Effects of limb autotomy and tethering on juvenile blue crab survival from cannibalism

L. David Smith

Smithsonian Environmental Research Center, PO Box 28, Edgewater, Maryland 21037, USA
and Department of Zoology, University of Maryland, College Park, Maryland 20742, USA

ABSTRACT: High frequencies of limb loss (18 to 39 %) in blue crab *Callinectes sapidus* Rathbun populations over broad temporal and spatial scales suggest that the autotomy response is an important escape mechanism. Limb loss, however, may increase vulnerability of prey in future encounters with predators. If individual survival is reduced significantly and injury frequency in the population is density-dependent, such nonlethal injury could affect population size. Annual frequencies of limb loss were positively correlated to blue crab abundances in the Rhode River, Maryland, USA, between 1986 and 1989, but results of open-field tethering experiments indicated that, overall, missing limbs did not increase juvenile vulnerability to predators. Limitations imposed by the tether on normal escape behavior, however, may have masked real survival differences among limb-loss treatments. To test for interactive effects of limb loss and tethering on survival from predation, I conducted a set of field experiments in 10 m² enclosures, using adult blue crabs as predators and intact and injured (missing 1 or 4 limbs), tethered and untethered juvenile conspecifics as prey. A second experiment, conducted in small wading pools, tested the impact of limb loss on escape speed and direction of juvenile blue crabs. Results of enclosure experiments demonstrated that: (1) under typical field conditions and crab densities, larger conspecifics do inflict lethal and nonlethal injury on juveniles; and (2) in encounters with predators, prior limb loss does not handicap crabs if escape is possible (untethered treatments), but does impose a defensive cost if escape is restricted (tethered treatments). In addition, survivorship patterns suggest that prey missing multiple limbs altered their activity patterns to decrease vulnerability. In wading pools, limb loss altered escape speed and direction, although effects varied depending on the type and number of missing limbs. Together, these experiments indicate that prior limb loss can have complex effects on escape effectiveness, defensive ability, and anti-predator behavior. They also suggest that, despite density-dependence, prior limb loss does not reduce blue crab fitness sufficiently to regulate population size.

KEY WORDS: Autotomy · Nonlethal injury · Blue crab · *Callinectes sapidus* · Predation · Cannibalism · Density-dependence · Escape response · Tethering · Enclosures

INTRODUCTION

Autotomy, the self-amputation of a body part at a breakage plane (Wood & Wood 1932, McVean 1982), is thought to function principally as a mechanism for escape from predators (Vermeij 1982, 1987). Experimental work on lizards and salamanders has shown that tail autotomy effectively distracts predators and prevents subjugation of prey (Congdon et al. 1974, Ducey & Brodie 1983, Dial & Fitzpatrick 1983, 1984). Nevertheless, for the individual, loss of an appendage can slow growth rate (Kuris & Mager 1975, Vitt & Cooper 1986, Smith 1990a), hinder foraging ability (Smith & Hines 1991a), decrease reproductive output (Smyth 1974, Maiorana 1977, Dial & Fitzpatrick 1981, Smith 1992), and lower social status (Fox & Rotsker 1982). Furthermore, autotomy can leave an animal more vulnerable in later encounters with predators by impairing defensive capacity (Bildstein et al. 1989, Davenport et al. 1992), reducing escape effectiveness (Congdon et al. 1974, Ducey & Brodie 1983, Dial & Fitzpatrick 1984, Vitt & Cooper 1986, Robinson et al. 1991a, b), or adversely modifying behavior (Robinson et al. 1991b).

Limb autotomy has the potential to affect not only individual fitness, but also population dynamics. Theoretical models suggest that nonlethal injury could regulate prey population size if: (1) injury rates were density-dependent, and (2) injury significantly reduced survival or reproduction (Harris 1989). This regulatory effect requires close coupling between predator and prey abundances; such coupling is most likely to occur if predator and prey are conspecifics. These models have important implications for animal populations exhibiting autotomy, because intraspecific predation is common in many taxa (Fox 1975, Polis 1981, Stevens et al. 1982, Kurihara & Okamoto 1987, Reaka 1987, Kurihara et al. 1988, Spence & Cárcamo 1991, Elgar & Crespi 1992) and injury frequency often correlates positively with population density (Baker & Dixon 1986, Petranka 1989, Robinson et al. 1991b, Smith & Hines 1991b, Van Buskirk & Smith 1991).

High frequencies (18 to 39%) of limb loss have been documented in blue crab *Callinectes sapidus* Rathbun (Portunidae) populations over broad temporal and spatial scales (Smith & Hines 1991b), suggesting that the autotomy response is an important survival mechanism in this species. Blue crabs are dominant predators in soft-bottom benthic communities in nearshore waters of the western Atlantic Ocean (Virnstein 1977, Holland et al. 1980, Hines et al. 1990) and are prey for a number of fish and crustacean species (Millikan & Williams 1984, Shirley et al. 1990). If nonlethal injury regulates population size in *C. sapidus*, direct and indirect effects on the community could be far-reaching. The potential for density-dependent injury exists, because cannibalism is known to occur in this and in other crab species (Botsford & Wickham 1978, Hankin 1985, Kurihara & Okamoto 1987, Peery 1989, Lipcius & Van Engel 1990). Limb-loss patterns observed in juvenile blue crabs tethered in the open field were strikingly similar to those found in natural populations of *C. sapidus* from 1986 to 1989 (Smith 1990b, Smith & Hines 1991b) indicating that unsuccessful predatory attacks may be the primary cause of autotomy. Although several predatory species could potentially have been responsible for these injuries (e.g. *Opsanus tau*; Hines et al. 1990), larger conspecifics were the only predators I observed attacking and consuming tethered juveniles during these experiments (author's pers. obs.). Based on these findings, I conducted a set of experiments in 10 m² field enclosures in the Rhode River, Maryland, USA, to test whether larger conspecifics were a source of lethal and nonlethal injury to juvenile blue crabs and whether missing limbs increased prey vulnerability to cannibalistic adults.

Enclosure experiments were also designed to compare prey survival as a function of tethering. Results of open-field tethering experiments indicated that, in most cases, intact juvenile blue crabs and those missing 1 to 4 limbs had similar mortality rates (Smith 1990b). Tethering, however, may have substantially altered normal escape response in this highly mobile species (Zimmer-Faust et al. 1994) and masked real survivorship differences among autotomy treatments. By employing large field enclosures, I was able to compare survivorship of tethered and untethered, injured and intact juvenile blue crabs. These experiments are among the first to examine: (1) the role of cannibalism as an agent of nonlethal injury, and (2) the effects of prior limb loss and tethering on prey survival using typical crab densities and natural field conditions.

A second set of experiments was conducted in small wading pools to test the effect of limb loss on escape behavior. Juvenile blue crabs were subjected to a number of limb-loss treatments and their escape speed and direction of movement over a short distance were measured. Results of these enclosure and escape response experiments, when compared to patterns of autotomy observed in natural populations, elucidate the role of autotomy as a survival mechanism and its potential for population regulation.

METHODS

Study site and collection methods. I conducted enclosure experiments in an embayment of the Rhode River, Maryland (38° 51' N, 76° 32' W) in 1989 (Fig. 1).
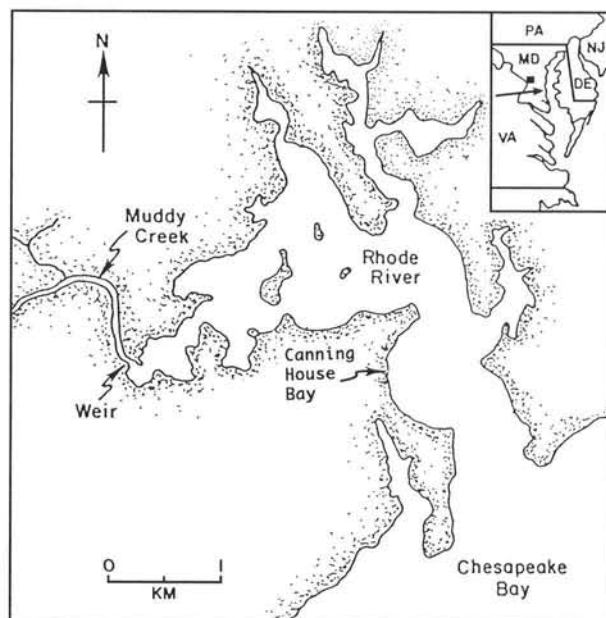

Fig. 1. Rhode River subestuary, Maryland, USA, and site of enclosure experiments in Canning House Bay

The Rhode River is a shallow (maximum depth 4 m), mesohaline (4 to 15‰) subestuary located on the western side of central Chesapeake Bay (Hines et al. 1987). Bottom sediments were composed of muddy sand and lacked submerged aquatic vegetation. Coarse woody debris was the dominant structural component in shallow, nearshore waters (Everett & Ruiz 1993). Water temperatures ranged from 26 to 32°C. Salinity was unusually low (2 to 4‰) in 1989. I carried out tests of escape response in 1989 in small wading pools at the Smithsonian Environmental Research Center, Edgewater, Maryland.

Intermolt blue crabs were collected for experiments at a fish weir, by seine, and by crab pots in shallow areas near the head of the Rhode River. Crabs were fed 1 or 2 fish (*Brevoortia tyrannus*) daily and held no longer than 3 d in floating cages anchored in shallow water. Crabs were starved 24 h prior to an experiment.

Intraspecific predation experiments. *Enclosure design:* Experiments designed to test the effects of limb loss and tethering on the survival of small blue crabs from larger conspecifics were conducted in enclosures. I constructed 12 adjoining 10 m^2 (2.5 × 4 m) enclosures in water approximately 0.5 m deep (mean low tide). The substrate within each enclosure was muddy sand lacking structural components. Enclosure sides were 1.2 m high, made of plastic mesh (1.27 cm mesh Vexar™) held up by wooden poles, and lined with 18 cm of galvanized wire mesh (1.27 cm mesh hardware cloth) along the bottom edge. I buried the hardware cloth 15 cm into the sediment to prevent escape by crabs. I placed a small section (15 cm wide × 1.2 m high) of Vexar and hardware cloth in each corner to round the corners off and remove a potential refuge for smaller crabs. Enclosures were oriented so that the long axis of each unit was parallel to shore.

Preliminary experiments indicated that recovery of untethered live crabs or shell fragments of eaten crabs would be difficult in murky water. To facilitate recovery, I attached a 45 cm length of floating fly line to a short (7 cm) steel leader 'antenna' rising off the dorsal carapace of all experimental crabs. The part of the floating line at the water surface marked the crab's location. The floating line nearest the crab, though, was painted black so that the line would not be visible to benthic predators. Observations showed that crab movement and ability to bury were not hindered by the floating line. Mean swimming speeds of intact juvenile blue crabs (mean CW ± 1 SD, 53.9 ± 13.8 mm) with and without floating lines were not significantly different ($t = 1.24$, df = 18, $p = 0.23$).

Experimental design: I subjected small, intermolt crabs between 41 and 72 mm CW (mean ± 1 SD, 54.1 ± 7.2 mm) to 1 of 3 limb-loss treatments and 1 of 2 tethering conditions (tethered or untethered) 24 h

before placing them in enclosures. Limb-loss treatments consisted of: (1) intact crabs, (2) crabs missing 1 cheliped, or (3) crabs missing both chelipeds, 1 walking leg, and the opposing swimming leg. Half of the small crabs were fitted with tethers. Tethering involved looping monofilament fishing line between the crab's lateral spines and cinching the line to form a halter across the dorsal carapace. The knotted end of a 1.2 m long nylon-coated, black steel leader was placed beneath the monofilament and both the steel leader and monofilament were anchored to the dorsal carapace using cyanoacrylate glue (Krazy Glue™). I attached the free end of the steel leader to a swivel secured to the top of a 10 cm stake, which I later embedded into the bottom sediment.

I tethered 2 small crabs in each of 6 enclosures and staked them so that both had access to the enclosure walls, but neither crab could physically contact the other. I introduced 2 untethered small crabs into each of the 6 remaining enclosures. Within any enclosure, both crabs had received the same autotomy treatment. I duplicated each treatment combination so that a single experiment consisted of 3 limb-loss treatments × 2 tethering conditions × 2 enclosures (= 12 enclosures). Treatment combinations were randomized among the 12 enclosures.

Two hours after small crabs had been placed in the enclosures, a single intact, large, intermolt male crab (mean CW ± 1 SD, 141.0 ± 16.0 mm) was placed in each of the 12 enclosures and left undisturbed for 48 h. Based on previous tethering experiments conducted in the open field in the Rhode River and monitored at 24 and 48 h, a 48 h period was deemed sufficient time to see an effect from predation (Smith 1990b). At the end of 48 h, I removed large crabs and collected small crabs or their remains. I repeated the experiment 8 times between 13 June and 22 July 1989. A new set of 36 crabs was used in each experiment. I checked cages before and during each experiment for signs of damage (e.g. holes, undercutting of sides by waves) and made necessary repairs.

Escape response experiments. I conducted experiments to test for direction and speed of escape response as a function of limb loss in wading pools (1 m diameter × 20 cm depth) filled with water from the Rhode River. Water temperature was 28°C and salinity was 2‰ during the experiments. To prevent a burial response by the crabs, the bottom of the wading pool was kept bare of sediment. Juvenile intermolt crabs (mean CW ± 1 SD, 45.8 ± 12.1 mm) were used. I randomly applied 8 limb-loss treatments (Table 1) to crabs and caused limbs to autotomize 24 h before an experiment.

In each experimental trial, I placed a crab underneath an opaque inverted container in the center of the pool and allowed it to settle for 30 s. The container top

Table 1. *Callinectes sapidus*. Type and number of limbs removed in autotomy treatments in escape trials in wading pools. INT: all limbs intact; R: right, L: left; CH: cheliped; WL: 1st walking leg; SL: swimming leg

Type	Number	n
INT	0	15
RCH	1	15
LCH	1	15
RSL	1	10
LSL	1	10
RCH, RWL	2	10
LCH, LWL	2	9
RCH, LCH, RWL, LSL	4	11
RCH, LCH, LWL, RSL	4	4

was perforated to eliminate suction when raised. After 30 s, the container was raised and the crab was allowed to move to the pool wall. I noted its direction of movement (right or left), and I recorded the time taken to move 50 cm to the pool wall using a stopwatch. This technique measured mean rather than maximum escape speed. I then recaptured the crab and repeated the process for a total of 6 trials per crab. If a crab failed to move or moved only part of the way to the wall (<2 % of 588 trials), the trial was discounted.

Statistical analyses. The primary focus of the intraspecific predation experiments was to determine how limb loss and tethering affected survival and further injury of juvenile blue crabs in the presence of larger conspecifics. Data were treated as categorical, and I used a logistic analysis (Cox & Snell 1989; PROC CATMOD with maximum likelihood estimate option, SAS Institute 1985) to determine whether limb-loss treatment, tethering condition, or their interaction affected survival and injury. If a model showed a significant association between response and independent variables, I used linear contrasts to make a priori comparisons (Day & Quinn 1989). Data for each combination of limb-loss treatment and tethering condition were pooled for the 8 experiments.

I used repeated measures procedures to test for autotomy treatment differences in escape time (ANOVA) and escape direction (logistic regression). If escape time differed significantly among treatments, mean individual escape times were compared using unplanned multiple comparisons (Ryan's Q-test; Day & Quinn 1989). For these and other comparisons using ANOVA, group variances were tested to assure homogeneity (F_{max}-test) and residuals were examined for normality. Among-treatment differences in escape direction were compared using a simultaneous test procedure (Sokal & Rohlf 1981). Within-treatment differences in escape direction were tested against an

expected 1:1 ratio. I performed all statistical analyses using Statistical Analysis Systems (SAS) software (SAS Institute 1985).

RESULTS

Intraspecific predation experiments

Seventeen of 192 small crabs (9 %) and 6 of 96 (6 %) large crabs used in the experiments were not recovered and were excluded from analysis. Frequencies of missing crabs did not differ among experiments ($G = 8.2$, df = 7, p > 0.10). Although missing crabs were not distributed evenly among enclosures or treatment combinations (G-tests, p < 0.05), sample sizes for all treatment combinations were sufficiently large for analysis. For combined treatment combinations, predation levels were significantly higher in the final experiment than in the second or third experiments (STP tests, p < 0.01). No significant differences in mortality and injury were found among any other experiments. Survivorship was not affected by enclosure location ($G = 16.8$, df = 22, p = 0.77). Juvenile crabs did not appear to be clustered at any particular location inside the enclosures; I recovered them in the center as well as along the sides. Mean size of juvenile crabs did not differ among treatment combinations (2-way ANOVA, $F = 0.25$, df = 5, p = 0.94), experiments ($F = 0.20$, df = 7, p = 0.99), or treatment combinations across experiments (treatment × experiment interaction, $F = 1.16$, df = 35, p = 0.27). For combined treatments over all experiments, surviving juveniles were significantly larger than those that were eaten (Wilcoxon 2-sample test, p = 0.021).

The effect of limb loss on juvenile blue crab survival was dependent on their tethering status (limb-loss treatment × tether status interaction, $G = 12.9$, df = 2, p = 0.002). Among tethered crabs, intact specimens had significantly higher survivorship than crabs missing 1 cheliped, but did not differ from those missing 4 limbs (Fig. 2, Table 2). In contrast, survivorship of untethered crabs did not differ among autotomy treatments (Fig. 2, Table 2). Untethered crabs that had been subjected to autotomy were twice as likely to survive as their tethered counterparts (Fig. 2, Table 2). In contrast, survival did not differ between untethered and tethered intact crabs. For combined treatments over all experiments (n = 163 juveniles), survival with additional limb autotomy (4 %) was rare compared to fatality (33 %). Additional limb loss (1 to 3 limbs) was observed for untethered individuals that were initially intact (n = 3 crabs) or missing 4 limbs (n = 2 crabs) and for 1 tethered individual missing 4 limbs. Large crabs used as predators did not lose limbs during the experiment.
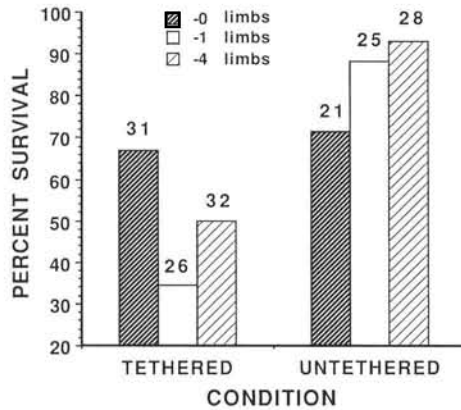
Fig. 2. *Callinectes sapidus*. Percent survival of blue crabs in enclosure experiments for 3 autotomy treatments (−0, −1, −4 limbs) and 2 tethering conditions (tethered, untethered). Sample sizes for each limb-loss treatment × tethering condition combination are presented above each bar

Nearly equal proportions of male and female juvenile crabs occurred in all treatment combinations permitting *a posteriori* testing for sex-related survival differences in encounters with predators. Survival was independent of sex for all limb-loss treatments (2-way logistic regressions, $\chi^2 = 0.47$, df = 1, p = 0.49) and tether conditions ($\chi^2 = 0.01$, df = 1, p = 0.94).

Escape response experiments

Although no natural predators were used to provoke a swimming response in these experiments, my observations and comparative data indicate that juvenile blue crabs were swimming in escape. Mean swimming speeds (22 cm s^{-1} for intact juveniles) measured over short distances in my experiments were similar to

Table 2. *Callinectes sapidus*. Linear contrasts comparing survival in enclosure experiments between intact (−0) crabs and treatments missing 1 (−1) or 4 (−4) limbs for tethered and untethered conditions, and intact (−0) or injured (−1 & −4) tethered (T) and untethered (U) crabs. Survival: directionality of survival. ns: no difference by sequential Bonferroni test (Rice 1989) where experimentwise α = 0.05

Contrast	df	χ^2	p	Survival
Tethered				
−0 vs −1	1	6.3	0.01	−0 > −1
−0 vs −4	1	2.1	0.15	ns
Untethered				
−0 vs −1	1	2.0	0.16	ns
−0 vs −4	1	4.1	0.04	ns
Tethered vs untethered				
−0	1	0.8	0.79	ns
(−1 & −4)	1	12.8	0.001	T < U

those recorded for untethered juvenile blue crabs when approached by larger conspecifics (Zimmer-Faust et al. 1994).

The number and type of missing limbs had a significant effect on escape time among experimental crabs (repeated-measures ANOVA for autotomy treatment; $F = 5.8$, df = 8,90, p < 0.001). Individual escape times varied significantly ($F = 7.4$, df = 5,450, p < 0.001) and increased linearly (polynomial contrast; $F = 21.7$, df = 1,90, p < 0.001) over repeated trials. Time differences among individual runs were consistent across all autotomy treatments (time × treatment interaction; $F = 1.2$, df = 40,450, p = 0.26). Mean escape times per individual were used to make comparisons among limb-loss treatments. Treatments that differed only by side (e.g. right vs left cheliped) did not differ in escape times ($F = 0.43$, df = 1,90, p = 0.52); hence, these were combined for subsequent comparisons. Escape times did not differ between intact crabs and those missing either 1 cheliped or 4 limbs (Fig. 3). These 3 treatment groups showed significantly faster movement than crabs missing either a single swimming leg or a cheliped and adjacent walking leg.

The direction of movement (right vs left) during an escape was not consistent among limb-loss treatments (repeated measures logistic analysis: treatment × direction interaction, $G = 58.3$, df = 35, p = 0.008). Crabs missing both chelipeds, a right first walking and left swimming leg moved to the left in 70% of the trials; while their counterparts (i.e. crabs missing both chelipeds, a left first walking and right swimming leg) moved to the right in 67% of the trials (Table 3). Escape direction between other treatment pairs in
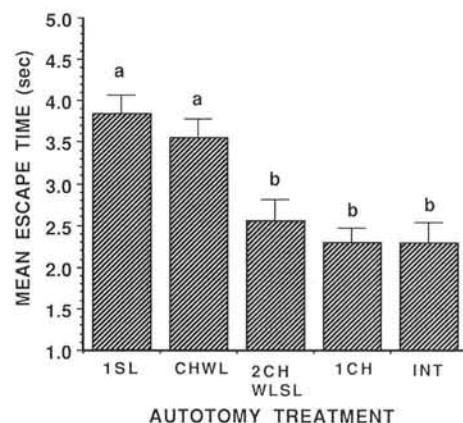

Fig. 3. *Callinectes sapidus*. Mean escape times (± 1 SE) of blue crabs subjected to different limb-loss treatments. Treatments that differed only by side were pooled for presentation. 1SL: missing one swimming leg; CHWL: missing cheliped and adjacent 1st walking leg; 2CHWLSL: missing both chelipeds, 1st walking and opposing swimming leg; 1CH: missing one cheliped; INT: all limbs intact. Means with the same superscript are not significantly different (Ryan's Q-test, p > 0.05)

Table 3. *Callinectes sapidus*. Frequencies of right and left escape movements summed for individual trials are compared among and within limb-autotomy treatments. Among treatments, those with the same superscripted letter do not differ in their direction of movement (STP test, 8 df, p > 0.05). Within treatments, L:R (% left: % right) is tested against expected pattern of random (50:50) directional movement (*G*-tests, 1 df). See Table 1 for limb loss codes

Limb loss	Escape direction		L:R	G	p
	Left	Right			
INT[a]	41	49	46:54	2.0	> 0.1
RCH[a]	41	49	46:54	2.0	> 0.1
LCH[ab]	54	36	60:40	3.6	> 0.05
RSL[ab]	32	28	53:47	0.3	> 0.5
LSL[ab]	35	25	58:42	1.7	> 0.1
RCH, RWL[ab]	30	30	50:50	0.0	> 0.99
LCH, LWL[a]	25	29	46:54	0.3	> 0.5
RCH, LCH, RWL, LSL[b]	46	20	70:30	10.5	< 0.005
RCH, LCH, LWL, RSL[a]	8	16	33:67	2.7	> 0.05

which opposing limb types were removed did not differ (STP test, df = 8, p > 0.05). Escape direction deviated significantly from an expected random pattern only for crabs missing both chelipeds, a right first walking, and left swimming leg (p < 0.005). A similar trend was observed for the matched treatment missing both chelipeds, a left first walking, and right swimming leg (0.05 < p < 0.01), but the sample size was too small to detect a difference.

DISCUSSION

Cannibalism and autotomy

Enclosure experiments demonstrated that cannibalism is a source of mortality and limb autotomy for juvenile blue crabs. These results are particularly meaningful, because experiments were conducted over a relatively large area (10 m^2), used realistic densities for the Rhode River (0.3 crabs m^{-2}; Hines et al. 1990), and occurred under ambient field conditions. Together with gut analyses (Laughlin 1982, Hines et al. 1990), population dynamics models (Lipcius & Van Engel 1990), open-field tethering (Smith 1990b, Ruiz et al. 1993) and aquarium experiments (Peery 1989), these data indicate that cannibalism is common in *Callinectes sapidus* populations. Larger conspecifics are likely the chief agents of death and injury for juvenile blue crabs in the Rhode River subestuary, because: (1) abundances of other potential predator species in the Rhode River are low (Hines et al. 1987, 1990, Ruiz et al. 1993); and (2) other sources of injury (e.g. intraspecific competitors, fisheries) are unimportant in this size class (Smith & Hines 1991b). Density-dependent

injury is strongly suggested by the positive correlation (r = 0.99, p < 0.05) between annual frequencies of limb loss and blue crab abundances in the Rhode River from 1986 to 1989 (Smith & Hines 1991b).

Autotomy and antipredator responses

The evolution of an autotomy response in diverse marine taxa (e.g. polychaetes, echinoderms, crustaceans) suggests its importance in preventing subjugation by predators (Vermeij 1982, Endler 1986). Unexpected patterns of blue crab survivorship in my experiments, however, suggest potentially complex effects of limb loss on future escape effectiveness, defensive ability, and activity levels of decapod crustacean prey. Following detection and approach by a predator, the most effective antipredator mechanism for juvenile crabs is escape or, if captured, autotomy followed by escape (e.g. 5 of 6 instances of autotomy in enclosures occurred among untethered individuals; see also Lawton 1989, Davenport et al. 1992). Tethering limits escape effectiveness (Zimmer-Faust et al. 1994) and should force prey either to actively defend themselves or reduce their activity to avoid detection. In field enclosures, intact juveniles were able to defend themselves to such a degree that survival rates among tethered and untethered intact crabs did not differ (Fig. 2, Table 2). In contrast, tethered juveniles missing 1 or both chelipeds experienced significantly higher mortality than their untethered counterparts (Table 2). These results suggest a defensive cost to autotomy if escape is restricted and illustrate the importance of escape for injured juvenile blue crabs. Under natural conditions, such restrictions are probably rare; however, defensive weaknesses will prove detrimental whenever escape proves ineffective (e.g. the predator is adept at pursuit) and injured prey are being subdued.

Prey will modify their activity in proportion to the risk of predation (Sih 1980, 1982, Lima & Dill 1990). In the presence of cannibalistic adults, smaller, more vulnerable backswimmers *Notonecta hoffmanni* reduced their movements and increased their use of suboptimal edge space to a greater degree than larger, less vulnerable instars (Sih 1982). Similar behavioral modifications in blue crabs missing 4 limbs could explain: (1) the lack of difference in survival rates between multiply injured and intact crabs in tethered treatments (Fig. 2, Table 2), and (2) a tendency towards higher survivorship in multiply injured versus intact crabs in untethered treatments (Fig. 2, Table 2). For tethered crabs missing 4 limbs, not only was escape hindered by the tether, but the absence of both chelipeds precluded any defensive posture. While re-

duced activity could increase the chances of surviving until limbs regenerate, such behavior might also decrease feeding rates or mating success (Sih 1982, 1992, Dong & Polis 1992).

Any reduction in speed (Punzo 1982, Daniels 1985, Robinson et al. 1991a) or evasiveness due to missing limbs could be detrimental for crabs that rely primarily on escape. In escape response experiments, asymmetrical injuries involving loss of a single swimming leg or a cheliped and walking leg from the same side slowed swimming speed by ca 36 % compared with intact controls (Fig. 3). In contrast, single cheliped autotomy had no effect on escape time. The latter outcome might be expected, because unlike swimming and walking legs, chelipeds provide little, if any, propulsive power (Spirito 1972). Removal of 4 limbs did not diminish escape speed relative to intact crabs. This surprising result may be due to the symmetry of the injury (2 limbs per side) and substantial loss of mass (ca 20 % of total wet weight; Smith 1990a) that allowed these individuals to maintain normal swimming speed. The direction of escape movement for crabs missing 4 limbs, however, became less random (Table 3). These individuals tended to be propelled by the remaining swimming leg in the direction of the missing swimming leg. Random directional movement by escaping prey can reduce predator capture efficiency (Schall & Pianka 1980); conversely, more consistent movement might expose injured crabs to greater risk of capture. I did not, however, observe increased mortality for juveniles missing 4 limbs in enclosure experiments. In the turbid conditions of the Rhode River, visual acuity is sufficiently limited that reduced escape speed and consistent directional escape responses by injured crabs may not be extremely costly.

Autotomy as a regulatory mechanism

While density-dependent intraspecific predation can potentially regulate population size in many brachyurans (e.g. Kurihara & Okamoto 1987, Lipcius & Van Engel 1990), the regulatory effect of nonlethal injury is uncertain. Using models, Harris (1989) demonstrated that nonlethal injury could regulate population size if injury rates were density-dependent, and injury significantly reduced survival or reproduction. The dynamics of limb loss in *Callinectes sapidus* populations meet the first of Harris's model criteria (density-dependent injury), but not the second. This study and other experiments (Smith 1990a, b, Smith & Hines 1991a, b) indicate that costs of injury to long-term survival or reproduction are insufficient to regulate population size. The most common form of injury in blue crab populations (single cheliped loss; Smith

1990a, Smith & Hines 1991b) did not increase blue crab vulnerability to predation in either enclosure (untethered treatments) or open-field tethering experiments (Smith 1990b) and had no observable effect on escape speed or direction. In addition, single cheliped loss had no effect on size increase at the molt or intermolt duration (Smith 1990a) or on foraging rate on an important bivalve prey species (Smith & Hines 1991a). In terms of reproductive success, cheliped loss in male blue crabs adversely affected competition for mates in experimental arenas (Smith 1992), but in natural populations male body size was a greater determinant of success (Smith unpubl. data). Autotomy of a single limb is unlikely to affect fecundity in female blue crabs. Energetic tradeoffs between reproductive output and regeneration found in chordate taxa (Smyth 1974, Maiorana 1977, Dial & Fitzpatrick 1981) should be absent in blue crabs, because sexually mature females cannot regenerate limbs (Millikin & Williams 1984). Severe multiple autotomy (–4 limbs) is costly to individuals in terms of reduced growth (Smith 1990a), foraging ability (Smith & Hines 1991a), and, for certain sizes, predator avoidance (Smith 1990b), but injuries of this magnitude are rare (< 1 % of the Rhode River population; Smith & Hines 1991b).

Sacrifice of 1 or 2 limbs appears to be an effective survival strategy for highly mobile, non-territorial decapods such as blue crabs. Costs of limb loss to survival and reproduction, however, undoubtedly vary among species. For species that must defend a burrow, cheliped loss could result in eviction by conspecifics (Conover & Miller 1978, O'Neill & Cobb 1979) or greater vulnerability to attack by predators (Bildstein et al. 1989). Autotomy could reduce reproductive output in species that are able to molt and regenerate missing limbs following their molt to maturity (e.g. cancrid crabs).

Effects of tethering and enclosures on prey survival

Tethering has been employed in marine (e.g. Heck & Thoman 1981, Aronson 1987, Wilson et al. 1990, Ruiz et al. 1993) and terrestrial (Belovsky et al. 1990) systems to assess the potential for predation among different habitats, latitudes, and species. While tethering is a useful technique for exposing prey to a suite of predators in a natural environment, few studies have tested for differential effects tethering might have on experimental treatments (see review by Peterson & Black 1994). My enclosure experiments are the first to test for such interactions under field conditions, and results indicate that the technique should be applied judiciously. As expected, tethering generally decreased survival of juvenile blue crabs relative to untethered

individuals. Zimmer-Faust et al. (1994) have shown that, while tethers have no significant effect on mean or maximum escape speeds in juvenile blue crabs, they do shorten the distance travelled during each swimming burst so that tethered prey are subject to repeated attack. Survivorship patterns in my enclosures illuminated injury-dependent behavioral and defensive differences in juvenile blue crabs. They illustrate the importance of maintaining uniform physical condition of tethered prey lest interpretation for other variables be confounded. The degree of handicap tethering imposes on prey also can depend on the type of habitat (Barshaw & Abele 1990), predator type (Peterson & Black 1994), and body size (Smith 1990b, Ruiz et al. 1993) and escape mode (Zimmer-Faust et al. 1994) of prey.

As with tethering, enclosures can potentially affect experimental treatments unequally. In all likelihood, enclosure walls provided a structural refuge for juvenile crabs. Injured free-swimming crabs may have utilized cage walls to a greater degree than tethered crabs or untethered intact prey. For tethered prey, encounter rates with predators and the chances of being captured or killed were likely higher in enclosures than in the open field. In enclosure experiments, tethered prey were potentially subject to repeated attacks by the same predator over 48 h. In contrast, in the open field, any one predator is more likely to search elsewhere after an unsuccessful attack. Whereas overall mortality for small tethered crabs was similar between enclosure (48%) and open-field experiments (43%; Smith 1990b), the likelihood of death versus injury was much greater in enclosures (43:1) than in the open field (ca 3:1).

Despite the potential for higher-order interactions between tethering and enclosure artifacts and autotomy treatments, field enclosures provided an assessment of escape success from a known predator under natural conditions of turbidity, salinity, temperature, and tidal action. These parameters are difficult to duplicate in the laboratory and may be critical for accurately estimating predation success. For example, foraging blue crabs use chemoreception to locate prey and their searching efficiency is greatest under low-flow conditions (Weissburg & Zimmer-Faust 1993).

Most experiments that have compared vulnerability of animals with and without appendages have concluded that autotomy significantly lowers the chances of prey surviving an attack (e.g. Dial & Fitzpatrick 1984, Vitt & Cooper 1985, Robinson et al. 1991). This cost is probably exaggerated because these experiments have typically been conducted in small terraria or aquaria. Under such circumstances, escape distances are severely restricted, and encounter rates between predator and prey are unnaturally elevated.

Separation distances of 20 cm are sufficient for juvenile blue crabs to evade larger conspecifics (Zimmer-Faust et al. 1994); thus, my enclosures provided ample room for escape even if encounter rates increased. Significantly, my results demonstrated that limb loss does not dramatically increase mortality from predators if prey have an opportunity to escape. Furthermore, low incidences of autotomy and high survivorship of untethered crabs (86%) suggest that while conspecifics do inflict nonlethal injury, the autotomy response is used infrequently when compared to other escape mechanisms.

LITERATURE CITED

Aronson, R. B. (1987). Predation on fossil and Recent ophiuroids. Paleobiology 13: 187–192

Baker, R. L., Dixon, S. M. (1986). Wounding as an index of aggressive interactions in larval Zygoptera (Odonata). Can. J. Zool. 64: 893–897

Barshaw, D. E., Able, K. W. (1990). Tethering as a technique for assessing predation rates in different habitats: an evaluation using juvenile lobsters *Homarus americanus.* Fish. Bull. U.S. 88: 415–417

Belovsky, G. B., Slade, J. B., Stockhoff, B. A. (1990). Susceptibility to predation for different grasshoppers: an experimental study. Ecology 71: 624–634

Bildstein, K. L., McDowell, S. G., Brisbin, L. L. (1989). Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predation. Anim. Behav. 37: 133–139

Botsford, L. W., Wickham, D. E. (1978). Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Bd Can. 35: 833–843

Congdon, J. D., Vitt, L. J., King, W. W. (1974). Geckos: adaptive significance and energetics of tail autotomy. Science 184: 1379–1380

Conover, M. R., Miller, D. E. (1978). The importance of the large chela in the territorial and pairing behaviour of the snapping shrimp, *Alpheus heterochaelis.* Mar. Behav. Physiol. 5: 185–192

Cox, D. R., Snell, E. J. (1989). Analysis of binary data. Chapman & Hall, New York

Daniels, C. B. (1985). The effect of tail autotomy on the exercise capacity of the water skink, *Sphenomorphus quoyii*. Copeia 1985: 1074–1077

Davenport, J., Spikes, M., Thornton, S. M., Kelly, B. O. (1992). Crab-eating in the diamondback terrapin *Malaclemys terrapin*: dealing with dangerous prey. J. mar. biol. Ass. U.K. 72: 835–848

Day, R. W., Quinn, G. P. (1989). Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59: 433–463

Dial, B. E., Fitzpatrick, L. C. (1981). The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). Oecologia 51: 310–317

Dial, B. E., Fitzpatrick, L. C. (1983). Lizard tail autotomy: function and energetics of postautotomy tail movement in *Scincella lateralis*. Science 219: 391–392

Dial, B. E., Fitzpatrick, L. C. (1984). Predator escape success in tailed versus tailless *Scincella lateralis* (Sauria: Scincidae). Anim. Behav. 32: 301–302

Dong, Q., Polis, G. A. (1992). The dynamics of cannibalistic populations: a foraging perspective. In: Elgar, M. A., Crespi, B. J. (eds.) Cannibalism: ecology and evolution among diverse taxa. Oxford Univ. Press, New York, p. 13–37

Ducey, P. K., Brodie, E. D. Jr (1983). Salamanders respond selectively to contacts with snakes: survival advantage of alternative antipredator strategies. Copeia 1983: 1036–1041

Elgar, M. A., Crespi, B. J. (eds.) (1992). Cannibalism: ecology and evolution among diverse taxa. Oxford Univ. Press, New York

Endler, J. A. (1986). Defense against predators. In: Feder, M. E., Lauder, G. V. (eds.) Predator-prey relationships: perspectives and approaches from the study of lower vertebrates. Univ. Chicago Press, Chicago, p. 109–134

Everett, R. A., Ruiz, G. M. (1993). Coarse woody debris as a refuge from predation in aquatic communities. Oecologia 93: 475–486

Fox, L. R. (1975). Cannibalism in natural populations. A. Rev. Ecol. Syst. 6: 87–106

Fox, S. F., Rostker, M. A. (1982). Social cost of tail loss in *Uta stansburiana*. Science 218: 692–693

Hankin, D. G. (1985). Proposed explanations for fluctuations in abundance of Dungeness crabs: a review and critique. In: Proceedings of the Symposium on Dungeness Crab Biology and Management. Alaska Sea Grant Report No. 85-3. Univ. Alaska, Fairbanks, p. 305–326

Harris, R. N. (1989). Nonlethal injury to organisms as a mechanism of population regulation. Am. Nat. 134: 835–847

Heck, K. L. Jr, Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habiitats. J. exp. mar. Biol. Ecol. 53: 125–134

Hines, A. H., Lipcius, R. N., Haddon, A. M. (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. 36: 55–64

Hines, A. H., Haddon, A. M., Weichert, L. A. (1990). Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. Mar. Ecol. Prog. Ser. 67: 105–126

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

Kurihara, Y., Okamoto, K. (1987). Cannibalism in a grapsid crab, *Hemigrapsus penicillatus*. Mar. Ecol. Prog. Ser. 41: 123–127

Kurihara, Y., Sekimoto, K., Miyata, M. (1988). Wandering behaviour of the mud-crab *Helice tridens* related to evasion of cannibalism. Mar. Ecol. Prog. Ser. 49: 41–50

Kuris, A. M., Mager, M. (1975). Effect of limb regeneration on size increase at molt of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. J. exp. Zool. 193: 353–360

Laughlin, R. A. (1982). Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. Bull. mar. Sci. 32: 807–822

Lawton, P. (1989). Predatory interaction between the brachyuran crab *Cancer pagurus* and decapod crustacean prey. Mar. Ecol. Prog. Ser. 52: 169–179

Lima, S. L., Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68:619–640

Lipcius, R. M., Van Engel, W. A. (1990). Blue crab population dynamics in Chesapeake Bay: variation in abundance (York River, 1972–1989) and stock-recruit functions. Bull. mar. Sci. 46: 180–194

Maiorana, V. C. (1977). Tail autotomy, functional conflicts and their resolution by a salamander. Nature 265: 533–535

McVean, A. (1982). Autotomy. In: Bliss, D. E. (ed.) The biology of Crustacea, Vol. 4. Academic Press, New York, p. 107–132

Millikin, M. R., Williams, A. B. (1984). Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. FAO Fish. Synopsis 138

O'Neill, D. J., Cobb, J. S. (1979). Some factors influencing the outcome of shelter competition in lobsters (*Homarus americanus*). Mar. Behav. Physiol. 6: 33–45

Peery, C. A. (1989). Cannibalism experiments with the blue crab (*Callinectes sapidus* Rathbun): potential effects of size and abundance. M.Sc. thesis, College of William and Mary, Williamsburg

Peterson, C. H., Black, R. (1994). An experimentalist's challenge: when artifacts of intervention interact with treatments. Mar. Ecol. Prog. Ser. 111: 289–297

Petranka, J. W. (1989). Density-dependent growth and survival of larval *Ambystoma*: evidence from whole-pond manipulations. Ecology 70: 1752–1767

Polis, G. A. (1981). The evolution and dynamics of intraspecific predation. A. Rev. Ecol. Syst. 12: 225– 251

Punzo, F. (1982). Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. J. Herpetol. 16: 329–331

Reaka, M. L. (1987). Adult-juvenile interactions in benthic reef crustaceans. Bull. mar. Sci. 41: 108–134

Rice, W. R. (1989). Analyzing tables of statistical tests. Evolution 43: 223–225

Robinson, J. V., Hayworth, D. A., Harvey, M. B. (1991a). The effect of caudal lamellae loss on swimming speed of the damselfly *Argia moesta* (Hagen) (Odonata: Coenagrionidae). Am. Midl. Nat. 125: 240–244

Robinson, J. V., Shaffer, L. R., Hagemeier, D. D., Smatresk, N. J. (1991b). The ecological role of caudal lamellae loss in the larval damselfly *Ischnura posita* (Hagen) (Odonata: Zygoptera). Oecologia 87: 1–7

Ruiz, G. M., Hines, A. H., Posey, M. H. (1993). Shallow water as a refuge habitat for fish and crustaceans in nonvegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. 99: 1–16

SAS Institute. (1985). SAS User's Guide: Statistics, Version 5 edn. SAS Institute Inc., Cary, NC

Schall, J. J., Pianka, E. R. (1980). Evolution of escape behavior diversity. Am. Nat. 115: 551–566

Shirley, M. A., Hines, A. H., Wolcott, T. G. (1990). Adaptive

significance of habitat selection by molting adult blue crabs *Callinectes sapidus* (Rathbun) within a subestuary of central Chesapeake Bay. J. exp. mar. Biol. Ecol. 140: 107–119

Sih, A. (1980). Optimal behavior: can foragers balance two conflicting demands? Science 210: 1041–1043

Sih, A. (1982). Foraging strategies and the avoidance of predation by an aquatic insect *Notonecta hoffmanni*. Ecology 63: 786–796

Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. Am. Nat. 139: 1052–1069

Smith, L. D. (1990a). Patterns of limb loss in the blue crab, *Callinectes sapidus* Rathbun, and the effects of autotomy on growth. Bull. mar. Sci. 46: 23–36

Smith, L. D. (1990b). The frequency and ecological consequences of limb autotomy in the blue crab, *Callinectes sapidus* Rathbun. Ph.D. dissertation, Univ. of Maryland, College Park

Smith, L. D. (1992). The impact of limb autotomy on mate competition in blue crabs, *Callinectes sapidus* Rathbun. Oecologia 89: 494–501

Smith, L. D., Hines, A. H. (1991a). The effect of cheliped loss on blue crab *Callinectes sapidus* Rathbun foraging rate on soft-shell clams *Mya arenaria* L. J. exp. mar. Biol. Ecol. 151: 245–256

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

Smyth, M. (1974). Changes in fat stores of the skinks *Morethia boulangeri* and *Hemiergis peronii* (Lacertilia). Austral. J. Zool. 22: 135–145

Sokal, R. R., Rohlf, F. J. (1981). Biometry. W. H. Freeman, New York

Spence, J. R., Cárcamo, H. A. (1991). Effects of cannibalism and intraguild predation on pondskaters (Gerridae). Oikos 62: 333–341

Spirito, C. P. (1972). An analysis of swimming behavior in the portunid crab *Callinectes sapidus*. Mar. Behav. Physiol. 1: 261–276

Stevens, B. G., Armstrong, D. A., Cusimano, R. (1982). Feeding habits of the Dungeness crab *Cancer magister* as determined by the index of relative importance. Mar. Biol. 72: 135–145

Van Buskirk, J., Smith, D. C. (1991). Density-dependent population regulation in a salamander. Ecology 72: 1747–1756

Vermeij, G. J. (1982). Unsuccessful predation and evolution. Am. Nat. 120: 701–720

Vermeij, G. J. (1987). Evolution and escalation. Princeton University Press, Princeton

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

Vitt, L. J., Cooper, W. E. Jr (1986). Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): age specific differences in costs and benefits. Can. J. Zool. 64: 583–592

Weissburg, M. J., Zimmer-Faust, R. K. (1993). Life and death in moving fluids: hydrodynamic effects on chemosensory-mediated predation. Ecology 74:1428–1443

Wilson, K. A., Able, K. W., Heck, K. L. Jr (1990). Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). Mar. Ecol. Prog. Ser. 58: 243–251

Wood, F. D., Wood, H. E. (1932). Autotomy in decapod Crustacea. J. exp. Zool. 62: 1–55

Zimmer-Faust, R. K., Fielder, D. R., Heck, K. L. Jr, Coen, L. D., Morgan, S. G. (1994). Effects of tethering on predatory escape by juvenile blue crabs. Mar. Ecol. Prog. Ser. 111: 299–303