

ULTRASONIC TELEMETRY OF SMALL-SCALE MOVEMENTS AND MICROHABITAT SELECTION BY MOLTING BLUE CRABS (*CALLINECTES SAPIDUS*)

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ABSTRACT

We have designed a new ultrasonic transmitter to track free-ranging premolt blue crabs and signal the event of ecdysis. The transmitter (15 g in air, 5 g in water) operates for 6-8 weeks on a small lithium battery, producing 75-kHz tracking pulses at about 1-sec intervals. It is attached to the crab's carapace, with a magnetic reed switch placed near the line where the carapace will separate from the abdomen as the molting crab backs out of its old shell. A magnet attached to the abdomen pulls away at ecdysis, signalling the event by allowing the switch to open and doubling the pulse rate of the transmitter. During field tests with 11 premolt male blue crabs in a small tributary of central Chesapeake Bay, the devices allowed us to assess movement patterns and selection of microhabitats for molting at scales of <1 m. Even with this small sample size several trends were evident. Distance traveled per day (average 130 m, range 0-569 m) and movement patterns were highly variable in the days prior to molt. Crabs moved more during the day, and molted by day or night in roughly equal proportions. All crabs selected shallow (<0.5 m) marsh-lined banks of a tidal creek for ecdysis. This study, the first in which arthropod molting has been telemetered in the field, provides a technique applicable to intra- and interspecific comparisons with other large species.

Although premolt and ecdysis occupy a small proportion of a crustacean's life, they represent a critical life history event required for growth and, in females of some species like blue crabs (*Callinectes sapidus*), for mating. While their armor is soft, crustaceans cannot defend themselves and are vulnerable to injury, predation, and cannibalism (Reaka, 1976; Botsford and Wickham, 1978; Laughlin, 1982; Lipcius and Herrnkind, 1982). Most decapod crustaceans reduce and eventually cease feeding during the period immediately prior to ecdysis through early postmolt (Van Engel, 1958; Hartnoll, 1982).

Because decapod crustaceans tend to hide during ecdysis, we know little about the microhabitats selected for molting in nature, and the process of site selection. The lucrative "soft crab" fishery for fresh postmolt blue crabs provides some of the best information available for any species on habitat selection for ecdysis (see Warner, 1976; Millikin and Williams, 1984, for summaries). According to fishermen's lore, male "peelers" (premolting crabs) tend to be found in shallow water, often in nearshore beds of submerged vegetation or up tidal creeks, where they may be caught with beach seines or dip nets. Female peelers are thought to seek out structures or submerged vegetation, often in deeper, more open water, where they are taken in "peeler pots" (unbaited traps) or "jimmy pots" (traps using intermolt adult males as sexual attractants). Both sexes can be caught by trawling or dredging in grass beds, or in "peeler pounds"—mesh fences perpendicular to shore that direct premolt crabs into a box net in shallow (<1 m) water.

Information available from the fishery is largely anecdotal and could reflect the premolt crabs' accessibility to crabbers (catchability) more than the crabs' actual patterns of habitat choice and utilization. Several recent quantitative studies, however, also indicate habitat partitioning. Juveniles are found in greater abundance in submerged vegetation than on unvegetated substrate, where they and molting blue crabs appear to find some protection from predation (Tagatz, 1968;

Heck and Orth, 1980; Heck and Thoman, 1981; 1984; Kennish et al., 1984; Penry, 1982; Orth et al., 1984; Leber, 1985; Wilson et al., 1987). In one of the best documented cases of habitat partitioning by molting crustaceans, Hines et al. (1987) showed that males utilize salt creeks for molting in areas of Chesapeake Bay lacking submerged vegetation, while females appear to remain in open-water basins for ecdysis.

Observation of exact microhabitats that blue crabs select for molting, and determination of detailed behavioral responses leading to selection of those sites, is rendered very difficult by the nature of the estuarine environment. The water is usually so turbid that visibility is limited to a few centimeters. Blue crabs have good vision, are extremely alert, and can swim much faster than a scuba diver. All of these considerations preclude direct observation of the behavior of unrestrained premolt crabs during microhabitat selection. To compound the difficulties, the fragile exuvia are easily moved and broken in nature, and are consumed by intermolt blue crabs (possibly for the calcium). Consequently, cast shells must be located promptly to find out exactly where ecdysis occurred.

Ultrasonic telemetry has given unprecedented insights into the movements and foraging activity of blue crabs in Chesapeake Bay (Hines and Comtois, 1985; Wolcott and Hines, 1989a). In a similar approach, we have developed an ultrasonic "molt-signalling" transmitter to circumvent the problems mentioned above, and for the first time provide information about selection of microhabitats for ecdysis by free-ranging arthropods. In a feasibility study the devices were used to test the hypothesis that male crabs in a subestuary of central Chesapeake Bay preferentially select microhabitats within a tidal creek to molt. This study demonstrated that the technique can provide as detailed a picture of microhabitat selection behavior as the investigator's endurance permits.

MATERIALS AND METHODS

This study was conducted during July–August 1987 at the Smithsonian Environmental Research Center on the Rhode River, a small subestuary in the mesohaline zone of Chesapeake Bay (Fig. 1). Salinities in the shallow (maximum depth = 4 m) subestuary fluctuate seasonally between 4‰ in spring and 15‰ in fall. Sediments in the study area are mostly fine silty mud with no submerged aquatic vegetation. The study focused on blue crabs moving in Muddy Creek, the main freshwater tributary of the subestuary (Fig. 1). The creek channel averages 1.5 m deep and is about 40 m wide at its mouth, where it opens into a broad (500 m), shallow (1.0 m) area before flowing into the head of the Rhode River. Mixed semidiurnal tides with a vertical range of about 0.5 m influence the creek, which is never emptied completely. Cattail (*Typha angustifolia*) and salt hay (*Spartina patens*) marshes line the creek banks and are flooded on 70% of high tides. Water temperature in the creek cycles seasonally from 0°C in January to 33°C in July. Salinities at the mouth of the creek fluctuate from 0‰ in April to 14‰ in October, and those 1 km upstream are similar. Large numbers of male blue crabs utilize the creek as a molting habitat in summer months (see Hines et al., 1987 for further details).

The ultrasonic transmitters (15 g in air, 5 g in water) produce a regularly recurring signal, timed by CMOS digital logic (adapted from Wolcott, 1979), that serves as a locating beacon. The pulse rate changes to provide a distinctive indication of ecdysis. The ultrasonic output pulses are 10–15 ms long, repeated at 1-s ("pre-molt") to 0.5-s ("post-molt") intervals, at a frequency of about 75 kHz. The transmitters are fabricated on printed circuits (1.5 cm × 3 cm), using surface-mounted components. The output transducer, a piezoceramic tube 12.5 mm diameter × 6.3 mm long, is driven by the buffered signal of either an LC (Hartley) or crystal (Pierce) oscillator. Average current drain is about 100 microamps, and a 160-milliamp-hour lithium cell (CR 1/3 N) provides power for about 6–8 weeks' operation. A functional diagram of the transmitter is presented in Figure 2; details of the electronic design and construction are presented elsewhere (Wolcott and Hines, 1989b).

The transmitter uses separation of the carapace from the abdomen (where the crab backs out of its old shell) as an unequivocal indicator of ecdysis. To detect the separation, a magnetic reed switch is fastened to the carapace and held (electrically) closed by an apposed magnet fastened to the ventral exoskeleton. This transducer has the advantage of consuming no power itself. As a molting crab backs out of the old shell, the old carapace is lifted away from the lower exoskeleton, the magnet is pulled

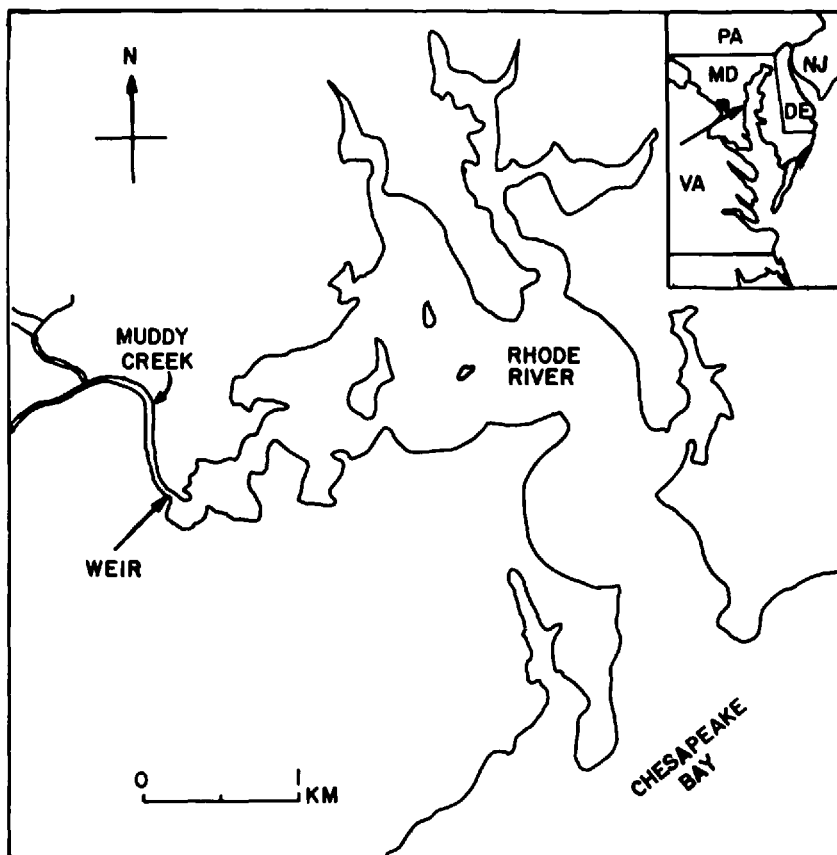


Figure 1. Location of the study site in the middle Chesapeake Bay. Muddy Creek, at left, is the major freshwater input to the Rhode River.

away from the switch, and the circuit is opened. This switches a capacitor, roughly doubling the pulse repetition rate of the transmitter when the crab molts. Transmitters are packaged in lengths of 16-mm diameter vinyl electrical insulation sleeving (Alpha PVC-80- $\frac{3}{8}$ "") with the ends glued shut. To bring the reed switch outside the package, its leads are embedded in the glue joint at one end. The package is filled with mineral oil as an insulating and sound-transmitting medium.

The transmitters were fastened to the crabs by loops of wire passing around the lateral spines and through holes punched in the glued ends of the vinyl tubing (Fig. 3). The reed switch at the end of a pair of flexible wires was laid along a 2-cm length of plastic soda straw and embedded in wax. Using cyanoacrylate adhesive (Dexter Hysol 2-C-500) and a strip of thin rubber, this assembly was affixed to a crab's carapace. The magnet was cemented to a piece of 6.8-kg test monofilament fishing line with adhesive and thinly covered with wax to prevent rust. Once the magnet was slid into the soda straw adjacent to the switch, the end of the monofilament was glued to the crab's abdomen with another small piece of rubber. Attachments of the switch assembly and magnet/monofilament had to be sufficiently close together that the monofilament could not snag, nor the magnet escape from the straw, prior to ecdysis. When ecdysis occurred, the springiness of the monofilament pulled the magnet away from the carapace (Fig. 4). This prevented the magnet from re-entering the straw and closing the switch again, even if the upper and lower portions of the exuvium fell back together once ecdysis was complete.

Laboratory tests with premolt crabs in aquaria confirmed that the transmitters operated physically and electronically as predicted. The flexible packages conformed to the animals' backs and did not appear to hinder swimming, feeding, or agonistic behaviors. Our extensive prior use of similar transmitter packages on free-ranging blue crabs also showed no significant effects on their feeding, locomotory, burying or sexual behaviors (Wolcott and Hines, 1989a).

Field tests were conducted in August 1987 with 11 male premolt crabs collected during routine

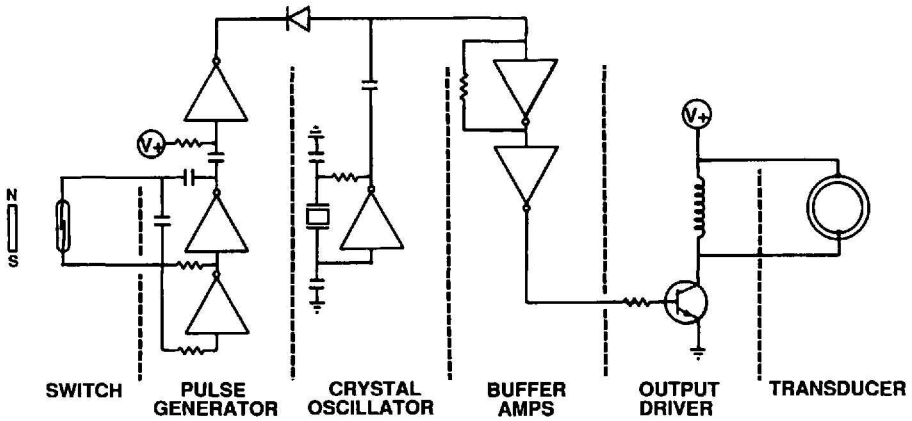


Figure 2. Functional block diagram of the "molt/tracking" transmitter.

sampling at a weir located at the mouth of Muddy Creek (Fig. 1; see Hines et al., 1987, for description). Molt stage was assessed by apolysis and pigmentation changes visible in the penultimate segment of the swimming leg (5th pereopod) described in Warner (1976) as: "white sign" = 7-14 days premolt; "pink sign" = 3-6 days premolt; or "red sign" = 1-2 days premolt. While awaiting fitting with transmitters in the laboratory, crabs were held in buckets containing about 3 cm depth of creek or river water. Within 24 h the prepared crabs were released back into Muddy Creek within 50 m upstream of the weir. Until they molted, the crabs were located each morning and evening from an inflatable dinghy using a directional hydrophone and ultrasonic receiver. The location of each site,

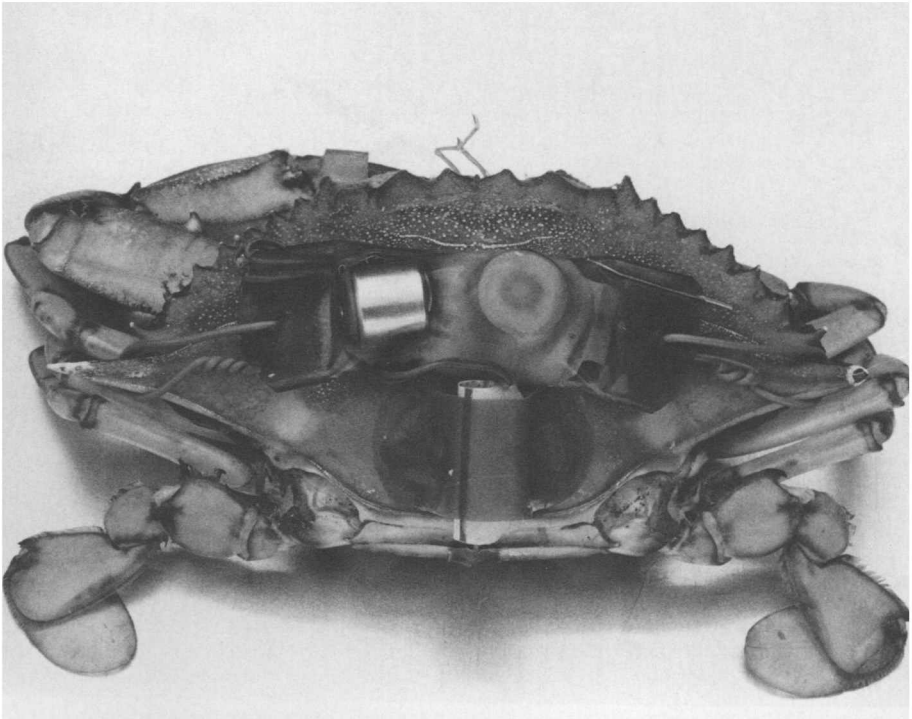


Figure 3. Blue crab fitted with "molt/tracking" transmitter. Transmitter package does not appear to substantially affect crabs' balance or locomotion.

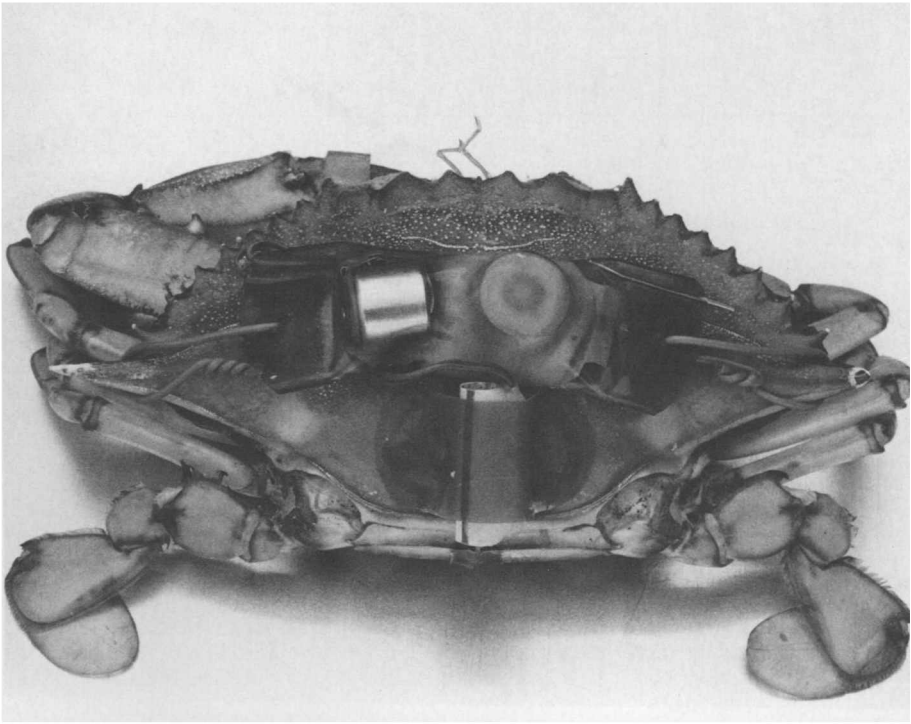


Figure 4. Operation of reed switch for signalling molting: magnet is withdrawn from tube as old carapace is elevated; magnet is held away from tube and reed switch by monofilament "spring" as shell falls back together (from Wolcott and Hines, 1989b).

relative to natural landmarks, was plotted on a map traced from aerial photographs of Muddy Creek. Time of day, depth, sediment type and presence of submerged vegetation were also recorded. As soon as the transmitter indicated that the crab had molted, the exuvium was collected and characteristics of the molting site noted as above.

The ultrasonic transmitters allowed precise tracking of movements and location of molting sites of 9 crabs. Some additional data were obtained from two other crabs carrying transmitters of an old design which produced weak signals. Both of these transmitters were lost to tracking after 2–3 days; one was found loose 3 days later. The only other problems resulted from the propagation characteristics of ultrasound in water. Thermal stratification during the heat of the day (which causes acoustic signals to refract downward), internal reflection in shallow water, scattering from a wind-roughened surface, and bubbles increase the absorption of the signal in the water column or at the bottom, and hence reduce the receiving range (Stasko and Pincock, 1977). On hot afternoons receiving range could drop below 50 m, and on a few sampling times some of the crabs could not be located. However, all the crabs usually could be located without difficulty, particularly early in the day, when the water was calm and thermally uniform.

RESULTS

Spatial Patterns of Movement.—Molting in the field produced a clear change in the signal, and intact exuvia with transmitters still affixed were collected for all nine crabs. This occurred as soon as 1 day after release for late premolt (red sign), whereas early premolt (white sign) crabs were tracked for up to 17 days.

All of the recovered transmitters indicated that male crabs remained within Muddy Creek to molt. Three of the 11 crabs initially moved upstream, but then reversed direction and began moving back down the creek. One of these molted while still upstream of the weir (Fig. 5); the other two moved downstream of the

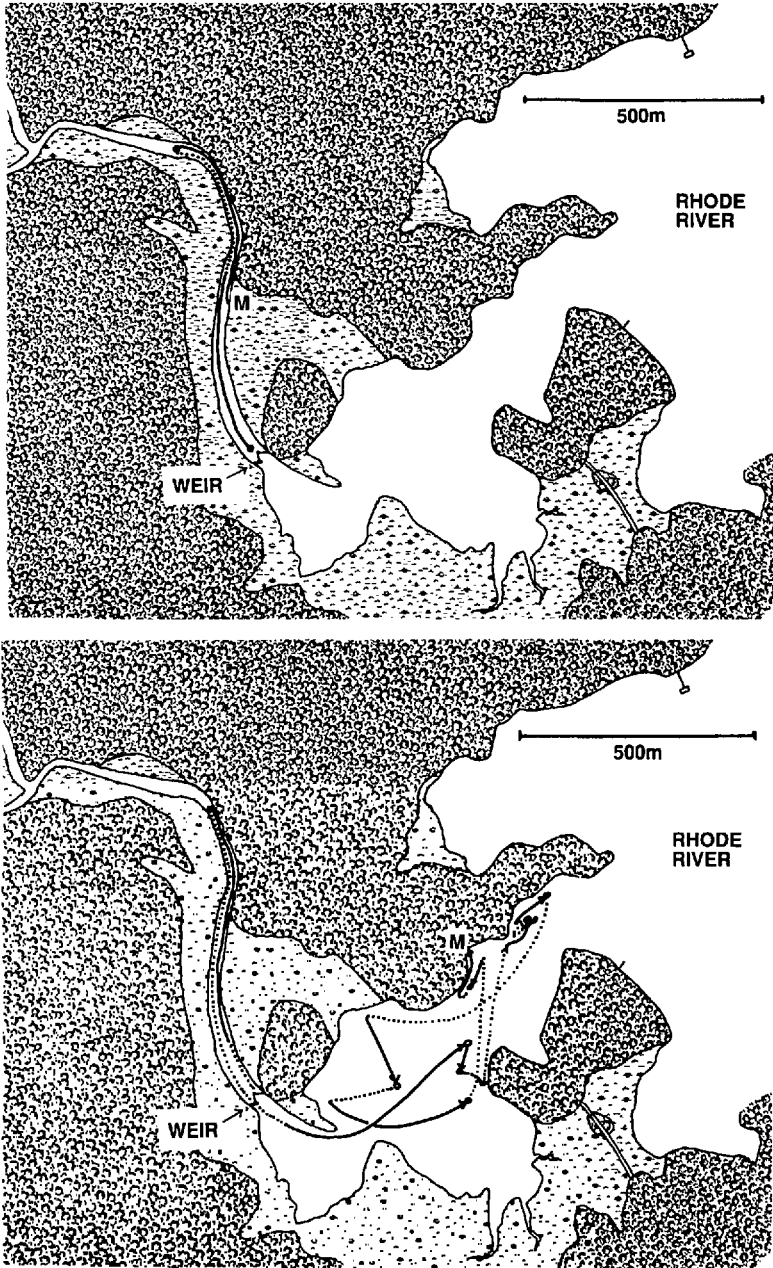


Figure 5 (upper). Three-day track of a 116-mm male that moved upstream for its first 24 h (to the top of the "creek" arrow), then headed back downstream the next day, but molted before reaching the weir. (Here and in Figs. 6–9, movements during the day are denoted by dotted lines, and those at night by solid lines; small circles represent daily intervals; "M" denotes the molting site.) Molt occurred by day in 5 cm of water, on muddy bottom at the edge of the marsh.

Figure 6 (lower). Fifteen-day track of a white-sign male that initially went upstream, but by the second day of tracking had moved below the weir. After moving around extensively in the Muddy Creek basin for nearly two weeks, the crab spent three days in a small area near the north shore. It molted at night, 1 m from shore, in less than 50 cm of water, on a peaty, snaggy bottom.

weir and, like the remaining recovered crabs, molted in the lower reaches of the creek. Mean length of the tracks (shortest path connecting all observations) was 1,717 m, but due to variation in tracking time prior to the molt as well as inherent variation among individuals, lengths of the tracks ranged from 138–4,241 m. The mean net distance (shortest possible path) from point of release to molting site was much shorter (364 m; range = 79–681 m), reflecting the highly meandering paths exhibited by the crabs in the lower reaches of the creek (Figs. 6–9). The mean index of meander (i.e., the ratio of net to total distance traveled, varying from 0.0 for random movement to 1.0 for straight-line movement) was 0.342 (range = 0.069–0.847).

Temporal Patterns of Movement.—Most of the crabs moved substantial distances during the days preceding ecdysis, averaging 130 m/day, but ranging from 0–569 m·day⁻¹. Speeds averaged 15.5 m·h⁻¹, but ranged from 0–137 m·h⁻¹ for short intervals of a few hours. The crabs moved significantly faster (averaging 22 m·h⁻¹) during daylight hours than during night (10 m·h⁻¹) (ANOVA, $P < 0.01$). The mean distance traveled per 24 h decreased markedly from 215 m several days prior to molt, to 60 m during the last day before molting (Fig. 10). However, distance·24 h⁻¹ was highly variable, with some crabs showing periods of little movement during the earlier portion of the tracks as well. Some individuals seemed to reduce wandering 2 days (Fig. 6) to 7 days (Fig. 7) before molting, while others continued moving long distances between tracking fixes up to a few hours before ecdysis (Figs. 8, 9).

Microhabitats Selected for Molting.—A consistent feature of the tracks was that all the premolt males selected shallow water within Muddy Creek for ecdysis (Figs. 6–9). The molting sites averaged 28 cm deep (range = 5–50 cm) on muddy or peaty bottoms, at an average of 3.5 m (range = 0–20 m) distance from shorelines vegetated predominantly by either cattail (*Typha angustifolia*) or saltmarsh cordgrass (*Spartina alterniflora*). These microenvironments comprise less than 10% of the area presumably investigated by the crabs as they moved along the upstream channel or repeatedly traversed the broad basins of lower Muddy Creek. We prepared and cut out tracings of various habitat types from a map of the basin, based on previous studies of Muddy Creek benthos (arbitrarily using a line tangent to the two points at the mouth as the boundary). Approximate proportions of other habitats not selected for molting are: narrow upstream creek channel 1–2 m deep, 5%; shallow downstream basin mudflats 0.5–1 m deep, >78%, and river head channel 1–3 m deep, 12%.

Timing of Molting.—Four of the crabs molted during the day, and three during the night. Time of molt could not be determined for the other two crabs due to missed location fixes. Exact time of ecdysis in the diel or tidal cycle could not be determined for any of the crabs because position fixes were made only twice a day.

Telemetry Data vs. Weir Samples.—During August 1987, when we were tracking the premolt crabs, blue crabs sampled at the weir continued to show the same pattern described by Hines et al. (1987). Over 95% of the crabs in the creek were male. Of those, over 61% moving upstream were in premolt, and 62% moving downstream were in postmolt (Table 1). Temporal variability in this pattern is evident when the data are examined at shorter intervals. In the first half of August 1987, nearly three fourths of the crabs moving upstream were in premolt; of those moving downstream, nearly half were in premolt and over a third were in postmolt. In the second half of the month, about half of the crabs moving upstream were

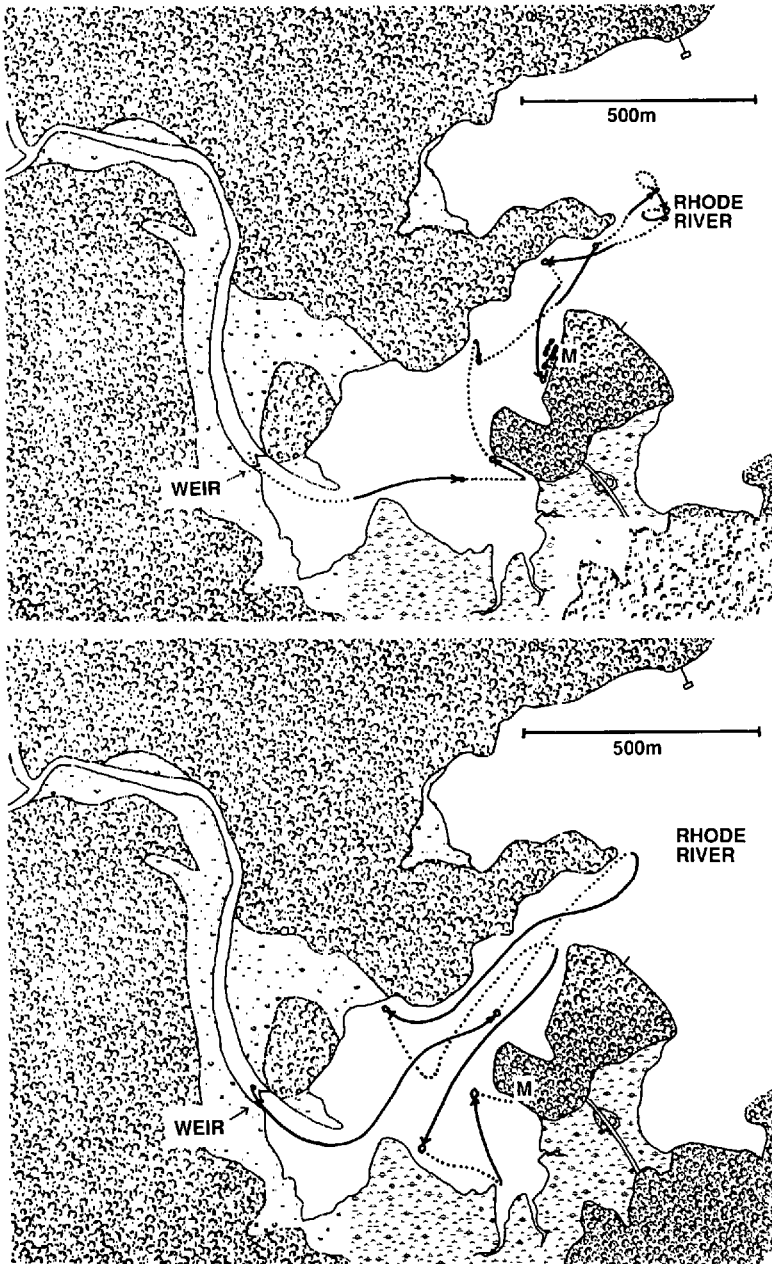


Figure 7 (upper). Seventeen-day track of a white-sign male that immediately moved downstream and on out into the Rhode River, but returned to Muddy Creek after about a week and restricted its movements to a small area off the south shore for the remaining 9 days. It molted in 10 cm of water at the edge of the shore grasses. The exuvium was recovered in early afternoon after missed sampling periods the preceding evening and morning. From its very fresh condition we infer that molt occurred by day.

Figure 8 (lower). Five-day track of a 128-mm white-sign male that continued to move long distances right up to the time of ecdysis. The exoskeleton was found in the morning, after being missed the preceding evening. Its condition suggested that molt occurred the previous day, probably within 2 m of the west shore of forested Corn Island, in about 40 cm of water, on a muddy bottom.

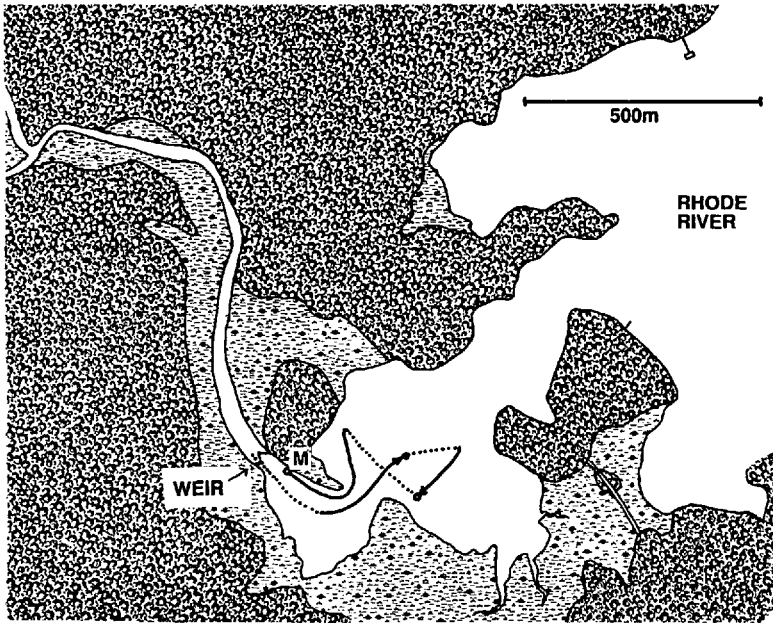


Figure 9. Three-day track of a 112-mm pink-sign male that continued extensive movements close to the time of ecdysis. Molt occurred by day about 2 m off the marsh edge, on a muddy bottom in 40 cm of water, about 10 h after the crab arrived at that location.

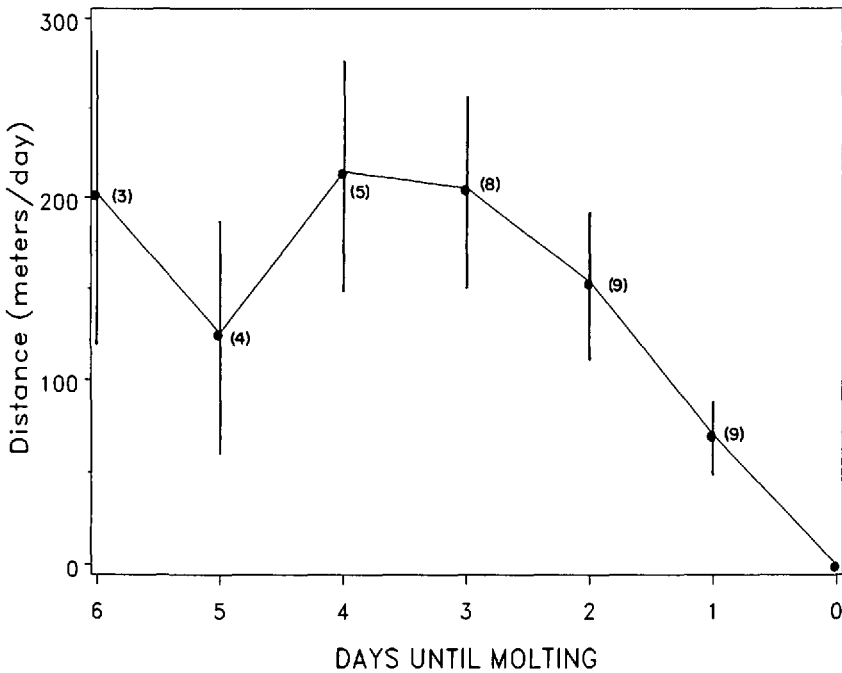


Figure 10. Distance travelled by premolt male crabs in Muddy Creek, as a function of the days remaining until molt (mean and SEM). Number of observations indicated in parentheses.

Table 1. Per cent composition, by sex and molt stage, of crabs moving upstream and downstream through the Muddy Creek fish weir during the study period in August 1987

Time period: Direction:	Whole month, N = 202		First half, N = 91		Second half, N = 111	
	Up	Down	Up	Down	Up	Down
By Sex						
Male	98	96	95	92	100	98
Female						
Juvenile	2	4	5	8	0	9
Mature	0	0	0	0	0	0
By Molt Stage						
Premolt	61	28	73	48	51	13
Postmolt	16	62	0	36	29	82
Intermolt	23	10	27	16	20	5

in premolt and nearly a third were in postmolt, while over 80% of crabs moving downstream were in postmolt (Table 1). Previous sampling at the weir showed only minor lunar components in the large temporal variances.

DISCUSSION

This new device for telemetering arthropod molting in the field proved effective for both tracking the movements prior to the molt and signalling the event of ecdysis. Had we chosen to track the instrumented individuals continuously, we could have described completely the crabs' wanderings with spatial resolution of less than a meter and (presumably) no lost data. Thus, precision in determining the crabs' exact path and the time of ecdysis was limited only by the frequency with which we relocated each individual.

Even with approximately twice-daily fixes, we have a clear picture of how the nine premolt males utilized creek habitats during the premolt period and eventually selected shallow microhabitats along the marsh-lined creekbank for ecdysis. The transmitters also revealed a high degree of variability in behavior among crabs, with the speeds and distances varying an order of magnitude between individuals and even from day to day in a single individual. Consequently, we regard the results of this initial study as indicative rather than definitive.

As we had hypothesized, all of the crabs we tracked remained within the creek to molt rather than moving into the Rhode River. However, they did not move consistently upstream prior to ecdysis as we expected from data collected with the fish weir across Muddy Creek. Most of the numerous crabs moving upstream through the weir (Fig. 1) in previous years were in premolt, while those moving downstream were predominantly in postmolt and significantly larger (Hines et al., 1987). Given the variability in direction of movement among crabs sampled by the weir during this study (Table 1), the apparent lack of an upstream trend in the crabs bearing telemetry transmitters may simply be an artifact of the small sample size. In any event, both the weir and telemetry data clearly indicate that in the Rhode River system many male blue crabs are using the tidal creek as molting habitat. The restriction of molting to a small proportion of the available microhabitats is strong presumptive evidence for selective behavior since these unrestrained animals apparently had equal access to the whole basin. However, our equipment provided no information on stimuli which could have provided the basis for microhabitat choices nor on selection behaviors per se.

Why the creek might have adaptive value as a molting habitat remains unclear. Hines et al. (1987) postulated that at least five factors might cause selection pressure for molting in the creek. We cannot evaluate the relative importance of three of these potential advantages: 1) reduced predation pressure on vulnerable postmolt crabs if there are fewer species and/or numbers of predators in the creek than in the river basin; 2) reduced cannibalism on soft crabs by partitioning of intermolt (feeding) crabs from molting (non-feeding) crabs; and 3) increased availability of key dietary requirements of post-molt crabs (e.g., calcium in exuvia) concentrated in the creek. However, knowledge gained from telemetry of the microhabitat for ecdysis provides some insight about two other factors.

One hypothesis is that the creek provides more or superior refuges from predation, relative to the river basin (Hines et al., 1987). However, the shallow zone along the marsh edges that the crabs selected for ecdysis did not, in most cases, provide structural refuges such as submerged or emergent vegetation, relief in the bottom sediment or tree snags. The shallows of the creek banks presumably provided partial refuge from aquatic predators. On the other hand, they presumably offered increased risk from wading birds (herons) and terrestrial predators (raccoons, otters). Furthermore, the same could be presumed about marginal shallows of the river basin. If predation is a dominant selective force, crabs might be expected to molt under cover of darkness. In fact, molts were about evenly distributed between day and night. Without additional knowledge of differences in predation pressures among habitats, there is no demonstrable advantage to selecting creek sites for molting.

Similarly, there is no clear evidence that physico-chemical conditions in the creek are more suitable for molting than are those in the river. Lower salinities in creek habitats might be more favorable for osmoregulation or water uptake during ecdysis, but drought conditions during our study period produced nearly identical salinities and temperatures in the creek and the head of the river basin. High levels of dissolved oxygen would help meet the elevated oxygen demands of ecdysis (deFur, this volume). Well-oxygenated water would be found in shallow creek microhabitats, but also around the margins of the river basin.

Since refuge and physico-chemical attributes did not indicate selective advantages of creek sites as molting microhabitats, it is critical to assess variation in predation pressure, cannibalism and availability of food (in terms of both calories and specific nutrient requirements) between the creek and river basin. Clearly, more behavioral observations and manipulative experiments will be needed to sort out the adaptive and mechanistic factors regulating selection of microhabitats for molting. Ultrasonic telemetry of movement and the ability to signal the event of ecdysis will allow collection of comparative data from other habitats like submerged aquatic vegetation, high salinity zones, and creeks with a more pronounced salinity gradient than our Muddy Creek study site. Additional data may be required to understand the role of interannual climatic variability. The transmitter design and method of application we have presented here also will be useful for comparisons with other large arthropods, including other brachyurans, lobsters and horseshoe crabs (*Limulus*).

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