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## UTILIZATION OF A SEAGRASS MEADOW AND TIDAL MARSH CREEK BY BLUE CRABS *CALLINECTES SAPIDUS*. II. SPATIAL AND TEMPORAL PATTERNS OF MOLTING

*Clifford H. Ryer, Jacques van Montfrans and Robert J. Orth*

### ABSTRACT

Blue crabs were collected weekly from a lower Chesapeake Bay seagrass meadow and adjacent tidal marsh creek over 2 months (July-August 1987) and molt staged. Molting activity, determined from a total of 1,220 crabs, was greater in the grassbed than in the marsh creek, and greater for small crabs and females. The difference between the two habitats in molting activity decreased from the first to the second month of sampling, possibly in response to seasonal decline in seagrass biomass. The proportion of small (<70 mm) females in both habitats was greatest on full moons. There was a lunar rhythm of molting activity by large crabs (2:70 mm), with peak molting activity on full moons. Small crabs demonstrated a similar, but nonsignificant rhythm of molting. We suggest that blue crabs approaching ecdysis aggregate in seagrass meadows, taking advantage of the refuge from predation that this structurally complex habitat affords. Lunar rhythmicity of molting activity may further reduce predation mortality through a dilution effect.

Crustaceans periodically undergo ecdysis (molting) whereby the existing exoskeleton is shed and replaced by a larger one. Physiological and morphological changes associated with the molt cycle have been described (Drach, 1939; Passano, 1960; Stevenson, 1972; Aiken, 1980). Yet, for the commercially and ecologically important blue crab (*Callinectes sapidus*), where and when molting occurs, and the selective pressures involved are not well understood. After molting, a crustacean's new exoskeleton remains soft for some time. Although not explicitly addressed by field studies, laboratory observations suggest that molting crustaceans may be susceptible to increased predation and physical stress (Lipcius and Herrnkind, 1982). Motility may also be decreased, further reducing the ability of molting individuals to flee or defend themselves. Nearing ecdysis, some crustaceans seek shelter (Tamm and Cobb, 1978; Reaka, 1976) or aggregate in habitats that segregate them from nonmolting conspecifics, thereby reducing injury or mortality due to aggression or cannibalism (Lipcius and Herrnkind, 1982). Molt-related habitat segregation in *C. sapidus* has been documented in the Rhode River, a subestuary of the central Chesapeake Bay (Hines et al., 1987). Crabs nearing ecdysis move into a tidal marsh creek tributary where molting occurs, followed by migration back to the river mainstem. It is unknown whether marsh creeks are used as molting refugia throughout the blue crab's geographical range.

Rhythmicity of activity and behavior is common among marine crustacea (DeCoursey, 1976; and refs. therein). Nocturnal (Fielder, 1964; Lasker, 1966; Thomas, 1966), or less commonly diurnal (Tamm and Cobb, 1976) patterns of molting are associated with avoidance of predators (Tamm and Cobb, 1976) or conspecifics (Lipcius and Herrnkind, 1982). For intertidal species molting may follow a semi-lunar pattern, being synchronized with tidal amplitude to avoid desiccation (Klapow, 1972; Williams, 1979). Reaka (1976) suggested that, irrespective of temporal patterns of predation or physical factors, synchronized ecdysis may be evolutionarily selected for according to a temporal variant of Hamilton's "selfish herd" hypothesis. When molting is synchronized, predators become limited by the rate at which they can utilize prey during brief peaks in molting activity,

resulting in lower individual risk than if molting is spread out over time. While there is little scientific data concerning diel or lunar molting patterns in *C. sapidus*, information from commercial shedding operations indicates that peak molting activity occurs during several days prior to, and immediately following, full moons (Oesterling, 1984).

Our observations on the use of shallow water habitats by blue crabs in the lower Chesapeake Bay and interpretation of local crabbing practices have led to the formulation of two hypotheses: 1) blue crabs nearing ecdysis aggregate in seagrass meadows, taking advantage of the refuge from predation and cannibalism that this habitat provides, and 2) there is a lunar rhythm in molting activity, with a peak occurring on full moons. The present study was designed to test these hypotheses by comparing the relative frequency of blue crab molting activity in a seagrass meadow and adjacent tidal marsh creek over an 8-week period.

#### MATERIALS AND METHODS

Study sites were located on the western shore of Browns Bay, in the lower Chesapeake Bay (Fig. 1). An unnamed creek, 12 m wide near its mouth and several hundred m long, which drained an extensive *Spartina alterniflora* marsh was selected as the marsh creek site (Ryer, 1987). A nearby (0.6 km) grassbed of mixed *Zostera marina* and *Ruppia maritima* constituted the seagrass meadow site (Orth and van Montfrans, 1987). The tidal amplitude at both sites is roughly 1 m, and summer water temperatures rarely exceed 30°C.

Both sites were sampled eight times at approximately 1-week intervals from 10 July 1987 to 1 September 1987 during quarter phases of the moon over two lunar cycles. Crabs in the grassbed were collected 1-2 h prior to low tide with a 4.9-m otter trawl (22-mm mesh wings, 6-mm cod end liner). Crabs were seined (10-mm mesh) from the lower half of the creek at low tide. Crabs were dislodged from hiding places in the creek bank or under logs using a dip net, making them available for collection by the seine. Collections in each habitat continued until at least 50 crabs were captured. Over the 8-week study period 1,220 crabs were collected, 735 and 485 from the grassbed and marsh creek, respectively. Size selective biases for the two gears were evaluated by comparison of size frequency distributions from this study with those reported by Orth and van Montfrans (1987) for the same grassbed and a neighboring marsh creek.

Crabs were returned to the lab and scored for size (carapace width, as measured from point to point of lateral spines), sex, and molt stage. Crabs were classified into four molt stage categories using criteria defined by Oesterling (1984). This technique involves qualitative examination of epidermal coloration and degree of retraction from the cuticle in the propodus of the fifth pereopod, and the degree of recalcification and re-chitinization of the carapace, as summarized below (terminology used by commercial crabbers is capitalized in parentheses): 1) postmolt-soft (SOFT CRAB), papery or leathery (PAPER SHELL) carapace, indicative of recent (hours to 1-2 days) molting. Corresponds to stages A-B of classification system that is based upon calcification, epidermal retraction and setogenesis (Drach, 1939; Aiken, 1973; Peebles, 1977; Vigh and Fingerman, 1985). 2) intermolt-hard (HARD CRAB), epidermis not yet retracted from cuticle. Corresponds to stage C. 3) early premolt—hard carapace, epidermis retracted from cuticle, appearing as a narrow green line (GREEN LINE PEELER) or broader white line (WHITE LINE PEELER). White line corresponds to stage Do, while green line may correspond to stage Do or the later phase of stage C (R. Lipcius, pers. comm.). 4) late premolt—molting imminent (hours to days), carapace hard, epidermis retracted, line broad and either pink or red (RED LINE PEELER) in color. Suture lines may be open (BUSTER). Corresponds to stages D,-E.

Multidimensional contingency table analysis was conducted using Log-Linear Models (Fienberg, 1980). Due to computational limitations and the difficulty associated with interpretation of higher level interactions, any given analysis was limited to four main effects and their interaction effects. Preliminary population analysis was conducted with classifying variables of SIZE (<70 mm or ~70 mm), SEX (male or female), HABITAT (grassbed or marsh creek), and DATE (1-8) to address differences in size and sex of crabs from the two habitats over the sampling periods. On the basis of these results, three additional analyses were conducted upon 1) all crabs, 2) those <70 mm, 3) and those ~70 mm, using classifying variables of SEX, HABITAT, LUNAR (lunar phase: full, waning half, new, waxing half), and CYCLE (1st or 2nd lunar month) to examine lunar changes in sex ratios.

Molt stage frequencies were analyzed in two ways. The first utilized classifying variables of STAGE (intermolt, early premolt, late premolt, and postmolt), HABITAT, SIZE, and SEX. For the second

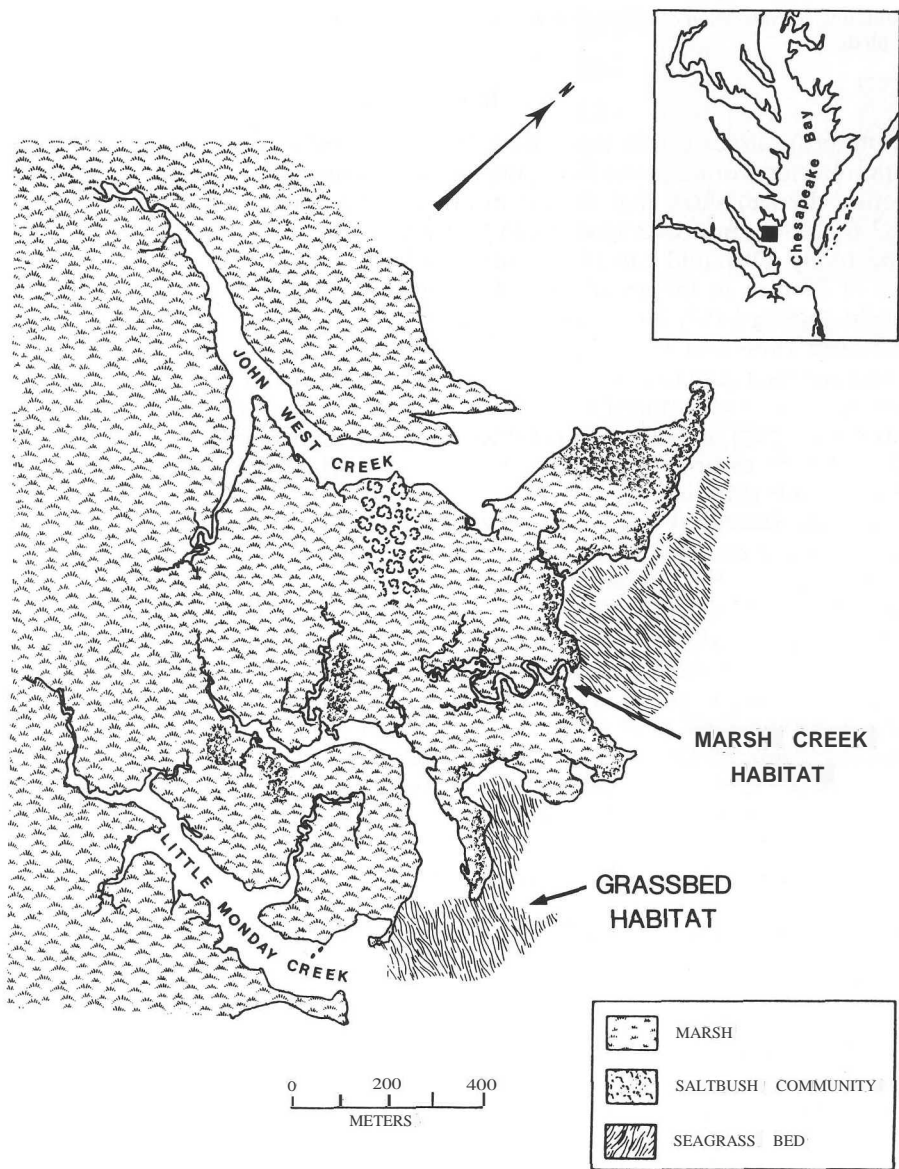


Figure 1. Location of study sites in lower Chesapeake Bay.

analysis the categories of STAGE were collapsed into nonmolting (intermolt and early premolt) and molting (late premolt and postmolt) to form a new variable, MOLT, and analyzed in conjunction with HABITAT, LUNAR, and CYCLE.

Results of preliminary analyses of STAGE and MOLT indicated that SEX, SIZE, HABITAT, LUNAR, and CYCLE may have confounded one another. To isolate these effects, data were divided into four subsets based upon combinations of SIZE and SEX (males <70 mm, males ~70 mm, females <70 mm, females ~70 mm) and analyzed separately with respect to MOLT, HABITAT, LUNAR, and CYCLE.

Effects were deemed significant at the  $P < 0.05$  level. While all interactions that significantly increased goodness-of-fit are included in the resultant models, only those interactions that include either SIZE or SEX in the population analysis, or STAGE or MOLT in the molting analysis are reported, thereby

eliminating consideration of effects that were controlled by sampling design (i.e., the number of crabs sampled).

## RESULTS

Both gears used in this study were biased towards the capture of large crabs. Data collected from Browns Bay using a relatively unbiased sampling methodology (suction dredge) show that for the months of July and August combined, from 1983 to 1986, crabs averaged 26 and 53 mm from grassbeds and marsh creeks, respectively (Orth and van Montfrans, 1987). Our sampling indicated mean crab sizes of 77 mm in the grassbed and 88 mm in the marsh creek for these same months during 1987. No crabs less than 30 mm were captured, indicating they were from 1986 and 1985 year classes (Orth and van Montfrans, 1987). Errors in interpretation due to potential differences in size-related sampling bias between gears have been minimized by control for crab size in our analysis. We have no basis upon which to evaluate molt stage related capture efficiency of the two gears, and therefore assume both gears have similar relative capture efficiencies for different molt stage crabs.

Crab size increased from a mean of 73.0 mm on 10 July to 95.9 mm on 1 September and grassbed crabs were smaller than those from the marsh creek (Fig. 2), although the magnitude of this difference varied with date (SIZE\*HABITAT\*DATE,  $P < 0.05$ ,  $\chi^2 = 14.15$ ,  $df = 7$ ). Sex composition was the same (approximately 55% female) for both size classes in the grassbed, while in the marsh creek there were relatively fewer females and the proportion of sexes differed between small (19% female) and large (37% female) crabs (SIZE\*HABITAT\*SEX,  $P < 0.01$ ,  $\chi^2 = 7.14$ ,  $df = 1$ ). Lunar phase had an effect upon sex composition for small crabs (SEX\*LUNAR,  $P < 0.01$ ,  $\chi^2 = 11.28$ ,  $df = 3$ ), with the highest percentage of females occurring on the full moon (Fig. 3). This pattern did not differ by lunar month or habitat, although overall sex composition was different between habitats. Similar trends in sex composition were noted for large crabs, and for all crabs combined, but were not significant (Figs. 2, 3).

A greater proportion of individuals from the grassbed were in pre- or postmolt, compared with the marsh creek (Fig. 4, STAGE\*HABITAT,  $P < 0.001$ ,  $\chi^2 = 162.43$ ,  $df = 3$ ). In addition, females (Fig. 5, STAGE\*SEX,  $P < 0.001$ ,  $\chi^2 = 23.36$ ,  $df = 3$ ) and smaller crabs (Fig. 6, STAGE\*SIZE,  $P < 0.001$ ,  $\chi^2 = 33.72$ ,  $df = 3$ ) were more likely to be in pre- or postmolt stages (Figs. 4, 5, 6).

Lunar phase affected molting activity (Fig. 7), with the proportional abundance of crabs showing signs of either imminent or recent molting being greatest on full moons, intermediate on half moons, and lowest on new moons (MOLT\*LUNAR,  $P < 0.001$ ,  $\chi^2 = 28.55$ ,  $df = 3$ ). This pattern did not differ by habitat or lunar month. Differences in molting activity between habitats were greater during the first lunar month than during the second (Fig. 8, MOLT\*HAB\*CYCLE,  $P < 0.01$ ,  $\chi^2 = 7.26$ ,  $df = 1$ ) (Figs. 7, 8).

When data were examined by cross-classification of size and sex, the effect of habitat and lunar periodicity changed in some instances (Table 1). There were no significant effects of habitat, lunar phase or lunar cycle upon molting activity for either small females or small males. For large males, molting activity was greater in the grassbed than in the marsh creek (MOLT\*HABITAT,  $P < 0.001$ ,  $\chi^2 = 30.38$ ,  $df = 1$ ). Molting activity for large females was also greater in the grassbed, but the magnitude of the difference between habitats was greater during the first lunar month (MOLT\*HABITAT\*CYCLE,  $P < 0.005$ ,  $\chi^2 = 7.74$ ,  $df = 1$ ). Molting activity was affected by lunar phase for both large males (MOLT\*LUNAR,  $P <$

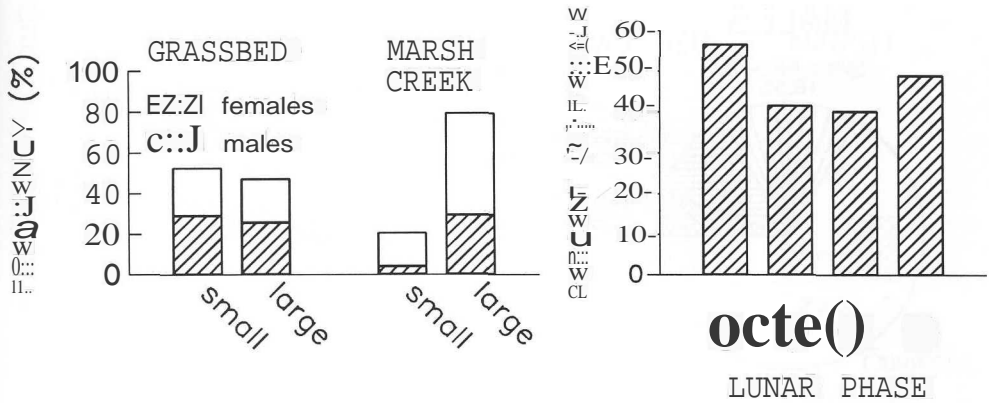


Figure 2 (left). Size (small <70 mm; large ~70 mm carapace width) and sex frequency distributions (%) for crabs collected from study sites, for all dates combined. Hatched sections of bars denote females, open sections denote males.

Figure 3 (right). Percent (%) female representation among small (<70 mm carapace width) crabs by lunar phase, for grassbed and marsh creek combined. Bars, from left to right, represent full, waning half, new, and waxing half moons.

0.05,  $\chi^2 = 10.50$ ,  $df = 3$ ) and large females (MOLT\*LUNAR,  $P < 0.005$ ,  $\chi^2 = 13.15$ ,  $df = 3$ ), with greatest activity on full moons (Table 1).

DISCUSSION

A greater percentage of *C. sapidus* in the grassbed was molting when compared to the marsh creek. Blue crabs approaching ecdysis may aggregate in grassbeds to take advantage of the refuge from predation and cannibalism that this structurally complex habitat affords. In general, benthic prey experience lower mortality in vegetated, as opposed to unvegetated habitats, in both laboratory (Heck and Thoman, 1981) and field tethering (with blue crabs) studies (Heck and Wilson, 1987; Wilson et al., 1987). The mechanism by which premolt blue crabs aggregate in grassbeds is unknown. It is possible that, where present, seagrass beds are the preferred molting habitat, being actively sought out by premolt crabs. Alternatively, premolt crabs may utilize the first suitable molting habitat they encounter. Since grassbeds are typically positioned between marshes and offshore waters,

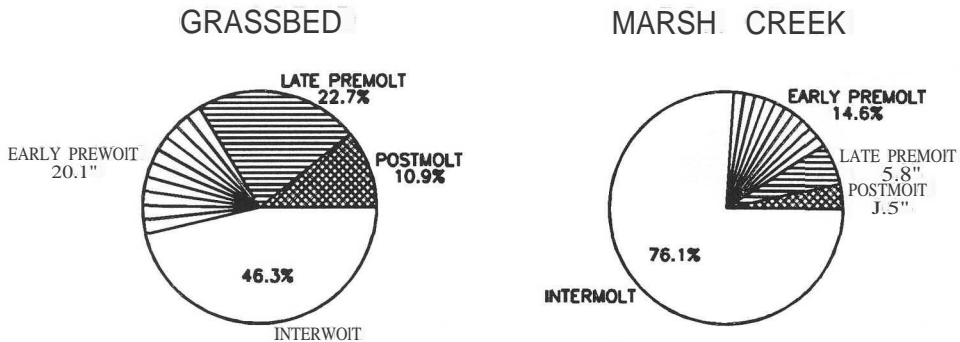


Figure 4. Comparison of grassbed and marsh creek with respect to molt stage, for all sexes, sizes and dates combined.

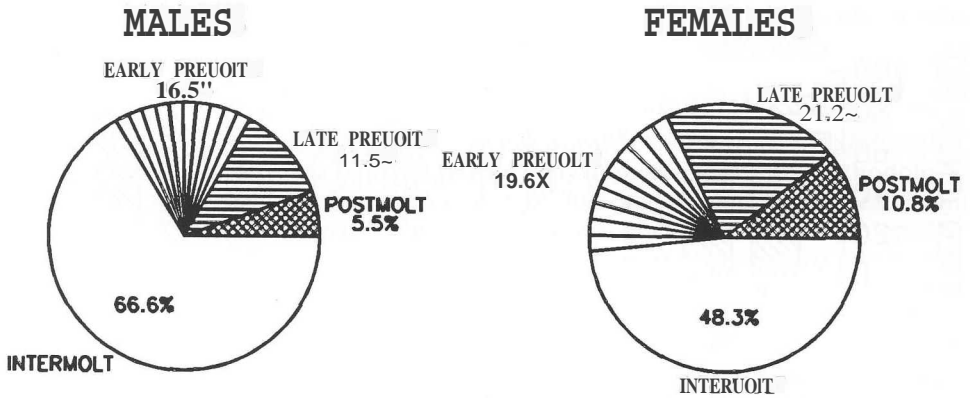


Figure 5. Comparison of sexes with respect to molt stage, for all habitats, sizes and dates combined.

crabs moving inshore to molt would encounter seagrasses first, resulting in their accumulation there.

Differences between the grassbed and marsh creek in molting activity decreased during the second month. The effort required to capture crabs from the grassbed also increased at this time, indicating a decrease in crab abundance or activity. Seagrass biomass in the lower Chesapeake Bay peaks during the late spring and early summer, followed by a decrease during the warmer summer months (Orth and Moore, 1986). The seasonal decline in the above ground biomass of vegetation may have decreased the value of the grassbed as a molting refugium during the second month, resulting in decreased utilization of the grassbeds by blue crabs.

Migration and concomitant habitat partitioning for the purpose of molting occurs in the Rhode River, where blue crabs, predominantly male, utilize a tidal marsh creek (Muddy Creek) as a molting refugium (Hines et al., 1987). There are no seagrasses in the Rhode River. Female crabs are thought to molt in the near-shore shallows of the Rhode River basin (Hines et al., 1987). Whereas habitat partitioning by sex between the marsh creek and the grassbed was observed in our study, both sexes had higher molting frequencies in the grassbed. Overall, the lower molting frequency among males, regardless of size, suggests they are less specific in their habitat requirements for molting, or prefer molting elsewhere. The marsh creek was not utilized extensively by either sex for molting, perhaps

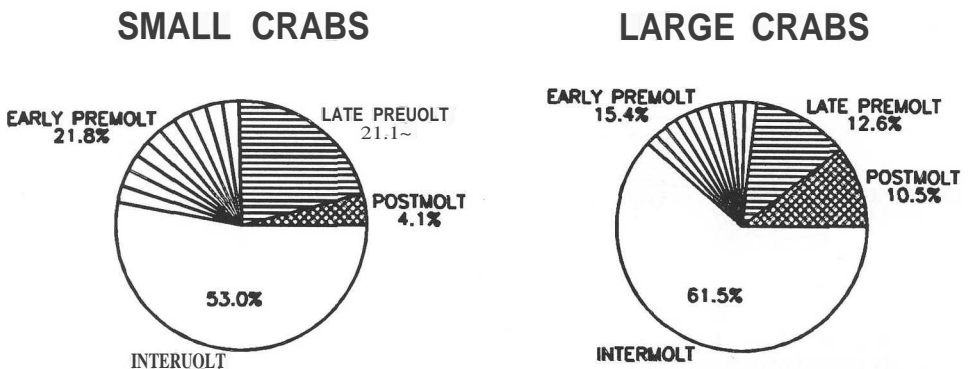


Figure 6. Comparison of small (<70 mm) and large (~70 mm carapace width) crabs with respect to molt stage, for all habitats, sexes and dates combined.

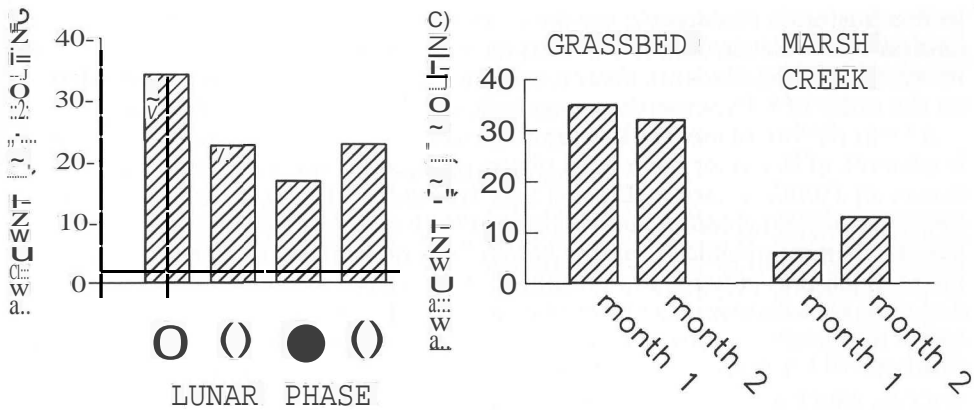


Figure 7 (left). Percent (%) of crabs showing signs of molting (imminent or recent) by lunar phase, for all sexes, sizes and habitats combined. Bars, from left to right, denote full, waning half, new, and waxing half moons.

Figure 8 (right). Percent (%) of crabs showing signs of molting (imminent or recent) by habitat and lunar month, for all sizes, sexes, and lunar phases combined.

due to the presence of nearby seagrass beds. However, Muddy Creek and our creek site also differ with respect to salinities. Hines et al. (1987) discuss the potential advantages of molting in a hypo-osmotic environment, such as the upper reaches of Muddy Creek. The creek we examined had little freshwater input, except during storm events, and did not differ in salinity from the seagrass bed habitat.

An alternative explanation for the observed differences in molting activity between the grassbed and the marsh creek takes into account possible differences in the forage base available to crabs in the two habitats. Ryer (1987) observed a trend for crabs to consume a larger quantity and better quality of food in a Browns Bay grassbed than in the marsh creek. Increased feeding could result in a shortened intermolt period, more frequent molting, and more rapid growth. However, for greater consumption to be translated into increased molting, crabs would have

Table I. Percentage (%) of blue crabs showing signs of recent or imminent molt for various combinations of size (small < 70 mm, large ≥ 70 mm) and sex by lunar phase, in both the grassbed and tidal marsh creek. Data are summed over the two lunar months sampled. N indicates the total number of crabs captured.

	Lunar phase							
	Full		Half		New		Half	
	%	N	%	N	%	N	%	N
<b>Grass</b>								
Small d	38.2	34	16.9	65	23.4	47	25.9	27
Large d	33.3	42	25.6	43	19.4	31	30.2	43
Small ♀	47.8	67	23.1	78	29.5	44	32.0	25
Large ♀	59.6	47	48.3	60	32.5	40	47.6	42
<b>Marsh</b>								
Small d	11.5	26	5.3	19	9.1	22	7.1	14
Large d	11.9	42	6.2	65	1.5	66	11.6	69
Small ♀	9.1	11	50.0	2	50.0	2	0.0	4
Large ♀	19.4	31	23.1	39	2.6	38	2.9	35



to demonstrate considerable residency in seagrass systems. While there are no data on the residence time of crabs in grassbeds, telemetry studies from the Rhode River, where seagrasses are absent, indicate that crabs frequently move distances on the order of kilometers during a single day (A. Hines, unpubl. data).

A lunar rhythm of molting by blue crabs was observed in both habitats. Rhythmic patterns of behavior have been observed in other species. Nocturnal molting occurs in *Panulirus argus* (Lipcius and Herrnkind, 1982), *P. cygnus* (Thomas, 1966), *Jasus novaehollandiae* (Fielder, 1964) and *Euphausia pacifica* (Lasker, 1966), whereas juvenile *Homarus americanus* molt diurnally (Tamm and Cobb, 1976). Such die! patterns are presumed to be associated with avoidance of predation or cannibalism. The intertidal sand-beach isopod *Excirologa chi/toni* exhibits the greatest molting activity several days prior to new and full moons (Klapow, 1972). Since tidal amplitude is increasing, this assures that newly molted isopods, which are less capable of maintaining position in the intertidal and more prone to desiccation, will not be stranded above the high tide mark for more than one tidal cycle. A similar rhythm of molting has been observed in the sand-beach amphipod *Talitrus saltator* (Williams, 1979). The fiddler crabs *Uca annulipes* and *U. triangularis* mate in synchrony with new and full moons so that after 2 weeks of development the larvae can be released on the next spring tide (von Hagen, 1970). In our study, molting activity was greatest on full, intermediate on half, and lowest on new moons, and therefore not related to spring tides, which are semi-lunar. This lunar pattern may be a temporal variant of Hamilton's (1971) "selfish herd" hypothesis (Reaka, 1976), in which temporal aggregation of a vulnerable activity (molting) decreases individual risk of predation through a dilution effect (Bertram, 1978). It is questionable whether the molting rhythm we observed, as distinct from synchronization where all individuals would molt at the same time, was strong enough to result in significant reduction of individual risk of predation. However, were cannibalism the major source of molting mortality such a rhythm would be more effective.

Sex composition data support our contention that crabs move to structured habitats to molt. In both the grassbed and the marsh creek the greatest percentage of females occurred on full moons, although this pattern was only significant for small crabs. Females also had a higher overall frequency of molting, regardless of habitat or size. From this we infer that females predominated among crabs that moved into these habitats to molt, although it is possible that the sex composition pattern was the result of reverse male movement.

Small crab molting activity, although similar to that for large crabs, was not significantly affected by lunar phase. Crabs may be able to delay ecdysis until environmental stimuli (lunar phase) trigger rapid completion of premolt (Reaka, 1975; 1976). Regardless of the selective pressures that have resulted in lunar periodicity of blue crab molting, for small crabs, immediate molting might outweigh the benefits of postponement until the next full moon, as less time would be spent at a smaller size. Vulnerability to predation increases with decreasing size in blue crabs (D. Smith, unpubl. data). The lack of a significant difference in molt frequency for small crabs between the grassbed and the marsh creek may also indicate that smaller crabs are less likely to risk movement between habitats for the purpose of molting.

Habitat partitioning and lunar patterns of molting in blue crabs have long been common knowledge among commercial watermen and recreational fisherman of the lower Chesapeake Bay, but have hereto remained scientifically undocumented. While large scale seasonal patterns of migration associated with recruitment, growth, and reproduction in blue crabs have been extensively studied, the results

of this study suggest that smaller scale movements over short time scales may also occur. Further investigation of the spatial and temporal aspects of interhabitat movements would greatly increase our understanding of blue crab population dynamics and interactions within estuarine communities.

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