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# VARIATION IN THE EXPRESSION OF LUNAR AND TIDAL BEHAVIORAL RHYTHMS IN THE HORSESHOE CRAB, *LIMULUS POLYPHEMUS*

*Anne Rudloe*

The value of lunar and tidal rhythms to inhabitants of both intertidal and subtidal zones is substantial. A number of major physical environmental parameters vary with the tide including salinity, turbulence, visibility and hydrostatic pressure, and the value to an animal of tracking these rhythmic environmental shifts is great. Tidal and lunar patterns in locomotion and feeding have been described for the crustaceans *Synchelidium, Emerita, Excirolana* (Enright, 1963), *Carcinus* (Naylor et al., 1971), *Tylos* (Kensley, 1972), *Hyale* (Joseph, 1972), *Uca* (Honnegger, 1976), for mites (Schulte, 1976), chitons (Smith, 1975), pycnogonids (Isaac and Jarvis, 1973) and gastropods (Zann, 1973a; 1973b).

Lunar and tidal reproductive rhythms occur in crabs (Saigusa and Hidaka, 1978; Barnwell, 1968; Greenspan, 1982; Forward et al., 1982); amphipods (Fish and Mills, 1979), gastropods (Grahame, 1975; Ohgaki, 1981), polychaetes (Hauenschild, 1961) and fish (Walker, 1949; Middaugh, 1981; Spratt, 1981; Radtke and Dean, 1982).

Tidal cycles, however, vary greatly along the coastline, creating a dilemma for species whose range encompasses several different tidal patterns—a common situation for species of the Carolinean faunal province that stretches from the Carolinas to the northern Gulf of Mexico (Barnwell, 1976). Variation within a species in the expression of tidal and lunar breeding patterns under varying tidal regimes has been recorded for the hermit crab *Pagurus geminus* (Imafuku, 1981), however. In addition Naylor (1960; 1961) and Gibson (1965; 1969) showed, in the crab *Carcinus* and the blenny *Blennius* respectively, that species exhibiting lunar and tidal periodicities under semi-diurnal tides often revert to circadian activity patterns in areas with little or no tidal influence. Further, seasonal variations in the expression of semi-lunar spawning rhythms have been recorded for the amphipod *Corophium volutator* (Omori et al., 1982).

Rudloe (1979; 1980) has shown lunar, tidal and circadian rhythms in the reproductive activity of adult horseshoe crabs in Apalachee Bay, Florida and in the emergence of the larvae, with activity concentrated on night spring high tides particularly at the full moon. In contrast, intertidal juvenile horseshoe crabs actively feed and move about on falling tides during daylight hours (Rudloe, 1981). Cohen and Brockman (1983) studied breeding *Limulus* at Seahorse Key, Florida approximately 150 km south of the Apalachee Bay site of Rudloe. While breeding was more strongly concentrated on daytime high tides than in Apalachee Bay, breeding peaks on full and new moon were similar to those observed in Apalachee Bay. Both of these sites experience mixed semi-diurnal tides (two unequal high and two unequal low tides per day). While crabs in Delaware Bay appear on breeding beaches at high tide throughout May and June, there are suggestions of full and new moon peaks in that population as well (Botton, pers. comm.).

Recent field observations on both foraging and breeding behavior in adult horseshoe crabs as well as feeding in juveniles have suggested substantial differences in the expression of lunar and tidal activity rhythms of this species in St. Joseph Bay, Florida as compared to populations studied earlier (Rudloe, 1983). The appearance of crabs in this area did not appear to coincide with either full or new moon, or the predicted high tide despite the fact that 80 miles to the east in Apalachee Bay massive breeding was occurring during this period on the full and new moons at high tide as described in prior studies (Rudloe, 1980).

There are major differences in the tidal regime between St. Joseph Bay and the breeding beaches previously studied in adjacent Apalachee Bay, at Seahorse Key, and Delaware Bay, however. Like most of the Atlantic coast and the western coast of Florida, Apalachee Bay, Seahorse Key and Delaware experience mixed semi-diurnal tides (i.e., two high and two low tides of unequal height each day). The tidal range is approximately 2 m with maximum differences coinciding with the new and full moon. However, beginning at Cape Sanblas and St. Joseph Bay, and moving westward in the Gulf of Mexico, tides become diurnal, with a single high and a single low each day. Amplitudes are much less, about one half meter in St. Joseph Bay and maximum differences in water depth occur in conjunction with the neap tides, off set from full and new moon by 1 week. Meteorological conditions often influence water depth to a greater degree than do predicted tides.

Lunar and tidal activity patterns in breeding and foraging behavior of adults as well as in foraging of juvenile *Limulus* was subsequently studied over a 3-year period under this tidal regime in St. Joseph Bay from 1980–1983. The objective was to determine if the relatively clear-cut lunar and tidal rhythms of behavior observed elsewhere would be maintained in a population exposed to erratic diurnal tides.

## Materials and Methods

Teams of one to four individuals established and monitored transect lines at sites within St. Joseph Bay between May 1980 and June 1983 (Fig. 1). Data was collected on activity patterns relative to tidal and lunar cycles by counting the number of animals observed while walking the transect lines.

*Lunar Rhythms.*—An initial 100-m transect was monitored for one lunar month in May–June 1980 on an intertidal sand flat along the east shore of the bay immediately south of Presnell's camp. Animals were engaged in feeding activity at this site. This transect was walked once a day at the time of the predicted high tide. Temperature and depth were recorded at the start of each transect. In April–June 1983, a 100-m transect on the breeding beach at Conch Island was established and checked once a week for 2 months on the dates of full and new moon and on the dates of the neap tides 1 week before and after those days. All animals present along the beach transect at the time of predicted high tide were counted as were the number observed feeding on the flats while walking a marked course from the mainland shore out to the island, a distance of approximately 1,000 m. Temperature, salinity and depth were recorded at the beginning of each transect, as were wind speed, direction and weather conditions.

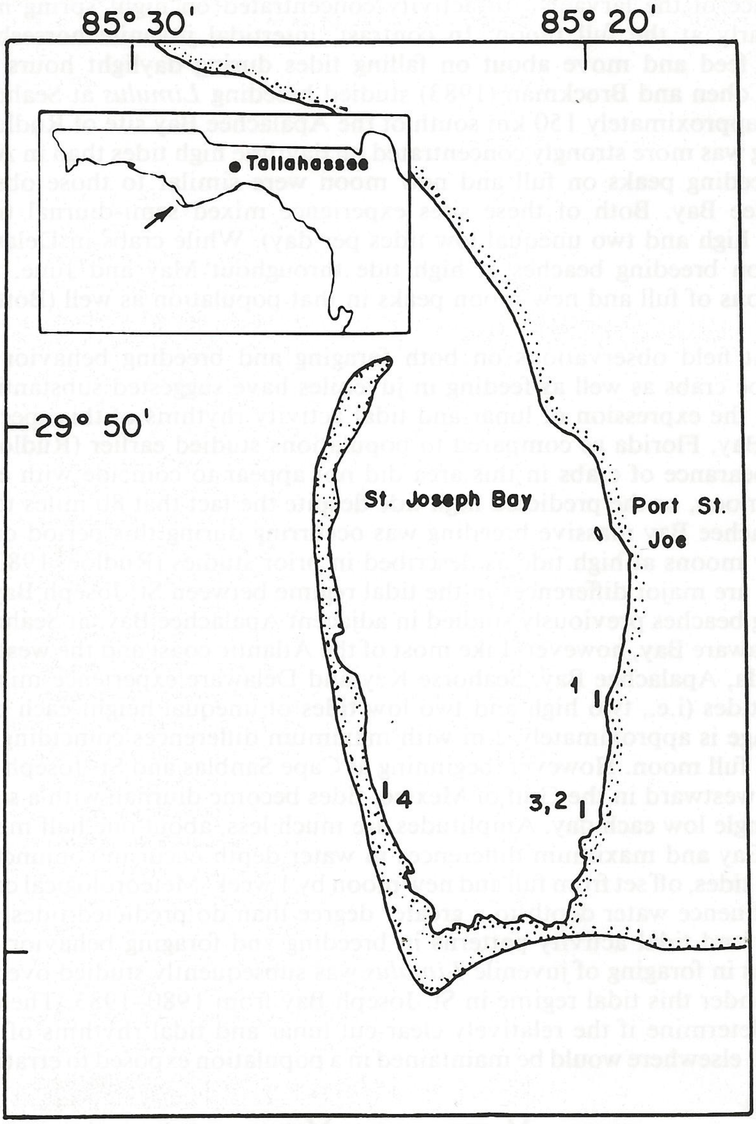
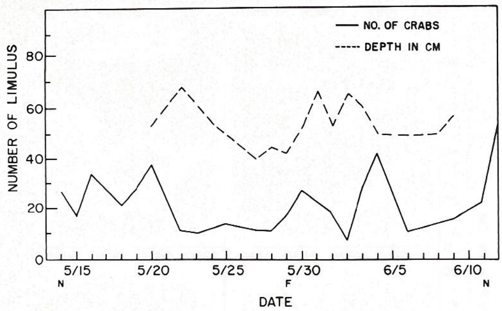



Figure 1. St. Joseph Bay study sites: (1) adult foraging transect, 1980, (2) Conch Island breeding transect, (3) Conch Island flat foraging transect, 1982–1983, (4) juvenile transect, 1982.

*Tidal Rhythms.*—In April–May 1982, data on tidal activity patterns was collected in St. Joseph Bay by establishing two transects, one on the beach at Conch Island, and one on the sand flat between Conch Island and the mainland shore. A grid was laid out on the sand flat with six parallel transect lines 166 m long and 30 m apart. For 6 days in May 1982, these were checked at 30-min intervals and all *Limulus* seen were counted. Teams of observers were on the site for 1.5 h prior to and 1.5 h following the predicted high tide. All high tides during this period occurred during daylight hours. Activity was also monitored on these transects on six additional nights during September 1982, when high tides occurred at night. Since it was noted during the spring observations that the actual time of maximum water depth rarely coincided with the predicted high tide, the period of observation was lengthened to 3 h prior to and 3 h following the predicted high tide to insure being present at the time



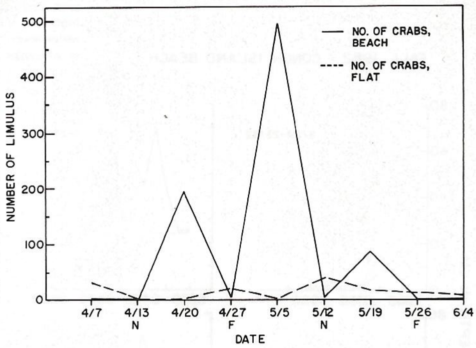




Figure 2. (Left) Activity of foraging adult *Limulus* and water depth over 1 lunar month in May–June 1980, on a 100-m transect. F = full moon, N = new moon, solid line = number of crabs, broken line = depth in centimeters.

Figure 3. (Right) Adult activity on intertidal flat and beach at Conch Island over 2 lunar months in April–June 1983. F = full moon, N = new moon, solid line = number of crabs on beach, broken line = number of crabs on intertidal flat.

of actual high water. Temperature and salinity were recorded at the beginning of each period of observation and depth was recorded at a fixed location on the sand flat and beach transects at 30-min intervals to determine the actual time of high water.

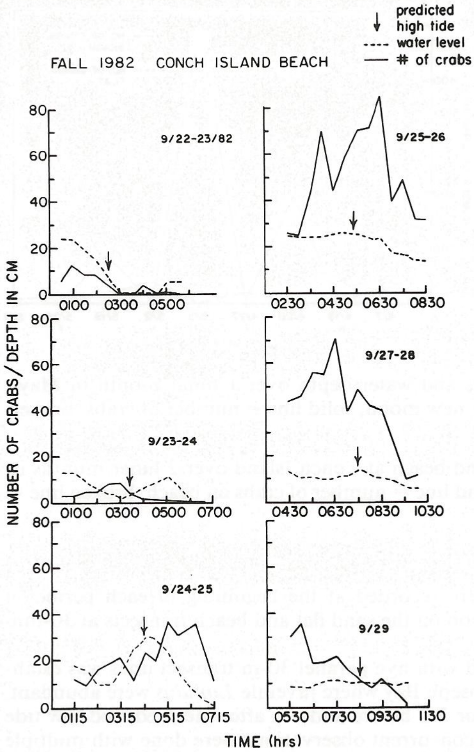
Also during the September 1982 field work, a grid with five parallel 30-m transect lines was established on an intertidal flat on the west shore of St. Joseph Bay where juvenile *Limulus* were abundant. The transects were monitored as described above for 3 h before and 3 h after the predicted low tide to record tidal activity patterns of juveniles. These concurrent observations were done with multiple teams of adult volunteer workers from Earthwatch/Center for Field Research.

## Results

*Lunar Cycle.*—Figure 2 shows activity in terms of the number of feeding adult crabs counted along the transect over 1 lunar month on the intertidal feeding flat in May and June 1980. No lunar peaks in activity were apparent. However, the distribution does differ statistically from uniformity (Kolomorov-Smirnov Goodness of Fit Test; $D = 0.09$, $P < 0.001$) and closely parallels changes in water depth. The deeper the water, the larger the number of crabs active. Water temperature varied between 26–31°C and depths ranged from 40–61 cm.

Figure 3 shows activities over two lunar months in April–June 1983 on both the Conch Island beach and the intertidal flats behind the island. Water temperature varied from 2–28°C, salinity was 32–33 ppt and depth varied from 27–42 cm. Among feeding animals on the intertidal flats, there were slight, but statistically significant elevations in activity on the full and new moon weeks ($D = 0.19$, $P < 0.001$) as compared to the other lunar phases. However, activity on the adjacent Conch Island beach peaked sharply on a bi-weekly basis during this period on the weeks of first and third quarter moons, with little or no activity on the full and new moon. Water depth at a fixed point on the beach at the time of predicted high tide was consistently higher although not statistically significant on these weeks of first and third quarter moon (spring tide mean depth at predicted high tide = 28 cm; neap tide mean depth = 38 cm/$t = 1.15$, NS) as compared to the weeks of full and new moon.

*Tidal Rhythms.*—Activity of adults is presented over six individual high tides in September 1982 from the transects on both the Conch Island beach (Fig. 4) and



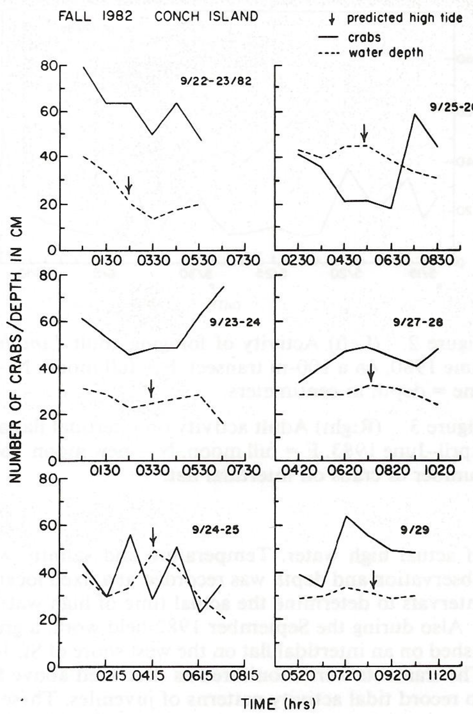




Figure 4. (Left) Activity of adult *Limulus* over predicted high tides for 6 days in 1982 on Conch Island breeding beach.

Figure 5. (Right) Activity of adult *Limulus* over predicted high tides for 6 days in 1982 on Conch Island intertidal flat.

the adjacent intertidal flat (Fig. 5). Water temperature was 20–25°C, salinity 30–31 ppt, and depth 14–41 cm on the flat and 2–30 cm on the beach. At both sites, there was no correlation of number of animals active with either the predicted or actual high tides, which frequently were not concurrent. All high tides during this period occurred at night. Activity during the daytime high tides in April and May 1982 at both sites also showed no consistent tidal activity patterns. Although no precise correlation of activities with either predicted or actual high tide occurred, activities ceased and the animals buried if the flats became exposed at low tide. While total numbers of crabs observed were comparable for both day/spring and night/fall tides on the intertidal flat, total numbers on the beach were an order of magnitude greater during the day/spring tides than during the night/fall high tides.

Figure 6 shows tidal activity patterns of juvenile *Limulus* (mean carapace width less than 8 cm) over six low tides in September 1982 on the intertidal flat. Temperature ranged from 22–29°C, salinity was 26–30 ppt and depth ranged from 8–42 cm. Activity does not peak at the predicted low tide but is clearly inversely correlated with the water depth. Again, the actual time of low water does not often coincide with the predicted time of low tide.

*Other Observations.*—Foraging adult *Limulus* disturb the sediment extensively as they burrow along approximately one third buried in the sand. Frequently, the

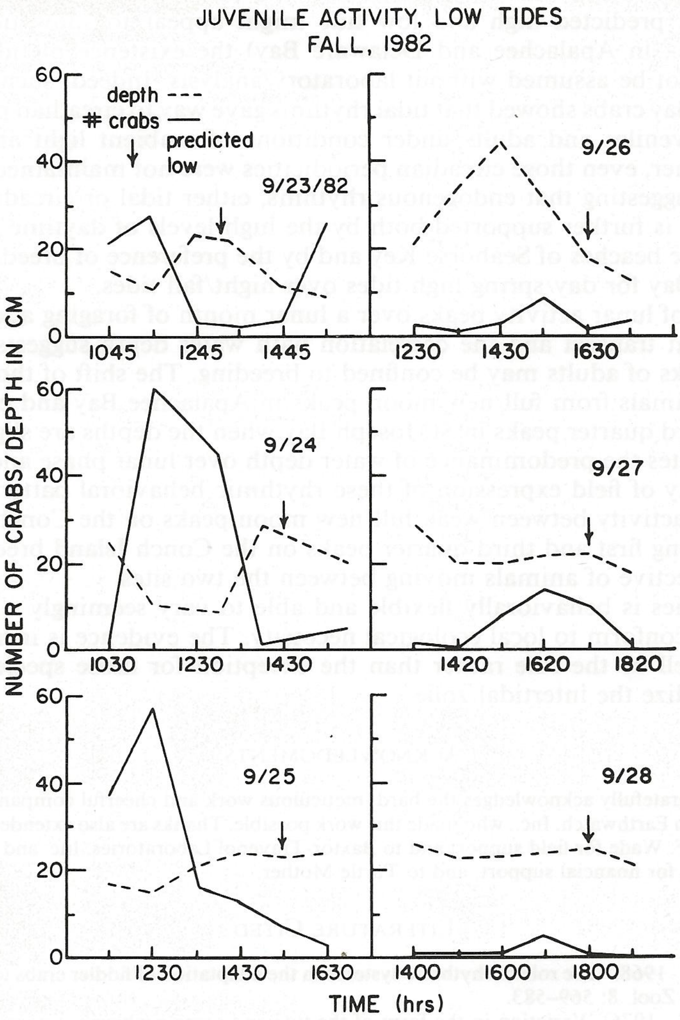



Figure 6. Activity of juvenile *Limulus* over predicted low tides for 6 days in 1982.

opisthosomal region remains slightly above the substrate surface. Juvenile pinfish (*Lagodon rhomboides*) and blue crabs (*Callinectes sapidus*) were frequently observed to accompany such horseshoe crabs and feed on particles of detritus and smaller organisms stirred into the water column. Both species would take shelter underneath the horseshoe crab's opisthosoma at the approach of an observer and pinfish actively and aggressively defended their horseshoe crab "territory" against other pinfish.

## Discussion

Juvenile and adult *Limulus* in St. Joseph Bay do not exhibit clearcut daily tidal activity patterns coinciding with times of predicted, astronomical low or high tides as do those in Apalachee and Delaware Bays. Rather they seem to respond to water depth. While populations in areas where high and low water corresponds closely with predicted high and low tide might appear to show tidal activity patterns (i.e., in Apalachee and Delaware Bay) the existence of tidal rhythms clearly cannot be assumed without laboratory analysis. Indeed, such analysis of Apalachee Bay crabs showed that tidal rhythms gave way to circadian periodicities for both juveniles and adults under conditions of ambient light and constant depth. Further, even those circadian periodicities were not maintained under DD in adults, suggesting that endogenous rhythms, either tidal or circadian, are not active. This is further supported both by the high levels of daytime breeding in adults on the beaches of Seahorse Key and by the preference of breeding crabs in St. Joseph Bay for day/spring high tides over night/fall tides.

The lack of lunar activity peaks over a lunar month of foraging adult crabs on the 1980 flat transect and the correlation with water depth suggests that lunar activity peaks of adults may be confined to breeding. The shift of those peaks of breeding animals from full/new moon peaks in Apalachee Bay and elsewhere to first and third quarter peaks in St. Joseph Bay when the depths are slightly higher again indicates the predominance of water depth over lunar phase and illustrates the flexibility of field expression of these rhythmic behavioral patterns. The oscillation of activity between weak full/new moon peaks on the Conch Island flat and the strong first and third quarter peaks on the Conch Island breeding beach may be reflective of animals moving between the two sites.

This species is behaviorally flexible and able to vary seemingly rigid activity patterns to conform to local ecological necessity. The evidence is increasing that this may well be the rule rather than the exception for those species that successfully utilize the intertidal zone.

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ADDRESS: *Panacea Institute of Marine Science, Panacea, Florida 32396.*