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Rhythmic Locomotor Activity in the Intertidal Shorecrab *Hemigrapsus oregonensis* (Brachyura, Grapsidae) from the Oregon Coast

Abstract

Sixteen adult male shorecrabs, *Hemigrapsus oregonensis* (Dana 1851), were collected from the 1.52 m (+ 5 ft) level at Coquille Point in the Yaquina Bay Estuary (44° 37' N. Lat., 124° 04' W. Long.), Oregon, U.S.A. The crabs were held in testing chambers at 10° ± 1° C under varying artificial light conditions. About half of the crabs showed both a tidal and a diurnal rhythmicity. The activity progression reflected greatest activity during predicted periods of dark-high tide at the collection site followed by dark-low tide followed by light-high tide, with least activity occurring during periods of light-low tide. Results are based on over 3000 h of monitoring time.

Introduction

Hemigrapsus oregonensis is a common inhabitant of the North American intertidal from Alaska to the Gulf of California (Schmitt 1921, Hart 1968). Within this range, it is most common in habitats ranging from muddy to a pea-sized gravel substratum (Way 1917, MacKay 1943, Hiatt 1948, Ricketts *et al.* 1968). It is quite tolerant of high silt loads and is considered to be both euryhaline and eurythermal (Dehnel 1960, Gross 1963, Dehnel and Carefoot 1965).

The periodicity of the tides, as expressed in varying exposure times at different tidal levels, would be expected to exert a great influence on the foraging patterns and behavioral activities of intertidal organisms. Tidally linked behavioral rhythms have been demonstrated in numerous marine organisms, including clams (Bennett 1954), oysters (Loosanoff and Nomejko 1951), prawns (Rodriguez and Naylor 1972), amphipods (Fincham 1970), isopods (Enright 1971, 1972), and several species of intertidal crabs (Fingerman 1955, Naylor 1958, Williams 1966). *H. oregonensis*, which is exposed to a fluctuating tidal regime, might be predicted, then, to exhibit tidally linked behavioral rhythms. The present study attempted to determine if locomotor activity patterns existed and, if so, to determine if they were related to a fluctuating tidal regime.

Methods

Adult male crabs with a minimum carapace width of 2.5 cm were collected during October and November 1972, during low tide at Coquille Point in the Yaquina Bay Estuary (44° 37' N. Lat., 124° 04' W. Long.) on the central Oregon coast from the 1.52 m (5 ft) tidal level. They were immediately transported to the laboratory in Corvallis, Oregon, about 80 km (50 mi) inland. Experiments were initiated within 3 h

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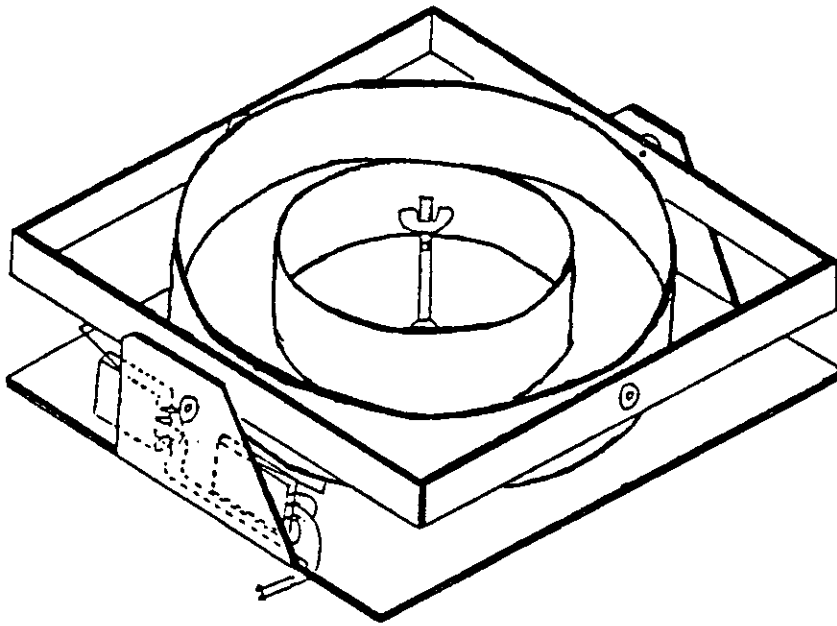


Figure 1. Activity chamber used in locomotor analysis of *Hemigrapsus oregonensis*. Chamber was suspended from yoke and gimbal framework to allow displacement in any plane from the horizontal. Microswitches were activated when the crab crossed an axis of rotation. Microswitches were connected to an Esterline-Angus event recorder which allowed continuous activity monitoring. Activity events were recorded as vertical marks on the continuously moving chart and were tabulated as number of events per hour.

after removal from the collection site and before the next high tide would have covered the collection area. All activity experiments were conducted in a cold room maintained at $10^{\circ} \pm 1^{\circ}$ C. The crabs were placed in an activity chamber, one per chamber, and their locomotor activity responses monitored for up to nine consecutive days. The animals were not fed during the experimental period. The test chambers (Fig. 1) were constructed from two cylindrical pieces of plexiglass 5 cm high, one having a diameter of 15 cm and the other a diameter of 25 cm. The smaller diameter piece was placed into the larger piece and spaced evenly to give a circular runway. The floor of the chamber was fitted with sea water saturated filter paper, and a lid was placed over the chamber to prevent the crab from escaping. The chamber was suspended from a ballbearing pivoted yoke and gimbal framework. Because the pivotal axes were at right angles to each other, the suspended activity chamber could be tilted in any direction. Microswitches were placed under the movable frameworks. Each time a crab crossed a quadrant of the chamber (rotational axis), the displacement of the chamber activated a micro-switch mechanism. The microswitches were connected to an Esterline-Angus 12 volt D.C. series 80 M continuous event recorder. The number of activity events per hour were counted, and compared with the natural daylight (sunrise-sunset) hours and the tidal regime during the experimental period. The light regime in the experimental chamber (abrupt lights on-lights off) was, early in the experiments, identical in length to the natural sunrise-sunset period but was later reduced to a constant low level red light (dark) regime. The tidal regime during the study period was established by plotting

the predicted mixed semi-diurnal tidal heights and then calculating the time during which the 1.52 m (5 ft) tidal height (from which the crabs were collected) was covered and exposed both during natural daylight and night time periods. No distinction was made between the collection site being covered by a lower high tide or a higher high tide. The length of time the collection site was covered by either type of high tide was, however, a major consideration. The number of activity events per hour was compared between periods of light, dark, covered (high tide) exposed (low tide), and several combinations of these. Student's t-test between means was applied as a statistical test to determine if significant variation in activity patterns correlated with natural light or tidal cycles. Results are based on over 3000 h of total monitoring time, an average of 190 h monitoring time on each of 16 individual male crabs.

Results

Subjective field observations suggested greater crab activity during night low tide periods than during day low tide periods. Experiments were performed to determine if this apparent day-night difference existed. Additional experiments were performed to determine if activity periods were regulated by a solar day cycle (light regime), a lunar day cycle (tidal regime), or a combination of both. Data showed that subjective field observations were not valid in all cases. In about half of the experiments, less activity occurred during dark periods than during light periods. Activity seemed most dependent on the state of the tide, however. Greatest activity occurred during high tide periods, regardless of the light regime. Both solar day (24.0 h) and lunar day (24.8 h) length seemed to affect crab activity patterns.

The activity pattern of one crab over a five day period under a natural light regime (L = 12 h, D = 12 h) (Fig. 2) has been superimposed on the tidal regime during the experimental period. This crab had activity bursts coinciding with periods of high tide. Both low tide and dark periods were periods of low activity. Few crabs were ever seen moving about during daytime low tide at the collection site, suggesting that periods when the crabs were covered (high tide) were periods of increased activity. The mean length between activity bursts was found to be 24.6 h, corresponding quite closely to a 24.8 h periodicity between successive higher high tides.

Figure 3 shows a persistent activity rhythm over seven tidal cycles. However, rather than relatively low activity during darkness, great activity bursts were recorded during periods of light or high tide. The mean length between bursts was 12.2 h, almost half that of the lunar periodicity. The periods of greatest activity were not precisely coincident with periods of high tide. The crab's activity peaks preceded the predicted high tide by about 3 h. Not all crabs showed a clear rhythmic pattern when subjected to a light-dark regime. Some crabs showed decreasing activity during the experiment. In one case, an average of 9.7 events per hour was recorded for the first two tidal cycles, but by the sixth and seventh tidal cycles only 2.3 events per hour were recorded. The greatest hourly activity in this less active crab corresponded to the initiation of dark and light periods.

It was apparent, then, that not all crabs exhibited a well-defined locomotor activity rhythmicity. Since it was indicated that both light and high tide may be cues for initiating activity periods, an experiment was run to minimize the effects of light on the apparent activation of the crabs. Two additional crabs were subjected to a natural (L = 7 h, D =

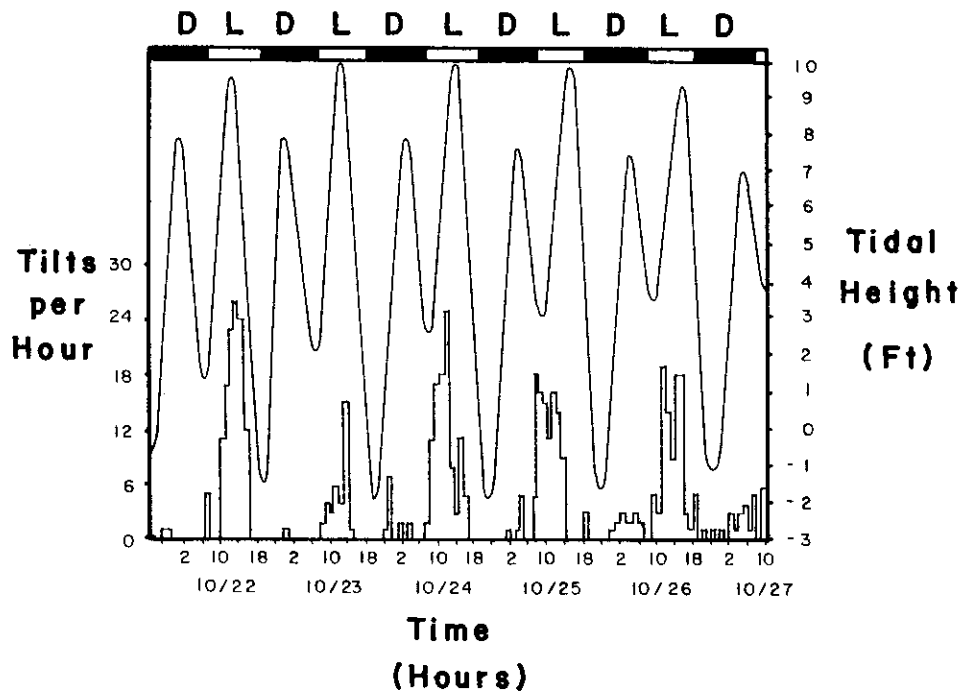


Figure 2. Activity pattern of an isolated *Hemigrapsus oregonensis* subjected to an artificial light regime (L = 12h, D = 12h). The activity pattern is superimposed on the predicted tidal regime at Coquille Point in the Yaquina Bay Estuary, Oregon.

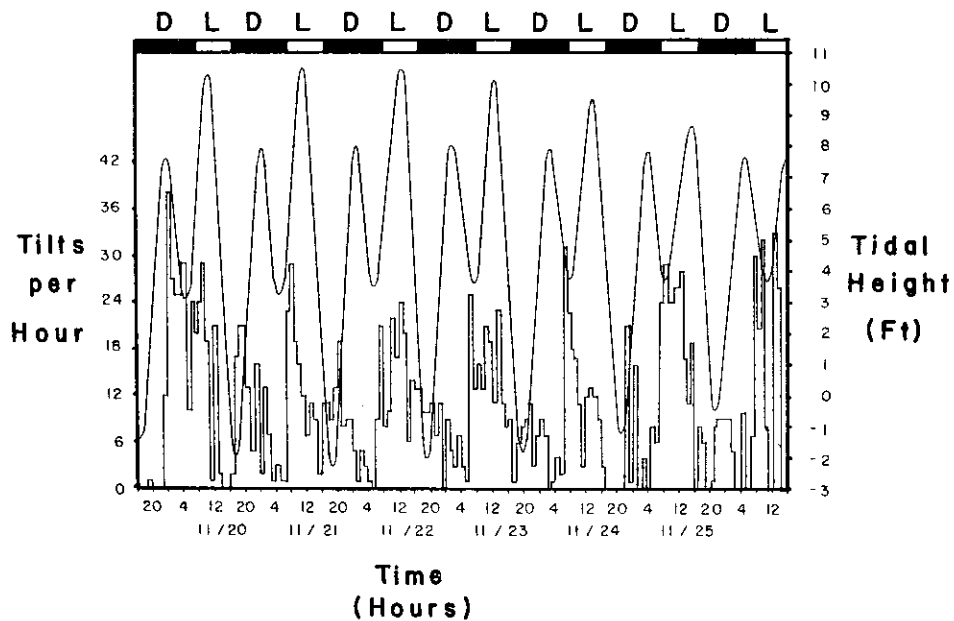


Figure 3. Activity pattern of an isolated *Hemigrapsus oregonensis* subjected to an artificial light regime (L = 7h, D = 17h). The activity pattern is superimposed on the predicted tidal regime at Coquille Point in the Yaquina Bay Estuary, Oregon.

17 h) light-dark regime for three full tidal cycles and then denied any light intensity increases for the next six full tidal cycles. A clear rhythmicity emerged after the crabs were subjected to constant darkness. Since the light regime was not in effect, the rhythmicity which emerged (Fig. 4) presumably was not cued on increasing light intensity (solar regime). The mean length between activity bursts was 29.0 h, with an average duration of 21.6 h. It thus appeared that under constant darkness the periodicity of the locomotor response tended to expand and become out of phase with the high tide within five tidal cycles.

Similarly, Figure 5 shows a definite rhythmicity emerging during the constant dark

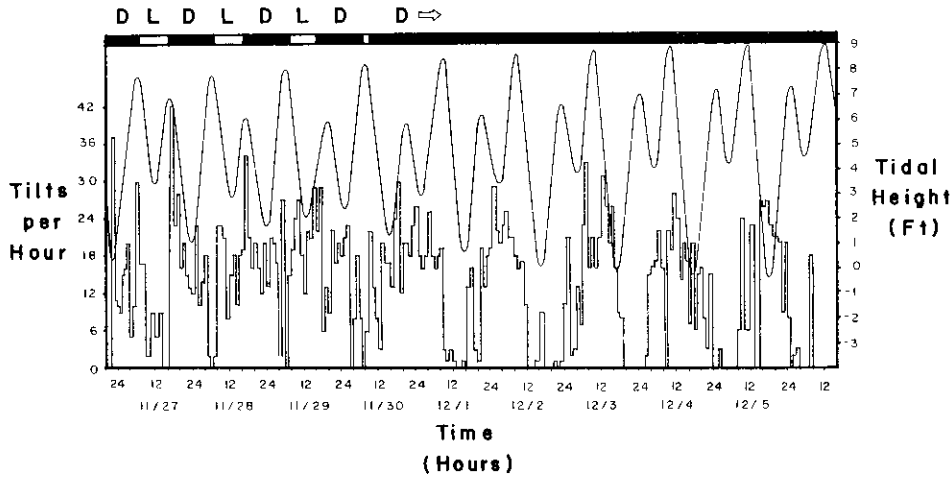


Figure 4. Activity pattern of an isolated *Hemigrapsus oregonensis* subjected to an artificial light regime (L = 7h, D = 17h) for the first three photoperiods and then subjected to a constant low level light regime for the next six consecutive tidal cycles. The activity pattern is superimposed on the predicted tidal regime at Coquille Point in the Yaquina Bay Estuary, Oregon.

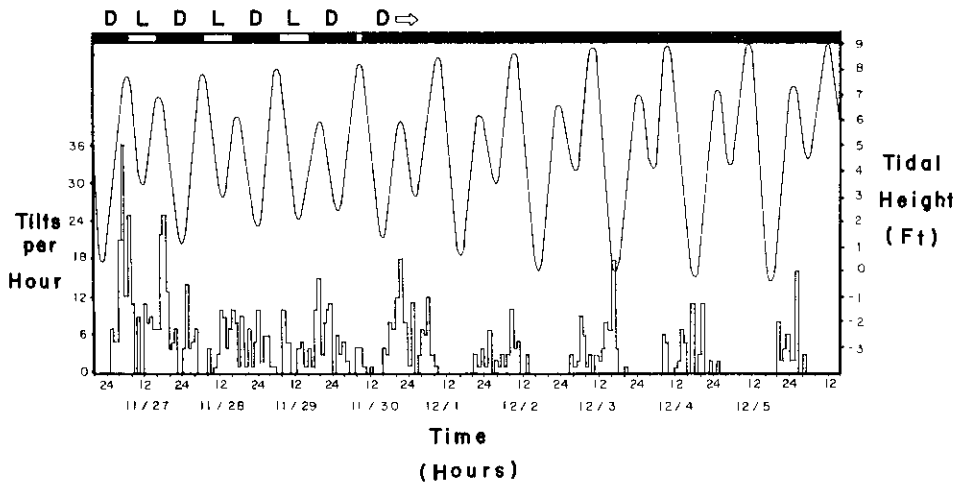


Figure 5. Activity pattern of an isolated *Hemigrapsus oregonensis* subjected to an artificial light regime (L = 7h, D = 17h) for the first three photoperiods and then subjected to a constant low level light regime for the next six consecutive tidal cycles. The activity pattern is superimposed on the predicted tidal regime at Coquille Point in the Yaquina Bay Estuary, Oregon.

portion of the experiment. The average duration between activity bursts was again 29.0 h, suggesting an endogenous rhythmicity which was longer than the lunar day cycle (24.8 h). Additional experiments under constant darkness showed initial activity peaks corresponding to high tide periods during the first two or three tidal cycles, but later appearing to become more random. The interval between activity peaks before disintegration of the pattern was considerably less (25.7 h and 23.0 h) than the 29.0 h periodicity found in those activity patterns which did not decay.

It was suspected, then, that two different entrainment factors were operative: light regime and tidal regime. The periodicity of activity relative to light, dark, and to whether the habitat was covered (high tide) or exposed (low tide) was investigated. A t-test between mean number of events per hour indicated that the crabs that exhibited a rhythmic cycle were significantly more active ($p < .05$) during periods of darkness than during periods of light. These crabs were also more active ($p < .05$) during periods of high tide than during periods of low tide, during periods of high tide than during light ($p < .05$), and during darkness than during low tide ($p < .05$). It thus appeared that greatest periods of overall activity occurred during high tide; the next greatest period of activity coincided with darkness followed by low tide, and with least activity recorded during daylight hours.

Periods of darkness were further divided into dark-high tide and dark-low tide periods. Light periods were similarly divided into light-high tide and light-low tide periods in an effort to couple the light regime and tidal regime effects. Greater crab activity ($p < .05$) occurred during light-high tide than during light-low tide, reflecting a true tidal rhythmicity. Greater activity ($p < .05$) occurred during dark-high tide than during light-high tide, suggesting a diurnal rhythmicity. Greater activity was also found during dark-high tide than during light-low tide. In order of decreasing magnitude, the greatest activity was found during dark-high tide followed by dark-low tide followed by light-high tide, with least activity recorded during light-low tide periods.

In some crabs, however, a comparison of activity during the light regime with the combined effect of the tidal regime indicated that the greatest activity occurred during periods of light-low tide followed by light-high tide, with equal activity during dark-high tide and dark-low tide (means not significantly different at $.05$). These findings support the interpretation that for some crabs the rhythmicity due to tidal fluctuation is absent or completely masked by the light regime rhythmicity.

The results of t-tests between mean number of events per hour showed that, in the absence of reinforcing light or tidal stimuli, greater activity occurred during predicted dark periods than during predicted light periods or predicted low tide periods ($p < .05$). Activity was also greater during high tide than during low tide ($p < .05$) or during daylight ($p < .05$). During dark periods, greater activity occurred during high tide than during low tide ($p < .05$). During light periods, however, no statistical differences ($p > .05$) were found between means at high tide and low tide. During high tides, greater activity occurred during dark hours than during light hours ($p < .05$). Similarly, during low tides greater activity was found during darkness than during light hours ($p < .05$). Under a constant dark regime, then, some crabs were still capable of maintaining a rhythmicity based on both tidal cycles and light cycles; others, however, under the same conditions apparently lost the tidal component. In those crabs that showed both a diurnal and a tidal rhythmicity under constant darkness, the activity

progression was the same as for those under the experimental light regime: greatest activity during predicted dark-high tide followed by dark-low tide followed by light-high tide with least activity during light-low tide.

Discussion and Conclusion

Symons (1964) found variability in locomotor activity (walking behavior) of *Hemigrapsus oregonensis*. Although he did not investigate tidally linked rhythms, he did demonstrate a diurnal component in male crabs, with maximal activity occurring during dark hours (0530 h, 1/2 ft-c). During this study, periods of activity in *Hemigrapsus oregonensis* were also found to be quite variable. Not all crabs tested showed a rhythmicity of locomotor patterns. Similarly, only about 50 percent of tested fiddler crabs (*Uca crenulata*) showed a rhythmicity (Honegger 1973). *Hemigrapsus edwardsi* from New Zealand showed a seasonal variation in activity which corresponded to vertical migrations in the intertidal (Williams 1969). During warmer water months (December, January, February) *H. edwardsi* showed a persistent tidal rhythm, with peak activity occurring one or two hours preceding high tide. This tidal rhythm, however, was not as apparent during cold water months (June, July, August), when the crabs would migrate down into the lower regions of the intertidal. Under constant conditions, this crab would lose its tidal periodicity after two to three weeks; but, under the same constant conditions, it would slowly re-establish its rhythmicity. The cue for initiating this re-entrainment was not established, but it was thought to be endogenous in origin.

H. edwardsi seems to lack a strong circadian component. The crabs *Sesarma reticulatum* and *Carcinus maenas* displayed a tidal and a diurnal rhythm for about three to four days, with peak activity bursts at a periodicity of 24 h (diurnal component) and 12.4 h (tidal component). Maximum activity during the tidal component occurred during high tide periods.

About half of the *H. oregonensis* were shown to display tidal and diurnal rhythmicities. Greatest activity occurred when the collection site was covered by high tide and was usually intensified during dark hours.

It is speculated that *H. oregonensis* is most active at high tide periods when moving from cover would not result in excessive desiccation, heating, or predation from shore-birds. Activity also appears to be greatest when high tide was coupled with darkness. During these conditions (dark-high tide), it is speculated that foraging would present the least chance for visual detection by fish predators.

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