Adaptive significance of habitat selection by molting adult blue crabs *Callinectes sapidus* (Rathbun) within a subestuary of central Chesapeake Bay

Michael A. Shirley[1], Anson H. Hines[2] and Thomas G. Wolcott[1]

[1]*Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina, USA;* [2]*Smithsonian Environmental Research Center, Edgewater, Maryland, USA*

Abstract: In the Rhode River subestuary, higher proportions of molting male blue crabs occupy a tidal creek, while molting and mating pubertal females are more common in the adjacent river basin. Predation pressure, mate availability, and physiological costs or benefits (competency to molt, survive ecdysis, and postmolt size increment) were estimated for these two habitats using a combination of caging and tethering techniques. Predation on molting crabs was less in the tidal creek; however, cannibalism may not explain these site-specific predation differences. There were no site-specific differences in survival, postmolt size increment, or competency for premolt crabs to molt when protected from predators. The results suggest that by molting in the creek males avoid higher predation in the river. Habitat selection by pubertal females may depend more on mate availability. Females may actively select the river or simply molt in the habitat in which they encounter a mate. Further experiments are needed to resolve the selection pressures eliciting the observed distribution of pubertal females.

Key words: Blue crab; *Callinectes sapidus*; Habitat selection; Mating; Molting; Predation

INTRODUCTION

In the Rhode River, a subestuary of central Chesapeake Bay, available habitats are partitioned by blue crabs according to their sex, size, maturity, or molt stage (Hines et al., 1987). Specifically, medium-sized (carapace width, 80–120 mm) males tend to molt in a tributary tidal creek while intermolt males and mating (pubertal) females remain in the main river basin. Several studies have documented shifts in habitat selection by blue crabs (Darnell, 1959; Perry, 1975; Orth & van Montfrans, 1987), but few studies address the adaptive significance of these behaviors (Ryer, 1987; Wilson et al., 1987; deFur et al., 1988). The present research examined three selective pressures deemed most likely to influence the distribution of molting blue crabs within the Rhode River system: predation, mate availability, and physiological costs or benefits (estimated here as the competency of crabs to molt, survive ecdysis, and increase in size within each habitat).

Food availability (Ryer, 1987), physiological constraints or benefits (Loesch, 1960), predation pressure (Heck & Wilson, 1987; Johns & Mann, 1987) and mating success (Hooper, 1986) influence habitat selection by decapod crustaceans. For blue crabs, the relative importance of these selective pressures changes with life history stage.

After early development in high salinity waters, megalopae move back into estuarine waters. Within an estuary, megalopae and juvenile blue crabs are most abundant in vegetated habitats (Heck & Thoman, 1984; Orth & van Montfrans, 1987). Possible reasons for this association include increased settlement of megalopae, greater food availability and reduced predation rates. Growing juvenile blue crabs continue to migrate up the estuary. As a result, greater numbers of mating blue crabs are found in the upper, less-saline regions of an estuary (Millikin & Williams, 1984).

The selective pressures influencing this large-scale migration of blue crabs into less saline water are not well understood. There may be benefits associated with this migration, such as larger size increments with each molt (de Fur et al., 1988), escape from less euryhaline predators, or increased reproductive success because of the concentration of mating crabs in the upper ends of estuaries.

As with megalopae and juvenile blue crabs, there are small-scale components to the migration patterns of adult crabs (Hines et al., 1987). Unlike larvae, juvenile and adult blue crabs can tolerate a wide range of temperature and salinity. However, their movement patterns are continually being influenced by physico–chemical factors. For example, the migration of blue crabs into deeper waters to overwinter coincides with the onset of declining temperatures (Van Engel, 1958). Blue crabs are also known to aggregate in shallow waters in response to deep-water hypoxia (Loesch, 1960; May, 1973). Changes in respiration (Mangum et al., 1985) and ion transport (Towle & Mangum, 1985) which accompany ecdysis may also affect microhabitat selection.

Predation also has a strong influence on habitat selection (Major, 1977; Wilson et al., 1987). Adult blue crabs are most vulnerable to predation and cannibalism during and immediately after ecdysis. Selecting molting sites segregated from intermolt crabs would reduce the risk of cannibalism, since late premolt and early postmolt crabs are non-feeding (Johnson, 1980; Millikin & Williams, 1984) and less aggressive. Tidal creek habitats provide a refuge from predation for other aquatic species (Hackney et al., 1976; Shenker & Dean, 1979; Rozas & Hackney, 1984) and may provide a similar function for molting crabs.

The habitat utilized by molting and mating females (pubertal females) may be influenced less by predation and more by where they encounter a mate. A female approaching her maturation molt releases a pheromone that attracts males and elicits male courtship behavior (Gleeson, 1980). Some male decapods, including blue crabs, "cradle-carry" their mates and provide protection from predation, supply food, and assist in molting (Williams, 1984; Hooper, 1986). These courtship behaviors are likely to influence habitat selection by pubertal females and may reduce their susceptibility to predation during ecdysis.

The adaptive significance of habitat selection by molting blue crabs may be viewed

as a balance between the costs and benefits of molting at various locations. In this study we examined three primary selective pressures known to influence habitat selection by marine species: physiological constraints, predation, and mate availability. The purpose of this study was to assess the relative influence of these selective pressures on molting and mating blue crabs within the Rhode River subestuary. Study sites were chosen based on the distributions of molting and mating blue crabs within this system (Hines et al., 1987). Predator exclusion cages were used to examine the physiological responses of molting study crabs while simultaneously collecting potential mates and predators. In addition, tethering techniques were used to estimate site-specific predation pressure.

METHODS

STUDY SITE

The Rhode River is a 485 hectare subestuary of central Chesapeake Bay (Fig. 1). Two study sites, river and tidal creek, were chosen based on the distribution of molting adult
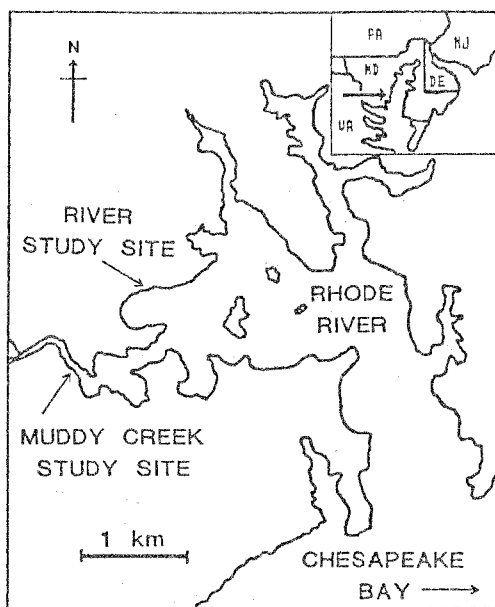

Fig. 1. Map of Rhode River subestuary, showing location of marsh creek and river study sites. Inset shows location of Rhode River on Chesapeake Bay.

male and pubertal female crabs (Hines et al., 1987). The maximum water depth at both sites was ≈ 1.5 m. The river basin site had sandy sediments and was adjacent to a forested shore. Sediments of the marsh creek site were loosely packed, silty mud. A

cattail *Typha* sp. marsh lined the shores of the creek site, but there was no submerged vegetation at either study site.

PHYSICOCHEMICAL DATA

Studies were conducted from July through September 1987 to coincide with the peak mating season for Chesapeake blue crabs (Williams, 1984). During this period 15 sets of measurements, one every 4–6 days, were made of salinity, temperature and dissolved oxygen at each study site. Measurements at both sites were made within 2 h of midday to minimize diel effects. An American Optical Instruments' refractometer, a YSI Model 57 dissolved oxygen meter and a standard mercury thermometer were used for these measurements. All measurements were from a depth of ≈0.5 m. Paired *t* tests were used to compare the salinity, dissolved oxygen and temperature between sites.

COLLECTION AND MAINTENANCE OF STUDY CRABS

Premolt crabs were captured from local crab populations using cages, pound nets and a weir. Maturity of the male crabs was determined by testing for separation of the abdomen from the carapace (Van Engel, 1958). Females approaching their maturation molt (pubertal females) were identified by the color and shape of their abdomen (Gleeson, 1980). Stage of molt was determined from the color of the penultimate segment of the swimming paddles (Passano, 1960; Perry et al., 1979).

Captured crabs, which were ≈7 days premolt ("white-sign"), were randomly assigned to holding pens within both study sites. Crabs were held in isolation to prevent injury and fed fresh or frozen fish every day. Crabs for study were chosen at random from those that had acclimated to the study site for at least 48 h. Only crabs that were ≈4 days premolt ("pink-sign") and were no longer feeding were used for the physiological response experiments. Thus, the effects of their initial nutritional state were minimized.

CAGING STUDIES

Premolt crabs were protected from predation by being placed in a wire mesh (12-mm mesh) enclosure. The enclosure was fastened to the floor of the upper level of a modified crab pot (Fig. 2). These cages were designed to capture organisms attracted to the study crab. 25 cages were placed at each site, 10 containing premolt males, 10 containing pubertal females, and five control (empty) cages. Each caging experiment was repeated seven times over an 8-wk period.

Difficulties in obtaining sufficient numbers of premolt crabs of the correct molt stage precluded strict adherence to the planned experimental design. Any additional empty cages were either used as cage controls or deployed enclosing white-sign pubertal females for use in the mate-availability experiments. The data from all caging studies were pooled to increase the power of the analyses.
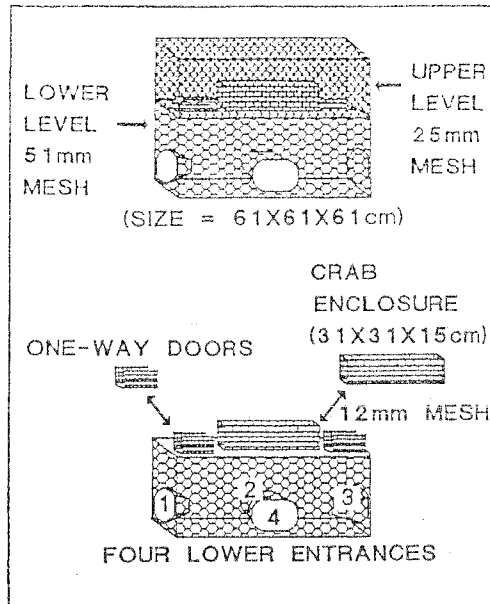
Fig. 2. Cage design: top diagram depicts the entire cage. Bottom diagram is a cut-away view of upper cage section showing crab enclosure box and one-way entrance doors.

Catch data

The various cage types (empty, male-enclosed and female-enclosed) were equally proportioned between each site. Therefore, the combined catch of all the cages within a site could be used to compare the proportion of captured crabs having a similar molt stage, sex and stage of maturation within each site. G tests (Sokal & Rohlf, 1981) were used for these analyses.

Physiological responses

After 4 days the condition of the late premolt (pink-sign) crabs which were enclosed in cages within each site were assigned to one of four categories: not-molted dead, not-molted alive, molted dead or molted alive. The total number of crabs in each category for each study site was compared using log-linear analyses (Sokal & Rohlf, 1981).

Premolt mortality was estimated by the proportion of the total number of crabs which died without molting. The competency of premolt (pink-sign) crabs to molt was estimated by the proportion of the total number of premolt crabs that did not molt yet survived. Ecdysial mortality was estimated by the proportion of the total number of premolt crabs that died during or immediately after molting. Total survival through ecdysis was estimated by the proportion of the total premolt crabs which survived to postmolt.

To estimate the size increment at the molt, the carapace width (spine tip to spine tip) of all cage and pen-held crabs was measured before and after ecdysis. The postmolt size increment was calculated as the proportional increase in carapace width after ecdysis. Since the holding method did not influence size increment, data from the holding pen records and caging studies were pooled. A two-way ANCOVA with premolt carapace width as a covariate was used to test the effects of site and sex on postmolt size increment.

Mate availability

To estimate the number of mates available to pubertal females placed at each site, empty cages served as cage controls and cages containing premolt males served as crab controls. The number of potential mates (mature intermolt males) captured per female-containing cage after 4 days was used to estimate mate availability during each study. The effects of site and cage-type were analyzed using ANOVA procedures with LSD contrasts. The contents of control cages which captured pubertal females or newly molted mature females or cages in which the study crab molted or died were not included in these analyses.

Predator abundance

To estimate predator abundance at each site, all potential predators captured in cages containing molting males were counted. Empty cages served as cage controls. ANOVA procedures were used to test the effects of study site on the mean number of predators captured per cage. The contents of cages which captured pubertal females or postmolt mature females, or cages in which the study crab died, were not included in the analyses.

TETHERING STUDIES

Fiberglass window screening ($\approx$2-mm mesh) bags were used to hold premolt (pink-sign) crabs until ecdysis. These bags were large enough (30 × 30 × 15 cm) for molting, but pliable enough to allow predators to damage the study crab. One premolt crab was placed inside each bag and the open end was tied with wire. 10 bags were placed at each study site and examined after 4 days. Seven such experiments, four using premolt males and three using pubertal females, were conducted.

Predation pressure

Recovery of a damaged and dead newly molted crab or pieces of an exuvium was scored as a predation event. Holes torn in the tethering bags were measured and compared to premolt size records to assure that the crab had not merely escaped. Predation pressure was estimated as the percent eaten (i.e., the proportion of total molting events scored as predation events). The effects of sex and site on predation pressure were analyzed using log-linear analyses. A Clopper–Pearson procedure was used to calculate confidence intervals (Hollander & Wolfe, 1973).

RESULTS

PHYSICO-CHEMICAL DATA

Creek water temperatures ranged from 20 to 28 °C ($\bar{x}$ = 24.3 °C), salinities ranged from 10 to 11‰ ($\bar{x}$ = 10.3‰) and dissolved oxygen levels ranged from 1.7 to 9.2 ppm ($\bar{x}$ = 5.1 ppm). On average, the river site was slightly more saline (extremes 10–12‰, $\bar{x}$ = 10.7‰ paired t test, P = 0.014), warmer (extremes 24–29 °C, $\bar{x}$ = 26.1 °C, paired t test, $P < 0.001$) and had higher dissolved oxygen concentrations (extremes 4.2–12.4 ppm, $\bar{x}$ = 7.2 ppm, paired t test, $P < 0.001$) than the creek.

CATCH DATA

A total of 180 crabs was collected in cages from the river site and 221 crabs from the creek site. Premolt and postmolt males composed significantly more (G test, $P < 0.001$) of the creek catch than of the river catch (Fig. 3, Sectors C, E). The proportion of mature
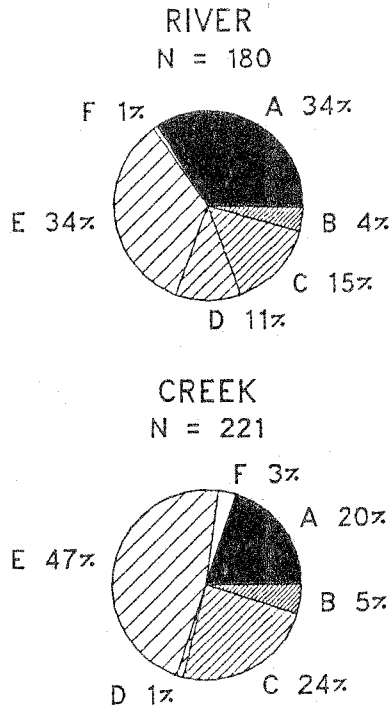

Fig. 3. Site-specific frequency distribution of crabs captured in study cages: (A) mature intermolt males, (B) immature intermolt males, (C) mature pre- and postmolt males, (D) pubertal females, (E) immature pre- and postmolt males and (F) mature and immature females.

intermolt males captured in cages was significantly greater (G test, $P < 0.001$) in the river than in the creek (Fig. 3, Sector A). Of the total creek catch, only 1.4% were

pubertal females, compared with 11.1% of the river catch (Fig. 3, Sector D, G test, $P < 0.001$).

PHYSIOLOGICAL RESPONSES

The condition of the study crabs after 4 days is summarized in Table I. Of the 175 premolt (pink-sign) crabs placed in cages that excluded predators 47% reached ecdysis of which 90% survived. Total premolt mortality was 5% and there were no

TABLE I

Summary of condition of caged crabs after 4 days for each site and sex. Confidence intervals by Clopper-Pearson procedure (Hollander & Wolfe, 1973).

Condition	Males			
	River (n)	95% CI	Creek (n)	95% CI
Not molted dead	3% (1)	0.1–14%	7% (3)	2–19%
Not molted alive	37% (14)	22–52%	30% (13)	16–44%
Molted dead	5% (2)	0.4–17%	5% (2)	0.7–16%
Molted alive	55% (21)	39–71%	58% (25)	43–73%
Total	100% (38)		100% (43)	

Condition	Females			
	River (n)	95% CI	Creek (n)	95% CI
Not molted dead	6% (3)	1–16%	5% (2)	0.6–28%
Not molted alive	54% (29)	41–67%	70% (28)	56–84%
Molted dead	4% (2)	0.6–14%	5% (2)	0.6–28%
Molted alive	37% (20)	24–50%	20% (8)	8–32%
Total	100% (54)		100% (40)	

differences between sites for males or females (log-linear analyses, $P = 0.264$). The competency for crabs to molt was not different for each study site (log-linear analyses, $P = 0.534$) nor were there site-specific differences in the ecdysial mortality (log-linear analyses, $P = 0.899$). Total survival from premolt through ecdysis was not affected by study site (log-linear analyses, $P = 0.264$). Similarly, site-specific effects on size increment with molt (Table II) were not significant (ANCOVA, $P = 0.561$).

TABLE II

Summary of percent size increment at ecdysis for crabs held at each site. Values are $\bar{x} \pm$ SE.

Site	Sex	Size increment
Creek	Females	34 ± 1.03 (n = 29)
River	Males	25 ± 0.79 (n = 29)
Creek	Males	23 ± 0.71 (n = 55)
River	Females	33 ± 1.00 (n = 52)

MATE AVAILABILITY

River cages containing a pubertal female captured significantly more potential mates (mature intermolt males) than did similar cages placed in the creek (Fig. 4, ANOVA
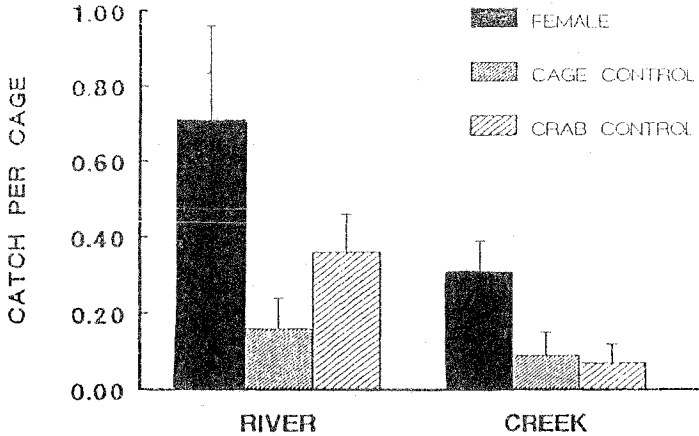

Fig. 4. Mean number ($\pm$ SE) of mature intermolt males captured per cage by site and cage-type. Female, cage containing a pubertal female (river, $n = 28$; creek, $n = 51$); cage control, empty cage (river, $n = 31$; creek, $n = 44$); crab control, cage containing a premolt male (river, $n = 25$; creek, $n = 27$).

with LSD comparisons, $P = 0.008$). Also, cages containing a pubertal female caught more potential mates than did empty cages (cage control, ANOVA with LSD comparisons, $P = 0.001$) or cages containing a premolt male (crab control, ANOVA with LSD comparisons, $P = 0.03$).
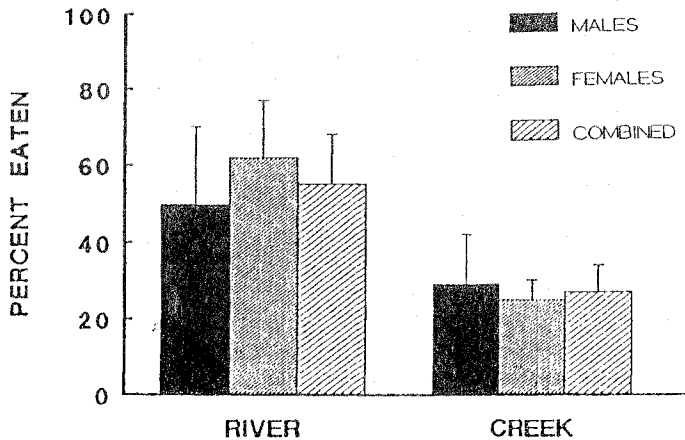

Fig. 5. Percent ($\pm$ 95% CI) of tethered molting crabs eaten at each site. Males: river, $n = 28$, creek, $n = 24$; Females: river, $n = 12$, creek, $n = 13$.

PREDATION PRESSURE

Significantly more of the crabs that molted in tethering bags placed in the river were eaten, compared with those placed in the creek (Fig. 5, log-linear analysis, $P = 0.022$). However, there were no sex-specific effects on these predation estimates (log-linear analyses, $P = 0.985$). Intermolt blue crabs represented the most abundant potential predators captured by cages containing a molting male crab. Empty cages captured fewer intermolt crabs than did cages containing molting males (ANOVA, $P = 0.02$). However, the number of intermolt crabs caught by cages containing molting males did not differ between sites (ANOVA, $P = 0.59$). Predators other than intermolt blue crabs, particularly American eels *Anguilla* sp., may have entered the cages and escaped. We occasionally observed that individual mesh holes were coated with mucus ("slime rings") which was similar to that coating eels, suggesting an eel had passed through the mesh.

DISCUSSION

The distribution of intermolt males, premolt males, postmolt males, and pubertal females estimated from this study's cage-catch data was similar to that reported by Hines et al. (1987) for the Rhode River–Muddy Creek system. Premolt and postmolt males were more abundant in the tidal creek habitat whereas intermolt males and pubertal females were more common in the river habitat.

There does not appear to be a physiological reason for the observed distribution of molting crabs. Habitat did not affect a premolt crab's competency to molt, survive ecdysis or increase in size. This is not surprising since the salinity, dissolved oxygen level and temperature of the creek and river were similar and within the physiological tolerance of this species (Williams, 1984). However, it is possible that the physiological responses measured were not sensitive enough to estimate more subtle site-specific costs or benefits.

Mate availability appears to be a primary factor determining habitat selection by premolt pubertal females. Habitat selection by a molting pubertal female is likely to be influenced by the mate that carries her. The degree to which a female can influence where her mate takes her is unknown. The habitat in which a pubertal female molts may simply depend on where she first encounters a mate. The chance of encountering an intermolt mature male as a mate is greater in the river habitat than in the creek, and pubertal females placed in the river attracted twice as many mature intermolt males as did pubertal females placed in the creek.

An alternative explanation is that females actively avoid the creek or select the river. Most of the crabs found in the creek are mature premolt and postmolt males. Prior to ecdysis, the exoskeleton of a premolt crab demineralizes and their claw muscles atrophy (Passano, 1960; Mykles & Skinner, 1982). Although they still exhibit courtship behaviors such as "cradle carrying" the female (pers. obs.), a premolt male's abilities to mate

successfully or to effectively protect females from predators are unknown. The energetic demands of approaching ecdysis may also interfere with male gamete production (Sastry, 1983). However, results of experiments being conducted at Pantego Creek, North Carolina, using ultrasonic telemetry to track premolt crabs until ecdysis, show that when premolt males and pubertal females are released from the same site they select similar locations and physicochemical conditions for ecdysis (Shirley & Wolcott, unpubl. data). This indicates that habitat selection by molting pubertal females is not an active choice of a habitat type different from that used by molting males.

Predation pressure on molting crabs was greater in the river and, based on these studies, seems to be the major selective pressure influencing habitat choice by molting males in the Rhode River Subestuary. Cannibalism, which makes up an unknown but important (L. D. Smith, Smithsonian Environmental Research Center, pers. comm.) component of the observed river predation rates, appears to have an equal influence in the creek and river, because the number of intermolt crabs attracted to molting males caged at each site was similar.

Unfortunately, the cage design was most effective at trapping blue crabs. The other predators causing the observed site-specific predation differences, measured by the tethering studies, may not have entered the cages, or may have escaped. Two other aquatic predators of blue crabs (Gunter, 1945; Jaworski, 1972; Wenner & Musick, 1975), the American eel *Anguilla* sp. and the spotted sea trout *Cynoscion* sp., were caught less frequently than blue crabs in otter trawls near the river site (Hines et al., in press; Hines, unpubl. data) and in cages containing molting crabs at both sites. However, our observations of mucous "slime rings" on the mesh of some cages suggests that eels were able to enter the cages and then escape. Furthermore, several of the eels that were caught by cages had soft postmolt crabs in their stomachs. This evidence suggests that predation by eels is an important component to the measured predation rates that was underestimated by the caging technique.

Differences in the physical properties of the creek and river may explain the observed predation rates. The turbidity of both sites limits visibility to secchi depths of <0.5 m (C. Gallegos, Smithsonian Environmental Research Center, pers. comm.). However, the river habitat is much wider (≈ 1 km) and deeper (maximum depth 4.5 m) than the creek, which quickly narrows upstream to a width of <20 m and a depth of <1 m. The river habitat is therefore more likely to support more and larger aquatic predators. Terrestrial-based predators of blue crabs, such as herons *Ardea* sp. and raccoons *Procyon* sp. (Steele, 1979), appear to dominate in the creek. However, further study is needed to determine if the differential predation rates reflect the relative effectiveness of terrestrial vs. aquatic predators at locating molting crabs in turbid waters.

In summary, this study examined the selective pressures maintaining habitat selection by molting crabs by estimating site-specific predation pressure, mate availability and the physiological differences. The results show that molting males which select the tidal creek habitat avoid higher predation in the river, thus suggesting the potential importance of tidal creeks as a refuge from predation for molting blue crabs. The distribution of

pubertal females may be the result of a decreasing concentration of females as they encounter mates while migrating up-estuary. Further study is needed to fully understand the benefits of increased mate (mature intermolt male) availability for pubertal females molting in the river.

ACKNOWLEDGMENTS

REFERENCES

Darnell, R. M., 1959. Studies of the life history of the blue crab (*Callinectes sapidus* Rathbun) in Louisiana waters. *Trans. Am. Fish. Soc.*, Vol. 88, pp. 294–304.

DeFur, P. L., D. Nusbaumer & R. J. Lewis, 1988. Physiological aspects of molting in blue crabs from the tidal fresh-water Potomac River, Virginia. *J. Crustacean Biol.*, Vol. 8, pp. 12–19.

Gleeson, R. A., 1980. Pheromone communication in the reproductive behavior of the blue crab, *Callinectes sapidus*. *Mar. Behav. Physiol.*, Vol. 7, pp. 119–134.

Gunter, G., 1945. Studies on the marine fisheries of Texas. *Publ. Inst. Mar. Sci. Univ. Tex.*, Vol. 1, pp. 1–190.

Hackney, C. T., W. D. Burbanck & O. P. Hackney, 1976. Biological and physical dynamics of a Georgia tidal creek. *Chesapeake Sci.*, Vol. 17, pp. 271–280.

Heck, K L., Jr. & T. A. Thoman, 1984. The nursery role of seagrass meadows in upper and lower reaches of the Chesapeake Bay. *Estuaries*, Vol. 7, pp. 70–92.

Heck, K. L., Jr. & K. A. Wilson, 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *J. Exp. Mar. Biol. Ecol.*, Vol. 107, pp. 87–100.

Hines, A. H., A. M. Haddon & L. A. Wiechert, in press. Variation in species composition, population dynamics, and foraging impact of epibenthic blue crabs and fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.*

Hines, A. H., R. N. Lipcius & A. M. Haddon, 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, Vol. 36, pp. 55–64.

Hollander, M. & D. A. Wolfe, 1973. *Nonparametric statistical methods.* John Wiley & Sons, New York, 503 pp.

Hooper, R. G., 1986. A spring breeding migration of the snow crab, *Chionoecetes opilio* (O. Fabr.), into shallow water in Newfoundland land *Crustaceana*, Vol. 50, pp. 257–264.

Jaworski, E., 1972. The blue crab fishery, Baratarrau Estuary, Louisiana. *La. Univ. Sea Grant Publ.*, No. LSU-SG-72-01, 112 pp.

Johns, P. M. & K. H. Mann, 1987. An experimental investigation of juvenile lobster habitat preference and mortality among habitats of varying structural complexity. *J. Exp. Mar. Biol. Ecol.*, Vol. 109, pp. 275–285.

Johnson, P. T., 1980. *Histology of the blue crab* Callinectes sapidus. *A model for the Decapoda.* Preager Sci. Publ., New York, 440 pp.

Loesch, H., 1960. Sporadic mass shoreward migrations of demersal fish and Crustacea in Mobile Bay, Alabama. *Ecology*, Vol. 41, pp. 292–298.

Major, P. F., 1977. Predator–prey interactions in schooling fishes during periods of twilight: a study of the silverside *Pranesus insularum* in Hawaii. *Fish Bull. NO.14.* Vol. 75, pp. 415–426.

Mangum, C. P., B. R. McMahon, P. L. DeFur & M. G. Wheatly, 1985. Gas exchange, acid-base balance, and the oxygen supply to the tissues during a molt of the blue crab *Callinectes sapidus*. *J. Crustacean Biol.*, Vol. 5, pp. 188–206.

May, E. B., 1973. Extensive oxygen depletions in Mobile bay, Alabama. *Limnol. Oceanogr.*, Vol. 18, pp. 353–366.

Millikin, M. R. & A. B. Williams, 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. FAO Fish. Synop., No. 138, NOAA Tech. Rep. NMF51, 38 pp.

Mykles, D. L. & D. M. Skinner, 1982. Crustacean muscles: Atrophy and regeneration during molting. In, *Basic biology of muscles: a comparative approach*, edited by B. M. Twarog et al., Raven Press, New York, pp. 337–357.

Orth, R. J. & J. Van Montfrans, 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.*, Vol. 41, pp. 283–294.

Passano, L. M., 1960. Molting and its control. In, *The physiology of Crustacea*, edited by T. H. Waterman, Academic Press, New York, pp. 473–536.

Perry, H. M., 1975. The blue crab fishery in Mississippi. *Gulf Res. Rep.*, Vol. 5, pp. 39–57.

Perry, H. M., J. T. Ogle & L. C. Nicholson, 1979. The fishery for soft crabs with emphasis on the development of a closed recirculating seawater system for shedding crabs. In, *Proceedings of the Blue Crab Colloquium*, edited by H. M. Perry & W. A. Van Engel, *Gulf States Marine Fisheries Commission, August 1982*, Vol. 7, pp. 137–152.

Rozas, L. P. & C. T. Hackney, 1984. Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. *Estuaries*, Vol. 7, pp. 213–224.

Ryer, C. H., 1987. Temporal patterns of feeding by blue crabs (*Callinectes sapidus*) in tidal-marsh creek and adjacent seagrass meadow in the lower Chesapeake Bay. *Estuaries*, Vol. 10, pp. 136–140.

Sastry, A. N., 1983. Ecological aspects of reproduction. In, *The biology of Crustacea*, edited by F. J. Vernberg & W. B. Vernberg, Academic Press, New York, Vol. 8, pp. 179–270.

Shenker, J. M. & J. M. Dean, 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: Abundance, diversity and temporal variation. *Estuaries*, Vol. 2, pp. 154–163.

Sokal, R. R. & F. J. Rohlf, 1981. *Biometry: the principles and practice of statistics in biological research*, W. H. Freeman & Company, New York, second edition, 859 pp.

Steele, P., 1979. A synopsis of the biology of the blue crab *Callinectes sapidus* Rathbun in Florida. In, *Proceedings of the Blue Crab Colloquium*, edited by H. M. Perry & W. A. Van Engel, *Gulf States Marine Fisheries Commission, August 1982*, Vol. 7, pp. 29–35.

Towle, D. W. & Mangum, C. P., 1985. Ionic regulation and transport ATPase activities during the molt cycle in the blue crab *Callinectes sapidus*. *J. Crustacean Biol.*, Vol. 5, pp. 216–222.

Van Engel, W. A., 1958. The blue crab and its fishery in the Chesapeake Bay. Part 1. Reproduction, early development, growth, and migration. *Commer. Fish. Rev.*, Vol. 20, pp. 6–17.

Wenner, C. A. & J. A. Musick, 1975. Food habits and seasonal abundance of the American eel, *Anguilla rostrata*, from the lower Chesapeake Bay. *Chesapeake Sci.*, Vol. 16, pp. 62–66.

Williams, A. B., 1984. *Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida*. Smithsonian Institution Press, Washington, DC, 550 pp.

Wilson, K. A., K. L. Heck Jr., & K. W. Able, 1987. Juvenile blue crab, *Callinectes sapidus*, survival: An evaluation of eelgrass, *Zostera marina*, as refuge. *Fish. Bull. NOAA*, Vol. 85, pp. 53–58.