

# Autotomy in Blue Crab (*Callinectes sapidus* Rathbun) Populations: Geographic, Temporal, and Ontogenetic Variation

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**Abstract.** Blue crab (*Callinectes sapidus* Rathbun) populations were examined at four sites in Chesapeake Bay and three additional sites along the southeastern Atlantic coast and Gulf of Mexico; the aims were to assess the incidence of limb autotomy and to determine whether injury patterns varied temporally, geographically, and ontogenetically. These data, which include four years of information from one site (Rhode River, Maryland, a subestuary of central Chesapeake Bay), make this study the most extensive and intensive survey of limb autotomy yet conducted in arthropods. A substantial percentage (17–39%) of the blue crab populations were either missing or regenerating one or more limbs, suggesting that autotomy is an important mechanism for their survival. The frequency of limb autotomy varied, both within and between years, and over broad geographical scales. Injury levels were generally correlated positively with crab size. Limb autotomy was independent of sex and molt stage, and frequencies varied little among sites in the Rhode River. Patterns of limb injury in *C. sapidus* were remarkably consistent among all sites. The most frequent injury involved loss of a single cheliped. Swimming legs suffered the least damage. Severe multiple limb loss was rare. Right and left limbs were lost with equal frequency in most populations. This consistency of autotomy pattern suggests differential vulnerability of limbs and standard behavioral response by blue crabs to various injury-causing agents. The frequency of autotomy was density-dependent in the Rhode River, indicating that intraspecific interactions (e.g., cannibalism) may be a major cause of limb

loss in populations in the Rhode River subestuary and elsewhere.

## Introduction

Many invertebrate and vertebrate species respond to injury or its threat by autotomizing (*i.e.*, severing) a body part along a breakage plane (Wood and Wood, 1932; Needham, 1953; Robinson *et al.*, 1970; Vitt *et al.*, 1977; McVean, 1982; McCallum *et al.*, 1989). While such behavior has immediate survival benefits (Dial and Fitzpatrick, 1983; Medel *et al.*, 1988; Smith, 1990a), autotomy may handicap individuals when foraging (Slater and Lawrence, 1980; Smith, 1990a), overwintering (Willis *et al.*, 1982); escaping predators (Vitt *et al.*, 1977; Dial and Fitzpatrick, 1984; Smith, 1990a), or competing for mates (Sekkelsten, 1988; Smith, 1990a) or shelter (Conover and Miller, 1978; Berzins and Caldwell, 1983). Energetic costs of regenerating body parts can reduce reproductive output (Maiorana, 1977) and growth (Kuris and Mager, 1975; Smith, 1990b). Theoretical models (Harris, 1989) have suggested that nonlethal injury could regulate population abundance, if injury rates were density-dependent and significantly reduced long-term survival or reproduction. Detailed knowledge of autotomy patterns and frequencies, for a single species, over both narrow and broad temporal and geographic scales, are needed to make more reliable inferences concerning the fitness benefits and consequences of autotomy.

Quantitative surveys of limb loss in decapod crustaceans exist for only a few species (*Cancer magister*, Durkin *et al.*, 1984; Shirley and Shirley, 1988; *Cancer pagurus*, Bennett, 1973; *Carcinus maenas*, Needham, 1953; McVean, 1976; McVean and Findlay, 1979; Sekkelsten,

1988, *Menippe mercenaria*, Sullivan, 1979; Simonson and Steele, 1981; Simonson, 1985; *Paralithodes camtschatica* and *Chionocetes bairdi*, Edwards, 1972). The percentage of injury in these species ranged from 13–66%. Inferences from these data regarding the fitness consequences of autotomy have been limited, however, because field data have not been collected for more than one complete growing season; smaller individuals in commercial species frequently have not been sampled; chelipeds have often been the only limbs assessed; and collections have been geographically restricted. To understand how the incidence of autotomy varies within and among populations, multiple-year and -site data on injury are needed for a range of body sizes for both sexes.

Nonlethal injury often results from unsuccessful attacks by predators (Vermeij, 1982). Variation in injury levels among populations and species has been thought to reflect differences in predation intensity and efficiency over altitudinal gradients (Ballinger, 1979; Shaffer, 1978), ecological habitats (Schoener and Schoener, 1980); biogeographic regions (Vermeij, 1976); geologic time (Vermeij, 1977, 1983), life histories (Vitt *et al.*, 1977), and behaviors (Jaksic and Fuentes, 1980; Schall and Pianka, 1980). Although specific agents responsible for autotomy in nature are rarely identified (*cf.*, Robinson *et al.*, 1970; Jaeger, 1981; Smith, 1990a), such information is needed to understand the patterns and impact of injury in populations. Intraspecific predation is common in the animal kingdom (Fox, 1975; Polis, 1981; Stevens *et al.*, 1982; Reaka, 1987; Kurihara and Okamoto, 1987), and may be an important cause of autotomy in some taxa (*e.g.*, salamanders; Jaeger, 1981). Large *Callinectes sapidus* are known to prey on smaller conspecifics (Laughlin, 1982; Hines *et al.*, 1990; Peery, 1989; Smith, 1990a). If intraspecific interactions are chiefly responsible for autotomy in blue crabs, then injury levels should correlate positively with population densities over temporal and spatial scales.

Costs of nonlethal injury to individuals will depend on the type and number of missing limbs. The relative importance of different limbs to survival, in turn, may be indicated by the frequency of their repair in the population. Limb regeneration in arthropods occurs upon molting, and crabs may require a number of molts (*e.g.*, 1–3 in *Callinectes sapidus*, Smith, 1990b; >4 in *Paralithodes camtschatica*, Edwards, 1972) before full limb length is restored. For most limbs, evidence of past injury disappears once symmetry has been restored. Following the loss of a major (crusher) claw, however, normal cheliped dimorphism is often not reestablished (Smith, 1990b); thus, the absence of such dimorphism can serve as a measure of survival of past injury.

To assess the impact of autotomy in a population, it is necessary to: (1) document spatial, temporal, and onto-

genetic variation in patterns and levels of injury; (2) identify causal agents; and (3) determine the various costs of injury to individuals. The present study examines incidences of autotomy in blue crabs (*Callinectes sapidus* Rathbun) at four sites in Chesapeake Bay and three additional sites along the southeastern United States Atlantic coast and the Gulf of Mexico. These data, which include four years of information from one site in central Chesapeake Bay, make this the most detailed survey yet conducted on autotomy in arthropods.

## Materials and Methods

### Sampling procedures

*Callinectes sapidus* individuals were collected from 1986 to 1989 in the Rhode River, Maryland; at three additional sites in the Chesapeake Bay in fall 1989; and at three sites along the southeastern Atlantic coast and the Gulf of Mexico of the United States (Figs. 1, 2) in spring 1989. At all locations, crabs were measured or examined for: (1) carapace width between tips of lateral spines, (2) sex, (3) sexual maturity in females (1986–89) and males (1988–89, only), (4) molt stage, (5) type and side of any missing or regenerating limbs, (6) lengths of limb buds, regenerating limbs, and contralateral intact limbs, and (7) side of the crusher claw.

Sexual maturity in female blue crabs was determined by examining differences in abdominal allometry (Van Engel, 1958). For males, sexual maturity was indicated by the ease with which the abdomen could be pulled away from the ventral surface of the cephalothorax (Van Engel, 1958; 1990). Molt stages were determined by assessing carapace hardness and by examining the propodus of the fifth pereopod for evidence of epidermal retraction (Van Engel, 1958; Johnson, 1980). A limb stump that was either scarred, or possessed a papilla or limb bud, was classified as a missing limb. A regenerating limb was considered to be a functional appendage that had undergone at least one molt since autotomy, but was shorter than the intact, contralateral limb. Crabs that possessed an unscarred stump wound, indicating possible injury caused during collection, were not measured. Limb length was measured as the distance from the autotomy plane in the basi-ischial segment to the dactyl tip of a fully extended limb.

### Site descriptions and collection methods

*Rhode River, Maryland.* *Callinectes sapidus* individuals were collected from the Rhode River near Edgewater, Maryland (38°51'N, 76°32'W), between July and November in 1986, and from May to November each year from 1987 to 1989 (Figs. 1, 2). The Rhode River is a

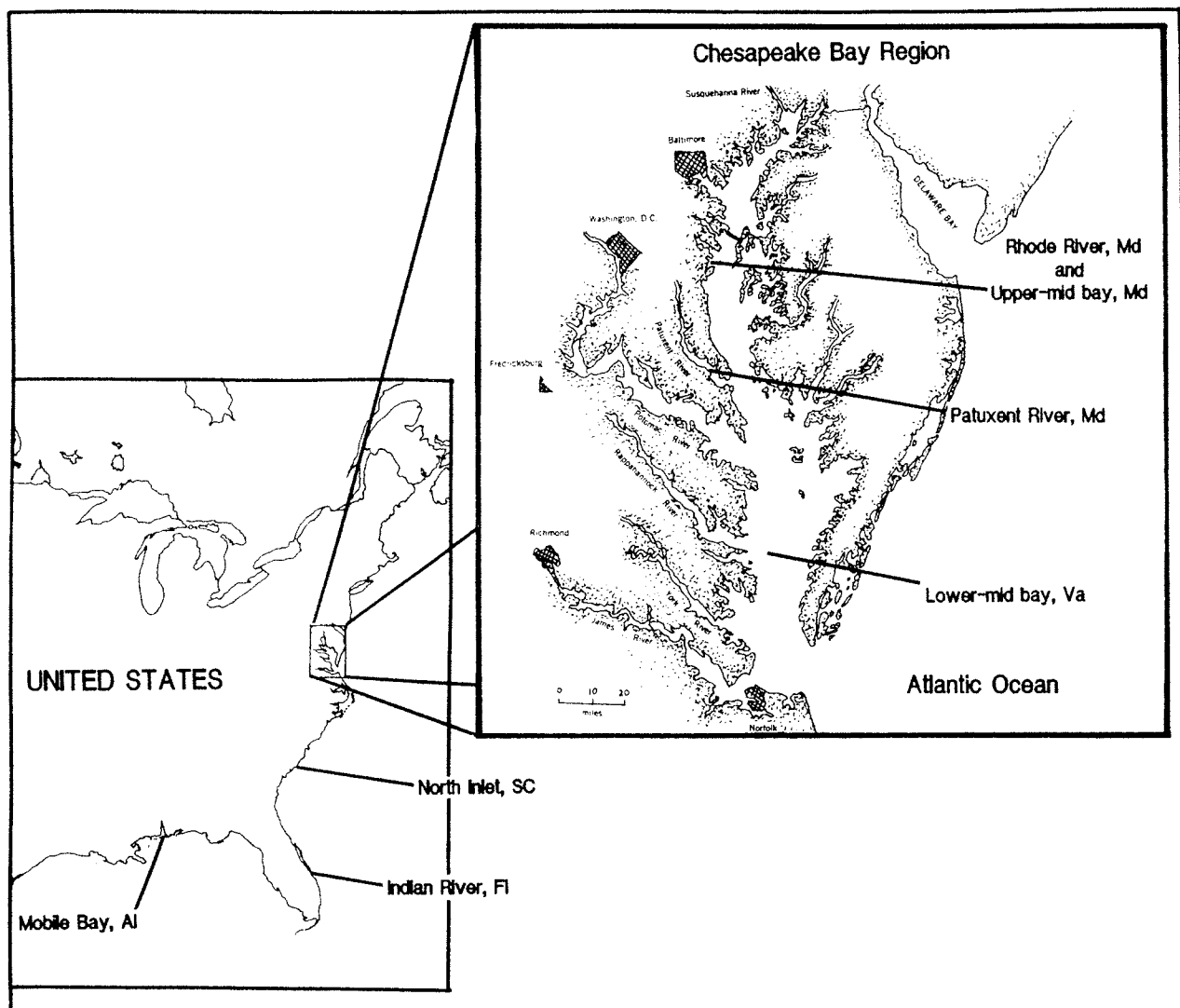


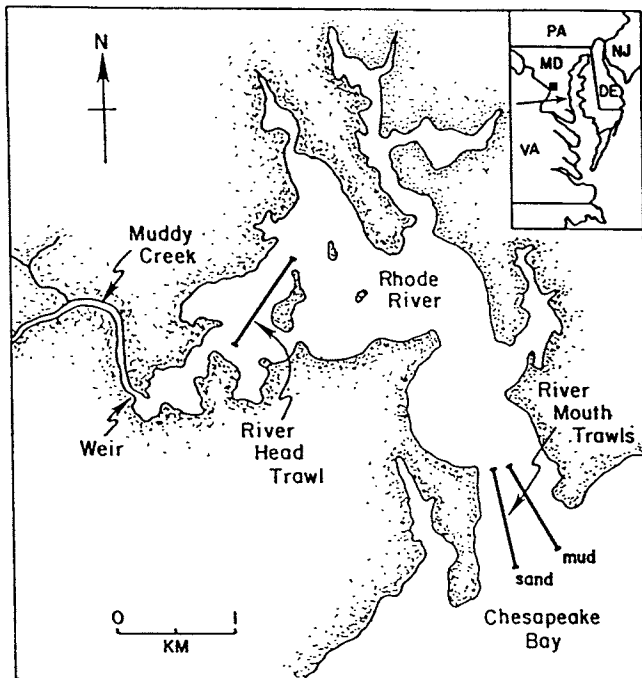
Figure 1. Map of the United States Atlantic coast and the Gulf of Mexico showing locations of blue crab sampling sites from 1986 to 1989.

shallow (maximum depth = 4 m), 485 ha mesohaline subestuary that empties into the western side of the upper-central Chesapeake Bay (Hines *et al.*, 1987a,b). Water temperatures ranged from 8°C to 34°C during the sampling period, with July temperatures averaging 28°C ( $\pm 2.4$ ). Salinities typically ranged from 4 to 14‰; but unusually low salinities (0–10‰) were recorded in 1989.

Several methods were used to sample blue crabs in the Rhode River as well as at other sites. Potential biases related to these different collection techniques were examined and are discussed below. In all four years, blue crabs were sampled monthly by otter trawl (3 m wide mouth; 5 mm mesh net body; 7 mm mesh cod end; with tickler chain; Hines *et al.*, 1987a) pulled for 900 m on two con-

secutive days at each of three stations in the Rhode River. Two stations were located at the river mouth, one over sandy substrate, and the other over muddy sediment; a third station was located at the river head over muddy sediment (Fig. 2).

From 1986 to 1988, blue crabs were also collected bi-weekly at a fish weir spanning the principal freshwater tributary (Muddy Creek) of the Rhode River. Crabs moving up- and downstream were captured separately in single hoop nets (7 mm mesh). No crabs were sampled at the weir in 1989 because of storm-related damage. Consequently, in 1989, crabs were collected biweekly at the river head (0.5–2 m depth); larger individuals were caught in baited commercial crab pots (57 mm mesh), and smaller crabs in specially designed crab pots (7 mm mesh). Blue



**Figure 2.** Map of the Rhode River subestuary, Maryland, showing sampling sites from 1986 to 1989. These include mouth sand and mouth mud trawl stations (1986–89) = River Mouth; river head trawl station (1986–89) and crab pot/seine sites (1989, only) = River Head; and Muddy Creek up- and downstream weir nets (1986–88) = Creek.

crabs were also sampled periodically in nearshore waters (depth 0.3–1.2 m) with a 10 m beach seine (7 mm mesh).

*Non-Rhode River sites.* Locations, dates, physical conditions (e.g., depth, salinity), and sampling techniques for

additional sites in Chesapeake Bay and for sites in South Carolina, Florida, and Alabama are summarized in Table I. Note that the upper-mid Chesapeake Bay site was only 1 km east of the mouth of the Rhode River, Maryland. Using a dipnet, blue crabs were collected from the sides of a commercial pound net at this site.

#### Statistical analyses

Data were treated as categorical, and frequencies were analyzed by logistic regressions (Cox, 1970; PROC CATMOD with maximum likelihood estimation, 0.5 added to all cells; SAS Institute, 1985) or two-way contingency tables. In the Rhode River, data were analyzed for only those months when 25 or more crabs were obtained. Locations in the Rhode River were combined into river mouth, river head, or creek sites, because differences in autotomy frequency were not detected between sample stations within each subregion (G-tests,  $P > 0.05$ ). Crabs were divided into small ( $<61$  mm carapace width), medium ( $61 \leq CW \leq 110$  mm), and large ( $>110$  mm CW) size classes. The division between medium and large size classes corresponded approximately with the onset of sexual maturity. Molt stages were classified as postmolt (stages A and B), intermolt (stage C), and premolt (stage D) (Johnson, 1980). Crabs in the act of molting (stage E) were very rare and were included as premolt animals.

The primary null hypothesis tested whether the frequency of injured crabs (i.e., those animals missing or regenerating at least one limb) in a population was independent of one or more of the following independent variables: (1) year (Rhode River, only), (2) month (Rhode

**Table I**

*Sampling sites, dates, physical conditions, and sampling methods used to collect blue crabs in 1989*

Site	Location (Lat., Long.)	Sampling dates 1989	Depth (m)	Salinity (‰)	Temp. (°C)	Sampling method
Upper-Mid Chesapeake Bay, Maryland	38°50'N, 76°31'W	Aug.–Sept.	5	6–11	24–28	dip net
Patuxent River, Maryland	38°23'N, 76°36'W	Oct.	9–21	12–14	14	otter trawl
Lower-Mid Chesapeake Bay, Virginia	37°25'N–37°39'N 75°56'W–76°17'W	Oct.	4–18	19	19	otter trawl
North Inlet, South Carolina	33°21'N, 79°11'W	May	.2–3	21	31	crab pots, dip net
Indian River, Florida	27°50'N, 80°29'W	May	.5–5	23–26	29–32	crab pots, dip net
Mobile Bay, Alabama	30°15'N, 88°00'W	May	.5–5	24	27	crab pots, seine

Latitudinal and longitudinal range of sampling transects are given for the lower-mid Chesapeake Bay site. See text for description of 1986–1989 Rhode River surveys.

Table II

Frequencies and percentages of crabs missing, regenerating, and both missing and regenerating limbs in the Rhode River from 1986 to 1989

Category	Rhode River, Maryland							
	1986 <sup>a</sup>		1987 <sup>b</sup>		1988 <sup>b</sup>		1989 <sup>b</sup>	
	n	%	n	%	n	%	n	%
Total intact	1050	75.0	505	81.2	536	82.5	569	82.2
Total injured:	350	25.0	117	18.8	113	17.5	123	17.8
Missing <sup>1</sup>	211	15.1	56	9.0	53	8.2	68	9.8
Regenerating <sup>2</sup>	123	8.8	55	8.8	57	8.8	46	6.7
Miss. + Regen. <sup>3</sup>	16	1.1	6	1.0	3	0.5	9	1.3
Total caught	1400	100.0	622	100.0	649	100.0	692	100.0
Sex ratio M:F	67:33		81:19		83:17		76:24	
Size ratio S:M:L <sup>4</sup>	12:48:40		20:26:54		21:38:41		32:18:50	

<sup>1</sup> Missing = crabs with one or more scarred stumps, papillae, or limb buds.

<sup>2</sup> Regenerating = crabs possessing one or more functional but shortened appendages.

<sup>3</sup> Miss. + Regen. = crabs possessing both missing and regenerating limbs.

<sup>4</sup> Size ratio: (S < 61 mm carapace width, M = 61–110 mm CW, L > 110 mm CW) for all crabs (injured and intact).

Years with the same superscripted letter did not differ significantly in total autotomy frequency.

River, only), (3) subestuarine location (Rhode River, only), (4) body size, (5) sex, (6) sexual maturity, (7) molt stage, and (8) geographic location. All relevant two factor combinations of these independent variables were tested by logistic regression for their relationship to the binary response variable (*i.e.*, frequency of injured *versus* uninjured crabs). Expected cell frequencies of injured animals were often low (<1) and prevented more than two independent variables from being tested reliably in a single model. Significant two-way interactions were not recorded between independent variables in most instances; hence, these results, except when specified, are not discussed. If a test revealed nonindependence, unplanned multiple comparisons controlling for experimentwise type I error were used to distinguish differences among frequencies (simultaneous test procedures, STP tests; Sokal and Rohlf, 1981, pp. 728). Two-way contingency tables were used to examine frequencies of injury as a function of limb type and number, right *versus* left side, and missing *versus* regenerating limbs.

Median carapace widths of injured and uninjured animals were compared within sites by nonparametric procedures (Mann-Whitney U-test; Sokal and Rohlf, 1981), because variances for carapace widths were heteroscedastic (F-max test; Sokal and Rohlf, 1981) even after attempts at data transformation.

## Results

### Population structure

In the Rhode River, sex ratios were consistently male-dominated, but relative frequencies of males and females

differed among all years except between 1987 and 1988 (STP test, 3 df; Table II). Annual size-frequency distributions differed among all years in the Rhode River and among all other sites in 1989 (Kornolgorov-Smirnov two-sample tests,  $P < 0.05$ ; Tables II, III). Outside the Rhode River, sex ratios were skewed towards females at all sites except South Carolina and the Patuxent River, Maryland (G-test, 5 df,  $P < 0.05$ ; Table III). Collections from the upper-mid Chesapeake Bay were designed to capture females and larger individuals; therefore, these sex and size ratios should not be compared to those from other sites, which were sampled randomly.

### Sampling methods

The frequency of autotomy in crabs collected from baited crab pots and seines at the Rhode River head (19%) did not differ from injury levels in otter trawls (22%) at that site in 1989 (G-test, 1 df,  $P > 0.05$ ). No significant differences in injury were observed between otter trawl and fish weir collections from 1986 to 1988 (G-tests, 1 df,  $P > 0.05$ ). At non-Rhode River sites, autotomy frequencies did not differ among crabs collected by otter trawl (Patuxent River, lower-mid Chesapeake Bay) and crab pots and seines (South Carolina, Florida, Alabama) (G-tests,  $P > 0.05$ ).

### Autotomy frequencies

*Yearly and geographic variation.* Frequencies of blue crabs missing or regenerating one or more limbs differed significantly among sites and years sampled (G-tests,  $P$

Table III

Frequencies and percentages of crabs missing, regenerating, and both missing and regenerating limbs at sites in the Chesapeake Bay and along the southeastern United States in 1989

Category	Chesapeake Bay										Mobile B.	
	Upper-Mid <sup>a</sup>		Patuxent R. <sup>b</sup>		Lower-Mid <sup>b</sup>		N. Inlet SC <sup>b</sup>		Indian R. FL <sup>b</sup>		AL <sup>ab</sup>	
	n	%	n	%	n	%	n	%	n	%	n	%
Total intact	549	80.9	63	61.2	150	67.0	139	68.1	132	65.7	191	73.5
Total injured:	130	19.1	40	38.8	74	33.0	65	31.9	69	34.3	69	26.5
Missing <sup>1</sup>	85	12.5	24	23.3	53	23.7	33	16.2	37	18.4	25	9.6
Regenerating <sup>2</sup>	39	5.7	11	10.6	17	7.6	27	13.2	32	15.9	40	15.4
Miss. + Regen. <sup>3</sup>	6	0.9	5	4.9	4	1.7	5	2.5	0	0.0	4	1.5
Total caught	679	100.0	103	100.0	224	100.0	204	100.0	201	100.0	260	100.0
Sex ratio M:F	40:60		51:50		26:74		61:39		32:68		37:63	
Size ratio S:M:L <sup>4</sup>	1:25:74		0:12:88		16:9:75		17:17:66		25:5:70		15:28:57	

<sup>1</sup> Missing = crabs with one or more scarred stumps, papillae, or limb buds.

<sup>2</sup> Regenerating = crabs possessing one or more functional but shortened appendages.

<sup>3</sup> Miss. + Regen. = crabs possessing both missing and regenerating limbs.

<sup>4</sup> Size ratio: (S < 61 mm carapace width, M = 61–110 mm CW, L > 110 mm CW) for all crabs (injured and intact).

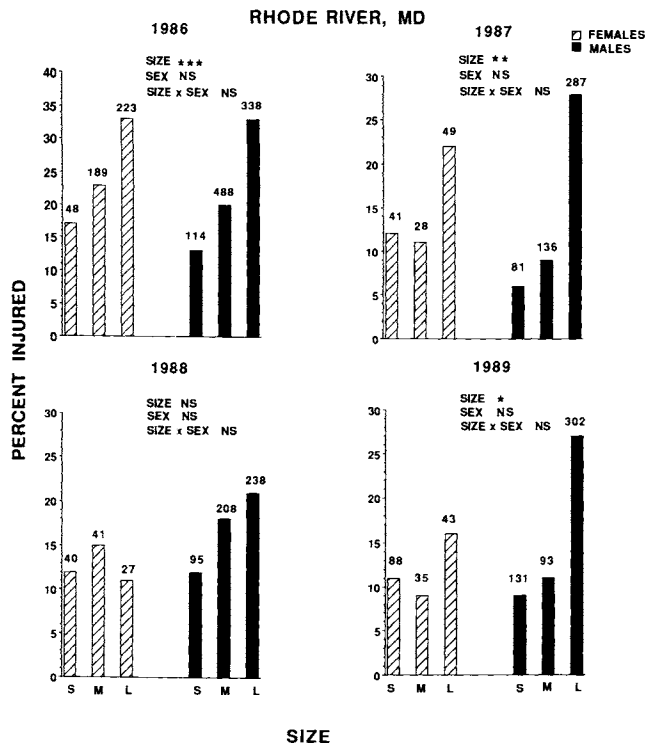
Sites with the same superscripted letter did not differ significantly in total autotomy frequency.

< 0.01; Tables II, III). In the Rhode River subestuary, limb loss frequency was significantly higher in 1986 (25.0%) than in 1987–89 (STP test, 3 df,  $P < 0.01$ ; Table II). Levels of injury in the latter three years did not differ significantly. The frequency of limb loss from 1986 to 1989 was positively correlated with estimated annual mean densities of crabs based on trawl net collections (Hines *et al.*, 1990) (Pearson's correlation coefficient,  $r = 0.99$ ,  $P < 0.05$ ).

Frequencies of limb loss in the Rhode River in spring (20.9%) and fall (19.1%) 1989 did not differ significantly from the overall frequency (17.8%) for the entire sampling season (May to October). This yearly value is used for comparison with injury levels at non-Rhode River sites in spring and fall 1989. The frequency of limb loss in the Rhode River subestuary in 1989 was identical to that recorded at the nearby upper-mid Chesapeake Bay site, but much lower than autotomy frequencies at two other sites in Chesapeake Bay (STP test, 2 df,  $P < 0.01$ ; Tables II, III). Similarly, the frequency of limb loss in the Rhode River in 1989 was significantly lower than springtime injury levels recorded at sites in South Carolina (31.9%) and Florida (34.3%), but not in Alabama (26.5%) (STP test; 3 df;  $P < 0.01$ ; Tables II, III). The incidence of limb autotomy did not differ significantly among Patuxent River, lower-mid Chesapeake Bay, South Carolina, Florida, or Alabama sites (STP test, 4 df,  $P > 0.05$ ), despite temporal and geographic differences among these samples.

*Missing versus regenerating limbs.* At all sites in the Chesapeake Bay and in two of four years in the Rhode River (1986, 1989), blue crabs were missing limbs more often than they were regenerating them (G-tests, 1 df,  $P < 0.05$ ; Tables II, III). Blue crabs collected from Mobile Bay, Alabama, showed the opposite trend, missing limbs less often than they were regenerating them (G-test, 1 df,  $P < 0.05$ ; Table III). No significant differences in frequencies of individuals missing or regenerating appendages were observed in Indian River, Florida; North Inlet, South Carolina; or the Rhode River, Maryland, in 1987 and 1988. Animals simultaneously missing and regenerating limbs were rare in all years and sites (Tables II, III).

*Size and sex.* Of all variables measured, body size correlated most often with autotomy frequencies (Figs. 3, 4). In the Rhode River, large animals were missing or regenerating limbs significantly more often than small or medium size individuals for all years except 1988 (Fig. 3). Limb loss frequencies did not differ significantly between small and medium size classes in any year (STP tests, 2 df, Fig. 3). Injury frequencies did not vary significantly among years in the smallest size class, but between-year variation in injury levels was observed in both medium and large size classes (G-tests, 3 df,  $P < 0.05$ ; Fig. 5). Median carapace widths of all injured crabs were significantly larger than those of all intact individuals in each year (Mann-Whitney U-tests,  $P < 0.001$ ). The frequency of autotomy was independent of sex for all years in the

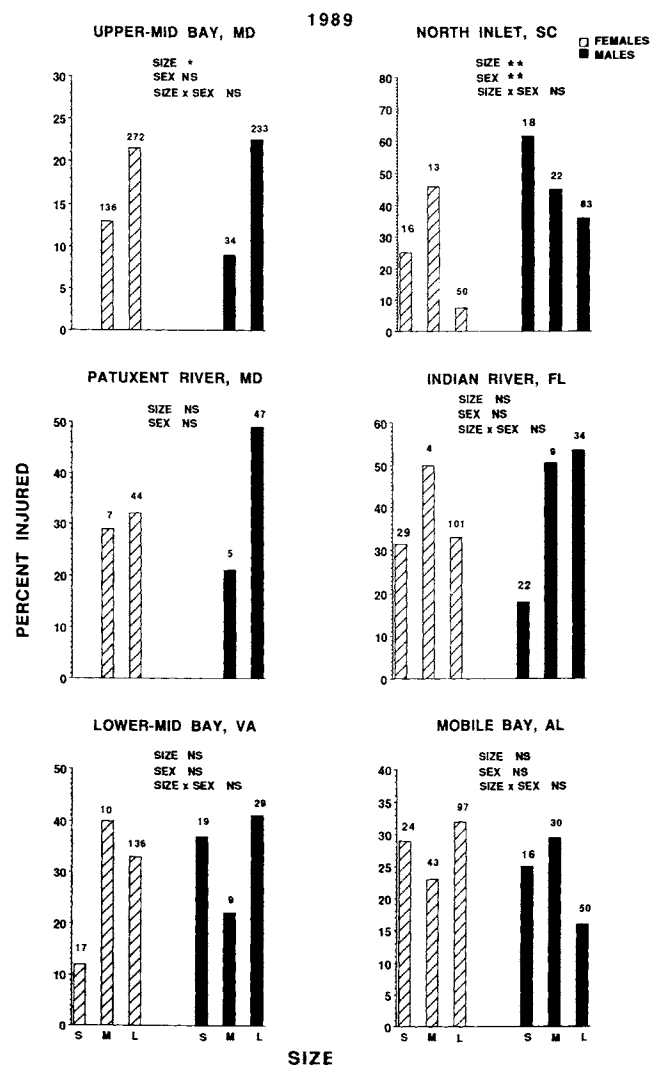


**Figure 3.** Histograms of the percentage of crabs injured in Rhode River, Maryland, as a function of size and sex for each year (1986–1989). S, M, and L represent small (carapace width < 61 mm), medium (61–110 mm), and large (>110 mm) size classes of crabs, respectively. Sample sizes of total crabs (*i.e.*, injured + uninjured animals) in each category are presented above each bar. Results of logistic model testing for association of size, sex, and the interaction of size and sex with injury frequency are presented for each year. NS, not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

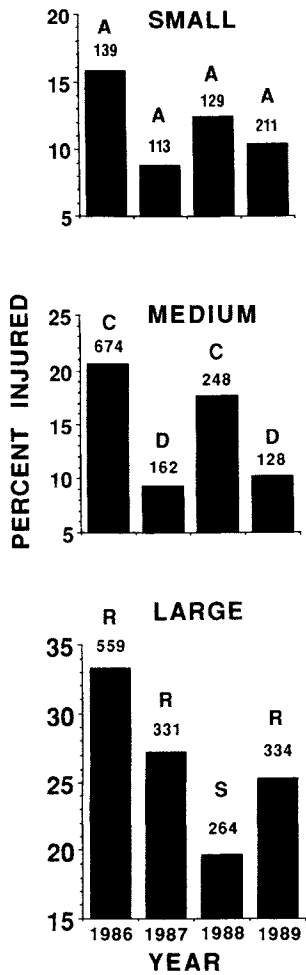
Rhode River and size differences were the same for both sexes (Fig. 3).

Outside the Rhode River, opposite size-related trends in autotomy frequencies were observed at upper-mid Chesapeake Bay and South Carolina sites (Fig. 4). Patterns at the upper-mid Chesapeake Bay site resembled those of the Rhode River, with large animals showing highest incidences of limb loss. In contrast, large crabs showed the least amount of limb loss in North Inlet, South Carolina and males were injured significantly more often than females (STP test,  $P < 0.05$ ). The frequency of injury was independent of size and sex at Patuxent River, lower-mid Chesapeake Bay, Indian River, and Mobile Bay sites (Fig. 4). At non-Rhode River sites, with one exception, median carapace widths of injured and intact crabs did not differ (Mann-Whitney U-tests,  $P > 0.05$ ). At the upper-mid Chesapeake Bay site, patterns again were similar to ones observed in the Rhode River; injured crabs were larger than uninjured animals (Mann-Whitney U-test,  $P < 0.002$ ).

**Reproductive maturity.** In the Rhode River, limb loss and reproductive maturity were significantly correlated for females in 1986 (male reproductive maturity was not measured) and for both sexes in 1989. In 1986, mature female crabs showed greater frequency of limb loss (34%;  $n = 132$ ) than juvenile females (25%;  $n = 312$ ) (G-test, 1 df,  $P = 0.05$ ). In 1989, adults of both sexes (26%;  $n = 324$ ) suffered higher levels of limb loss than did juveniles (10%;  $n = 359$ ) (logistic regression, 4 df,  $P < 0.001$ ). No significant differences in injury were observed between juveniles and adults in the Rhode River in 1987 and 1988, or at Chesapeake Bay and southeastern sites with the exception of South Carolina (logistic regression, 4 df,  $P$



**Figure 4.** Histograms of the percentage of crabs injured at sites in the Chesapeake Bay, South Carolina, Florida, and Alabama as a function of size and sex in 1989. Size categories and statistical tests are as described in Figure 3. In the Patuxent River site, separate tests were used to compare effects of (1) sex, and (2) size among females. Sample sizes were too low to test for the interaction of size and sex.



**Figure 5.** Between-year comparisons of percentages of crabs missing, regenerating, and both missing and regenerating limbs in the Rhode River by size from 1986 to 1989. Years with the same superscripted letter did not differ significantly in total autotomy frequency (STP tests,  $P > 0.05$ ).

< 0.006). At North Inlet, juvenile crabs showed anomalously high levels of limb loss (44%) compared to adults (25%).

**Season.** The percentage of injury for large crabs and for combined size classes in the Rhode River varied significantly over the season in 1987 and 1989 only (G-tests,  $P < 0.05$ , Fig. 6). In these years, overall levels of autotomy were high early in the season, declined in mid-summer (July–August), increased in September, and dropped again in October. These late season declines in injury level were due primarily to an influx of smaller, undamaged crabs into the subestuary (Hines *et al.*, 1987a, 1990). Large crabs continued to have high levels of damage in late fall (Fig. 6). No significant seasonal trends in autotomy frequency were observed for small or medium size crabs in any year.

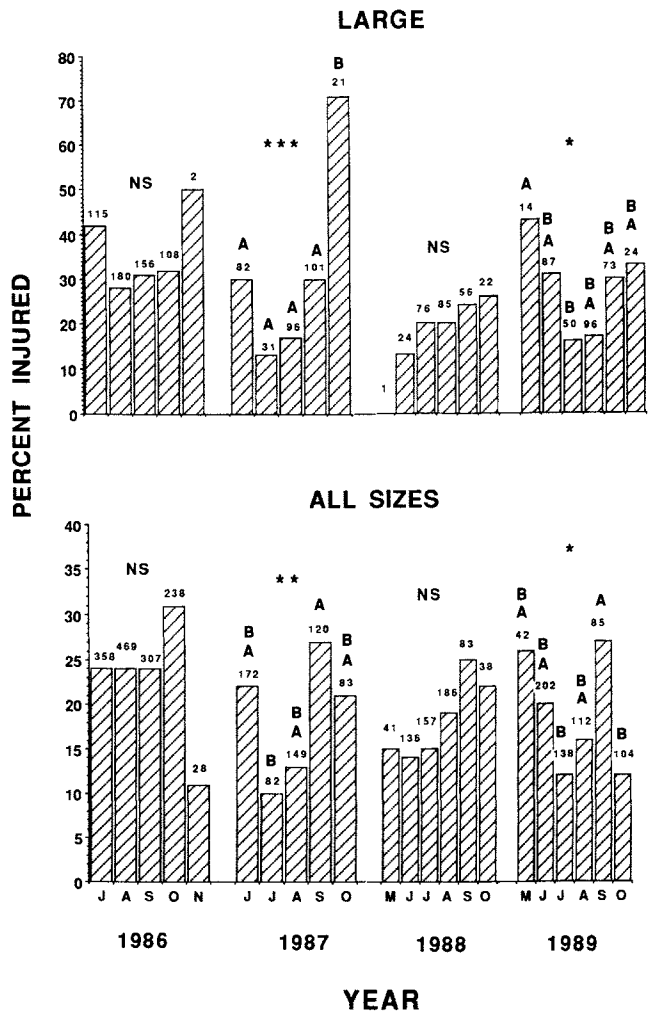
**Subestuarine location.** No significant differences in limb loss were found among sites within the Rhode River sub-

estuary from 1986 to 1988. In contrast, crabs caught at the river head in 1989 were missing or regenerating limbs more than twice as often (20%) as those caught at the river mouth (9%) (G-test, 1 df,  $P < 0.002$ ).

**Molt stage.** The frequency of limb loss was independent of molt stage for all years in the Rhode River and at all other sites, except South Carolina, where premolt animals were damaged almost twice as often as intermolt animals (G-test, 2 df,  $P < 0.05$ ).

*Patterns of autotomy*

**Limb number.** Single limb loss was the most common form of autotomy for all sites and years (Figs. 7, 8). In



**Figure 6.** Percentage of crabs injured (*i.e.*, missing or regenerating at least one limb) by month in the Rhode River, Maryland from 1986 to 1989. Large crabs (>110 mm CW) and combined size classes are presented. Sample sizes and results of 2-way contingency tests are presented above each bar. NS = Not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ , \*\*\*,  $P < 0.001$ . For each year, months with the same letter were not significantly different (STP tests,  $P > 0.05$ ).



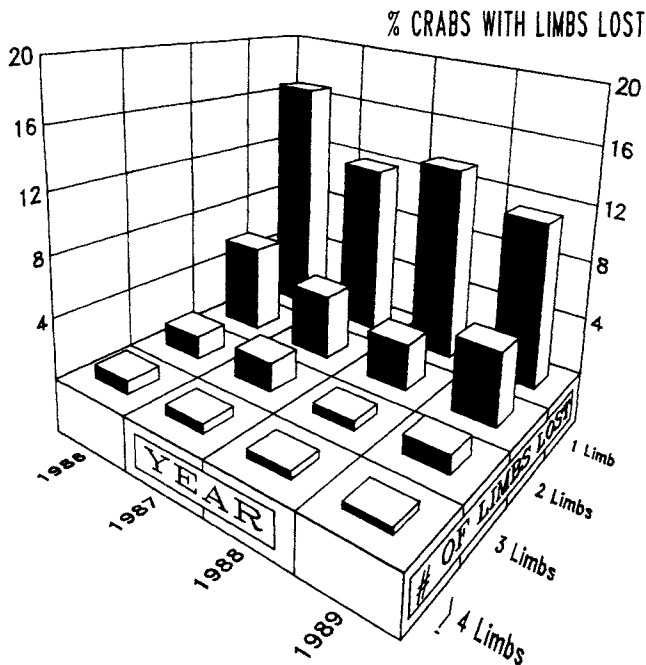


Figure 7. Histogram of the percentage of crabs missing or regenerating 1, 2, 3, or 4 or more limbs in the Rhode River, Maryland, from 1986 to 1989.

the Rhode River, 11–17% of the population were missing or regenerating a single limb, while injury to two appendages occurred less frequently (3–6%). Loss of three or more limbs was observed in less than 2.5% of the population in the Rhode River for any given year (Fig. 7). The maximum number of limbs missing or regenerating on a single crab was six. The mean number of limbs lost ranged from 1.3 to 1.6. The proportion of numbers of limbs (*i.e.*, 1, 2, 3,  $\geq 4$ ) lost among crabs in the Rhode River did not differ among years ( $G^2 = 9.0$ , 9 df,  $P > 0.1$ ).

The relative numbers of limbs lost also did not differ among blue crabs in Alabama, Florida, upper- or lower-mid Chesapeake Bay (Fig. 8). In North Inlet, South Carolina, single limb loss was proportionately higher than double limb loss when compared to other sites (STP test,  $P < 0.05$ ). In Patuxent River, injury to two limbs (15.5%) occurred nearly as often as single autotomy (19.4%). The proportion of crabs experiencing single *versus* multiple limb loss did not differ significantly with body size at any site ( $G$ -tests, 2 df,  $P > 0.05$ ) with the possible exception of the Rhode River in 1986. In that year, only 13% of the injured small crabs were missing or regenerating two or more limbs; medium (33%) and large (36%) crabs showed considerably higher levels of multiple autotomy ( $G$ -test, 2 df,  $P = 0.06$ ).

Although comparatively rare, in all years in the Rhode River and at upper- and lower-mid Chesapeake Bay sites, multiple autotomy occurred more often than would be

expected based on a binomial distribution in which: (1) the probability of losing any one limb was assumed equal, and (2) limbs were independent with respect to damage (Table IV). In contrast, observed and expected frequencies of single and multiple limb loss did not differ significantly at South Carolina, Florida, and Alabama sites. Observed and expected frequencies of limb loss were marginally non-significant ( $G$ -test, 2 df,  $P = 0.07$ ) in the Patuxent River.

*Limb type.* Chelipeds were the most common limbs lost in all populations (8–33%) (Figs. 9, 10). Few crabs were missing or regenerating the paddle-shaped fifth pereopod (1–5%). Different limb types were not lost with equal frequency at any site or in any year ( $G$ -tests, 4 df,  $P < 0.02$ ). The proportions of injured limb types did not differ in the Rhode River among years ( $G^2 = 18.3$ , 12 df,  $P > 0.1$ ). Damage to chelipeds was disproportionately high at Florida, lower-mid Chesapeake Bay, and Patuxent River sites when compared to other sites (STP tests, 20 df,  $P < 0.05$ , Fig. 10). With the exception of the South Carolina site and the Rhode River in 1988, there were no differences between the frequencies of right and left limbs lost. At both North Inlet in 1989 and Rhode River in 1988, right limbs were lost more often than left limbs ( $G$ -tests, 4 df,  $P < 0.05$ ).

*Cheliped morphology.* The majority (63–87%) of crabs at all sites and in all years possessed a right crusher cheliped

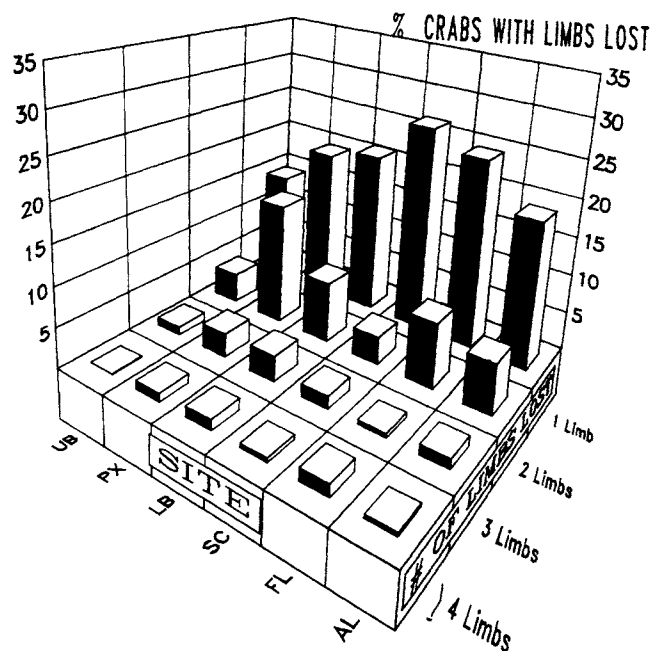


Figure 8. Histogram of the percentage of crabs missing or regenerating 1, 2, 3, or 4 or more limbs in the upper-mid Chesapeake Bay (UB); Patuxent River, Maryland (PX); lower-mid Chesapeake Bay (LB); North Inlet, South Carolina (SC); Indian River, Florida (FL); and Mobile Bay, Alabama (AL) in 1989.

Table IV

Comparisons of expected versus observed frequencies of intact crabs and those missing or regenerating 1, 2, 3, or 4 or more limbs in the Rhode River, Maryland from 1986 to 1989

Injury status	Rhode River, Maryland							
	1986		1987		1988		1989	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Intact	1050	960	505	463	536	514	569	528
-1 Limb	234	369	75	138	86	122	78	145
-2 Limbs	83	64	26	18	20	13	34	18
-3 Limbs	21	6	12	2	4	1	8	1
- ≥4 Limbs	12	0.5	4	0.7	3	0.4	3	0.1
G-test	$P < 0.001$		$P < 0.001$		$P < 0.005$		$P < 0.001$	

Expected frequencies were generated from a binomial distribution in which the probability of loss of each of 10 limbs was the same. Limbs were assumed to be lost independently. The probability of losing any one limb = # limbs lost in the population / (10 × # crabs in the population). The final two categories (-3 and -4 or more limbs) were pooled for analysis. (G-tests, 2 df).

and a left cutter cheliped (Table V). The frequency of crabs with a right crusher/left cutter did not differ among years in the Rhode River. Frequencies of crabs with right crusher/left cutter morphology in the upper-mid Chesapeake Bay and Rhode River in 1989, however, were significantly higher than those from other sites in that year. Crabs with two cutters were relatively common (7–21%); whereas, left crusher/right cutter morphological patterns were observed less frequently (0.6–10%). Crabs possessing double crushers were extremely rare ( $\leq 1\%$ ).

Frequencies of crabs bearing right crusher/left cutter morphologies decreased as size increased in the Rhode River in all years (Fig. 11). The frequency of female crabs bearing a right crusher/left cutter was greater than males in three of four years ( $P = 0.06$ ). Sex differences in the frequency of crusher/cutter patterns were generally consistent across size classes (but see 1986, size × sex interaction).

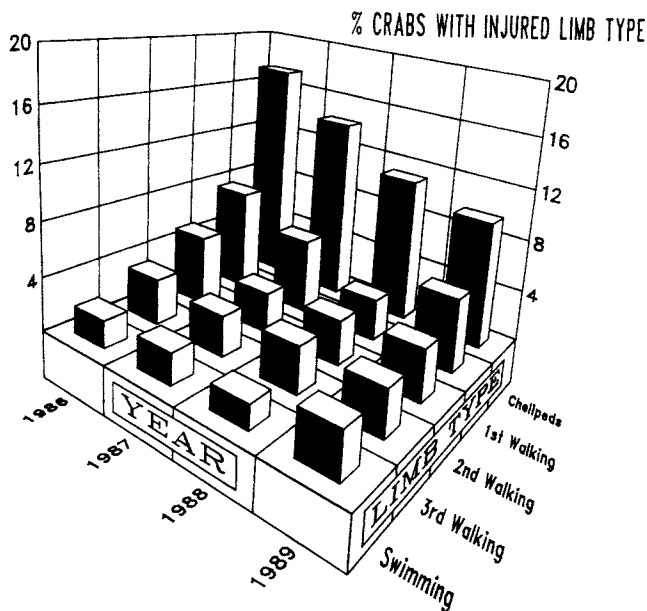


Figure 9. Histogram of the percentage of crabs missing or regenerating one or both chelipeds, 1st, 2nd, and 3rd walking legs and swimming legs in the Rhode River, Maryland, from 1986 to 1989.

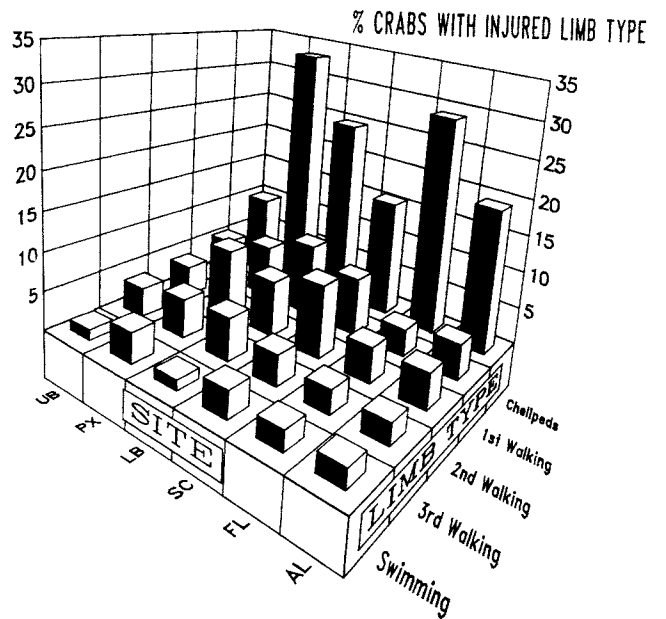


Figure 10. Histogram of the percentage of crabs missing or regenerating one or both chelipeds, 1st, 2nd, and 3rd walking legs and swimming legs in the upper-mid Chesapeake Bay (UB); Patuxent River, Maryland (PX); lower-mid Chesapeake Bay (LB); North Inlet, South Carolina (SC); Indian River, Florida (FL); and Mobile Bay, Alabama (AL) in 1989.

Table V

Frequencies and percentages of crusher and cutter cheliped morphologies from blue crabs collected in the Rhode River (1986-1989), and in the upper-mid Chesapeake Bay; Patuxent River; lower-mid Chesapeake Bay; North Inlet, SC; Indian River, FL; and Mobile Bay, AL in 1989

Site & Year	Morphological Patterns of Crab Chelipeds				
	Right crusher left cutter	Left crusher right cutter	Double cutters	Double crushers	Other
Rhode R. 86	1109 (79%)*	61 (4%)	148 (11%)	1 (.1%)	81 (6%)
Rhode R. 87	509 (82%)*	18 (3%)	68 (11%)	0 (0%)	27 (4%)
Rhode R. 88	537 (83%)*	4 (.6%)	88 (14%)	0 (0%)	20 (3%)
Rhode R. 89	576 (83%)* a	4 (.6%)	93 (13%)	0 (0%)	19 (3%)
Upper-Mid CB 89	593 (87%) a	20 (3%)	44 (7%)	2 (.3%)	20 (3%)
Patuxent R. 89	71 (69%) b	3 (3%)	12 (12%)	1 (1%)	16 (16%)
Lower-Mid CB 89	163 (73%) b	11 (5%)	21 (9%)	2 (1%)	27 (12%)
N. Inlet, SC 89	129 (63%) b	20 (10%)	42 (21%)	1 (.5%)	12 (6%)
Indian R., FL 89	146 (73%) b	11 (6%)	20 (10%)	1 (.5%)	23 (11%)
Mobile B., AL 89	192 (74%) b	20 (8%)	37 (14%)	2 (.8%)	9 (4%)

The category "other" included crabs missing one cheliped and possessing one cutter or crabs missing both chelipeds. Comparisons of frequency of crabs with a right crusher/left cutter for 4 years in the Rhode River (STP test, 3 df) and among all 1989 sites (STP test, 6 df) are presented. Sites with the same symbol or letter (to denote separate tests) are not significantly different ( $P > 0.05$ ).

The relationship of size and sex to cheliped morphology was less consistent at sites outside the Rhode River. The frequency of crabs possessing a right crusher/left cutter did not vary significantly with size or sex at any Chesapeake Bay site or in Mobile Bay. Low sample sizes in the Patuxent River prevented testing the interaction between size and sex. Size differences were recorded in North Inlet and Indian River (G-tests;  $P < 0.05$ ). At North Inlet, large males (47%;  $n = 84$ ) possessed fewest right crushers. Regardless of size, ca. 69% of female blue crabs ( $n = 82$ ) possessed a right crusher and left cutter. In Indian River, Florida, the incidence of right crusher/left cutters was lower in large individuals of both sexes when compared to small size classes.

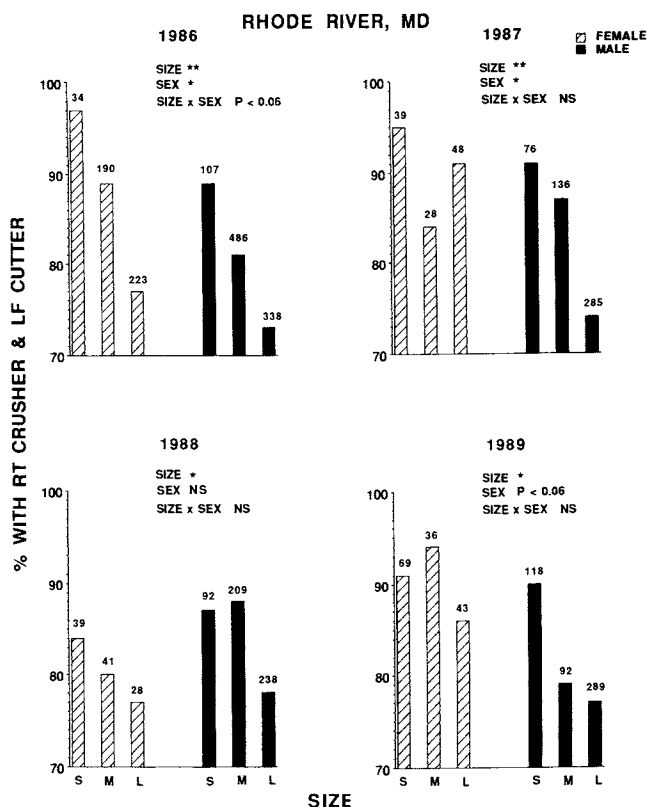
## Discussion

### Causal agents

High frequencies of limb loss recorded over broad temporal and geographic scales indicate that autotomy is an important mechanism for survival in *Callinectes sapidus*. Eighteen to 25% of blue crabs surveyed over a four year period in the Rhode River, Maryland, and 19–39% of blue crabs at six other sites along the eastern coast of the United States in 1989 were missing or regenerating one or more limbs. Autotomy is an effective escape response to predators (Robinson *et al.*, 1970; Congdon *et al.*, 1974; Medel *et al.*, 1988; Smith, 1990a). Variation in injury levels in populations may indicate differential predation pressure (e.g., Shaffer, 1978; Ballinger, 1979; Schall and Pianka, 1980; McCallum *et al.*, 1989) or predator effi-

ciency (Schoener, 1979; Schoener and Schoener, 1980; Jaksic and Fuentes, 1980). In the Rhode River, significantly higher levels of limb loss were recorded in blue crabs in 1986 (25%) than in three subsequent years (18–19%). If partial predation is responsible for autotomy (Smith, 1990a), then these differences indicate either increased predation pressure, decreased predator efficiency, or both during 1986.

Several lines of evidence indicate that unsuccessful predation by conspecifics may be the principal source of nonlethal injury in blue crabs in the Rhode River. Based on trawl catches (Hines *et al.*, 1987a, 1990), the Rhode River subestuary lacks abundant fish predators or decapod species capable of capturing and killing medium-to-large, hard-shelled blue crabs. American eel (*Anguilla rostrata*) and oyster toadfish (*Opsanus tau*), both known predators of small blue crabs (Wenner and Musick, 1975; Wilson *et al.*, 1987), occur in very low densities in the subestuary (Hines *et al.*, 1990). Gut analysis (Laughlin, 1982; Hines *et al.*, 1990) and experimental work (Peery, 1989; Smith, 1990a) have shown that cannibalism is an important cause of mortality in blue crabs. A long-term study in Chesapeake Bay (Lipcius and Van Engel, 1990) suggested density-dependent regulation of blue crab populations by conspecifics. Increased encounter rates between conspecifics during years of high abundance should lead to increased levels of both lethal and nonlethal injury. In the present survey, the frequency of limb loss was positively correlated with annual blue crab abundances (correlation coefficient,  $r = 0.99$ ) in the Rhode River. Mean abundances of crabs in the Rhode River between 1987 and



**Figure 11.** Histograms of the percentage of crabs possessing a right crusher and left cutter in the Rhode River, Maryland, as a function of size and sex for each year (1986–89). S, M, and L represent small (carapace width < 61 mm), medium (61–110 mm), and large (>110 mm) size classes of crabs, respectively. Sample sizes of total crabs (*i.e.*, animals with and without right crusher-left cutter combinations) in each category are presented above each bar. Results of logistic model testing for the association of size, sex, and their interaction with the frequency of crabs bearing a right crusher-left cutter combination are presented for each year. NS, not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

1989 (4–6 crabs/m<sup>2</sup>) were significantly lower than in any of the five previous years surveyed (Hines *et al.*, 1990). Injury levels in the Rhode River between 1987 and 1989 remained remarkably constant, which suggests temporal coupling between injury-causing agents and victims.

Factors besides partial predation (*e.g.*, intraspecific competition, fisheries) could contribute to observed autotomy frequencies, but these sources are probably minor. In most brachyuran crabs, intraspecific competitive interactions are highly ritualized and do not usually result in limb autotomy (Hazlett, 1972; Jachowski, 1974; Hyatt and Salmon, 1978). In *Callinectes sapidus*, instances of limb loss were rare when size-matched males competed for a sexually receptive female in small arenas (<1%; Smith, 1990a). Limb autotomy can occur during ecdysis in blue crabs, but such instances were observed infrequently (Smith, pers. obs.). Handling by fisheries also could contribute to injury in certain size classes (*e.g.*,

Kennelly *et al.*, 1990). Larger sublegal-size blue crabs (CW < 127 mm) may experience limb loss before being culled. Smaller crabs generally escape uninjured through the mesh of crab pots (Smith, pers. obs.), while larger, legal-sized crabs are harvested.

Autotomy frequencies were not biased by the various gear used to sample blue crabs. Severely injured (and potentially less mobile) animals should not have been underrepresented in collections, because active (otter trawls, seines) as well as passive (fish weir, crab pots) methods of capture were used. By using a variety of collection methods, a range of depths and habitats in the subestuary were sampled.

### Size effects

Positive correlations between autotomy frequency and blue crab body size indicate ontogenetic differences in both repair rates and susceptibility to predation. The average percentage of injury in medium- and small-size crabs for four years in the Rhode River was 37% and 58% that of large crabs, respectively. Similar size-related trends have been observed in a shore crab, *Carcinus maenas* (McVean, 1976; McVean and Findlay, 1979; Sekkelsten, 1988). Predator inefficiency often increases with increased prey size (Murtaugh, 1981; Vermeij, 1982; Reaka, 1987; Peery, 1989), and tethering experiments (Smith, 1990a) have demonstrated that larger blue crabs suffered appendage loss proportionately more often than mortality compared to smaller crabs. In the present survey, median carapace widths of injured crabs in the Rhode River were greater than those of uninjured individuals. Evidence of limb loss will also remain for longer periods in large than small animals. Limb regeneration requires molting, and blue crab molting frequency declines as size increases (Leffler, 1972; Smith, 1990b). In St. Johns River, Florida, the average length of the molt interval (*ca.* 40 days) for large (>110 mm CW) crabs was 2.5 times that of small crabs (16 days; 20–59 mm CW) and 1.5 times that of medium crabs (27 days; 60–110 mm CW) (Tagatz, 1968; see also Smith, 1990b). Based on these molt intervals, estimated daily injury rates for crabs in a given size class (*i.e.*, % injury/molt interval) over four years in the Rhode River were similar (*ca.* 0.74%/day for small crabs, 0.64%/day for medium crabs, and 0.69%/day for large crabs). Although small crabs are more vulnerable to fatal attack from predators than medium or large crabs (Smith, 1990a), they will regenerate missing limbs more quickly after nonlethal injury. In female blue crabs, molting ceases when sexual maturity is reached (Millikin and Williams, 1984), so subsequent injuries accumulate.

### Temporal variation

The lack of significant monthly variation in injury for small- and medium-size blue crabs within years in Rhode

River indicates that predator efficiency remained seasonally consistent for both size classes. Significant between-year differences among medium-size crabs, however, suggests that as annual predation levels change, medium-size animals may experience greater variability in survival than smaller animals. Injury levels in large crabs exhibited both significant within- and between-year variability. Higher frequencies of limb loss in the large size class late in the season (September–October) could have resulted from a combination of factors: (1) slower repair rates as average sizes increased over the summer; (2) decreasing molting frequency as water temperature declined (Leffler, 1972); and (3) increased levels of cannibalism as bivalve prey (e.g., *Mya arenaria*, *Macoma balthica*) became scarce (Hines *et al.*, 1990). High frequencies of limb loss seen at the beginning of each season may be a carryover from the previous fall. Because molt frequency declines over winter, regeneration is delayed.

### Sex

Male and female blue crabs, regardless of stage of sexual maturity, appeared equally vulnerable to injury in the Rhode River. This is consistent with observations in *Carcinus maenas* (McVean and Findlay, 1979) and *Cancer magister* (Shirley and Shirley, 1988). Given that adult male blue crabs continue to molt, it is surprising that injury frequencies in mature females were not proportionately higher. It is possible that: (1) large adult males are molting so infrequently that they rarely restore limb symmetry; (2) behavioral differences are making mature females less prone to injury (but see Smith, 1990a); or (3) females are migrating to spawning areas in southern Chesapeake Bay, so their injuries are not observed in the Rhode River.

### Spatial variation

Injury frequencies did not vary spatially within the Rhode River subestuary in three of four years. Hines *et al.* (1987a) have shown that blue crabs enter the Rhode River each spring and fall where they grow to maturity. Male crabs forage throughout the subestuary and use Muddy Creek as a molting habitat. These movement patterns may explain why observed injury levels are homogeneous across sites.

Significant differences among autotomy frequencies in the Rhode River region, other sites in the Chesapeake Bay, and southeastern United States indicate that these regions differ in the type, degree, or efficiency of injury-causing agents. Injury levels recorded in the Rhode River and upper-mid Chesapeake Bay in 1989 were markedly lower than at any other site (except Alabama) for that year. Higher frequencies of limb loss and regeneration

outside the Rhode River cannot be attributed to differences in sex ratio or size distributions among sites, because the elevated injury levels were maintained for most categories of size and sex. The relatively low salinities and shallow depths found in the Rhode River may limit the abundances and diversity of predators so that the subestuary serves as a refuge. Qualitative observations of trawl catches at the Patuxent River, lower-mid Chesapeake Bay, and Alabama sites showed higher diversity and abundances of large, known crab predators (e.g., striped bass, *Morone saxatilis*; oyster toadfish, *Opsanus tau*; white catfish, *Ictalurus catus*, Millikin and Williams, 1984) than were found in the Rhode River (Hines *et al.*, 1990).

Surprisingly, no significant differences in injury frequency existed among populations from the Patuxent River, Maryland south to Mobile Bay, Alabama, even though these populations spanned two biogeographic provinces (cold-temperate North Atlantic and warm-temperate Northwest Atlantic; Vermeij, 1978), were sampled in different seasons, and were subjected to different suites of predators. These data contrast with studies showing increased predation pressure at lower latitudes (Bertness *et al.*, 1981; Vermeij *et al.*, 1980; Heck and Wilson, 1987).

### Patterns of autotomy

The consistency of limb loss pattern observed in this study is probably due to limb function and the behavioral response to the injury-causing agent. Chelipeds were lost most often, followed by first walking legs. Similar patterns have been observed in other brachyuran crabs (e.g., *Carcinus maenas*, McVean, 1976; McVean and Findlay, 1979; *Cancer magister*, Durkin *et al.*, 1984; Shirley and Shirley, 1988). Crabs respond to threats from predators or competitors with outstretched claws (Schone, 1968; Robinson *et al.*, 1970; Jachowski, 1974; Vannini, 1980) making anterior limbs particularly vulnerable to injury. Strikes from behind may often prove fatal, so fewer crabs will be found missing swimming legs. Additionally, the autotomy response in swimming legs is greatly reduced in larger crabs; even severe damage to these limbs often would not result in autotomy (Smith, pers. obs.). Small and medium-sized crabs, however, autotomize all limb types readily. Escape responses by blue crabs showed no consistent directionality (Smith, 1990a), and the symmetry of limb loss suggests that the injury-causing agent is striking randomly. Similarity in injury frequency between right and left sides has also been observed in Dungeness crabs, *Cancer magister* (Durkin *et al.*, 1984).

Multiple autotomies could be caused either by single events damaging more than one leg or by cumulative damage from independent events. While single limb loss

was most common at all sites and in all years in *Callinectes sapidus* (also in *Carcinus maenas*, McVean and Findlay, 1979; *Cancer magister*, Shirley and Shirley, 1988), multiple limb loss was more frequent than chance predicts. McVean (1976) interpreted a similar pattern in *C. maenas* to indicate that injured animals are more susceptible to attack than intact individuals. Tethering studies in *C. sapidus* suggest that multiple limb loss occurs in a single attack event (Smith, 1990a). The percentage of animals simultaneously missing and regenerating limbs was rare (ca. 1%) in all years in the Rhode River, indicating that previous limb loss, in most instances, does not make an animal more vulnerable to future attacks.

### Cheliped regeneration

Substantial percentages of regenerating chelipeds were observed in all populations, which suggests that, despite their importance (e.g., defense, foraging), crabs could compensate temporarily for their loss. In many crustacean taxa, loss of the major claw results in the transformation of the opposing minor claw into a major claw over several molts (Hamilton *et al.*, 1976). The autotomized limb is simultaneously replaced by a minor claw. In blue crabs, transformation can be incomplete even after three molts (Smith, 1990b); consequently, those crabs losing a right crusher claw bear symmetrical, double cutters following regeneration. Presence of a left crusher/right cutter, double cutters, or double crushers is evidence of previous limb loss. In the Rhode River, frequencies of animals bearing a right crusher/left cutter generally declined as size increased. Up to 25% of large crabs (e.g., 1986; Fig. 11) showed evidence of having lost a right crusher during their lifetime, which suggests that survival following loss of a right crusher was high. Frequencies of these atypical claw morphologies were even higher in South Carolina (32%) and Florida (35%). Interestingly, the percentage of male crabs bearing a right crusher and left cutter was lower than in females in three out of four years in the Rhode River, which suggests that males were suffering greater incidence of cheliped injury during their lifetime.

### Conclusions

By examining the frequency of injury over both temporal and geographic scales, our study provides the most complete analysis to date on autotomy in any species. The magnitude of this data set allows inferences about causal agents of autotomy and about the impact of autotomy on blue crab survival following attack. Four years of autotomy data in the Rhode River, Maryland, provide evidence that: (1) the frequency of nonlethal injury in the population is positively correlated with density and is probably due to unsuccessful conspecific predation; (2)

the rate of autotomy is similar over the lifespan of the individual, but differences in molting rate and predator efficiency result in higher injury levels in larger animals; (3) chances of survival subsequent to single or double limb loss are good; and (4) lower frequencies of autotomy in the Rhode River compared to other sites indicate geographic differences in the intensity or efficiency of injury-causing agents. The high incidence of limb loss in all age groups, and in both sexes over broad temporal and geographic scales, indicates that autotomy is an important adaptation for avoiding predation.

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### Literature Cited

- Ballinger, R. E. 1979. Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona. *Ecology* 60: 901-909.
- Bennett, D. B. 1973. The effect of limb loss and regeneration on the growth of the edible crab, *Cancer pagurus* L. *J. Exp. Mar. Biol. Ecol.* 13: 45-53.
- Bertness, M. D., S. D. Garrity, and S. C. Levings. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution* 35: 995-1007.
- Berzins, I. K., and R. L. Caldwell. 1983. The effect of injury on the agonistic behavior of the stomatopod, *Gonodactylus bredini* (Manning). *Mar. Behav. Physiol.* 10: 83-96.
- Congdon, J. D., L. J. Vitt, and W. W. King. 1974. Geckos: adaptive significance and energetics of tail autotomy. *Science* 184: 1379-1380.
- Conover, M. R., and D. E. Miller. 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. 1970. *Analysis of Binary Data*. Methuen, London. 142 pp.

- Dial, B. E., and L. C. Fitzpatrick. 1983. Lizard tail autotomy: function and energetics of postautotomy tail movement in *Scincella lateralis*. *Science* 219: 391-393.
- Dial, B. E., and L. C. Fitzpatrick. 1984. Predator escape success in tailed versus tailless *Scincella lateralis* (Sauria:Scincidae). *Anim. Behav.* 32: 301-302.
- Durkin, J. T., K. D. Buchanan, and T. H. Blahm. 1984. Dungeness crab leg loss in the Columbia River estuary. *Mar. Fish. Rev.* 46: 22-24.
- Edwards, J. S. 1972. Limb loss and regeneration in two crabs: the king crab *Paralithodes camtschatica* and the tanner crab *Chionoecetes bairdi*. *Acta Zool.* 53: 105-112.
- Fox, L. R. 1975. Cannibalism in natural populations. *Ann. Rev. Ecol. Syst.* 6: 87-106.
- Hamilton, P. V. 1976. Cheliped laterality in *Callinectes sapidus* (Crustacea: Portunidae). *Biol. Bull.* 150: 393-401.
- Harris, R. N. 1989. Nonlethal injury to organisms as a mechanism of population regulation. *Am. Nat.* 134: 835-847.
- Hazlett, B. A. 1972. Responses to agonistic postures by the spider crab *Microphrys bicornutus*. *Mar. Behav. Physiol.* 1: 85-92.
- Heck, K. L., Jr., and 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.* 107: 87-100.
- Hines, A. H., R. N. Lipcius, and A. M. Haddon. 1987a. 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., P. J. Haddon, J. J. Miklas, L. A. Wiechert, and A. M. Haddon. 1987b. Estuarine invertebrates and fish: sampling design and constraints for long-term measurements of population dynamics. Pp. 140-164 in *New Approaches to Monitoring Aquatic Ecosystems*, ASTM STP 940, T. P. Boyle, ed. American Society for Testing and Materials, Philadelphia.
- Hines, A. H., A. M. Haddon, and 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.* 67: 105-126.
- Hyatt, G. W., and M. Salmon. 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: a quantitative analysis. *Behaviour* 65: 182-211.
- Jachowski, R. L. 1974. Agonistic behaviour of the blue crab, *Callinectes sapidus* Rathbun. *Behaviour* 50: 232-253.
- Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. *Am. Nat.* 117: 962-974.
- Jaksic, F. M., and E. R. Fuentes. 1980. Correlates of tail losses in twelve species of *Liolaemus* lizards. *J. Herpetol.* 14: 137-141.
- Johnson, P. T. 1980. *Histology of the Blue Crab, Callinectes sapidus. A Model for the Decapoda*. Praeger Sci. Publ. Co., New York. 440 pp.
- Kennelly, S. J., D. Watkins, and J. R. Craig. 1990. Mortality of discarded spanner crabs *Ranina ranina* (Linnaeus) in a tangle-net fishery—laboratory and field experiments. *J. Exp. Mar. Biol. Ecol.* 140: 39-48.
- Kuris, A. M., and M. Mager. 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.
- Kurihara, Y., and K. Okamoto. 1987. Cannibalism in a grapsid crab, *Hemigrapsus penicillatus*. *Mar. Ecol. Prog. Ser.* 41: 123-127.
- Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. *Bull. Mar. Sci.* 32: 807-822.
- Leffler, C. W. 1972. Some effects of temperature on the growth and metabolic rate of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. *Mar. Ecol. Prog. Ser.* 41: 123-127.
- Lipcius, R. M., and W. A. Van Engel. 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.
- McCallum, H. I., R. Endean, and A. M. Cameron. 1989. Sublethal damage to *Acanthaster planci* as an index of predation pressure. *Mar. Ecol. Prog. Ser.* 56: 29-36.
- McVean, A. 1976. The incidence of autotomy in *Carcinus maenus* (L.). *J. Exp. Mar. Biol. Ecol.* 24: 177-187.
- McVean, A. 1982. Autotomy. Pp. 107-132 in *The Biology of Crustacea*, Vol. 4, D. E. Bliss, ed. Academic Press, Inc., New York.
- McVean, A., and I. Findlay. 1979. The incidence of autotomy in an estuarine population of the crab *Carcinus maenas*. *J. Mar. Biol. Assoc. U.K.* 59: 341-354.
- Medel, R. G., J. E. Jimenez, S. F. Fox, and F. M. Jaksic. 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos* 53: 321-324.
- Millikin, M. R., and A. B. Williams. 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. *NOAA Technical Report NMFS 1. FAO Fisheries Synopsis No. 138*.
- Murtaugh, P. A. 1981. Inferring properties of mysid predation from injuries to *Daphnia*. *Limnol. Oceanogr.* 26: 811-821.
- Needham, A. E. 1953. The incidence and adaptive value of autotomy and of regeneration in Crustacea. *Proc. Zool. Soc. London* 123: 111-122.
- Peery, C. A. 1989. Cannibalism experiments with the blue crab (*Callinectes sapidus* Rathbun): potential effects of size and abundance. Master's thesis. College of William and Mary, Williamsburg, Virginia.
- Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *Ann. Rev. Ecol. Syst.* 12: 225-251.
- Reaka, M. L. 1987. Adult-juvenile interactions in benthic reef crustaceans. *Bull. Mar. Sci.* 41: 108-134.
- Robinson, M. H., L. G. Abele, and B. Robinson. 1970. Attack autotomy: a defense against predators. *Science* 169: 300-301.
- SAS Institute. 1985. *SAS User's Guide: Statistics*. Version 5 Edition. SAS Institute Inc., Cary, North Carolina. 956 pp.
- Schall, J. J., and E. R. Pianka. 1980. Evolution of escape behavior diversity. *Am. Nat.* 115: 551-566.
- Schoener, T. W. 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* 60: 1110-1115.
- Schoener, T. W., and A. Schoener. 1980. Ecological and demographic correlates of injury rates in some Bahamian *Anolis* lizards. *Copeia* 1980: 839-850.
- Schone, H. 1968. Agonistic and sexual display in aquatic and semi-terrestrial brachyuran crabs. *Am. Zool.* 8: 641-654.
- Sekkelsten, G. I. 1988. Effect of handicap on mating success in male shore crabs *Carcinus maenas*. *Oikos* 51: 131-134.
- Shaffer, H. B. 1978. Relative predation pressure on salamanders (Caudata: Plethodontidae) along an altitudinal transect in Guatemala. *Copeia* 1978: 268-272.
- Shirley, S. M., and T. C. Shirley. 1988. Appendage injury in dungeness crabs, *Cancer magister* in southeastern Alaska. *Fish. Bull.* 86: 156-160.
- Simonson, J. L. 1985. Reversal of handedness, growth, and claw striulatory patterns in the stone crab *Menippe mercenaria* (Say) (Crustacea: Xanthidae). *J. Crust. Biol.* 5: 281-293.
- Simonson, J. L., and P. Steele. 1981. Cheliped asymmetry in the stone crab, *Menippe mercenaria*, with notes on claw reversal and regeneration. *Northeast Gulf Sci.* 5: 21-30.

- Slater, A., and J. M. Lawrence. 1980. The effect of arm loss on feeding and growth rates in *Luidia clathrata*. *Fla. Sci.* **43**: 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. 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.* **46**: 23–36.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman, New York. 859 pp.
- Stevens, B. G., D. A. Armstrong, and R. Cusimano. 1982. Feeding habits of the Dungeness crab *Cancer magister* as determined by the index of relative importance. *Mar. Biol.* **72**: 135–145.
- Sullivan, J. R. 1979. The stone crab, *Menippe mercenaria*, in the southwest Florida fishery. *Fl. Mar. Res. Publ. No.* 36.
- Tagatz, M. E. 1968. Growth of juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fish. Bull.* **67**: 281–288.
- 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.* **20**: 6–17.
- Van Engel, W. A. 1990. Development of the reproductively functional form in the male blue crab, *Callinectes sapidus*. *Bull. Mar. Sci.* **46**: 13–22.
- Vannini, M. 1980. Notes on the behaviour of *Ocypode ryderi* Kingsley (Crustacea, Brachyura). *Mar. Behav. Physiol.* **7**: 171–183.
- Vermeij, G. J. 1976. Interoceanic differences in vulnerability of shelled prey to crab predation. *Nature* **260**: 135–136.
- Vermeij, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* **3**: 243–258.
- Vermeij, G. J. 1978. *Biogeography and Adaptation: Patterns of Marine Life*. Harvard University Press, Cambridge, MA. 332 pp.
- Vermeij, G. J. 1982. Unsuccessful predation and evolution. *Am. Nat.* **120**: 701–720.
- Vermeij, G. J. 1983. Shell-breaking predation through time. Pp. 649–669 in *Biotic Interactions in Recent and Fossil Benthic Communities*, M. J. S. Tevesz and P. L. McCall, eds. Plenum, New York.
- Vermeij, G. J., E. Zipser, and E. C. Dudley. 1980. Predation in time and space: peeling and drilling in terebrid gastropods. *Paleobiology* **6**: 352–364.
- Vitt, L. J., J. D. Congdon, and N. A. Dickson. 1977. Adaptive strategies and energetics of tail autotomy in lizards. *Ecology* **58**: 326–337.
- Wenner, C. A., and J. A. Musick. 1975. Food habits and seasonal abundance of the American eel, *Anguilla rostrata*, from the lower Chesapeake Bay. *Chesapeake Sci.* **16**: 62–66.
- Willis, L., S. T. Threlkeld, and C. C. Carpenter. 1982. Tail loss patterns in *Thamnophis* (Reptilia:Colubridae) and the probable fate of injured individuals. *Copeia* **1982**: 98–101.
- Wilson, K. A., K. L. Heck, Jr., and K. W. Able. 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. *Fish. Bull.* **85**: 53–58.
- Wood, F. D., and H. E. Wood, II. 1932. Autotomy in decapod crustacea. *J. Exp. Zool.* **62**: 1–55.