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DAILY AND TIDAL PATTERNS OF ACTIVITY IN INDIVIDUAL FIDDLER CRABS (GENUS UCA) FROM THE WOODS HOLE REGION[1]

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Fiddler crabs, *Uca* spp., and the shore crab, *Carcinus maenas,* possess persistent daily rhythms of color change (Abramowitz, 1937; Powell, 1962); thus, they are no exception to the proposition that circadian[2] rhythmicity is ubiquitous in organisms. Moreover, these same crabs may simultaneously exhibit rhythmic physiological adjustments to the tidal cycles of their littoral habitat. Persistent tidal rhythms have been reported in the color change of *Uca* (Brown *et al.,* 1953; Fingerman, 1960) and in the motor activity and metabolic rate of both *Uca* and *Carcinus.*

Edwards (1950) first examined the motor activity of the fiddler crabs, *U. pugilator, U. pugnax* and *U. minax.* He stated that all three species tended to be dark-active, with the exception of at least one *U. pugilator* which exhibited a bimodal daily pattern of activity occurring at sunrise and sunset. He reported a good correlation between the forms of the daily patterns of motor activity and oxygen consumption. It is worth remarking that all of his crabs were maintained in the laboratory for unspecified durations prior to recording.

Brown *et al.* (1954) recorded continuously the oxygen consumption of *U. pugnax* and *U. pugilator* in constant conditions. They reported the simultaneous presence in each species of both daily (24-hour) and semi-diurnal tidal (12.4-hour) rhythms. In discussing the metabolic rhythms in *U. pugnax,* Webb and Brown (1958) later reported that the correlation between rhythms in parallel samples of crabs tended to fall off after about seven days in the laboratory. This indicated loss of phase synchrony or rhythm among the crabs.

Bennett *et al.* (1957) demonstrated the presence of an overt, semi-diurnal

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[2] In this paper circadian (etymologically, about a day) rhythms are regarded as those persistent rhythms which can be entrained by the 24-hour cycle in natural conditions. These rhythms are distinguished on an ecological basis from the semi-diurnal tidal and diurnal tidal rhythms which, although they have a period length of about a day, are entrained by a tidal cycle in natural conditions.

tidal rhythm of spontaneous motor activity in *U. pugnax* in constant conditions. After about eight or nine days the average tidal pattern of the sample became less distinct, indicating again the loss of phase synchrony or rhythm among individual crabs. In this experiment the period length of the rhythm of activity was in some instances significantly longer than the semi-diurnal tidal period of 12.4 hours (Enright, 1965).

It was reported (Barnwell, 1963) that *U. maracoani* possessed an overt semi-diurnal tidal rhythm of motor activity which persisted for at least 11 days in constant low illumination and followed the actual changes in the periodicity of the tides at the beach of collection. *U. mordax,* maintained under the same conditions, possessed both daily and semi-diurnal tidal rhythms in motor activity.

In *Carcinus maenas* semi-diurnal tidal rhythms were found to persist for five or six days in spontaneous motor activity (Naylor, 1958) and oxygen consumption (Arudpragasam and Naylor, 1964). Both processes exhibited diurnal inequalities in the heights of the tidal peaks. For motor activity the greatest activity occurred during the nocturnal tidal peak, and for oxygen consumption, during the daytime tidal peak.

Blume *et al.* (1962) confirmed the findings of Naylor on the simultaneous occurrence of two periodic components with tidal and daily frequencies in the motor activity of *C. maenas.* In their studies the recording period was six or seven days.

In the foregoing summary, the short-term character of the experiments has been noted. Generally the curtailment of recording was due to the apparent warping or diminution of the tidal component after about a week in laboratory conditions. A second characteristic of these studies, perhaps related to the first, is that practically all of the published figures of tidal rhythms in these crabs have been *averages* of a few to many individual recordings. As the authors of these figures have usually remarked, the apparent breakdown of the average tidal pattern may be due in at least some cases to the loss of phase synchrony or divergence of pattern among individuals within the sample.

The purpose of the present study was to obtain information on the rhythms of individual crabs recorded continuously over longer intervals than in the preceding reports. Single specimens of *U. minax, U. pugilator* and *U. pugnax* were maintained in actographs for periods ranging up to 47 days. Recordings were made both in constant illumination and in natural cycles of daylight and darkness.

Materials and Methods

The specimens of *U. pugnax* and *U. pugilator* were collected on July 10 and 11, 1963, at the Chapoquoit marsh on the southwestern perimeter of West Falmouth Harbor. West Falmouth Harbor is located on Buzzards Bay about eight kilometers north of Woods Hole, Massachusetts. The *U. minax* were collected at Wild Harbor, which is about four kilometers north of West Falmouth Harbor. Collections were made on July 3, 5 and 11 and August 9, 1963. The crabs were returned to the laboratory and placed in actographs within a day of collection.

The actographs were similar to those used in earlier studies on *Uca* activity (Bennett *et al.,* 1957; Barnwell, 1963). Crabs were placed individually with about 10 mm. of sea water in aluminum tipping pans with transparent plastic covers. One end of each pan rested on a knife edge and the other end was suspended by a thread running to a spring scale recording system. Tipping of the pan caused by movements of the crab was translated through the spring scale into horizontal excursions of a pen on a moving strip of paper. By using a series of spring scales and pens the activity of as many as seven crabs could be recorded at once on the same strip of paper.

The actograph tracings were analyzed by measuring the duration of activity in each hour and expressing it as most nearly occupying either 0, 25, 50, 75, or 100% of the hour. All activity was recorded in terms of Eastern Daylight Time, EDT.

Six actograph assemblies, recording from four to seven crabs apiece, were in simultaneous operation. Three of the assemblies, each for a different species, were maintained under constant illumination with an intensity of between three and four foot-candles at the level of the actograph pans. During the study room temperature ranged from 23.0° to 26.5° C. without obvious daily variation. Additional recordings were made in an adjacent darkroom where illumination was constant at an intensity well below one foot-candle. Crabs maintained under both light intensities will be referred to as being in constant illumination, symbolized by LL.

In the basement of a nearby building the three remaining actograph assemblies, each with a different species, were placed in front of a northward-facing window. The lower half of the window was covered with white paper so as to shield the crabs from outside movements. On any day the maximum light intensity to which the crabs were exposed ranged from about 45 foot-candles to five foot-candles for the most shaded pans. Room temperature between July 21 and Aug. 26 exhibited a slight daily variation with an average low of 22.6° C. and an average high of 23.6° C. The extreme temperatures during this period were 21° and 24° C. These crabs will be referred to as being in natural illumination, symbolized by LD.

In order to keep the crabs for extended periods it was necessary to change the water in the tipping pans at intervals of two or three weeks. This process required only a minute or so for each crab. Changing of the water was sometimes followed by a temporary increase in the level of activity, but the timing of the pattern did not appear to be altered. The crabs were not fed during the experiments.

The times of tide used for both collecting sites are the predicted values published by the U. S. Coast and Geodetic Survey for West Falmouth Harbor. The times are obtained by applying correction factors to the tidal schedule supplied for Newport, R. I. In the absence of a correction factor for Wild Harbor, the use of the West Falmouth Harbor corrections appeared to be justified, since these corrections were essentially identical with those for two locations on the shore of Buzzards Bay just to the north of Wild Harbor.

Some small but statistically significant mean differences were found when the predicted times of high and low water at Newport were compared with the actual recorded times, which were later obtained from the USCGS. During the period of the experiments, July and August, 1963, the observed times of high water occurred at 8.7 ± 11.4 minutes (mean and standard deviation) later than the predicted times. For low water during the same period the observed times were 7.5 ± 22.2 minutes earlier than the predicted times.

Results

Individual recordings have been selected to illustrate the general types of patterns obtained in each species in LD and LL. For each group is listed the total number of crabs which were studied.

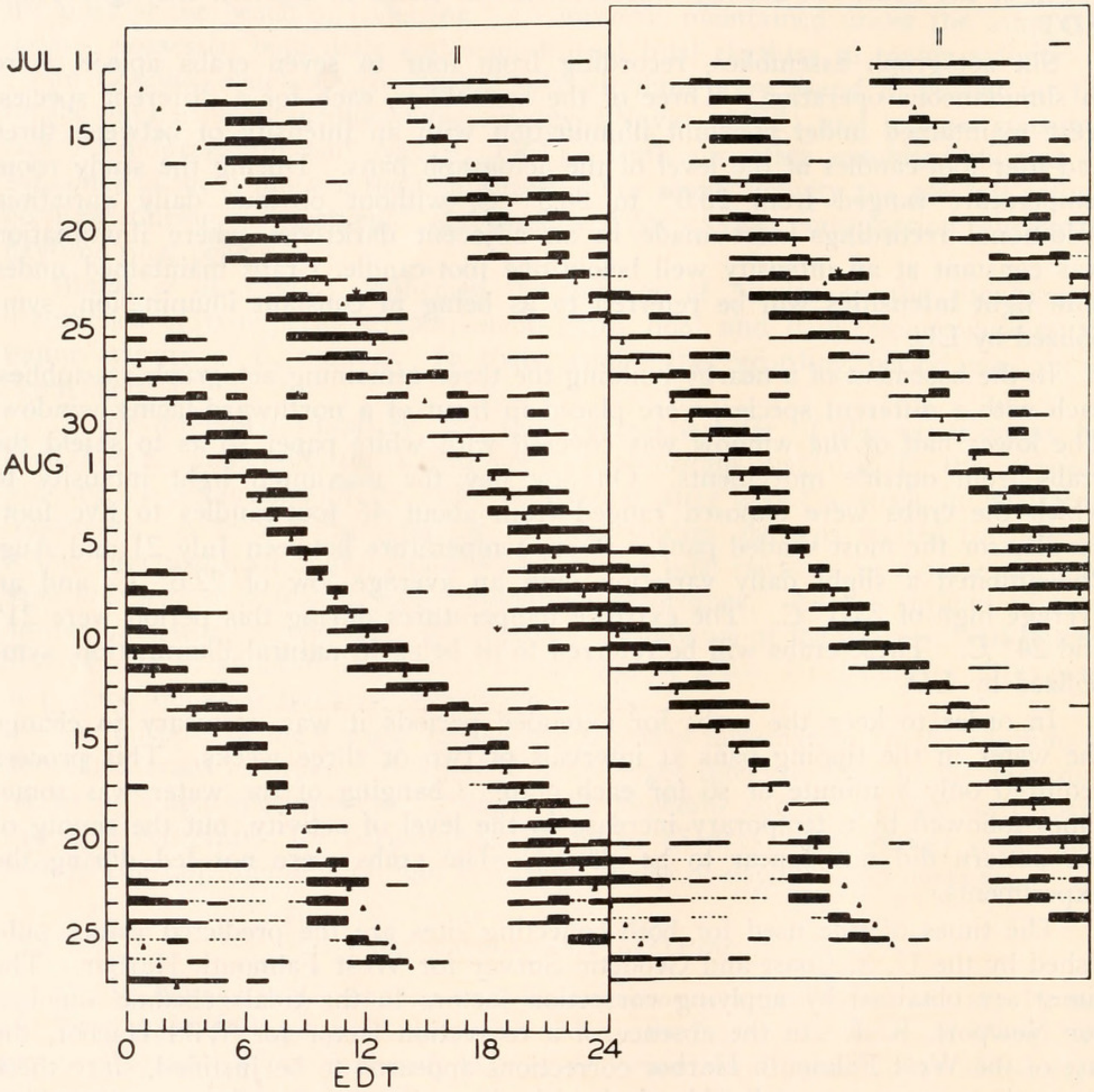

Figure 1. Activity pattern of a male *U. minax* in LD. The graph has been reproduced twice, with the right-hand graph displaced upward by one day, in order to facilitate the visualization of the drift of activity peaks across the solar day. The height of the blocks indicates the per cent of the hour during which activity was recorded, either 25, 50, 75, or 100 per cent. Parallel vertical lines at the beginning of the record mark the time of collection. Small triangles indicate the predicted times of high tide at the beach of collection. Small arrows point to times when water in the tipping pans was changed. Broken lines indicate failure of the recording system. These conventions are used for all figures.

U. minax—LD (7 crabs)

Crab 1 (Fig. 1). This male crab exhibited an overt semi-diurnal tidal rhythm which persisted through 46 complete days of recording. The frequency of the rhythm was very close to tidal frequency. A 24-hour component was expressed both as an initial suppression of tide-related activity between 24:00 and 05:00 (July 12 to about July 21) and as an enhancement of activity when the tidal peak occurred between 19:00 and 21:00 (July 17 to 22, Aug. 2 to 9, 17 to 24); at both times of day the initiation of activity tended to conform for several days to the time of sunrise or sunset. The tendency for the tidal peak to be suppressed during the morning hours disappeared with passing time, as subsequent tidal peaks were obvious between 24:00 and 05:00 (from July 24 to 30, Aug. 6 to 15, and Aug. 21 to 27). Daily activity related to sunset depended primarily on the presence of the tidal peak for its expression. Occasionally, a tendency for activity at sunset was expressed by isolated bursts of activity not associated with tidal peaks. However, the periods of greatest activity took place at semi-monthly (15-day) intervals when tidal activity coincided with sunset.

Crab 2 (Fig. 2). This is the first portion of the record of a female crab in which the tidal rhythm was evident for 40 days of recording. The record demonstrates that suppression of the tidal peak between 24:00 and 05:00 need not always occur when the crab is first removed from the beach to the experimental condition of LD.

Crab 3 (Fig. 3). This male attempted to molt between 09:00 and 10:00 on Aug. 7. The semi-diurnal pattern persisted with a high level of activity up to the time of molt. During the initial 11 days of recording, the activity peak in the first half of the day appeared to conform to a 24-hour schedule and effectively masked any tide-related activity.

U. minax—LL (14 crabs)

Crab 4 (Fig. 4). This male crab was collected on July 5 for a preliminary experiment. Its activity was recorded in LL at three to four foot-candles until 22:00 on July 10 when it was transferred to the lower light intensity of the

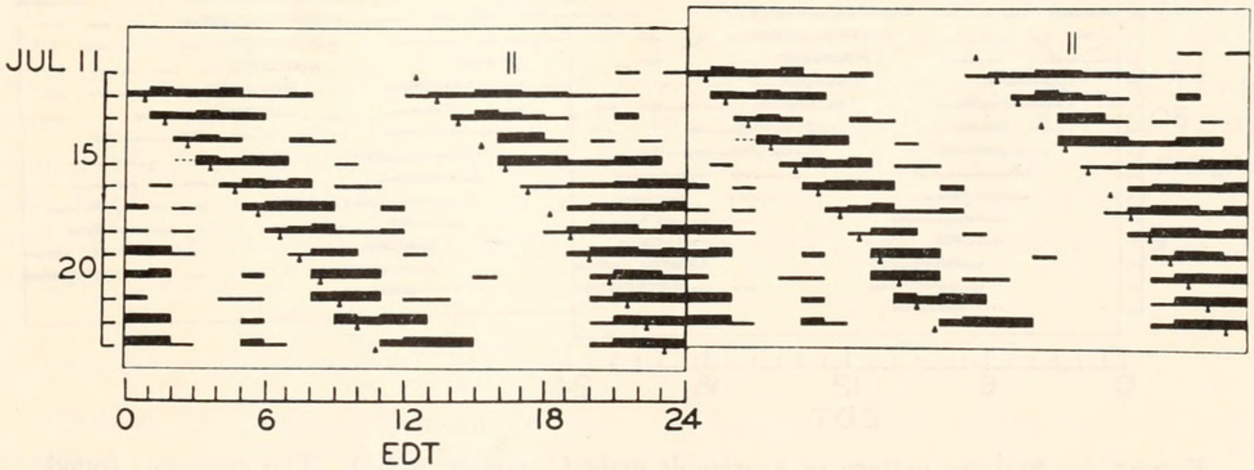

FIGURE 2. Activity pattern of a female *U. minax* in LD.

adjacent darkroom. Initially the semi-diurnal tidal rhythm bore the same relationship to the time of tide as that already observed for the crabs in LD, that is, initiation of activity within an hour or two of the time of high tide. However, the period of the rhythm in LL was clearly longer than 12.4 hours. Furthermore, there was not the pronounced suppression or enhancement of activity related to the time of sunrise or sunset that was evident in the crabs in LD. The tidal pattern persisted for at least five weeks. During the last week of recording it appeared to undergo a transition from a bimodal to a predominantly unimodal daily pattern, in which activity occurred mainly in the latter half of the day.

Of the 14 *U. minax* kept in LL, ten possessed a distinct semi-diurnal tidal rhythm, the period of which exceeded the natural mean tidal period of 12.4 hours. There were individual differences in the period length of the rhythm, and in some cases the period was not constant but increased gradually. Three of the remaining four crabs possessed tidal rhythms, but the activity became so diffuse that it was not possible to determine from inspection if the period length deviated from the natural tidal period. The pattern of the fourth crab is described next.

Crab 5 (Fig. 5). This crab was an ovigerous female which was collected on July 3 for a preliminary experiment. Its activity was recorded in LL at three to four foot-candles until 10:45 on July 8 when it was transferred to the lower light intensity of the photographic darkroom. By July 12, when water was replaced in the tipping pan, the larvae had emerged. Most striking in this case is the gradual disappearance of the tidal component and the eventual domination of the daily pattern by a major peak. Initially, activity was tide-related, with

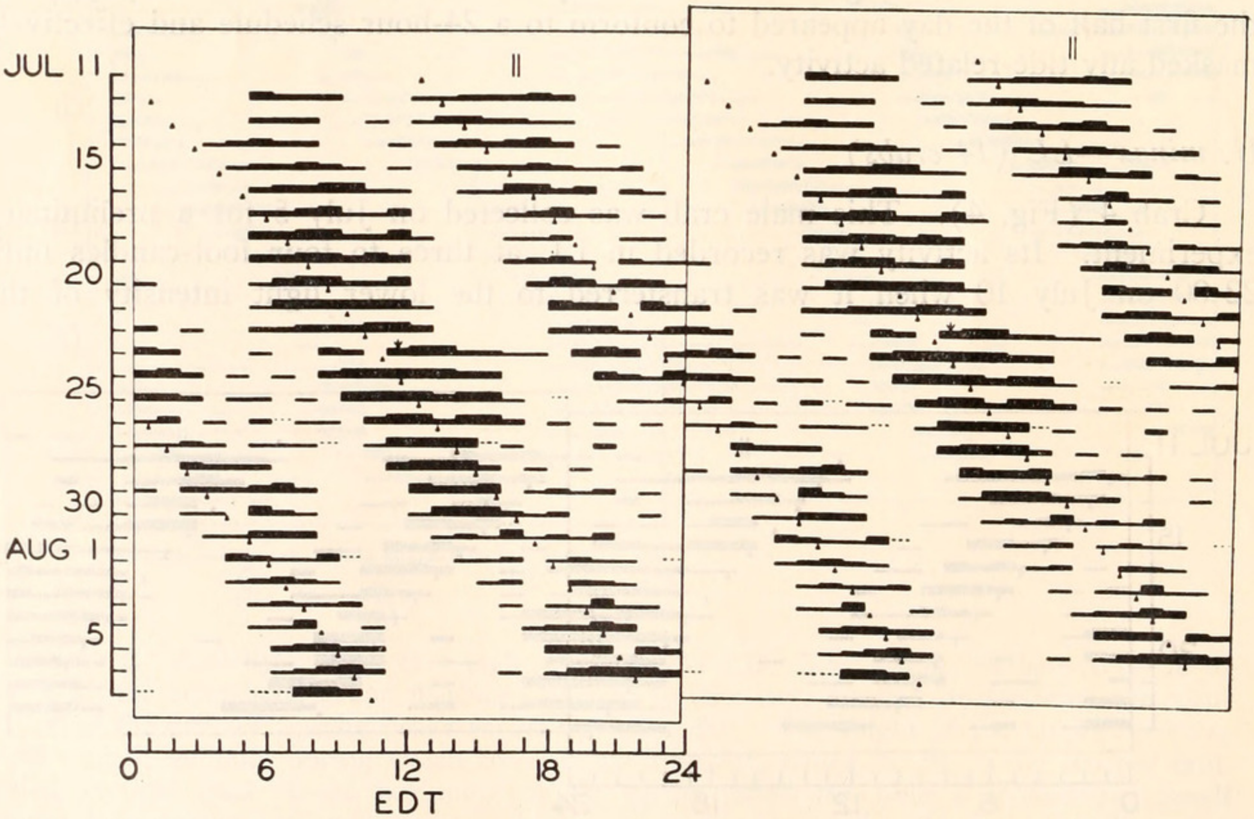

FIGURE 3. Activity pattern of a premolt male *U. minax* in LD. The crab was found attempting to molt at 10:00 on Aug. 7.

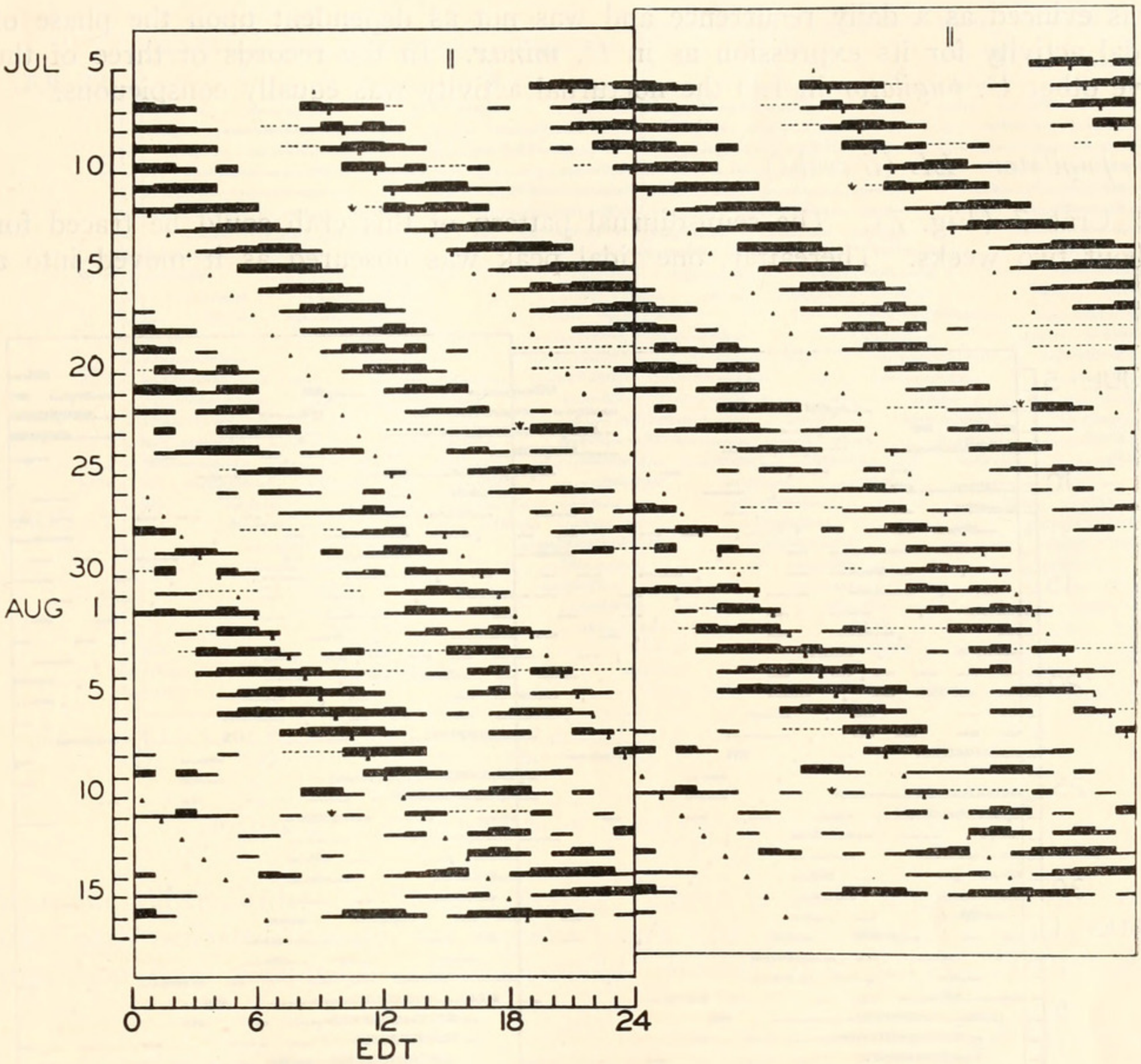

FIGURE 4. Activity pattern of a male *U. minax* in LL. At 22:00 on July 10 this crab was transferred to the lower light intensity of the photographic darkroom.

the nocturnal tidal peak being the more conspicuous of the two peaks. The nocturnal tidal peak appeared to drift into the daylight hours but then disappeared after a final peak at 15:00 on July 26. The original daytime tidal peak (07:00 to 10:00 on July 6) appeared to drift across the day and merge with a diffuse band of nocturnal activity. In addition to the two tidal peaks and the broad band of daily activity which eventually emerged, there seemed to be other component bands (*e.g.,* activity centered on 09:00 to 10:00 from July 26 to July 31, then on 11:00 to 12:00 from Aug. 1 to Aug. 3) which contributed to a generally complex pattern.

U. pugilator—LD (*6 crabs*)

Crab 6 (Fig. 6). Both an accurate semi-diurnal tidal rhythm and a daily rhythm, consisting of pronounced activity after sunset, were present for the 29 days of recording. For this species a 24-hour component of activity at sunset was evinced as a daily recurrence and was not as dependent upon the phase of tidal activity for its expression as in *U. minax*. In the records of three of the five other *U. pugilator* in LD the nocturnal activity was equally conspicuous.

U. pugilator—LL (6 crabs)

Crab 7 (Fig. 7). The semi-diurnal pattern of this crab could be traced for about two weeks. Thereafter, one tidal peak was obscured as it moved into a

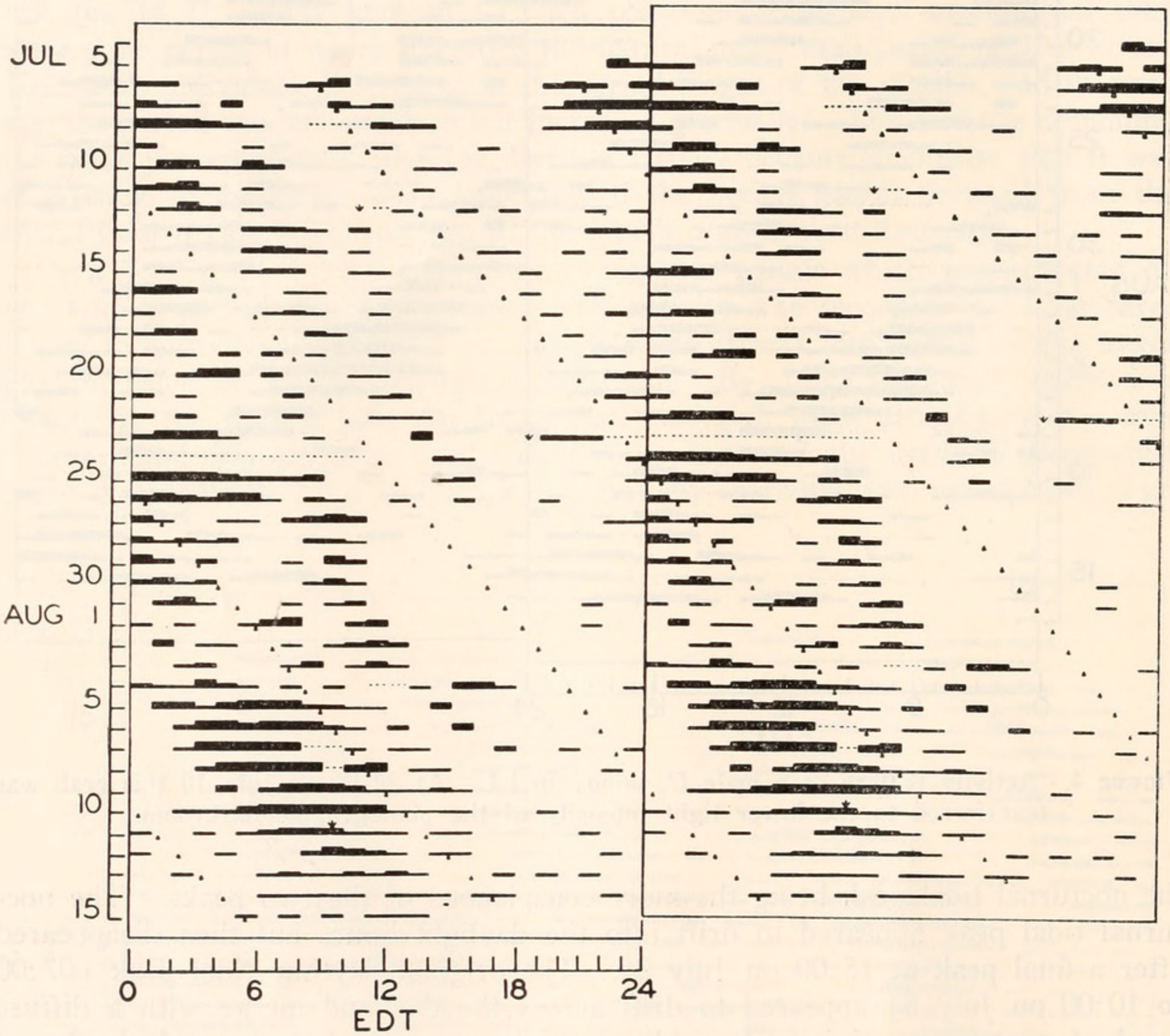

FIGURE 5. Activity pattern of a female *U. minax* in LL. At the time of collection, on July 3, this crab was ovigerous. At 10:45 on July 8 it was transferred to the lower light intensity of the photographic darkroom.

band of activity centered at 02:00 from July 21 to 28. The second tidal peak scanned across the daytime hours. It could perhaps be traced for somewhat longer than the other peak, but by the late afternoon of July 30 to 31 it had faded.

Crab 8 (Fig. 8). Conspicuous in this crab is the augmentation, early in the recording period, of a single major daily peak of activity. This major peak was initially a nocturnal one, and its period length appeared from inspection to be less

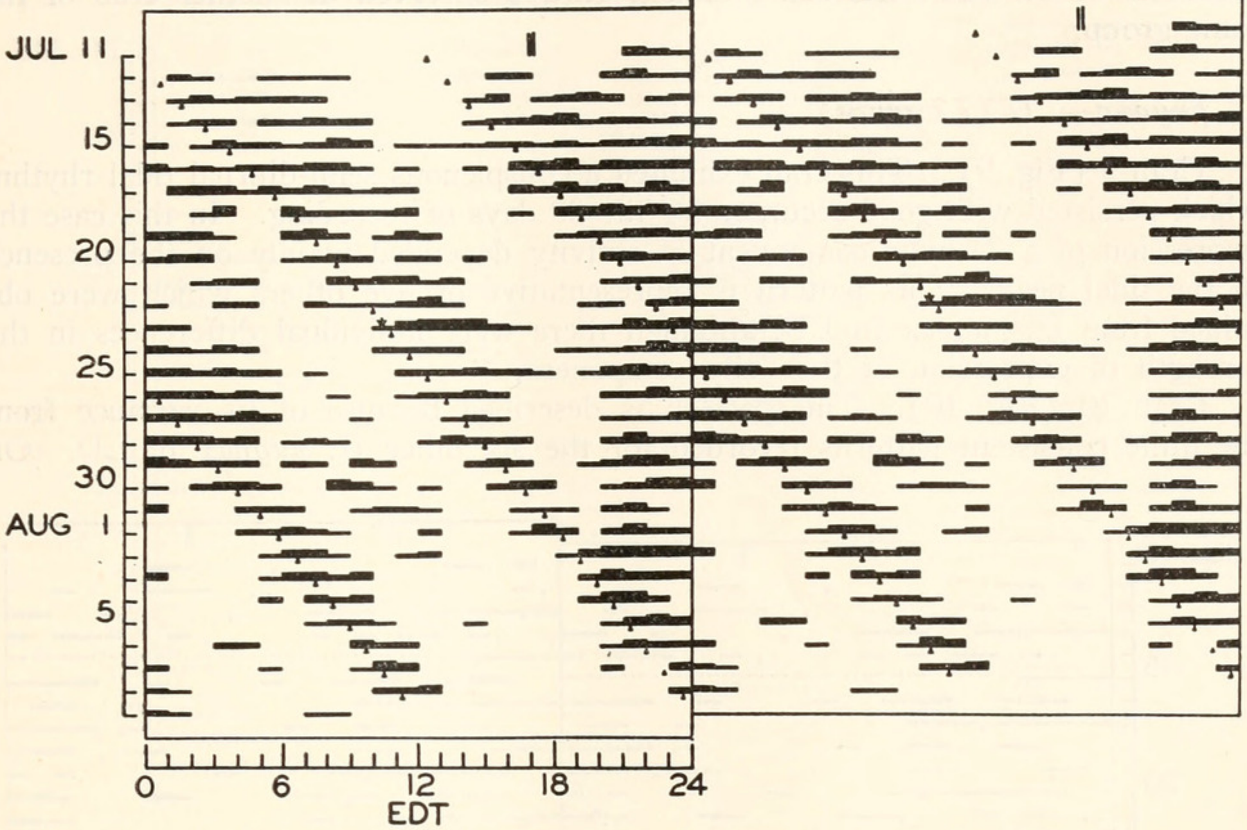

FIGURE 6. Activity pattern of a male *U. pugilator* in LD.

than the diurnal-tidal (24.8-hour) period. There is some suggestion that one tidal peak persisted through the daytime hours with close to tidal frequency. A transition from a bimodal to an essentially unimodal daily pattern of the same

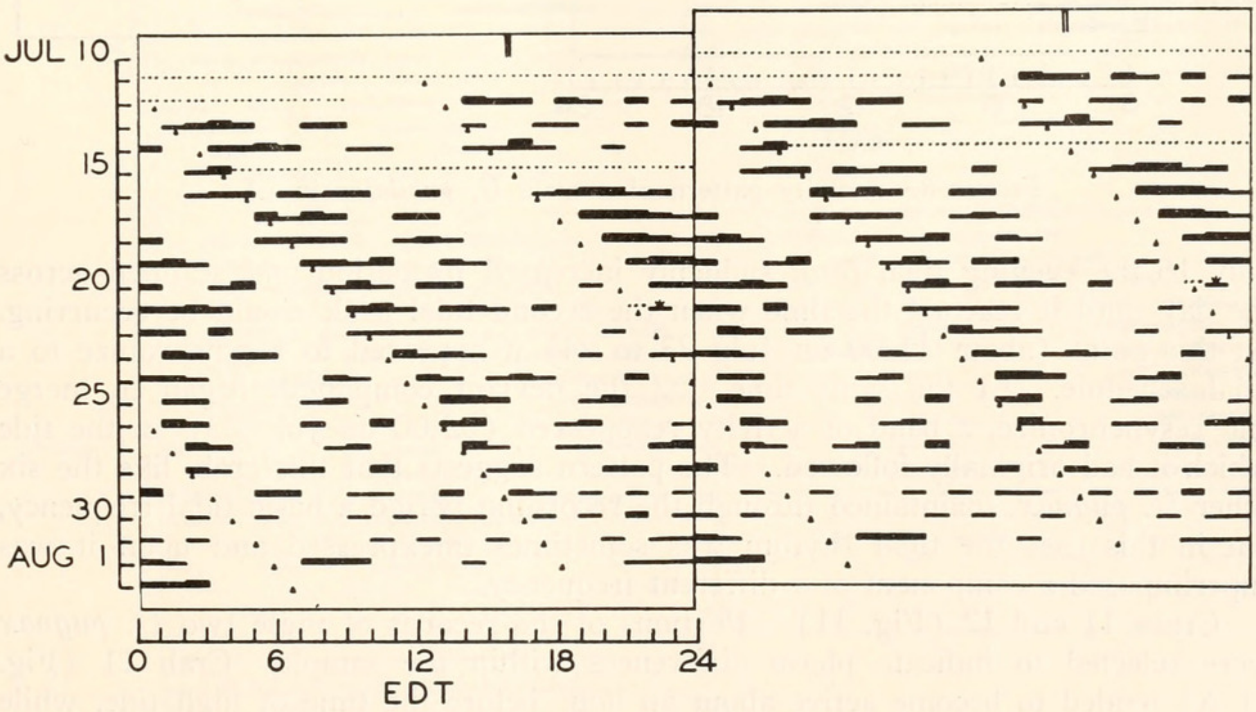

FIGURE 7. Activity pattern of a male *U. pugilator* in LL.

character as the one described in this case was observed in another crab of the same group.

U. pugnax—LD (7 crabs)

Crab 9 (Fig. 9). This crab exhibited a conspicuous semi-diurnal tidal rhythm which persisted with good accuracy for the 30 days of recording. In this case the expression of a 24-hour component of activity depended mainly on the presence of the tidal peak. This pattern is representative of five others which were obtained from *U. pugnax* in LD, although there were individual differences in the strength of expression of the daily component.

Crab 10 (Fig. 10). This pattern is described because of its variance from the quite consistent patterns recorded for the six other *U. pugnax* in LD. On

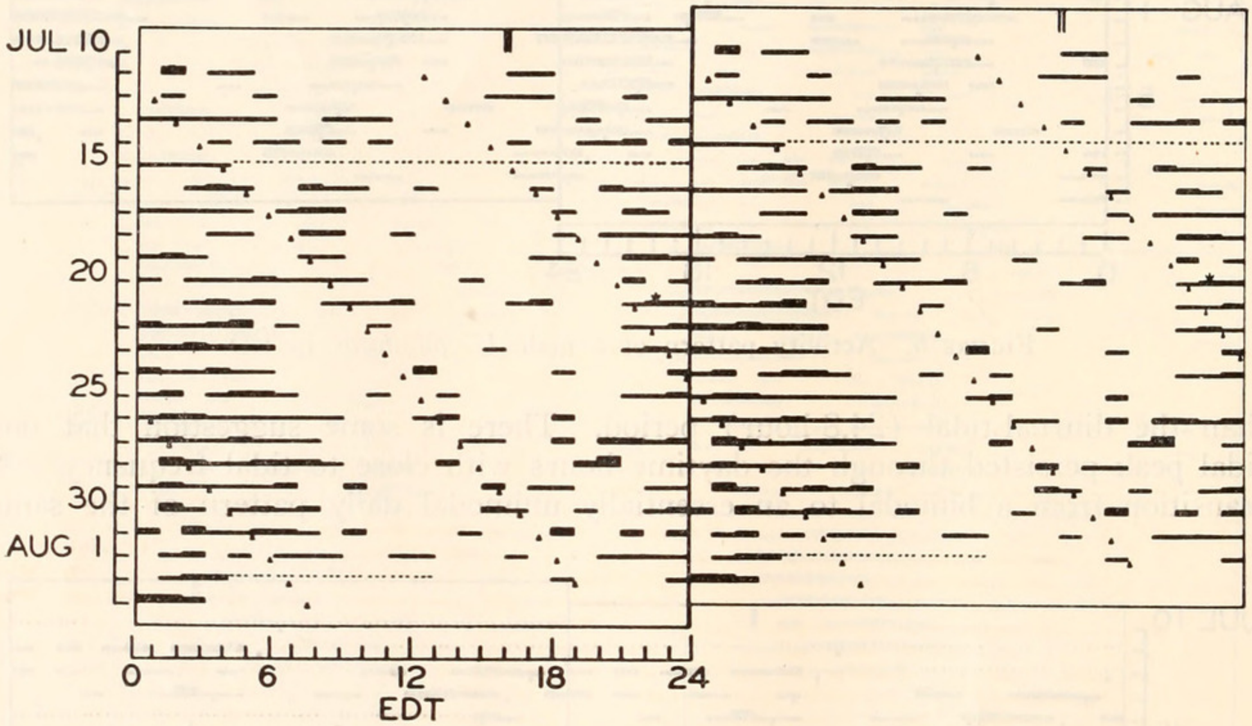

FIGURE 8. Activity pattern of a male *U. pugilator* in LL.

July 16 the evening tidal peak suddenly increased its period and scanned across the day until it reached the time when the second tidal peak would be occurring. At this point (about 11:00 on July 23 to 24) it appeared to resynchronize to a tidal schedule. At the same time that the deviant component began to merge and resynchronize, a band of activity reappeared (02:00 on July 23) on the tide which it had originally followed. The pattern suggests that this crab, like the six other *U. pugnax,* maintained through the recording period a basic tidal frequency, but in this case the tidal rhythm was sometimes unexpressed and upon it was superimposed a component of a different frequency.

Crabs 11 and 12 (Fig. 11). Portions of the records of these two *U. pugnax* were selected to indicate phase differences within the sample. Crab 11 (Fig. 11 A) tended to become active about an hour before the time of high tide, while the major period of activity for crab 12 (Fig. 11 B) was initiated about four to five hours after the time of high tide. In both patterns a 24-hour rhythm was

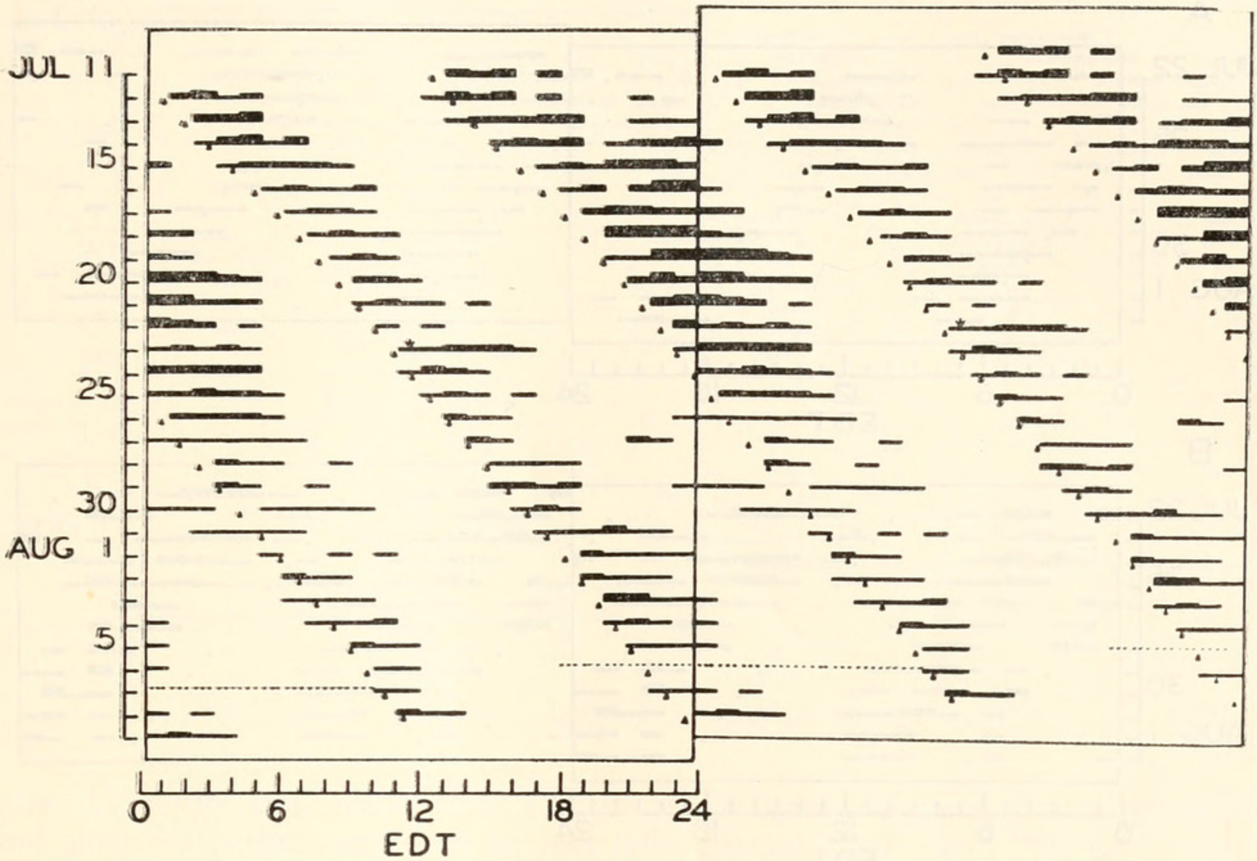

FIGURE 9. Activity pattern of a male *U. pugnax* in LD. The crabs of this group were collected on July 10.

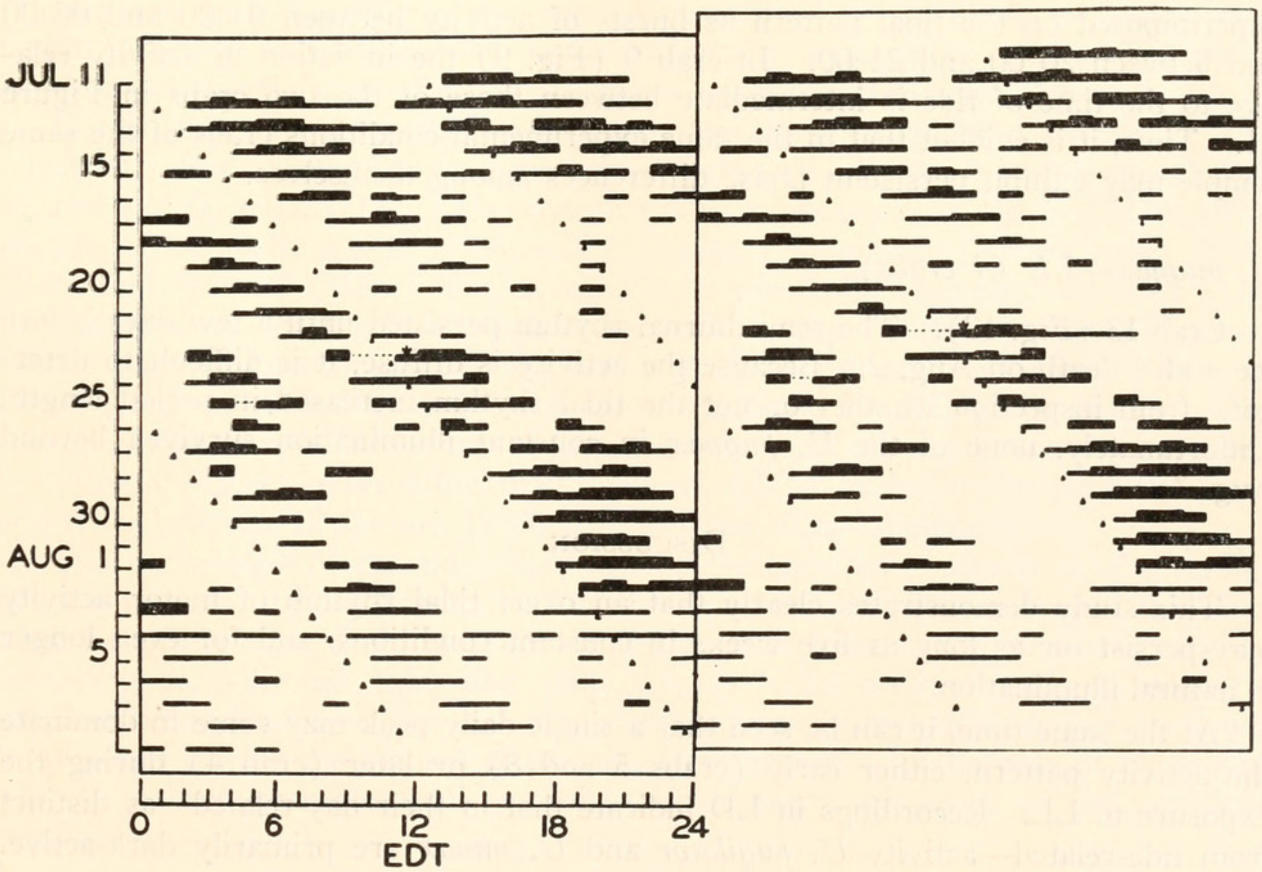

FIGURE 10. Activity pattern of a male *U. pugnax* in LD.

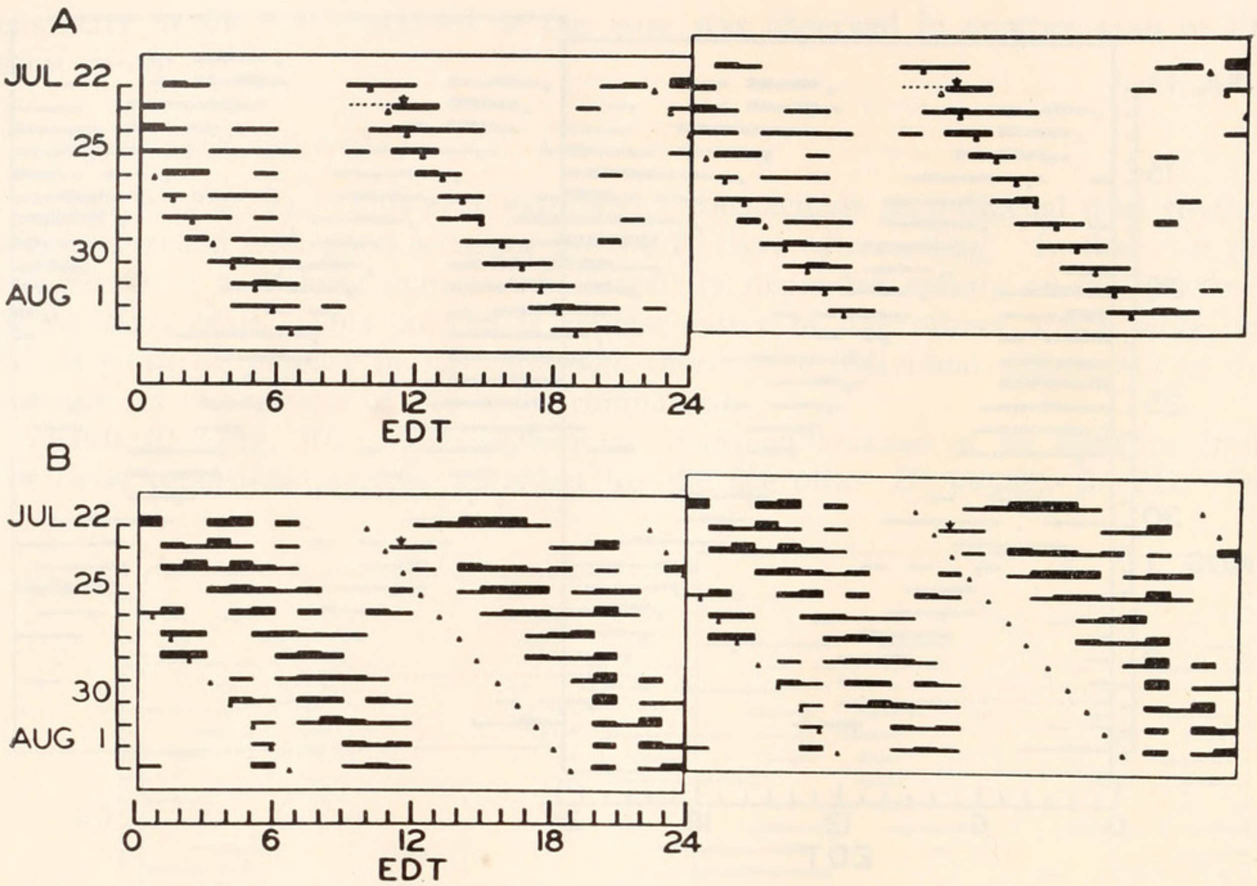

FIGURE 11 A AND B. Activity patterns of two male *U. pugnax* in LD.

superimposed on the tidal pattern as bursts of activity between 04:00 and 06:00 and between 20:00 and 21:00. In crab 9 (Fig. 9) the initiation of activity relative to the time of tide is intermediate between those of the two crabs in Figure 11. Thus, it is evident that in the same experimental conditions crabs of the same sample may exhibit persistent phase differences among themselves.

U. pugnax—LL (4 crabs)

Crab 13 (Fig. 12). The semi-diurnal rhythm persisted until a few days before the crab's death on Aug. 2. Because the activity is diffuse, it is difficult to determine from inspection whether or not the tidal rhythm increased in period length. Unfortunately, none of the *U. pugnax* in constant illumination survived beyond Aug. 3.

DISCUSSION

This study demonstrates clearly that an overt tidal rhythm of motor activity may persist for as long as five weeks in constant conditions, and for even longer in natural illumination.

At the same time, it can be seen that a single daily peak may come to dominate the activity pattern, either early (crabs 5 and 8) or later (crab 4) during the exposure to LL. Recordings in LD indicate that in their day-related—as distinct from tide-related—activity *U. pugilator* and *U. minax* are primarily dark-active.

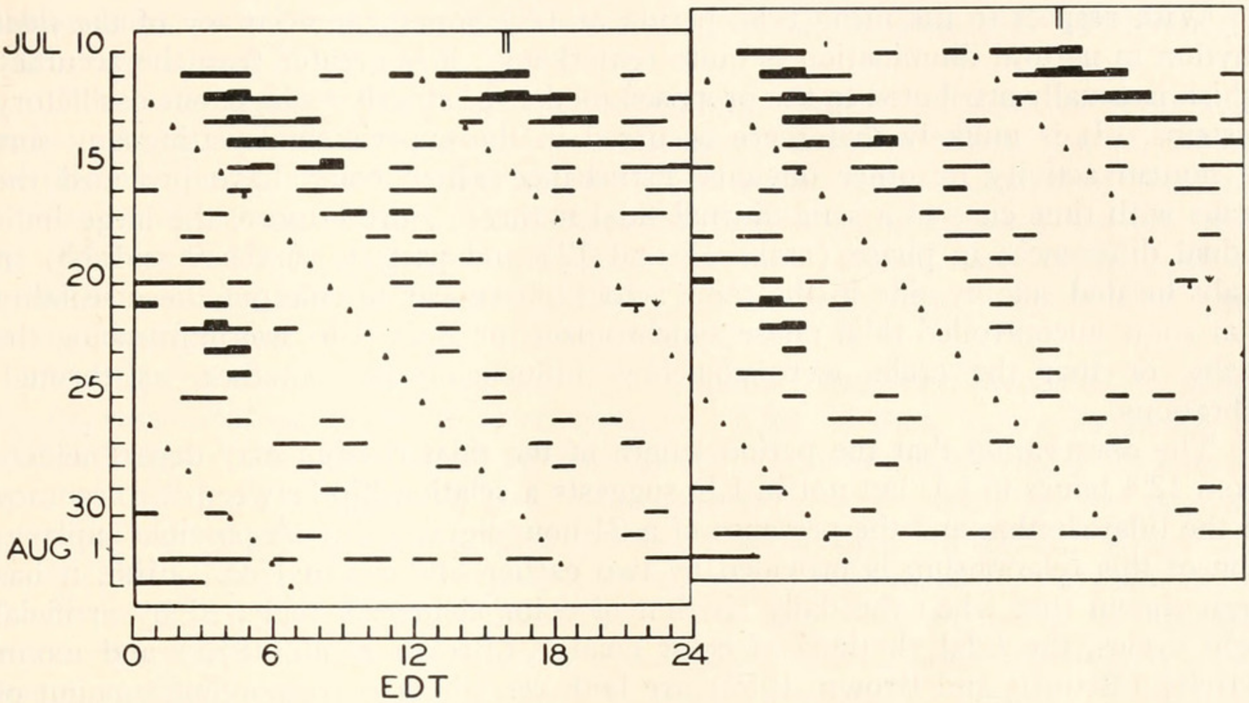

FIGURE 12. Activity pattern of a male *U. pugnax* in LL.

Since the major peak observed in LL was of nocturnal origin in two of the cases, and since its period tended to be less than diurnal tidal (24.8-hours), it seems likely that it represents a circadian component. Several years ago Prof. Hermann Schöne (personal communication) observed a circadian rhythm in the motor activity of *U. pugilator*. The rhythm persisted for many months in constant illumination with a period which was a function of light intensity. The period length increased as the logarithm of light intensity increased, a relationship which has been observed frequently in dark-active animals (Hoffmann, 1965).

For all three species a daily component was more pronounced in natural illumination. For *U. pugnax* it consisted of increased activity between sunset and sunrise (20:00 to 05:00). This rhythm has its counterpart in the persistent daily rhythm of metabolic rate of *U. pugnax* in constant conditions (Brown *et al.*, 1954; Webb and Brown, 1958). The average daily metabolic variation, obtained from five summers of recording, was characterized by a rapid increase in rate at about 20:00, a major maximum at 05:00, and a gradual decline to a minimum rate at 17:00 (Brown, 1960, Fig. 6 C, with times converted from EST to EDT). The ecological significance of the form of the persistent metabolic rhythm is also indicated by Crane's (1958) observation that for most fiddler crabs in the field the tides occurring between 12:00 and 17:00 appear to be disadvantageous.

The persistence of the tidal rhythm is of interest with regard to the timing of semi-monthly (15-day) cycles. It has been pointed out (Brown *et al.*, 1953) that a semi-monthly cycle could be timed by the periodic interference of simultaneously occurring semi-diurnal tidal and daily cycles. The present study provides a graphic demonstration of just such an accurate and persistent tidal rhythm as would be required for the mechanism of periodic interference. In the case of *U. minax* (Fig. 1) three accurate semi-monthly periods were measured off in non-tidal conditions.

With respect to the mean tidal period of 12.4 hours, the accuracy of the tidal rhythm in natural illumination is quite remarkable; it is greater than the accuracy which is usually attributed to the proposed models of strictly endogenous oscillatory systems. It is unlikely that there occurred in the experimental setting any sort of human activity or other obvious disturbance which could have provided the crabs with time cues of a semi-diurnal tidal nature. Furthermore, the large individual differences in phase (crabs 11 and 12) and pattern (crabs 9 and 10) in crabs located side by side in the same actograph appear to rule out the possibility that some uncontrolled tidal phase synchronizer, or *Zeitgeber,* was influencing the crabs, or that the crabs were somehow influencing one another, as through vibrations.

The observation that the period length of the tidal rhythm may depart widely from 12.4 hours in LL but not in LD suggests a relationship between the accuracy of the tidal rhythm and the presence of a 24-hour light cycle. A possible explanation of this relationship is provided by two earlier findings in *Uca.* First, it has been shown that when the daily rhythm of color change is rephased by artificial light cycles, the tidal rhythms of color change (Brown *et al.,* 1953) and motor activity (Bennett and Brown, 1959) are both reset by a corresponding amount of time. Second, in constant illumination the daily rhythm of color change in several species of *Uca* (Webb *et al.,* 1954; Sandeen and Wheatley, 1962) may exceed 24 hours in period length. Given (a) some sort of coupling between daily and tidal rhythms during phase shifting and (b) a lengthening of period, or phase drift, of the daily rhythm, then a lengthening of period of the tidal rhythm is not an unexpected consequence.[3] Thus, inaccuracy of the tidal rhythm could be explained simply as a result of inaccuracy of the circadian rhythm. When phase and period of the circadian rhythm are synchronized with a natural light cycle, an accurate tidal rhythm would be permitted to express itself.

It is also possible that the tidal rhythm, of itself and apart from the circadian component, was exhibiting deviations in period length which were analogous to those of circadian rhythms. Why this should have occurred in LL but not in LD is not clear. Furthermore, the interpretation of the circadian period is itself an unresolved question. Either the circadian period in the steady-state is the same as the period of its endogenous, driving oscillator (Pittendrigh, 1960; Aschoff, 1960), or it arises through intra-organismic frequency transformation of basic clock periods, proposed by Brown to be geophysically derived, accurate solar- and lunar-day ones. The theoretical possibility of frequency transformation has been acknowledged (Klotter, 1965), and its biological significance has been discussed (Brown, 1962, 1965). At present neither of the two alternative theories has been disproved, and both account for the properties of circadian rhythms. However, the theory of external timing accounts not only for circadian rhythms but for persistent rhythms of accurate daily and lunar (tidal) frequency.

The activity pattern recorded for crab 10 (Fig. 10) appears to be a case of dissociation of components of a tidal clock system. The record was obtained in LD, assuring, presumably, that the circadian component was phase-locked and could not contribute to the dissociation. Examples have been published of a similar

[3] Experimental evidence on this point has recently been presented by Webb and Brown (1965).

phenomenon in the circadian rhythms of certain arctic mammals (Pittendrigh, 1960, Figs. 10 and 11).

There was considerable variation among the activity patterns of individual crabs. At the species level several generalizations could be made. In *U. minax* the tidal rhythm was most distinct and persistent under both conditions of illumination, and under constant illumination exhibited the greatest tendency to deviate from the tidal period. *U. pugilator* exhibited the most conspicuous component of nocturnal activity and the greatest tendency to undergo transitions from a tidal to circadian pattern in constant illumination.

Among crabs of the same species several factors have been reported to affect the expression of daily and tidal components. One of these is the exposure to tidal influence. Altevogt (1959) reported that in the field the activity of *U. tangeri* in a non-tidal pool conformed to a daily schedule, while crabs in the near-by intertidal zone carried on the same activities on a tidal schedule. Fingerman *et al.* (1958) found that the persistent melanophore rhythm of *U. pugilator* from above the high water line was predominantly a daily rhythm, while the rhythm was conspicuously tidal in crabs from the intertidal zone. Naylor (1960) reported that *C. maenas* from a non-tidal dock exhibited principally nocturnal activity in LD rather than tidal activity. Blume *et al.* (1962) also reported that in *C. maenas* either a semi-diurnal tidal cycle or a daily cycle may dominate the activity pattern.

In *C. maenas,* Naylor (1960) showed that the tidal rhythm of crabs from a tidal habitat could be suppressed by maintaining the crabs in a non-tidal aquarium for four weeks. Their activity came to resemble that of crabs from the non-tidal dock. By chilling, a tidal rhythm could be induced in these non-tidal crabs (Naylor, 1963). The experimentally demonstrated lability of the tidal rhythm in *C. maenas* suggests that under natural conditions the rhythm can be switched off and on in accordance with changes in environmental circumstances.

A second factor influencing the pattern of activity is reproductive state. Hyman (1920) reported that ovigerous females of *U. pugnax, U. pugilator,* and *U. minax* emerged from their burrows during low tides at sunset, but were not to be seen running on the beach with the males during the low tides in the daytime. In this regard it is of interest that nocturnal activity dominated the activity pattern of the ovigerous *U. minax* (Fig. 5).

From extensive observations on individual fiddler crabs of several species, Crane (1958) was able to classify their social activity into six phases. Among these phases the amount of motor activity varied widely. In the "underground" phase the crab did not emerge at all from its burrow during low tide, while in the "non-aggressive wandering" and "aggressive wandering" phases the crab left its burrow and walked almost incessantly during the period of low tide. Populations of crabs tended to pass through the sequences of phases from least to most social in semi-monthly cycles, but large individual differences were evident. Thus, a third factor contributing to individual differences in activity could be internally controlled level of social behavior.

Bliss (1960) has reported that in constant darkness the circadian rhythm of the land crab, *Gecarcinus lateralis,* had significantly greater variability in eyestalk-less and intact premolt crabs than in intact intermolt crabs. In the present study only a single crab (Fig. 3) is known to have been in premolt condition. This crab exhibited in natural illumination an accurate tidal rhythm with a high level of activity up to the moment of molting. Unfortunately, there have not been more extensive reports on the effects of the premolt condition on the daily and tidal patterns of activity in fiddler crabs.

Up to the present, little has been done on the physiological control of the expression of daily and tidal components, although an experiment by Brown *et al.* (1954) is of some interest. These authors reported that eye-stalk ablation in *U. pugilator* abolished the tidal, but not the daily rhythm of metabolic rate in constant conditions. In this regard it is significant that the eyestalk is involved in the regulation of reproduction, molt, and level of motor activity, those factors which have just been discussed as contributing to differences in the expression of daily and tidal rhythms.

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Summary

1. The motor activity of individual specimens of *U. pugnax, U. pugilator,* and *U. minax* was recorded in actographs in both constant illumination and natural cycles of daylight and darkness for periods which exceeded six weeks in some crabs.

2. In the natural light cycle crabs exhibited overt, semi-diurnal tidal rhythms of high accuracy which persisted, in the case of *U. minax,* for at least 46 days. Superimposed on the tidal rhythm was a 24-hour component which consisted generally of activity between sunset and sunrise.

3. In constant illumination the tidal rhythm in *U. minax* clearly exceeded the natural tidal period of 12.4 hours. In some crabs of this species the tidal rhythm persisted for well over a month.

4. In both *U. minax* and *U. pugilator* transitions from a tide-related pattern to an apparently circadian pattern were observed in constant illumination.

5. Evidence was presented for dissociation of components of the tidal clock system in *U. pugnax.*

6. Variations in the activity pattern occur at the species level and within species. Within species individual variation may be due to such factors as exposure to tidal influence, reproductive state, phase of social activity, and molting.

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