Orientation of *Limulus polyphemus* in the Vicinity of Breeding Beaches

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1) Horseshoe crabs, *Limulus polyphemus*, emerge in mating pairs on sandy beaches to lay eggs then return offshore. Rapid offshore locomotion is exhibited during escape responses. A variety of potentially suitable orientational guideposts exist in the near-shore environment, including visual cues, bottom slope, wave surge and currents to direct such movements.

2) A series of experiments was performed in which horseshoe crabs were tagged with styrofoam floats and released in the vicinity of known breeding beaches under varying conditions of surge, current, bottom slope and turbidity. The direction of movement (interpreted as an escape movement) was recorded at one minute intervals for ten minutes and the last five bearings of each crab were averaged and plotted.

3) The direction of movement correlated most closely with the direction of wave surge even in the presence of bottom slope and currents. Horseshoe crabs distributed randomly in the absence of wave surge although they typically maintained relatively straight paths.

INTRODUCTION

Between approximately April and June of each year, depending on latitude, horseshoe crabs, *Limulus polyphemus*, emerge in large numbers to mate and lay eggs on sandy beaches of the eastern Gulf of Mexico and the Atlantic Coast to Cape Cod. Single males intercept and attach themselves to females in approximately 1 meter of water during spring high tides, after which the pair emerges onto the beach and deposits eggs in the sand at the high tide mark. Following egg deposition, taking up to two hours, the pair returns to the water and moves an unknown distance offshore.

Little is known about the orientational mechanisms directing this behavioral sequence. Research on the sensory capabilities of *Limulus* includes work by Waterman (1950; 1954a,b) demonstrating the sensitivity of the lateral eye to ultraviolet light. Wald and Krainan (1963) extended this work with electroretinograms of the median eye of young *Limulus* and found they too are sensitive to ultraviolet light. Spectral sensitivities of the lateral, ventral and median

eyes were measured (Millecchia and Mauro, 1969a,b; Nolte and Brown, 1969, 1970, 1972), while attempts to measure the animals' ability to discriminate visual patterns have been inconclusive (Campenhausen, 1967). Adolph (1971) recorded optic nerve spikes underwater and found continuous optic nerve activity under dim light in turbid water. Lall and Chapman (1973), working with intact animals in nature, found positive responses to full spectrum sunlight mediated through the lateral eyes and dorsal ocelli. Positive responses to near ultraviolet were shown to be mediated by the dorsal ocellus.

Work on the non-visual sensory systems of *Limulus* has included descriptions of chemoreceptors associated with respiration, responses to chemical, thermal, tactile and proprioceptive stimuli and descriptions of articular proprioceptors of the walking legs (Barber, 1950, 1956, 1958, 1960; Waterman and Travis, 1953; Pringle, 1956; Barber and Segel, 1960; Hayes and Barber, 1967; Ward, 1969). Eagles (1973) described the anatomy and innervation of the tailspine system relative to the behavioral function of the telson. Most of the literature, however, treats receptor physiology rather than exploring their functional significance to intact horseshoe crabs. Nevertheless, they establish a broad spectrum of possible modes of reception for guidance stimuli.

Several different physical phenomena of the near-shore environment are potentially available for orientational purposes by *Limulus*. These include bottom slope, bottom contour, wave surge and/or the resultant ripple patterns on the bottom, light gradients, and current. We investigated the movements of sexually mature horseshoe crabs while measuring concurrent physical factors under varying conditions at several known breeding beaches. At this time, *Limulus* exhibit clear onshore/offshore directionality in their movement patterns, facilitating analysis of orientation mechanisms.

MATERIALS AND METHODS

Seventeen experiments were conducted using a total of 148 horseshoe crabs, hereafter referred to as crabs, 15 of which were collected at Hilton Head, S. Carolina and the remainder from the Panacea, Florida area. Crabs were collected as they emerged onto breeding beaches in pairs and were held for periods of a few days to two weeks. They were then released individually in approximately $\frac{1}{2}$ meter of water adjacent to the shoreline, with a plastic surface buoy attached to the left posterior spine of the opisthosoma. Each crab was released from the surface and allowed to settle to the bottom and right itself. Once it moved away from the release point, compass bearings were taken on the surface buoy at 1 minute intervals for 10 minutes, using a prismatic hand bearing compass accurate to 2°. We observed no obvious impairment of the crabs' ability to maintain a steady course in any given direction while pulling a buoy.

Ten crabs were released in most experiments, while the smallest number used was five.

Experiments were conducted on both rising and falling tides. Midway through each experiment, a small styrofoam surface buoy was released and tracked to record the presence and direction of any current moving counter to the wave surge. The buoy was made as small and flat as possible to minimize the element of wind drift. High turbidity and surge oscillations obviated other current measuring techniques.

The experiments were conducted at various times of day between 0800–1800 hours in September–November, 1973, and May, 1974. A sphyrion identification tag was placed on each crab and a record was kept of sex, size, condition of lateral eyes and of carapace fouling. We used crabs with both normal and with naturally damaged or destroyed lateral eyes. Individuals were tested only once and were not recovered except in the experiments with current, where use of a boat made recovery and retesting of some crabs possible.

Seven of the seventeen experiments were conducted with wave heights of approximately 30 cm to 60 cm, as measured from trough to crest. Five were run in calm, still water while three experiments involving 22 crabs were also run without waves but in the presence of a strong tidal current.

Of the seven experiments with waves present, four were run off Mashes Sands Beach, Wakulla County, Florida, where the sand bottom is nearly level with a depth at high tide of approximately 1 meter. Three 30 meter transects made perpendicular to the shoreline revealed an average offshore slope of 0.7° due east (90°) at this site. Three experiments were run off a beach at the St. Joe Paper Company station at St. James, Franklin County, Florida, where the bottom was found to slope offshore 165° at a rate of 8.3° for the first 24 meters and then level off at a depth of approximately 2.1 meters (Figure 1). Thus the slope of the "level" beach was less than 10% of that of the beach at St. James.
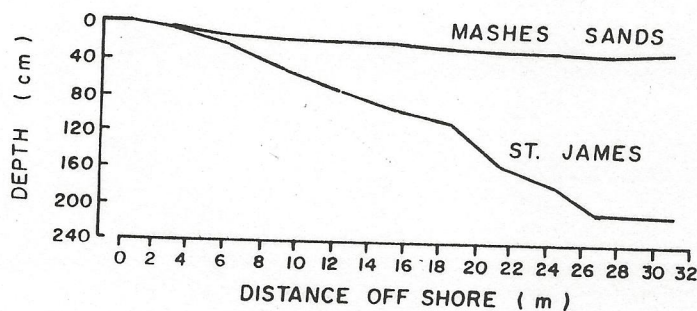

FIGURE 1   Shoreline slopes of the two experimental sites used to test orientational responses of *Limulus* showing onshore–offshore contour.

In all experiments with wave action, the water was sufficiently turbid that crabs released at a depth of 1 meter were not visible on the bottom. Surge on the bottom was detected at a depth of 1 meter in association with wave heights of 30 cm or more. Its presence was noted by visually monitoring a displacement indicator consisting of a metal dial embedded in the bottom with a freely swinging indicator needle just above the substrate that moved back and forth with the passage of each wave (May, 1973).

All five experiments without surge were conducted on level bottoms in a depth of approximately 1 meter. There the water was sufficiently clear that crabs were visible on the bottom.

Three experiments done with strong current, but no waves, were run in Dickerson Bay, Panacea, Florida. The crabs were released in approximately 2 meters depth from an anchored boat. The procedure was otherwise the same as outlined above. Current strengths were subsequently measured at 25 cm/sec on similar tides in the same location using a Gurley 665-E current meter.

In addition to the 15 experiments described above, two other control tests were made. One was conducted with surge at Mashes Sands with seven crabs whose vision was impaired by coating both lateral and median eyes with black India Ink. Their orientational performance was then compared to that of crabs in preceding trials whose eyes had not been artificially altered. To control for the possibility that the crabs derived orientational information from the drag of the surface buoy, we conducted another experiment using five untethered crabs with eyes painted as above. These were released approximately 1 km offshore from Panama City Beach, Florida, in 5 meters depth, each carrying a 70 KHz ultrasonic transmitter (see Herrnkind and McLean, 1971) glued to the prosoma. They were followed by a SCUBA diver, using a directional ultrasonic receiver, who took bearings of the direction of movement. Ten compass bearings were taken at 1 minute intervals as with the surface experiments.

RESULTS

Upon release, a crab generally landed on its dorsal surface, then righted itself and either moved away from the release point immediately or attempted to bury in the sand. In the latter case, we repeatedly lifted the crab to the surface of the sand until it ceased attempting to bury and began to move away from the release point. Both behaviors are typical escape responses; similar behavior was often noted when crabs on the beach were disturbed by humans. The movement direction of crabs away from a release point, or a site of disturbances appeared similar to movements approaching or leaving a beach when mating.

Figure 2 shows the final positions of crabs in the seven experiments with surge present. The final positions represent the mean of the last five compass bearings
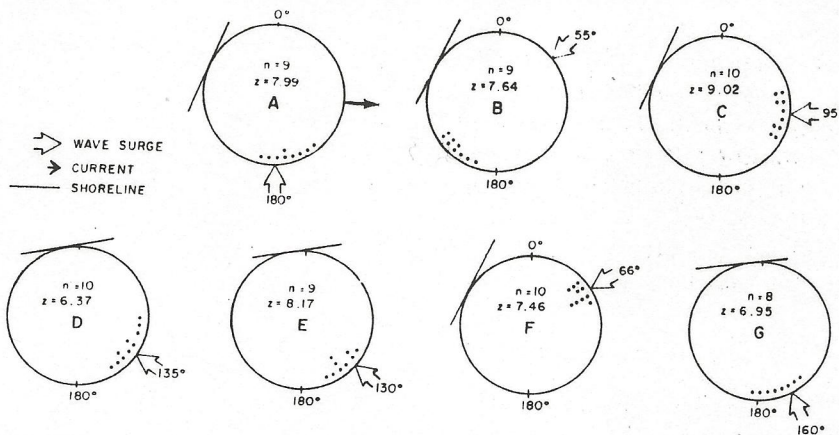
FIGURE 2 Distribution of horseshoe crabs released in the presence of wave surge: shoreline 7°–187°, Mashes Sands; shoreline 80°–260°, St. James. Direction of increasing slope and depth essentially perpendicular to shoreline. The Z values show statistical significance, $p < 0.01$, indicating a preferred response direction into the surge. Values of Z corresponding to $p \leq 0.01$ are n = 8, Z = 4.2; n = 9, Z = 4.25; n = 10, Z = 4.29. Mean vectors: A = 169°, B = 231°, C = 90°, D = 135°, E = 141°, F = 66°, G = 168°.

taken on each crab and in all cases indicates their positions at the greatest distance from the starting point. Use of the last five bearings, rather than just the last, serves to show path variability; this avoids erroneously recording an angular or zigzag path as a single "vanishing point". We did not include the first five bearings since these were the most likely to vary because of the previous handling of crabs and because the readings were most subject to parallax error.

Only in Experiment A was a detectable surface current running in a direction other than that of the surge. In that case, the waves approached from 180°(S) while the current ran perpendicular to the surge or toward 90°(E). Crabs clearly moved in the direction of the oncoming surge rather than the current in this instance. Experiments A, B, C and F were conducted at Mashes Sands (relatively level bottom) whereas Experiments D, E, and G were conducted at St. James (steeply sloping bottom). In all cases A–G, the wave heights were estimated at 30–60 cm (trough to crest). However, in Experiment D, waves decreased during the course of the testing and the second five crabs showed increasing deviation from the surge direction, with the exception of the tenth crab.

All crabs moved into the waves except in Experiment B where they moved with the waves and onto the shore. The crabs buried upon reaching the beach rather than pairing and proceeding with normal reproductive behavior. Final positions in that case represent the crabs' landing points on the beach.

The results of all experiments were examined for preferred direction with the

Rayleigh Test (Batschelet, 1965) and were found to be significant at the 0.01 level. Application of the V test (Batschelet, 1972) indicated that the sample bearings did not differ from the hypothesized preferred direction; i.e., the direction from which the waves were approaching (or the opposite bearing in Experiment B). The V test is a modification of the Rayleigh Test in which the distribution is significant only with adequate clustering about the predicted direction.

Figure 3 shows the crab distributions after 10 minutes in control runs without surge and without detectable current (except in run E). The Rayleigh test
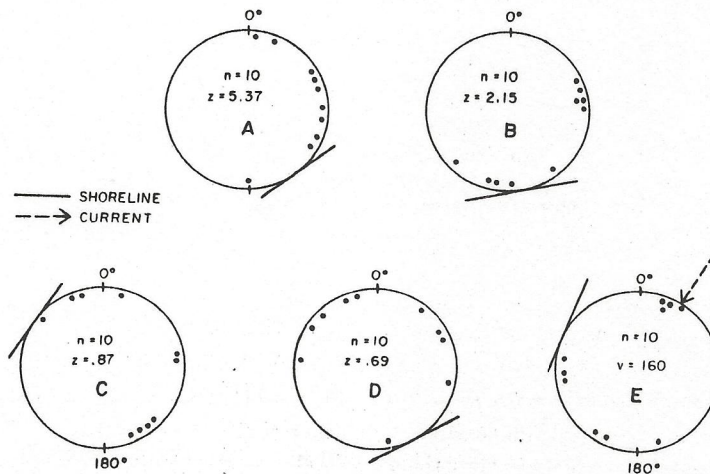

FIGURE 3 Distribution of horseshoe crabs released in the absence of wave surge, indicating no preferred direction.

indicated no preferred direction with the exception of Experiment A. Although crabs in A showed a statistically preferred direction, the scatter is much greater than under conditions of surge. Since Experiment E appears to represent a weakly bimodal response, the Rayleigh test was considered inappropriate. However, application of the Rao test (Batschelet, 1972) indicated random distribution.

Three experiments run under conditions of strong current but no waves, are presented in Figure 4. Although many of the crabs appeared to move either with or against the current to some extent, the final distributions were statistically random.

Figure 5 shows that the ability to orient was unaffected when the crabs' vision was artificially impaired. Figure 6 shows the responses of blinded, sonically tagged crabs; they oriented into the surge ($p < 0.01$) as did those released directly from shore with surface buoys.
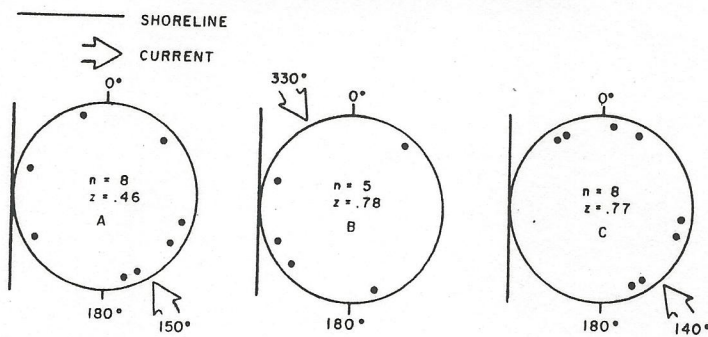
FIGURE 4   Distribution of horseshoe crabs released in the absence of wave surge and the presence of current: shoreline 5°–185°. Dickerson Bay. There was no statistically significant preferred direction although certain individual crabs do appear to move either with or against the current.
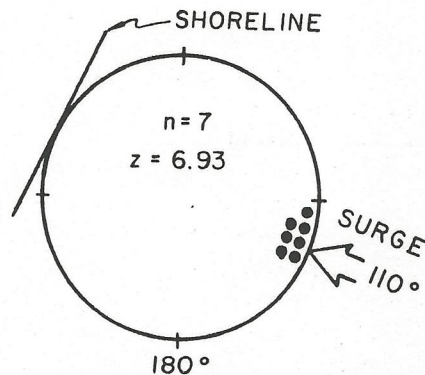

FIGURE 5   Distribution of visually impaired horseshoe crabs released in the presence of wave surge. The responses indicate a preferred direction into the surge. Value of Z, $p \leq 0.01$, is 4.2 for n = 7. Mean vector = 108°.

TABLE I

Surge response relative to sex and lateral eye condition[a]

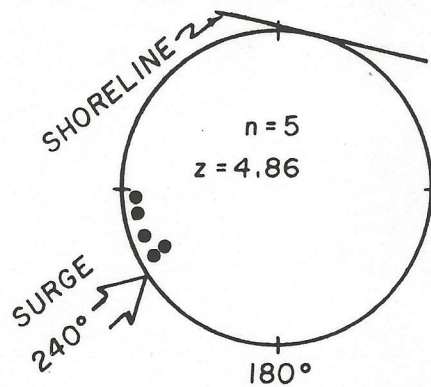|	No.	Z (Raleigh Test)	U (V Test)	Signif. Level
All males	43	39.2	8.9	0.0001
All females	12	8.6	4.1	0.0001
Opaque eye	24	22.3	6.7	0.0001
Partly opaque eye	10	9.7	4.4	0.0001
Clear eye	21	15.9	5.6	0.0001

[a] —surge trial D omitted.

F

FIGURE 6 Distribution of diver-tracked, sonically tagged horseshoe crabs (blinded) released with wave surge present. A statistically significant preferred direction corresponding to the surge direction is present. Value of Z, $p \leq 0.01$, is 3.9 for n = 5. Mean vector = 253°.

Table I presents a breakdown by sex and by condition of the lateral eyes, of the responses of 55 crabs in six of the experiments with surge. Experiment D was excluded due to the moderation of surge conditions in the course of the test. The table analyzes the responses of male versus female, and of crabs with clear lateral eyes versus those with partly or completely opaque lateral eyes in terms of their relative ability to orient relative to the surge. For each of the five categories, surge and crab response bearings were normalized to 0° and the distribution was tested with the Rayleigh and V tests. In all cases the sample bearings did not differ from the surge direction. It was concluded that neither sex nor condition of the lateral eyes affected the ability to orient.

Table II presents the four control and three surge experiments in which the number of buoys still in sight at the end of all runs was recorded. The crabs were clearly more prone to move far enough to disappear from sight after 10 minutes in the presence of surge than when in calm water. The buoys were

TABLE II

Limulus still in sight at end of all runs

Trial	Runs with Surge			Runs without Surge		
	No. Used	No. Sighted at End	%	No. Used	No. Sighted at End	%
1	9	3	33%	10	10	100%
2	10	1	10%	10	10	100%
3	10	3	30%	10	10	100%
4				10	8	80%
		% = 24.3%			% = 95%	

sufficiently large that they were as readily seen under surge conditions as in calm.

The effect of bottom slope in relation to surge is presented in Table III. Of 29 crabs used in three experiments on level bottom at Mashes Sands exclusive of Experiment B in which crabs move onto shore, 25 remained within 15° of

TABLE III

Limulus orientation to surge on level and sloping substrate

	Location			
	Mashes Sands: Level Bottom 25 trials		St. James Beach: Sloping Bottom 18 trials	
Limulus Became:	No. crabs	%	No. crabs	%
Increasingly accurate	12	48%	2	11.1%
Less accurate	13	52%	15	83.3%
Unchanged	0	0%	1	5.6%

the surge direction. Of these 25, 13 (52%) deviated more from the surge direction in the last five recordings of their position as they moved away from the release point than in the first five recordings, while 12 (48%) became more accurate. In the three surge experiments at St. James, 18 crabs oriented into the surge. Of these 18, 15 (83.3%) became less accurate, two (11.1%) became more accurate and one (5.6%) showed no change. Thus, crabs in this area were more prone to deviate from the direction of oncoming surge as they moved away from the starting point.

Ten crabs from the experiments with surge and ten crabs from the control group without surge were arbitrarily chosen and their individual paths examined for oriented versus random movement using Hodges test (Batschelet, 1972). Twenty sets of points were plotted in Figure 7 and Figure 8 for surge and control groups respectively. Crabs in both groups were statistically strongly oriented at the 5% level. However, the range of bearing variability for all crabs tested without surge was 60° ± 28° as opposed to only 20° ± 7° for animals tested with surge. Bearing variability is here defined as the maximum variation in bearing within one trail. Thus, although animals in both groups were statistically oriented, less deviation did in fact occur under surge conditions.

No differences were noted between responses of Atlantic and Gulf coast *Limulus* in any experiments.
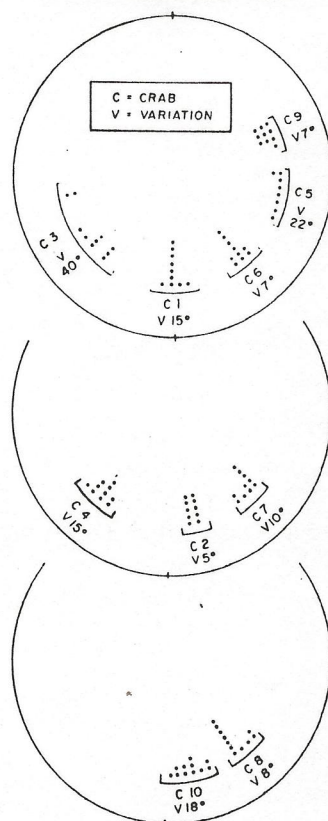
SURGE CRABS
MEAN VARIATION 15.2°

FIGURE 7   Individual trials of ten horseshoe crabs shown as bearings at one minute intervals (wave surge present). Paths are relatively straight as well as oriented into the surge.
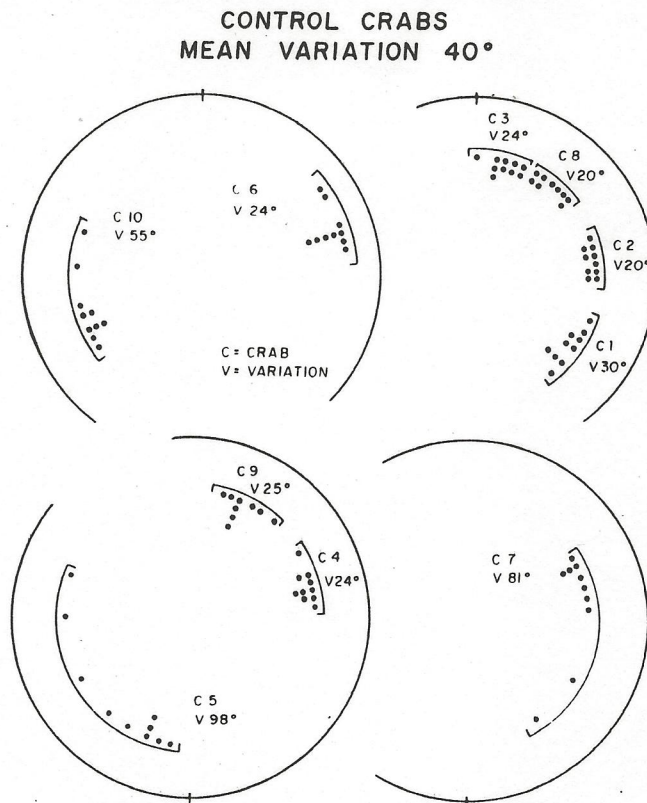
CONTROL CRABS
MEAN VARIATION 40°

FIGURE 8 Individual trials of ten horseshoe crabs shown as bearings at one minute intervals (wave surge absent). Paths indicate directionality but exhibit greater variability than those under surge conditions.

DISCUSSION

In both surge and control experiments, crabs moved in a fairly straight path in whatever direction chosen, indicating some degree of orientation. Totally disoriented animals, in the absence of any apparent cues, wander in circular patterns (pers. observation). In experiments with surge present, they clearly moved into or (in one case) with the waves. Thus, mature *Limulus* exhibit a definite orientation to some physical component related to waves. The responses of blinded animals in the absence of surge were not examined. Although Adolph (1971) recorded optic nerve activity from crabs in the field under poor light conditions, the high level of turbidity associated with water adjacent to breeding beaches seems sufficient to preclude any dynamic gradient of light

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intensity suitable for orientation in that situation. Only an even diffuse light is seen by the human eye underwater in such conditions. Visual orientation under other circumstances is certainly not precluded, however. That the orientation is mainly non-visual in submerged movements, immediately off-shore from breeding beaches, is also indicated by the oriented responses of animals with both median and lateral eyes coated with India Ink; by the similar responses of crabs with intact and with naturally damaged lateral eyes; and by the fact that animals in clear water with optimal light conditions did not have a preferred direction of movement in the absence of surge, whereas animals in highly turbid water in the presence of surge were highly oriented. Finally, large numbers of crabs were observed successfully approaching a beach, emerging and laying eggs, and returning to the water despite badly eroded lateral eyes.

Wave surge, the oscillation of water near the substrate as a wave passes over at the surface, seems the most promising orientational possibility. A major feature of such nearshore environments, surge can provide a generally reliable cue for moving either on or offshore in the vicinity of a beach, since swells moving obliquely into shallow water refract toward shore. It has been repeat-edly observed by the senior author that the greatest number of horseshoe crabs emerge on those spring high tides that coincide with high wind and maximum conditions of wave surge. The crabs also showed a clear tendency to move faster and farther in the 10 minute observation period when surge was present than when the water was calm.

The increasing path variation of crabs tested on a rapidly sloping bottom may result from the attenuation of surge as the animals move into greater depths or from the absence of slope as the bottom became level offshore, or both. Path variation did increase somewhat on the more level bottom of Mashes Sands as well, however, indicating some other mechanism may also be involved. Directions at Mashes Sands (Figure 9) indicated that the surge direction dominated any response to the slight degree of slope present. Applica-tion of the Rayleigh test to all experiments there indicated no overall preferred direction independent of the various surge directions. At the St. James Beach, however, the slope and surge directions coincided and animals moved directly offshore. Further testing on steeply sloping bottoms in the absence of any surge and with surge from a variety of directions is necessary to examine the relative importance of the two factors. Slope might well be of importance in longer movements from depths of 20 meters or more into shallow water where surge becomes effective to the bottom of the water column.

Sand ripples produced on the bottom by wave surge might also provide orientational information when surge itself has momentarily abated. They are, however, a direct result of wave surge and usually are aligned with the direction of the wave surge at any given time. Experiments under more controlled
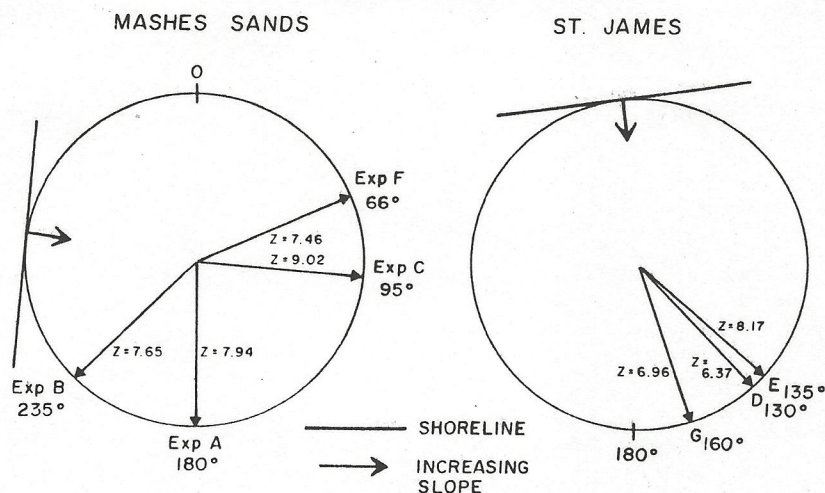
MASHES SANDS   ST. JAMES

FIGURE 9 Final distributions of horseshoe crabs in all surge experiments at Mashes Sands and St. James. Surge direction predominated over offshore direction at Mashes Sands while at St. James they coincided.

conditions will be necessary to differentiate the influence of ripples apart from the wave surge itself.

Although surge, and perhaps bottom slope, appear to be orientational guideposts in the vicinity of beaches, the fact that the crabs move in a straight line when released in the field both with and without surge and on level bottoms suggests additional guidance mechanisms. Furthermore, juvenile crabs on tide flats, the only other phase of the life cycle that has been observed in the field, do not appear to orient to surge in any degree. The overall orientational behavior of horseshoe crabs will likely prove to depend on a variety of mechanisms, the identification of which must await further data on the types of behavior and activity patterns of horseshoe crabs offshore.

It is probable that wave surge, as a persistent and characteristic feature of the marine environment, will prove to be of widespread use by a number of species as an orientational cue. A consistent directional response to surge has been demonstrated in the spiny lobster *Panulirus argus* (Herrnkind and Mc-Lean, 1971; Herrnkind, in prep.) and has been postulated for a number of other marine species.

The sensory basis of the surge response has yet to be defined. Hydro-dynamically, however, surge is merely a current oscillating over a short distance, and many animals known to sense water currents might well perceive surge as well. A number of external ciliary and setose mechanoreceptors have been described from various species of crustacea which respond to a variety of types of water movement (Laverack, 1962, 1963; Mellon, 1963; Clarac and

Vedel, 1973). Internal proprioceptors are also possible candidates for surge reception since they must direct compensation for forces tending to displace the animal. A number of different types of walking leg proprioceptors have been described from *Limulus* (Hayes and Barber, 1967) and may well represent sites for surge reception.

To further verify and quantify the response of the horseshoe crab to surge, and to investigate other potential orientational stimuli, we are conducting experiments under controlled conditions in a wave generating test-tank. The test-tank permits analysis of responses to completely isolated stimuli as well as known combinations of factors.

Acknowledgements

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