The effect of cheliped loss on blue crab *Callinectes sapidus* Rathbun foraging rate on soft-shell clams *Mya arenaria* L.

L. David Smith and Anson H. Hines

Smithsonian Environmental Research Center, Edgewater, Maryland, USA

(Received 21 September 1990; revision received 4 February 1991; accepted 9 May 1991)

Abstract: Loss of single chelipeds was common (4–17%) in populations of blue crab *Callinectes sapidus* Rathbun surveyed in Chesapeake Bay and along the southeastern Atlantic coast and Gulf of Mexico. In contrast, blue crabs missing both chelipeds were relatively rare (0–5%). Laboratory experiments were conducted to determine the effects of cheliped autotomy on blue crab foraging rate on soft-shell clams *Mya arenaria* L. In replicated aquarium experiments, clams (44–72 mm shell length) were allowed 48 h to burrow in sandy substratum before an intact male crab or one missing one or both chelipeds was introduced. After 48 h, clams were checked for evidence of siphon injury or mortality. Foraging rate (clams consumed/48 h) of crabs missing a single crusher cheliped did not differ significantly from that of intact crabs. Blue crabs compensated for the loss of a crusher by using the cutter cheliped and opposite first walking leg to forage. In contrast, crabs missing both chelipeds experienced a greater feeding handicap; their consumption of clams was significantly lower than that of intact crabs. The low incidence of individuals missing both chelipeds suggests that such injury does little to diminish blue crab predation on *M. arenaria* populations.

Key words: Autotomy; *Callinectes sapidus*; Foraging; *Mya arenaria*; Predator–prey interaction

INTRODUCTION

Many brachyuran decapods are capable of self-amputating (autotomizing) one or both chelipeds in response to injury or its threat (Robinson et al., 1970; McVean, 1982). While the ability to autotomize a body part may be an important tactic for evading predators (Robinson et al., 1970; Schall & Pianka, 1980; Medel et al., 1988; McCallum et al., 1989; Smith, 1990a), the animal loses the service of that structure until regeneration occurs. Potential costs associated with autotomy may vary with developmental stage (Maiorana, 1977; Vitt & Cooper, 1986; Smith, 1990a), the task (e.g., mating, foraging) (Ballinger, 1973; Fox & Rostker, 1982; Smith, 1990a), or the taxa involved (Jaksic & Fuentes, 1980). For example, tail loss in lizards and salamanders may have little direct impact on foraging performance, but arm loss in sea stars (Slater & Lawrence, 1980) or cheliped loss in decapod crustaceans (Elner, 1980; Edgar, 1990; Juanes & Hartwick, 1990) could directly reduce foraging rate and force dietary changes. If nutritional needs cannot be supplemented adequately, the energetic cost of limb

Correspondence address: L.D. Smith, Smithsonian Environmental Research Center, PO Box 28, Edgewater, MD 21037–0028, USA.

replacement (e.g., Kuris & Mager, 1975; Lawrence et al., 1986; Smith, 1990b) could be compounded and growth slowed further. The effect of autotomy on foraging rate in decapod crustaceans, however, has not been tested experimentally.

Blue crabs *Callinectes sapidus* Rathbun typically possess a pair of dimorphic chelipeds specialized for crushing and shearing prey (Hamilton et al., 1976; Brown et al., 1979; Smith, 1990a; Smith & Hines, 1991). These decapod crustaceans are important estuarine predators (Virnstein, 1977; Holland et al., 1980) whose foraging behavior can directly and indirectly affect the abundance and distribution of their soft-bottom prey (Hamilton, 1976; Virnstein, 1977; Blundon & Kennedy, 1982a; Lipcius & Hines, 1986; West & Williams, 1986; Hines et al., 1990). The soft-shell clam *Mya arenaria* L. is a major prey item in the diet of blue crabs (Hines et al., 1990). A common infaunal suspension-feeder in Chesapeake Bay (Hines & Comtois, 1985), adult *M. arenaria* gain a partial refuge from blue crab predation by burying deeply (10–25 cm) in sandy sediments (Blundon & Kennedy, 1982a). Cheliped loss in blue crabs could exacerbate difficulties of excavating and consuming large clams, thereby increasing clam survivorship. To determine the effects of cheliped autotomy on blue crab foraging on *M. arenaria*, we compared feeding rates of crabs missing no, one, or two chelipeds in the laboratory.

MATERIALS AND METHODS

FIELD SAMPLING

C. sapidus individuals were collected and measured for limb loss during 1986–89 in the Rhode River, Maryland (38°51′N, 76°32′W), a subestuary of the mesohaline zone in Chesapeake Bay. Blue crabs were also sampled at two additional sites in the Chesapeake Bay in fall 1989 and at sites along the southeastern Atlantic coast and Gulf of Mexico of the USA in spring 1989. A detailed description of the survey is provided elsewhere (Smith, 1990a; Smith & Hines, 1991); only summary information pertinent to the foraging experiments is given here. A cheliped was classified as missing if the limb stump was scarred or possessed a papilla or limb bud. Crabs that possessed an unscarred stump wound, indicating possible injury caused during collection, were not measured.

Juvenile and adult blue crabs of both sexes were sampled by otter trawl, seine, and crab pot in the Rhode River as well as at other sites. No bias in limb loss frequencies related to these different collection techniques was detected.

EXPERIMENTAL PROCEDURES

Foraging experiments were conducted in three closed-system 208-l aquaria (1.2 m length × 0.3 m width × 0.5 m depth) at the Smithsonian Environmental Research Center, Edgewater, Maryland, between 21 July and 13 September 1989. Exterior sides of each aquarium were covered with opaque plastic to minimize outside disturbance.

Each aquarium contained a 23-cm layer of sand covered by 24 cm of estuarine water. Sediment was coarsely sieved to remove macrofaunal organisms. Sediment composition was 86% medium-to-very fine sand and 14% silt and clay (J. Lin, pers. comm.). Water was aerated and filtered during each experiment and changed between experiments. Salinity ($\pm 0.5‰$) and water temperature ($\pm 0.5\,°C$) were consistent across aquaria in each experiment. Salinity ranged from 3 to 9‰ and matched ambient levels in the Rhode River. Water temperatures ranged from 23 to 26 °C. Blue crabs were captured in baited crab pots in the Rhode River and held $\leqslant 3$ days in floating cages prior to an experiment. Crabs were fed fish (*Brevoortia tyrannus*) daily, but then starved for 24 h before an experiment. Live *M. arenaria* were obtained locally from a commercial source and held in estuarine water tables for ≤ 1 wk before an experiment. Only clams with active siphon-withdrawal reflexes and undamaged siphons and shells were used in experiments.

FORAGING EXPERIMENTS

In each of 10 replicate experiments, three size-matched (± 5 mm carapace width, CW), adult, intermolt male blue crabs (130–150 mm CW range) were subjected to one of the following autotomy treatments: (1) a right crusher cheliped was removed, (2) both chelipeds were removed, or (3) no limbs were removed. Limb autotomy was caused 24 h before introduction into an aquarium by applying pressure to the meral segment. Crabs autotomized injured limbs immediately.

Shell length (SL) and width were measured for 24 *M. arenaria* in each experiment. Eight randomly selected clams (44–72 mm SL) were introduced into each of three aquaria. Clams were positioned 12.5 cm apart along the aquarium centerline (15 cm from each wall). Each clam was pushed into the substratum to $\approx 1/3$ its shell length and then allowed to bury further naturally. Clam burial was checked after 24 and 48 h.

48 h after clam introduction, a single crab was placed into each aquarium and allowed to forage for 48 h. The three autotomy treatments were randomized among aquaria and tested concurrently. After 48 h, crabs were removed from aquaria, and all surviving clams and all shell fragments of eaten clams were recovered. Evidence of predator-induced clam siphon damage was recorded. At the end of each experiment, sediment was remixed to eliminate burrows left by clams, and a new set of 24 clams was introduced.

In control experiments, eight *M. arenaria* were placed in each of three aquaria without a blue crab predator to determine whether: (1) burial depths were consistent between tanks, and (2) nonpredator related mortality or siphon damage occurred. A measured length of monofilament fishing line (≈ 39 cm) was attached to the center of one valve of each clam using cyanoacrylate glue (Krazy Glue), so that depth of burial could be determined. Clams were pushed into the substratum to $\approx 1/3$ their shell length and allowed 48 h in which to burrow. Burial depths (cm) were recorded at 24 and 48 h and survivorship was checked at the end of 96 h.

Observations of feeding behavior were not possible in aquaria containing sediment because movement by crabs resulted in turbid water and poor visibility. Instead, crabs were observed feeding in an aquarium lacking sediment. In separate trials, a single clam was placed in the aquarium with an intact crab or a crab missing one or both chelipeds. Observations were made from behind a blind for two crabs per autotomy treatment.

STATISTICAL ANALYSES

The primary focus of the experiment was to determine whether limb loss differentially affected blue crab foraging rate (i.e. clams or siphons eaten/48 h). Data were treated as categorical, and a logistic regression (Cox & Snell, 1989; PROC CATMOD with maximum likelihood estimate option, 0.5 added to all cells, SAS Institute, 1985) was used to determine whether limb loss treatment, experimental replicate, or their interaction affected mortality and injury of clams. If a test revealed significant heterogeneity, unplanned multiple comparisons controlling for experimentwise type I error were used to distinguish differences among frequencies (simultaneous test procedure, STP; Sokal & Rohlf, 1981, p. 729).

The relationship of predator and prey size for each treatment was examined using ANCOVA (crab size = covariate). Linear contrasts compared mean sizes of surviving clams with those of consumed clams for each treatment (one-way ANOVA). Burial depths in control experiments were compared between aquaria and times after adjusting for clam size (two-way ANCOVA). Variances were homogeneous (F_{max} tests, Sokal & Rohlf, 1981) and residuals were normally distributed in all tests. For ANCOVA models, tests for homogeneity of slopes showed no interaction among regression lines ($P > 0.05$).

RESULTS

FIELD SURVEY

During 1986–89, 7.5% of 3330 blue crabs caught in the Rhode River, Maryland, were missing one or both chelipeds. Loss of a single cheliped (6.9%) was significantly more common than loss of both chelipeds for pooled size classes (0.6%; $G^2 = 316.8$, 1 df, $P < 0.001$; Fig. 1). The proportion of crabs missing both chelipeds (0.006) is approxi­mately what would be expected if each cheliped were lost independently (i.e., $0.069^2 = 0.005$). Large blue crabs (> 110 mm CW) were missing one or both chelipeds more often than medium (61–110 mm CW) or small crabs (< 61 mm CW) ($G^2 = 36.1$, 2 df, $P < 0.001$). Right and left chelipeds were lost with equal frequency for pooled size classes ($G^2 = 2.6$, 1 df, $P = 0.1$; Fig. 1). With the exception of South Carolina, the frequency of cheliped loss was significantly greater at all sites sampled outside the Rhode River (STP test, 5 df, $P < 0.05$; Fig. 2). For example, 21.3% of the blue crabs
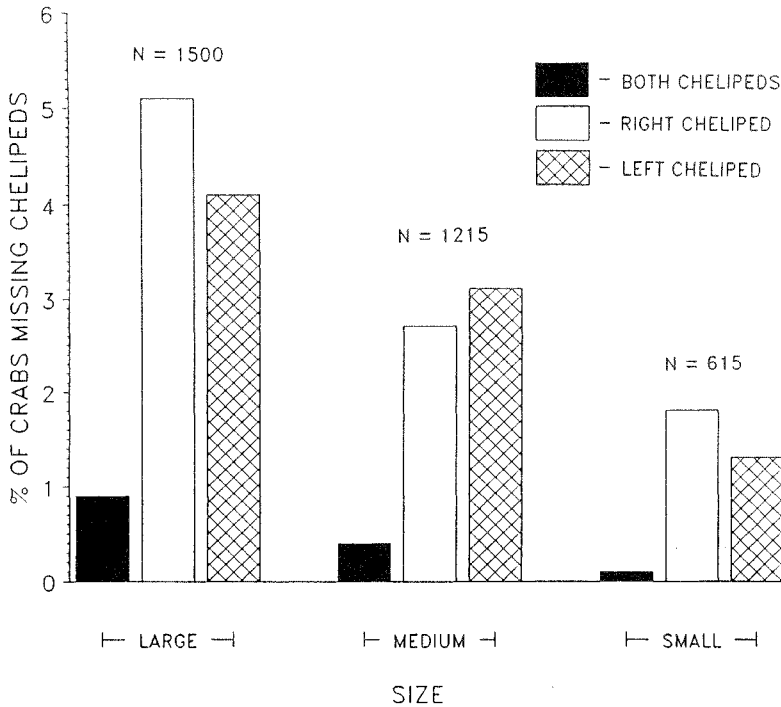
Fig. 1. Summary of the percentage of blue crabs missing right, left, or both chelipeds as a function of size in Rhode River, Maryland, during 1986–89. Size classes consist of small (CW < 61 mm), medium (CW 61–110 mm) and large (CW > 110 mm) crabs. Sample sizes for each size class are presented.

sampled in the Patuxent River, Maryland, were missing one or both chelipeds, while only 4.5% of the Rhode River population showed similar damage in 1989 (Fig. 2). Loss of both chelipeds was relatively rare at all sites.

FORAGING EXPERIMENTS

In control experiments, clam burial depth over 48 h in the absence of blue crab predators showed significant differences among tanks (two-way ANCOVA, *M. arenaria* shell length = covariate; $F = 3.9$, df = 2,41, $P = 0.03$) and between days ($F = 6.3$, df = 1,41, $P = 0.02$). Exclusion of one exceptionally deep burrower (≥ 2 SD from $\bar{x}$) resulted in nonsignificant differences among tanks (two-way ANCOVA, $F = 2.8$, df = 2,39, $P = 0.07$; Table I). Clams were found buried deeper at 48 h than at 24 h ($F = 9.7$, df = 1,39, $P = 0.004$). Burial depth was not significantly related to clam size ($F = 1.1$, df = 1,39, $P = 0.1$). No instances of clam mortality or siphon damage were observed among tanks after 96 h.

In experiments with crab predators, one crab missing a single cheliped died; data from this aquarium were excluded from analysis. Four clams ($<2\%$) died without
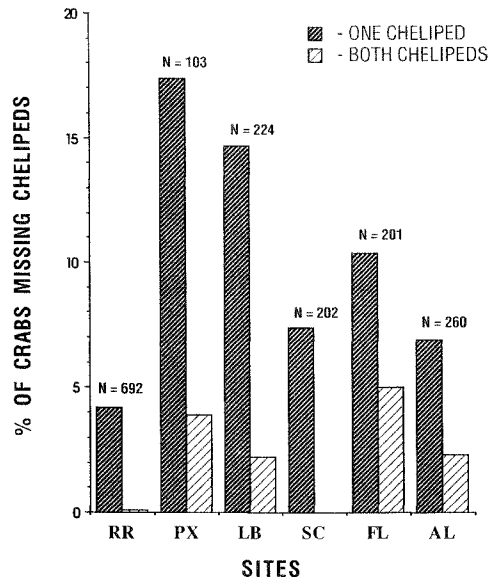
Fig. 2. Summary of percentage of blue crabs missing one or both chelipeds in 1989 in Rhode River, Maryland (RR); Patuxent River, Maryland (38°23'N, 76°36'W; PX); lower Chesapeake Bay, Virginia ($\approx$ 37°30'N, 76°00'W; LB); North Inlet, South Carolina (33°21'N, 79°11'W; SC); Indian River, Florida (27°50'N, 80°29'W; FL); and Mobile Bay, Alabama (30°15'N, 88°00'W; AL). Samples sizes of blue crabs for each site are given.

TABLE I

Comparison of mean clam burial depths (cm) in control tanks (1–3) over 24 and 48 h.

Source	$\bar{x}^1$	n	$\bar{x}^2$	n
Tank				
1	10.0^a	16	10.0^a	16
2	11.2^{ab}	16	10.2^a	14
3	8.7^b	16	8.7^a	16
Time				
24 h	9.0^a	24	8.6^a	23
48 h	11.0^b	24	10.6^b	23

[1] Includes all clams;

[2] Excludes one unusually deep burrowing clam. Superscripts with same letter are not significantly different (Ryan's Q test, $P > 0.05$).

evidence of siphonal or shell damage by crabs. These also were excluded. Five of the remaining 228 clams (2.2%) received damage to their siphons by crabs and survived. Siphon injury was not confined to any particular limb autotomy treatment. Blue crabs missing both chelipeds consumed significantly fewer *M. arenaria* than did intact crabs or crabs missing one cheliped (logistic regression, $G^2 = 10.8$, 2 df, $P = 0.004$; Fig. 3,
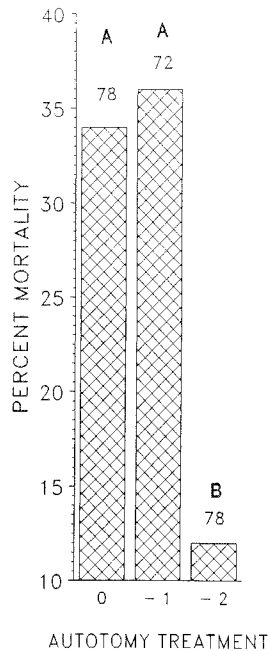
Fig. 3. Comparison of percent mortality of *M. arenaria* among three blue crab limb autotomy treatments (i.e., missing 0, 1, or 2 chelipeds) for combined experimental replicates. Treatments with same letter are not significantly different (log regression). Clam sample sizes are presented for each treatment.

Table II). Consumption rates did not differ between intact crabs and those missing one cheliped (STP test, 2 df, $P > 0.05$). The percentage of clams eaten differed among replicated experiments ($G^2 = 26.9$, 9 df, $P = 0.002$) but the differences were consistent

TABLE II

Mean consumption rates of clams ($\pm$ 1 SE) by intact crabs and those missing one or both chelipeds for 10 experiments.

Autotomy treatment	n	Mean consumption rate [clams/(crab $\times$ 48 h)]
Intact	10	2.7 (0.9)
One cheliped	9	2.9 (1.0)
Two chelipeds	10	1.0 (0.5)

for all treatments (treatment $\times$ experiment interaction, $G^2 = 23.0$, 18 df, $P = 0.15$). Clam mortality was not affected by horizontal position in aquaria ($G^2 = 3.1$, 7 df, $P = 0.87$).

Mean shell lengths of *M. arenaria* consumed by blue crabs were significantly smaller than those of surviving clams for all autotomy treatments (orthogonal linear contrasts, 1 df, $P < 0.001$, MSE $= 62.0$, $n = 228$; Fig. 4). Carapace widths for three crabs in one
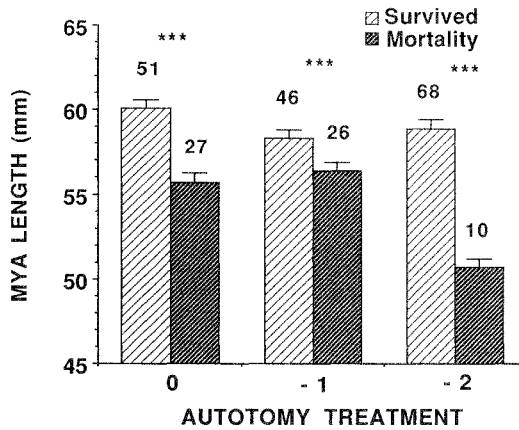
Fig. 4. Comparison of mean shell lengths (mm) of consumed and undamaged *M. arenaria* for each blue crab limb autotomy treatment (i.e., 0, 1, or 2 chelipeds missing). Sample sizes and $\pm$ SE of $\bar{x}$ are given. Significance levels of orthogonal linear contrasts for each comparison are presented. *** $P < 0.001$.

experimental replicate were not recorded, and this is reflected in analyses that include predator size. Size of predated clams correlated positively with blue crab carapace width (one-way ANCOVA, $F = 16.4$, df = 1,49, $P < 0.001$). Crab carapace widths differed among experiments (one-way ANOVA, $F = 24.0$, df = 8,17, $P < 0.001$), but not among treatments within experiments (± 5 mm). *M. arenaria* shell lengths differed among experimental runs (two-way ANOVA, $F = 67.2$, df = 9,199, $P < 0.001$), but not among autotomy treatments within experiments (treatment $\times$ experiment interaction, $F = 0.8$, df = 17,199, $P = 0.67$).

BEHAVIORAL OBSERVATIONS

Regardless of the number of chelipeds removed, blue crabs (> 140 mm CW) were capable of feeding on medium-size (≈ 45 mm SL) *M. arenaria*. Using both chelipeds, intact crabs manipulated and easily crushed a large (77 mm SL) and medium size (42 mm SL) clam in separate trials. Crabs missing a right cheliped picked up clams (one 80 mm, the other 48 mm SL) with their left cheliped, positioned the clams with their right first walking leg and third maxilliped, and then crushed the shells with their cheliped. Crabs missing both chelipeds manipulated clams using both right and left first (and occasionally second) walking legs. In one trial, a crab positioned a medium-size clam (47 mm SL) between its third maxillipeds and crushed the lower shell edge away from the siphon. The maxillipeds were used to hold and pull the prey while the mandibles shredded the soft tissue. In a second trial, a crab missing both chelipeds chipped at the shell margin of a large *M. arenaria* (82 mm SL) but was unable to crush it. Instead, the crab ate the fleshy mantle margin and siphon.

DISCUSSION

High frequencies of limb loss (18–39%) in *C. sapidus* populations from Chesapeake Bay to the Gulf of Mexico suggest that autotomy is an important mechanism for limiting injury and avoiding predation (Smith, 1990a; Smith & Hines, 1991). At all sites, the majority of those injured were missing or regenerating a single cheliped (Smith & Hines, 1991). Chelipeds perform a variety of important functions in decapod crustaceans, including mate display, prey capture, and predator defense (e.g., Robinson et al., 1970; Jachowski, 1974; Smith, 1990a). For autotomy to be cost-effective, loss of a cheliped must not significantly impair performance of such tasks. Our experiments demonstrated that blue crab consumption rates on *M. arenaria* were not reduced by the absence of a crusher cheliped. *C. sapidus* individuals compensated for the injury by utilizing the cutter cheliped and the opposite first walking leg to manipulate and crush their prey. Crushing forces exerted by either crusher or cutter claws in adult blue crabs are sufficient to break all sizes of *M. arenaria* found in Chesapeake Bay (Blundon & Kennedy, 1982b). Such compensatory adjustments following limb loss are common in crustacea (Reese, 1983). Substantial levels of cheliped regeneration observed in blue crab populations (Hamilton et al., 1976; Smith, 1990b) suggest that individuals are capable of surviving, at least temporarily, with only one cheliped.

For blue crabs missing both chelipeds, reduced foraging rate on *M. arenaria* could force changes in diet, slow growth, and adversely affect survival and reproduction. In the Rhode River, *M. arenaria* account for ≈76% of the biomass in sandy sediments (Hines & Comtois, 1985) and are a major item in the diet of blue crabs (Hines et al., 1990). Loss of both chelipeds could be particularly disadvantageous in late summer, when only larger *M. arenaria* persist and their abundances are low (Holland et al., 1980; Blundon & Kennedy, 1982a; Lipcius & Hines, 1986). Injured crabs may have greater difficulty capturing mobile prey, such as conspecifics (Smith, 1990a), or crushing molluscs with robust shells, such as *Rangia cuneata* and *Mercenaria mercenaria* (Blundon & Kennedy, 1982b). Energetic costs associated with multiple limb regeneration could be compounded by decreased foraging rate. In laboratory experiments, molt increments of blue crabs missing four limbs (both chelipeds, one walking and one swimming leg) were significantly smaller than those of intact crabs even though both groups were fed menhaden ad libitum (Smith, 1990b). Smaller body size in blue crabs can increase susceptibility to predators, reduce competitive ability for mates (Smith, 1990a), and decrease fecundity in females (Hines, 1982).

Feeding rates of blue crabs in these experiments are comparable to those observed by Lipcius & Hines (1986) for blue crabs exposed to treatment densities of 8 *M. arenaria*/208-l aquarium over 72 h. Their treatments, conducted in sandy sediments, showed that intact adult crabs removed ≈3.5 clams over 72 h (2.3 clams/48 h). In the present experiment, intact crabs and those missing one cheliped ate an average of 2.8 clams/48 h; whereas, blue crabs missing both chelipeds consumed an average of only 1 clam over the same period (Table II). These values are below satiation levels for individual crabs (5.5 clams/48 h extrapolated from Lipcius & Hines, 1986).

Consumption rates in aquaria should not have been significantly biased by experimental prey densities or burial depths. Clam densities (22 clams/m^2) and burial depths (10 cm) were comparable to natural densities and depths observed in Chesapeake Bay in mid-summer (Blundon & Kennedy, 1982a; Hines & Comtois, 1985). Lipcius & Hines (1986) demonstrated that, given a range of 2–32 clams of equivalent size per aquarium, maximum risk of mortality for *M. arenaria* in sandy substrata occurred at ≈4–8 clams. Blundon & Kennedy (1982a) showed that large *M. arenaria* buried below 10 cm gained a partial refuge from blue crab predators. In the present experiments, smaller *M. arenaria* were eaten more often than larger clams, even though burial depths did not differ among the size range of *M. arenaria* used. Larger clams may be more difficult to excavate or to manipulate than smaller clams. Similar size-related effects have been noted for bivalves with more robust shells. For example, large blue crabs did not eat the largest size class of hard clams *Mercenaria mercenaria* (>40 mm SL) offered in laboratory experiments, but did forage on 10 and 25 mm SL clams (Arnold, 1984). Similarly, blue crab handling time of mussels *Geukensia demissa* increased with mussel size, such that smaller mussels were eaten most often (Hughes & Seed, 1981). This behavior is not confined to blue crabs. Juanes & Hartwick (1990) demonstrated a size-selective feeding preference by Dungeness crabs *Cancer magister* for small hard-shelled clams *Protothaca staminea*.

Because individuals missing both chelipeds were relatively uncommon in the Rhode River, blue crab predation rates on *M. arenaria* were probably not diminished significantly. Higher frequencies of both single and double cheliped loss, however, were recorded in blue crab populations at other sites in the Chesapeake Bay (e.g., 21% in Patuxent River, Maryland) and along the southeastern coast of the USA. The effect of limb autotomy on blue crab foraging in these locations could potentially be significant at the population and individual level for both predator and prey. Alternative prey species may be more difficult to capture and subdue with only a single cheliped. Blue crabs are known to eat a wide range of bivalves, gastropods, polychaetes, fish, and crustaceans (Laughlin, 1982; West & Williams, 1986; Hines et al., 1990; Stoner & Buchanan, 1990). Future experiments should examine the effects of limb autotomy on a blue crab's prey preference, given a range of prey species and prey sizes. Empirical work is also needed to determine whether autotomy's effect on foraging rate varies as diet changes during crab ontogeny (Laughlin, 1982; Stoner & Buchanan, 1990).

supported by the Smithsonian Environmental Research Center. This paper is submitted in partial fulfillment of requirements for a Doctor of Philosophy at the University of Maryland.

REFERENCES

Arnold, W.S., 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linné). *J. Exp. Mar. Biol. Ecol.*, Vol. 80, pp. 207–219.

Ballinger, R.E., 1973. Experimental evidence of the tail as a balancing organ in the lizard *Anolis carolinensis*. *Herpetologia*, Vol. 29, pp. 65–66.

Blundon, J.A. & V.S. Kennedy, 1982a. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.*, Vol. 65, pp. 67–81.

Blundon, J.A. & V.S. Kennedy, 1982b. Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *J. Exp. Mar. Biol. Ecol.*, Vol. 65, pp. 47–65.

Brown, S.C., S.R. Cassuto & R.W. Loos, 1979. Biomechanics of chelipeds in some decapod crustaceans. *J. Zool. London*, Vol. 188, pp. 143–159.

Cox, D.R. & E.J. Snell, 1989. *Analysis of binary data*. Routledge, Chapman & Hall, 200 pp.

Edgar, G.J., 1990. Predator–prey interactions in seagrass beds. II. Distribution and diet of the blue manna crab *Portunus pelagicus* Linnaeus at Cliff Head, Western Australia. *J. Exp. Mar. Biol. Ecol.*, Vol. 139, pp. 23–32.

Elner, R.W., 1980. The influence of temperature, sex, and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). *Mar. Behav. Physiol.*, Vol. 7, pp. 15–24.

Fox, S.F. & M.A. Rostker, 1982. Social cost of tail loss in *Uta stansburiana*. *Science*, Vol. 218, pp. 692–693.

Hamilton, P.V., 1976. Predation of *Littorina irrorata* by *Callinectes sapidus*. *Bull. Mar. Sci.*, Vol. 26, pp. 403–409.

Hamilton, P.V., R.T. Nishimoto & J.G. Halusky, 1976. Cheliped laterality in *Callinectes sapidus* (Crustacea: Portunidae). *Biol. Bull.*, Vol. 150, pp. 393–401.

Hines, A.H., 1982. Allometric constraints and variables of reproductive effort in brachyuran crabs. *Mar. Biol.*, Vol. 69, pp. 309–320.

Hines, A.H. & K.L. Comtois, 1985. Vertical distribution of infauna in sediments of a subestuary of central Chesapeake Bay. *Estuaries*, Vol. 8, pp. 296–304.

Hines, A.H., A.M. Haddon & L.A. Wiechert, 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, Vol. 67, pp. 105–126.

Holland, A.F., N.K. Mountford, M.H. Hiegel, K.R. Kaumeyer & J.A. Mihursky, 1980. Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. *Mar. Biol.*, Vol. 57, pp. 221–235.

Hughes, R.N. & R. Seed, 1981. Size selection of mussels by the blue crab *Callinectes sapidus*: energy maximizer or time minimizer? *Mar. Ecol. Prog. Ser.*, Vol. 6, pp. 83–89.

Jachowski, R.L., 1974. Agonistic behavior of the blue crab, *Callinectes sapidus* Rathbun. *Behaviour*, Vol. 50, pp. 232–253.

Jaksic, F.M. & E.R. Fuentes, 1980. Correlates of tail losses in twelve species of *Liolaemus* lizards. *J. Herpetol.*, Vol. 14, pp. 137–141.

Juanes, F. & E.B. Hartwick, 1990. Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology*, Vol. 71, pp. 744–758.

Kuris, A.M. & M. Mager, 1975. Effect of limb regeneration on size increase at molt of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. *J. Exp. Zool.*, Vol. 193, pp. 353–360.

Laughlin, R.A., 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bull. Mar. Sci.*, Vol. 32, pp. 807–822.

Lawrence, J.M., T.S. Klinger, J.B. McClintock, S.A. Watts, C.-P. Chen, A. Marsh & L. Smith, 1986. Allocation of nutrient resources to body components by regenerating *Luidia clathrata* (Say) (Echinodermata : Asteroidea). *J. Exp. Mar. Biol. Ecol.*, Vol. 102, pp. 47–53.

Lipcius, R.M. & A.H. Hines, 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology*, Vol. 67, pp. 1361–1371.

Maiorana, V. C., 1977. Tail autotomy, functional conflicts and their resolution by a salamander. *Nature*, Vol. 265, pp. 533–535.

McCallum, H. I., R. Endean & A. M. Cameron, 1989. Sublethal damage to *Acanthaster planci* as an index of predation pressure. *Mar. Ecol. Prog. Ser.*, Vol. 56, pp. 29–36.

McVean, A., 1982. Autotomy. In, *The biology of Crustacea, Vol. 4*, edited by D. E. Bliss, Academic Press, New York, pp. 107–132.

Medel, R. G., J. E. Jimenez, S. F. Fox & F. M. Jaksic, 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos*, Vol. 53, pp. 321–324.

Reese, E. R., 1983. Evolution, neuroethology, and behavioral adaptations of crustacean appendages. In, *Studies in adaptation: the behavior of higher Crustacea*, edited by S. Rebach & D. W. Dunham, John Wiley and Sons, New York, pp. 57–81.

Robinson, M. H., L. G. Abele & B. Robinson, 1970. Attack autotomy: a defense against predators. *Science*, Vol. 169, pp. 300–301.

SAS Institute, 1985. *SAS user's guide: statistics. Version 5 edition.* SAS Institute, Cary, North Carolina, 956 pp.

Schall, J. J. & E. R. Pianka, 1980. Evolution of escape behavior diversity. *Am. Nat.*, Vol. 115, pp. 551–566.

Slater, A. & J. M. Lawrence, 1980. The effect of arm loss on feeding and growth rates in *Luidia clathrata*. *Fla. Sci.*, Vol. 43, p. 16.

Smith, L. D., 1990a. *The frequency and ecological consequences of limb autotomy in the blue crab*, Callinectes sapidus *Rathbun*. Ph. D. dissertation, University of Maryland, College Park, Maryland, 259 pp.

Smith, L. D., 1990b. Patterns of limb loss in the blue crab, *Callinectes sapidus* Rathbun, and the effects of autotomy on growth. *Bull. Mar. Sci.*, Vol. 46, pp. 23–36.

Smith, L. D. & A. H. Hines, 1991. Autotomy in blue crab (*Callinectes sapidus* Rathbun) populations: geographic, temporal, and ontogenetic variation. *Biol. Bull.*, Vol. 180, pp. 416–431.

Sokal, R. R. & F. J. Rohlf, 1981. *Biometry.* W. H. Freeman & Co., New York, 859 pp.

Stoner, A. W. & B. A. Buchanan, 1990. Ontogeny and overlap in the diets of four tropical *Callinectes* species. *Bull. Mar. Sci.*, Vol. 46, pp. 3–12.

Virnstein, R. W., 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology*, Vol. 58, pp. 1199–1217.

Vitt, L. J. & W. E. Cooper, 1986. Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): age-specific differences in costs and benefits. *Can. J. Zool.*, Vol. 64, pp. 683–792.

West, D. L. & A. H. Williams, 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *J. Exp. Mar. Biol. Ecol.*, Vol. 100, pp. 75–95.