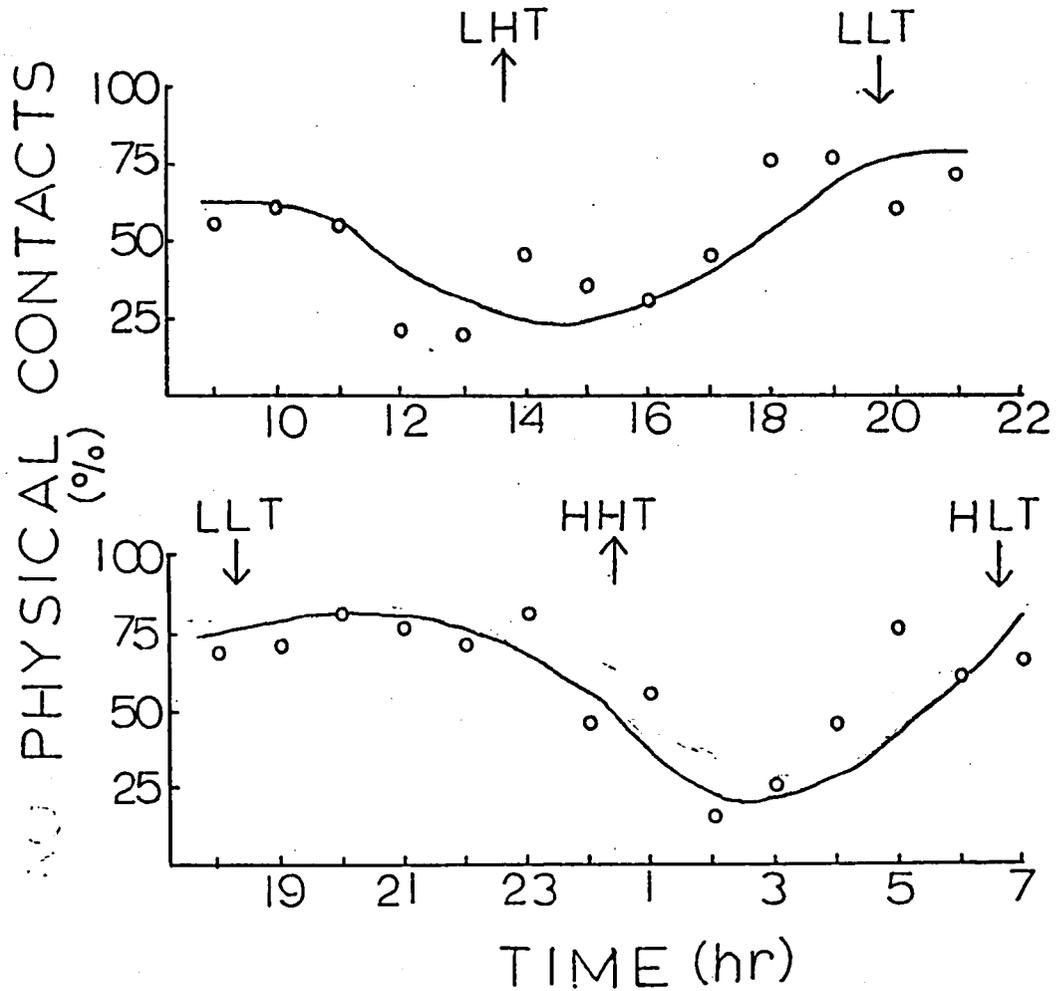


Figure 14. Tidal rhythm of physical contact in *C. digueti*.

Above, Oct. 7, 1972. Below, Oct. 20-21, 1972. Percentages of contacts are shown as a function of time and tidal stage (arrows above). The number of hermit crabs touching each other was determined from photographic sequences of the gregariousness tests.

light-dark substrates, the rhythm of gregariousness persisted for approximately two tidal cycles.

The mean oxygen consumption of individual hermit crabs (10) in two tests is seen in Table 1. A comparison of high and low tide values reveals that consumption at low tide was considerably higher than consumption at high tide. The mean oxygen consumption of the 10 hermit crabs for low and high tide were 26.4 and 20.2 microliters/hr, respectively. The difference for the eight hermit crabs consumption at low and high tide was not significant ( $.05 < p < .10$ , paired t-test), while the difference for the ten hermit crabs of the ten tests combined was significant ( $.01 > p$ , paired t-test).

Physiological tolerances of C. digueti were found to be great. The mean critical thermal maximum was  $45.4^{\circ}\text{C}$  with a competence range of  $\pm .8^{\circ}\text{C}$  (t-test), while the mean critical thermal minimum must lie between  $-1$  and  $4^{\circ}\text{C}$ . In the latter test, all hermit crabs were found to survive cooling to  $5^{\circ}\text{C}$  and 28 per cent survived cooling to  $-1^{\circ}\text{C}$ . Figure 15 illustrates this species' tolerance to different salinities. One hundred per cent of the hermit crabs survived salinities between 15 and  $45 \text{ ‰}$  for 24 hours. Resistance to desiccation is shown in Figure 16. At  $20^{\circ}\text{C}$  and a humidity of 38%, 100 per cent survived for eight hours, while the data indicate that 50 per cent of the hermit crabs would die only after 27 hours exposure.

Table 1. Mean oxygen consumption in microliters per hour of *C. digueti* at low and high tide on December 4, 1971, and February 20, 1972.

#	LT	HT
Test I		
1	42.8	36.6
2	23.7	20.6
Test II		
1	32.3	21.8
2	40.9	34.8
3	6.2	8.5
4	10.0	7.2
5	32.6	17.6
6	32.7	24.8
7	17.8	18.3
8	12.6	12.1
Mean =	23.1	18.1
$t_8 = 2.206$		
$p .07$		
Total Mean =	26.4	20.2
$t_{10} = 3.250$		
$p .01$		

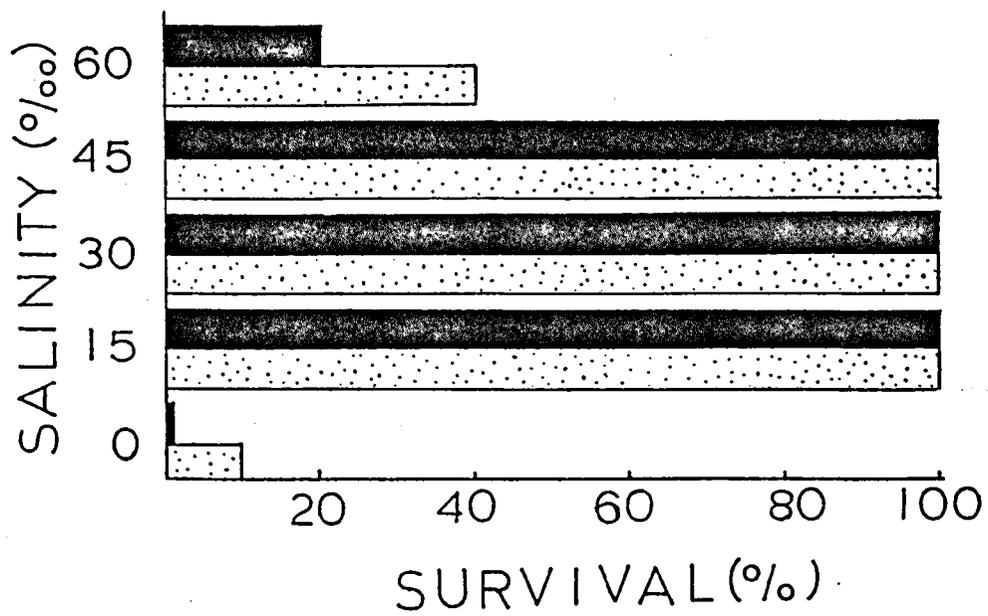


Figure 15. Salinity tolerance of *C. digueti*.

Survival of 10 hermit crabs each at five different salinities is shown after 1 hour (dots) and 24 hours (solid) time.

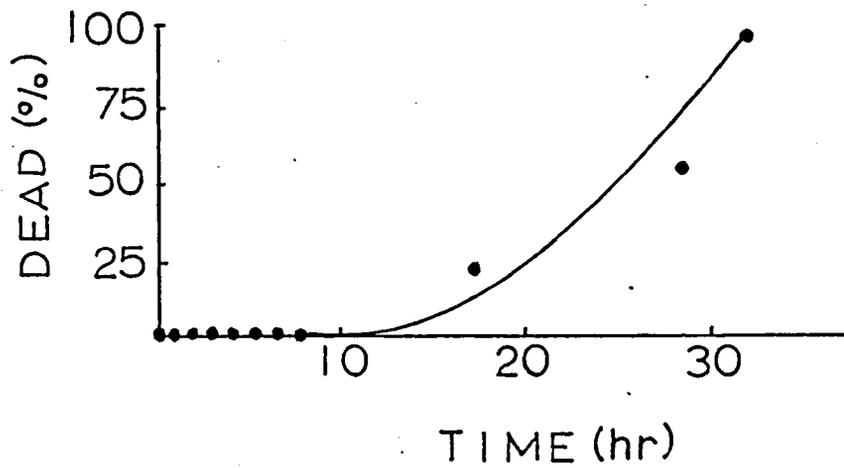


Figure 16. Resistance to desiccation in C. digueti.

Hermit crabs (n=123) were immersed to determine survival after exposure to drying under conditions of 20°C and 38% humidity.

## DISCUSSION

### Mechanism of Aggregation

The hypothesis that a phototactic rhythm might be a component of aggregative behavior in C. digueti was suggested by results of Drzewina (1907), who discovered a semilunar rhythm of phototactic response with possible diurnal tidal components in C. misanthropus. A number of molluscs maintain their intertidal positions by reversible phototactic responses (Newell, 1970). However, the results of tests to detect a tidal rhythm of phototaxis in C. digueti were negative.

Since populations of C. digueti shift from predominantly light substrates such as the sand and coquina limestone at high tide onto dark basalt boulders at low tide, it was postulated that a rhythm of preference for light or dark substrate might be involved in its aggregative behavior. Substrate color preference may be important in orientation and habitat selection of many marine organisms, but there has been a paucity of research on the subject. A large amount of work has shown that substrate color plays a role in the selection of attachment sites by barnacles (Walton Smith, 1948). However, light-dark color preference was not found to be involved in the substrate selection of the amphipod Corophium (Meadows, 1964). Fraenkel and Gunn (1961) discuss instances of response to dark objects or substrates (skototaxis), but conclude that experiments thus far reported may be reinterpreted as cases of negative phototaxis or primitive form vision.

Thus, considerable ambiguity exists on the subject of light-dark color preference as opposed to the tactic response to direct light or shade.

The tidal rhythm of light-dark preference shown in this study is obviously an important component in the rhythm of aggregation and dispersion manifested by C. digueti. Further, it is clearly distinguishable from a phototactic rhythm, since experiments under similar laboratory conditions revealed no phototactic rhythm. Also, form vision is probably not involved in this color preference rhythm as the hermit crabs tended to occupy central areas rather than choosing color interfaces. It is evident that reactions to both lightness and darkness of a substrate are distinct from phototactic responses. The term skototaxis, however, seems inappropriate, for Fraenkel and Gunn (1961) did not recognize the existence of negative skototaxis.

What is the nature of this tidal rhythm of preference for light and dark? Characteristically, periods of circadian rhythms are little affected by temperature change, with temperature coefficients normally ranging between 0.9 and 1.2 (Palmer, 1970). Likewise, although changing photoperiods or light shocks may induce period or phase changes, light intensity changes are of little importance in a number of species' rhythms, such as that of emergence in the Chironomid midge Pseudomittia studied by Remmert (Cloudsley-Thompson, 1961). Since no significant differences resulted from the various temperature and light intensities of separate experiments, this rhythm may be endogenous. In this case, then the free running periods of individuals, i.e., the different periods of self-sustained oscillation of individuals (Aschoff, Klotter and Wever, 1965), may have varied sufficiently to cause the apparent damping

of the rhythm in the population as a whole. On the other hand, because dissipation was relatively rapid, occurring within 24 hours usually, one or more zeitgebers, forcing oscillations which entrain the rhythm (Aschoff et al., 1965), must be present in this species' environment which synchronize the tidal rhythm in members of the population.

One possible zeitgeber is turbulence or mixing associated with the changing tides. The tidal rhythms seen in Figure 6 differ somewhat from patterns in other experiments in that the amplitude of the second peak for preference of the white substrate is far greater than the first. Also this preference is prolonged, lasting more than 10 hours. This aberrant reaction may be explained by the schedule of frequent water changes employed on that test date. The water was changed every three hours as opposed to once after 12 hours and not at all in the other two sets of experiments. These frequent water changes may have acted as zeitgebers which altered the rhythm of substrate color preference in the October 7-8 tests.

Although the tactic rhythm of light-dark preference is an effective part of aggregative behavior, it cannot be the only component of the rhythm of the hermit crabs. At night clumps do form, although these are generally smaller than those of the daytime. A non-visual component must therefore be involved in the clustering rhythm. As discussed earlier social interactions have seldom been explored in aggregative behavior. The preferred explanations of aggregation have been in terms of kineses and taxes. However, a few studies have revealed that gregariousness may indeed be involved in aggregations, and,

consequently, this aspect of behavior was investigated. Results indicate that a rhythm of gregariousness does indeed exist in this species, which manifests an increased tendency to cluster at times of low tide and to disperse at times of high tide.

The rhythm of gregariousness is to some extent related to the rhythm of preference for light and dark substrates. Comparison of the clumping rhythms on the all-white versus the all-black substrates on the October 20-22 test date (Figures 10 and 11) reveals differences in the two. The amplitude of the gregarious response at times of low tide appears to be suppressed on the all-white substrate. Contrastingly, dispersion at the times of high tide is less pronounced on the all-black substrate than on the all-white substrate. An examination of the mean chi square values, which indicate relative randomness or clumpiness, reveals that the average for the black substrate tests is 26.7, while the average for the white substrate tests is 18.6. These data indicating a greater state of clumping on the black substrate, support the conclusion above. However, visual cues in the rhythm of gregariousness may be supplemented by chemical cues, which could be utilized in clump formation in darkness. Again, this rhythm remained distinct for about two tidal cycles under laboratory conditions, and as suggested for the substrate color preference rhythm, this rhythm may also be endogenous, although periodic zeitgebers probably act to synchronize the rhythm.

Oxygen consumption of individuals was the reverse of that predicted from field and behavioral observations. The results showing higher oxygen consumption at low tide than at high tide, if regarded as significant, are unexpected as the time of low tide is the time when

the hermit crabs would normally be clumped on a black substrate and immobile. Therefore, low oxygen consumption would be predicted as a result of minimal activity. High oxygen consumption would be expected at the times of high tide, the time of feeding and locomotor activity. However, in the experimental situation individual hermit crabs were isolated on a light background. It is suggested that high activity occurred at times of low tide when the animals could not aggregate and seek a dark substrate, obscuring or reversing the expected pattern. If this is the case, then oxygen consumption data might be regarded as an unreliable index to rhythm in aggregating species, if the procedure involves isolation of individuals. This conclusion is supported by the results of Allee (1926) who found that oxygen consumption of land isopods was far greater in isolated individuals than that of clumping individuals. Alternate explanations may be offered for the oxygen consumption data. A phase shift, for example, might have been induced in the process of transportation.

I conclude from the results discussed thus far that aggregation in C. digueti has two components, a tactic rhythm of preference for light and dark substrates and a social rhythm of gregariousness. Further, these rhythms are strongly allied. A black substrate promotes the gregarious response, while a white substrate enhances dispersal.

#### Adaptive Value of Aggregation

Two schools of thought exist on the subject of why aggregation is of adaptive value. The first is championed by Allee (1931, 1938), who discussed numerous studies demonstrating that the functioning of

individuals is extensively altered in aggregations. Growth, rate of reproduction, and protection from toxins increased, while oxygen consumption decreased in aggregations of certain species. Allee then, propounded the idea that there is a physiological basis for aggregative behavior. That aggregation might have a social basis is suggested by the theory of Wynne-Edwards (1962) that species survival and dispersion depends on conditioned social behavior of individuals in the population. Species may avoid unchecked competition for food by controlling their own population densities, maintaining them at optimal levels for a particular habitat. Diverse functions such as mating, care of the family, group life, and fighting may all be related to means of dispersion and, consequently, to a mechanism for population balance.

What is the adaptive value of the aggregative behavior of *C. digueti*? Alternation of dispersal for scavenging purposes and then regrouping for the purpose of energy conservation, perhaps by way of lowered oxygen consumption, could be viewed as a mechanism for the species to maintain its intertidal position. In several respects the clumping of this species resembles the sleeping societies of insects, birds, and bats (Allee, 1938).

Is there a physiological basis for clumping? Thermal regulation is an unlikely function of clumping as this species was demonstrated to be eurythermal. Critical thermal maxima and minima of the hermit crabs exceeded the range of microhabitat extremes recorded for an exposed surface boulder at +5.6 feet at Puerto Penasco (Eger, 1971). Since clumping is a year-round activity, a thermoregulatory function must be ruled out. Also, this species is euryhaline within exceptionally

wide limits. Consequently, an osmoregulatory function of aggregating behavior may also be rejected. Does clumping occur to conserve moisture and thus resist desiccation? Clump formation might lead to creation of a humid microenvironment in which evaporation is retarded by decreasing the surface to volume ratio of the hermit crabs. In the test to check this out, the dried hermit crabs at first clumped in two corners of the tray. However, three hours later they became active and dispersed, after which no obvious clumping was noted. Since exposure at low tide lasts much longer than three hours, this observation suggests that conservation of moisture is not a function of the clump. Further, results show that this hermit crab can tolerate extensive periods of desiccation. In the summer, when temperatures are highest, clumping might help to conserve moisture, but the adaptive value of year-round aggregation probably involves other bases. This argument is further supported by the fact that clumping does occur under water, as well as out of water. I conclude then that conservation of moisture could not be primary function of clumping behavior.

One possible function of the clump may be escape from predators such as Eriphia, Heliaster, and Octopus, which crowd into residual pockets of deeper water and under rocks at low tide. Clumps are camouflaged against the basalt boulders as the shells adopted by C. digueti are predominantly dark, e.g., Morula ferruginosa, Tegula mariana, Cerithium scluptum, and Columbella fuscata. The adaptive value of aggregating suggested here is analogous to that proposed for schooling behavior in fish by Brock and Riffenburgh (Shaw, 1970), in which the area occupied by prey fish is minimized, reducing chances of predation.

Another likely function of the cluster is facilitation of intraspecific interactions. Although other organisms, such as the hermit crab Pagurus, aggregate in the same area, clumps of C. digueti are species specific, suggesting that species recognition plays a role in clump formation. Also, considerable activity, such as shell exchange, shell grooming, fighting, and breeding, may be observed to occur during formation of the clump and likely transpires after inundation by high tide water too. That breeding activity may be promoted by clump formation is indicated by the fact that the breeding period is extensive. Hermit crabs collected between June 25 and October 7 released larvae; the breeding period is perhaps even longer.

Therefore, I conclude that the adaptive value of clumping may be escape from predators and/or facilitation of intraspecific relationships, such as shell exchange, shell grooming, fighting, and breeding. From this study, little support is offered to the idea that the clump serves as a means of thermo- or osmoregulation or as a means of resisting desiccation. The rhythm of aggregation and dispersal, dictated by a rhythm of color substrate preference and a rhythm of gregariousness, thus seems to be most clearly related to social factors. The complexity of components of aggregation, however, suggest that the functions of clustering of C. digueti might be numerous.

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