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Growth and Claw Regeneration of the Stone Crab, *Menippe mercenaria*

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Florida Department of Natural Resources
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ABSTRACT

Savage, T. and J.R. Sullivan. 1978. Growth and Claw Regeneration of the Stone Crab, *Menippe mercenaria*. Fla. Mar. Res. Publ. No. 32. 23 pp. Laboratory-maintained and feral crabs were observed for incremental carapace width and major and minor claw growth. Morphometric relationships for male and female carapace width against length and carapace width against major and minor claw sizes were derived. Only slopes of carapace width *vs.* female major and male minor claws were not significantly different at the 95% confidence level. Feral normal male incremental growth exceeded that of normal females for all parameters. Normal laboratory females possessed greater average carapace width growth but less claw growth than did their male counterparts. All laboratory growth was more uniform but incrementally smaller than corresponding field growth. A hypothetical growth plot constructed from incremental growth of several crabs indicated ages at attainment of sexual maturity and legal size to be 10 and 30 months. A pictorial description of stone crab claw regeneration is presented. Minor claws realized greater regeneration after one and two molts (73.5% and 96.5% of pre-autotomized sizes) than did major claws (68.6% and 89.0%). Intermolt interval of laboratory crabs increased with larger carapace width sizes. Claw loss shortened or lengthened duration of the intermolt period depending upon whether the claw was removed shortly after a molt or later in the cycle.

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INTRODUCTION

The stone crab, *Menippe mercenaria* (Say, 1819), ranges from North Carolina to Mexico (Rathbun, 1930) and the Caribbean (Karandeyeva and Silva, 1966), but North American commercial utilization of this species is exclusive to Florida. The value of the ever expanding stone crab fishery to the State of Florida is considerable, ranking third in crustacean fisheries behind the shrimp and lobster industries in total revenues. Landings have increased steadily, with a few minor setbacks, from 200 thousand pounds in 1957 to 2.4 million pounds in 1976. Most crabs are landed in southwestern counties, although crabs are trapped on both coasts and in the panhandle section of the state (Savage et al., 1975). Two southwestern counties, Collier and Monroe, annually harvest over 50% of the state's total catch.

Even though *M. mercenaria* is a commercial species, most studies have dealt with non-commercial facets of stone crab biology. Binford (1913) investigated the reproductive apparatus of both sexes. Menzel and Hopkins (1955) first reported the stone crab's habit of preying on oysters. Further proof of oyster predation by stone crabs was documented by Menzel and Nichy (1958). Porter (1960) described zoeal stages of the species, while Manning (1960) reported on changes in carapace dimension as the crab progresses from juvenile to adult. Futch (1966) presented a general description of the stone crab in Florida. Karandeyeva and Silva (1966) established respiratory and osmoregulatory intensities. Sushchenya reported on stone crab nutrition and energy with Claro (1966) and Madruga (1967). Noe (1967) furthered knowledge of stone crab reproduction. Cheung published reports on stone crab endocrinology (1967), molting (1968) and growth and reproduction (1969). Powell and Gunter (1968) accomplished the first field investigation of stone crabs in Texas waters. Savage and McMahan (1968) described incremental growth rates of laboratory-held juvenile stone crabs. Salinity and temperature optimum requirements for larval rearing were established by Ong and Costlow (1970), while Yang (1970) predicted a bright future for stone crab mariculture. Savage described the mating process (1971a) and effects of maintenance parameters on growth (1971b) in stone crabs. Bender (1971) and Sinclair (1972) separately investigated stone crab behavior patterns. Cheung (1973) researched claw regeneration on "aged" male stone crabs. Mootz and Epifanio (1974) reported on the energy budget of *Artemia*-fed larval stone crabs. Sandifer and Smith (1974) and Yang and Krantze (1976) detailed the successes and failures of stone crab rearing and pond culture. Savage et al. (1974) described claw extraction during molting of a stone crab, and subsequently (1975) analyzed Florida west coast stone crab landings. Cheung (1976) reported statistical evidences of claw reversal.

There are few dynamic processes of crustacean life more important to the success of growth and regeneration than molting. Superficially, molting appears only to be an interruption in the crustacean life cycle when growth occurs, after which the animal can resume normal activities. In actuality, molting affects every aspect of the animal's life, including reproduction, behavior, and metabolism (Passano, 1960). The Florida Department of Natural Resources Marine Research Laboratory initiated a study in 1968 to investigate growth and regeneration of male and female stone crabs in captivity and in the field. Major emphasis was placed on normal growth rates and regeneration of the claws. This study, designed to reveal the natural processes supporting the fishery, is the subject of this report.

METHODS AND MATERIALS

FIELD PROCEDURES

Stone crabs are available along Florida's shorelines throughout the year, permitting the gathering of experimental material when needed. During the course of this study, animals were captured by hand at low tide and brought into the laboratory singly or in groups to determine some aspect of subsequent molting (e.g., carapace or claw growth, regeneration). Stone crabs were collected in the greater Tampa Bay area and elsewhere along Florida's west coast (Figure 1).

The most frequently sampled location was Pinellas Point (PP), a small public park at the southern end of Pinellas County (Figure 2). Intertidal shoreline contained rock and shell rubble material which served as a habitat for mostly small and medium sized crabs. Other medium and large crabs were received from a local crabber trapping the Gulf waters just west of the Sunshine Skyway Bridge (SB). Occasionally, small and medium crabs were collected in the intertidal zone fronting the seawall of the Sky Harbor Condominium (SH) adjacent to the Sunshine Skyway.

In the Sarasota Bay area, surveys were periodically conducted on an offshore oyster bar to examine the undisturbed habitat of a population of resident and transient stone crabs for comparison with Pinellas Point. Other moderately large collections of crabs were provided by a restaurant owner who permitted us to collect whole crabs from traps set offshore from Anna Maria Island (AM).

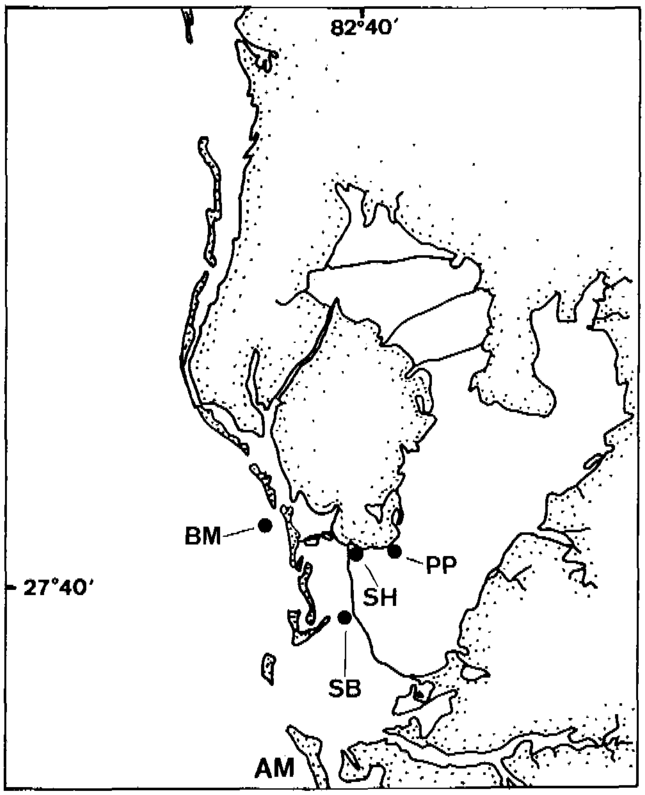

Figure 1. Sources of crabs from Florida's west coast. Tampa Bay sampling locations were Sunshine Skyway Bridge (SB), Sky Harbor Condominium (SH), Pinellas Point (PP), Bill McGarry (BM) and Anna Maria Island (AM).

Figure 2. Low tide at public park pier (a), Pinellas Point, where most live crabs were collected; rock and rubble (b) at base of pier.

Most crabs used for laboratory investigations were provided by three large wholesale firms located along Florida's west coast. Intact crabs in damp, burlap bags were brought to the laboratory from Chokoloskee, Cedar Key and Crystal River. Crab procurements, as well as the contribution each shipment made to the overall project, are summarized in Table 1.

The great bulk of field observations involved monitoring individuals of the local stone crab population at Pinellas Point. During visits, crabs over 20 mm CW were collected and observed for intermolt condition, handedness, sex (Figure 3), and claw stridulatory pattern (*pars stridens*, Guinot-Dumortier and Dumortier, 1960), and measured for carapace width, length, and claw size (Figure 4). Carapace length was measured from the frontal groove to the posterior edge; carapace width was measured between lateral spines. Claw size was measured as the length of the base of the propodus, a measurement also used to determine legal size. Measured crabs were released some distance away to allow different crabs to migrate into the station before the next visit. Sarasota Bay and Sky Harbor sites were surveyed in a similar manner. Generally, field observations augmented observations and data gathered from laboratory investigations.

LABORATORY PROCEDURES

Laboratory investigations were conducted in two covered, circular (4.6 m diameter), outdoor, fiberglassed concrete tanks (Figure 5). An open-water system, maintained at a depth of 56 cm by a stand pipe drain, pumped water from adjacent Bayboro Harbor. Concrete building blocks placed around the tank perimeter provided shelter. Crabs were fed chopped fish or whole, fresh or frozen oysters every other work day. Tanks were drained and cleaned after each feeding. Solar radiation provided the only illumination.

Supplementing these two habitat tanks were various types of apparatus used for acclimating crabs after field collection. One type used was a 91 cm x 31 cm x 152 cm epoxy-coated wooden tub holding recirculated water from Bayboro Harbor. It was maintained in a wet laboratory whose ambient temperature was elevated somewhat by steam pipes along the ceiling in proximity of an adjacent boiler room. Lighting was provided by overhead fluorescent bulbs. Another type, used for elevated temperature studies conducted in an isolated, insulated room, was constructed of green plastic, with dimensions of 213 cm x 61 cm x 61 cm and with a capacity of 414 1. Recirculated water from

TABLE 1. SOURCES AND DISPOSITION OF STONE CRABS.

Source	Series Prefix	Total Crabs	Data Use				
			Measurements	Field Growth	Laboratory Growth	Claw Regeneration	No Data
Moore's Restaurant Longboat Key	A	27	16			3	8
Unknown	L	24	19				5
Tierra Verde St. Petersburg	TV	6	6				
Municipal Pier St. Petersburg	MP	25					25
Sky Harbor St. Petersburg	SH	7					7
Cedar Key	CK	22	10				12
Bill McGarry St. Petersburg	BM	48	8		1	7	32
Skyway Bridge St. Petersburg	SB	24	1		1	1	21
Pinellas Point St. Petersburg	PP	93	27	40	7	1	18
Unknown	EX	8					8
Hamilton's Crabs Chokoloskee	C	40	22			5	13
Hamilton's Crabs Chokoloskee	T	24	16				8
Hamilton's Crabs Chokoloskee	2C	20	7				13
Crystal River Seafood Crystal River	CR	60	20		28		12
Crystal River Seafood Crystal River	2CR	130	46		30	5	49
Totals		558	198	40	67	22	231

Bayboro Harbor was provided as well as overhead fluorescent bulbs. Smaller crabs were usually placed in a series of 0.22 l plastic jars, 0.44 l plastic beakers, or 20 cm diameter dishes until sufficient sizes were attained to allow survival in larger containers. Sand-shell fragments and pieces of PVC pipe were provided for shelter. Other crabs were placed in the wooden tub until adequately adjusted to their surroundings and then introduced into the circular tanks.

All crabs brought to the laboratory were examined for intermolt condition, handedness, sex, and stridulatory pattern, and measured for carapace width, length, and claw size. Many methods of marking to identify individual crabs were tried before a reasonably successful one was discovered. Marking the carapace with a felt-tipped pen, after scouring with light sandpaper, worked well initially but subsequently rubbed off. Red nail polish produced no better results, even when applied after abrading the carapace with sandpaper and drying with alcohol or acetone. Scarring the carapace with a soldering iron and engraving tool also failed. Notching various segments of the abdomen with a paper punch was more successful. However, notched areas often became infected, adversely affecting the molting cycle. We did not pursue this type of marking further because of time limitation, but, since notching has proven successful with lobsters, additional studies in this area may be warranted. Another marking technique involved dyeing thick rubber bands with various identifying colors and then placing them on each crab. The band encircled the crab's waist, i.e., that portion laterally where the carapace meets the legs, anteriorly to just below the mouth parts and posteriorly to the tip of the telson. A major drawback of this method was that the band impeded the molting process by preventing the crab from backing out of its old exoskeleton, consequently killing it. Most commonly affected were intact crabs because proecdysis was difficult to observe. Proecdysis symptoms could be observed in captives that were regenerating appendages. Such crabs were removed from habitat tanks and isolated without bands in separate aquaria. Upon completion of molting and hardening of the shell, crabs were returned to habitat tanks with bands reaffixed. A walking leg was autotomized prior to return to the circular tanks to insure that future proecdysis symptoms could be recognized.

Photographs of the carapace of individual crabs supplemented the last method of marking (Figure 6).

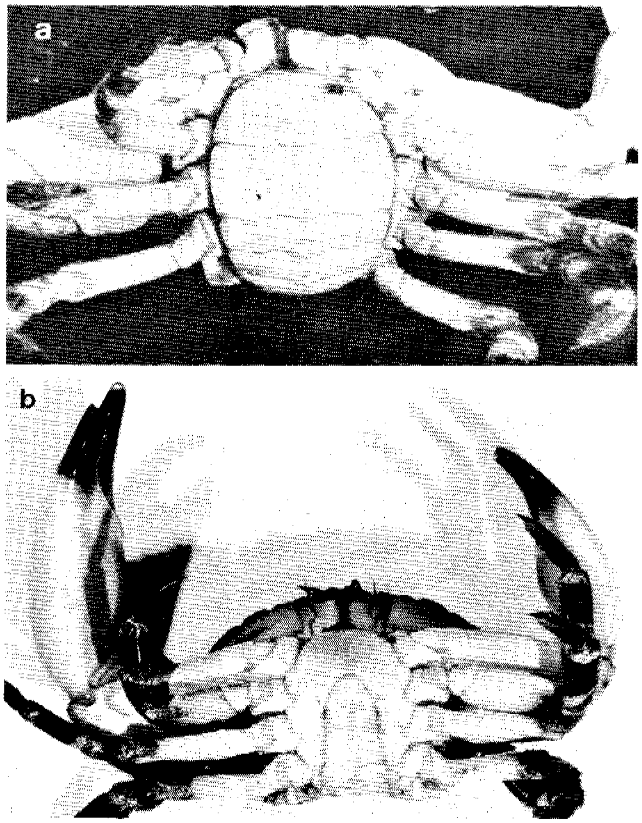

Figure 3. Abdominal differences used for sex determination of stone crabs: a. female; b. male.

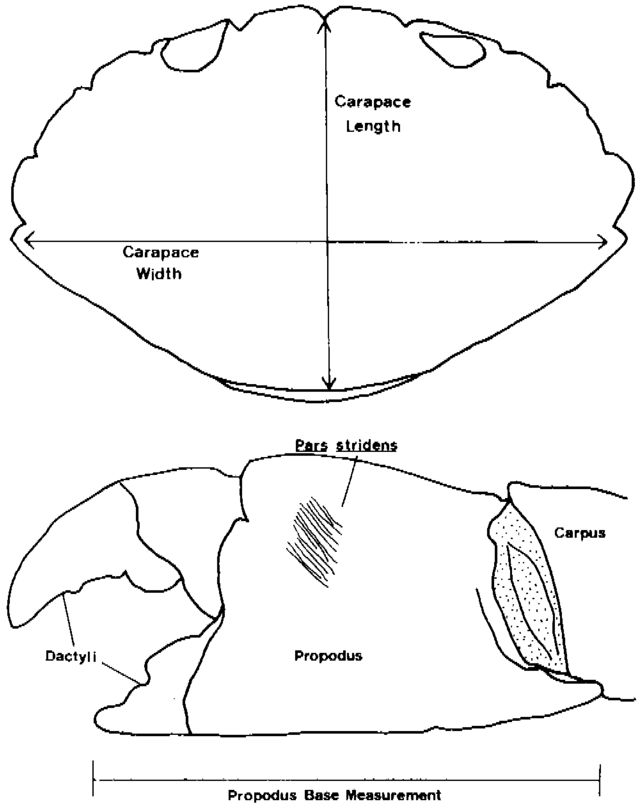

Figure 4. Locations of measurements to determine carapace width and length, and claw size; note *pars stridens* pattern on upper distal portion of propodus.

The pattern of each specimen's carapace is unique and retained throughout life (Savage, 1971b). Exuvia found during tank cleaning were matched with corresponding photographs and recorded. The newly molted animal could then be found during subsequent tank cleaning after shell hardening and remeasured to reveal growth and regeneration of any appendages, if applicable.

If an appendage is severed or autotomized at the fracture plane, located on the basi-ischium between the merus and coxa (Figure 7), and conditions are favorable for regeneration, a black scab will cover the wound. Within several days following scab formation, a tissue bud encased by a protective, transparent, cuticular sheath will push through the black scab. In ensuing weeks, this limb bud will continue to grow and differentiate into furrows defining the various parts of the claw. Just prior to molting, an extremely rapid increase in size of the regenerating appendage occurs (Hiatt, 1948).

Improper autotomization of claws frequently causes death or severely disrupted growth. Initially, claws were induced to autotomize in the customary manner employed by commercial fishermen (Savage et al., 1975). However, it was realized early that this technique did not insure that the crabs would survive. A subsequent method, whereby a probe was inserted into the fleshy joint of the carpus (wrist) and directed proximally until stimulation of the autotomizer muscle occurred, proved most effective (Figure 8). The major effort associated with the conduct of this study involved the daily routine activities designed to maintain healthy crabs in captivity. Once the technique insuring recovery from induced autotomy was perfected, deaths and other failures occurring during this study resulted from our inability to solve maintenance problems.

RESULTS AND DISCUSSION

MORPHOMETRIC ANALYSES

Because of the general lack of knowledge regarding the life history of stone crabs, basic measurements of most crabs captured were taken to gain knowledge of crab dimensions. Morphometric analyses between carapace width (CW) and length (CL), and major and

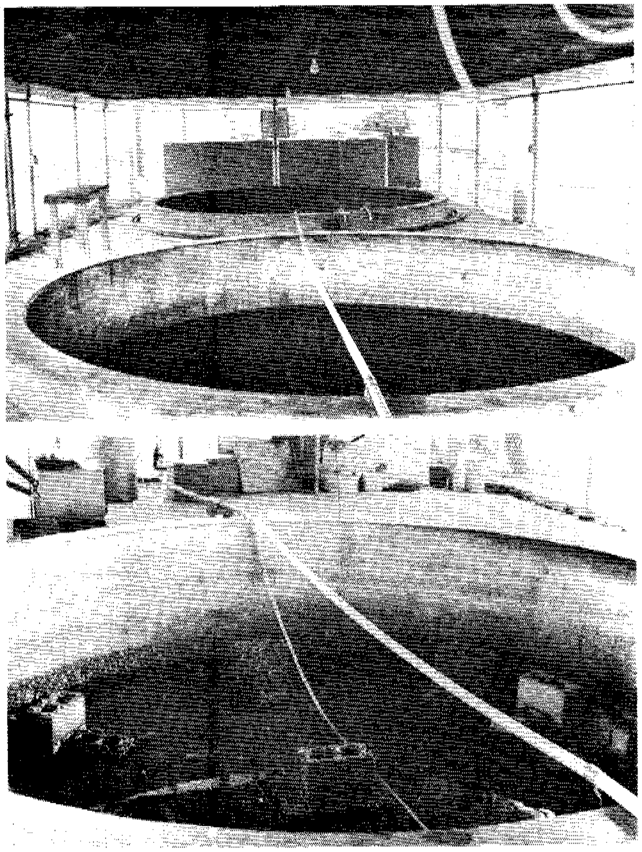

Figure 5. Habitat tanks used for most laboratory investigations; concrete blocks provided shelter.

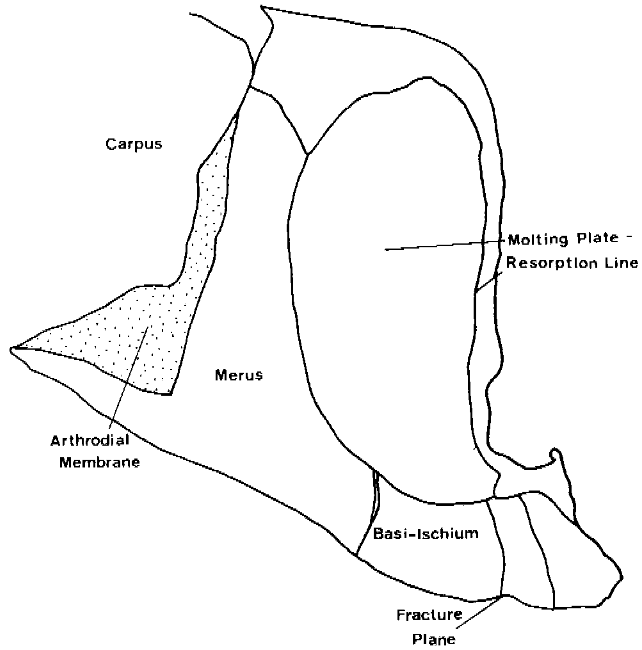

Figure 7. Location of fracture plane in relation to other features on stone crab claws.

minor claw sizes of both sexes were compiled and formulas for these relationships derived (Table 2). Only intact, "normal" crabs, i.e., crabs whose claws possess the normal striae configuration (Savage et al., 1975), were used in these analyses because of the variation in growth inherent in animals regenerating lost appendages.

CARAPACE WIDTH VS. LENGTH RELATIONSHIPS

Carapace width vs. length relationships of 72 female and 47 male crabs are depicted in Figure 9. The two linearly-regressed lines differed significantly (Table 3). Females displayed a larger carapace length than males for respective carapace widths greater than 35 mm. Below this size, however, there appeared to be no difference in the relationship of these two parameters between sexes. This point of divergence coincides with what may be the approximate size at sexual maturation of females. Powell and Gunter (1968) collected one egg-bearing female with CW = 33.8 mm;

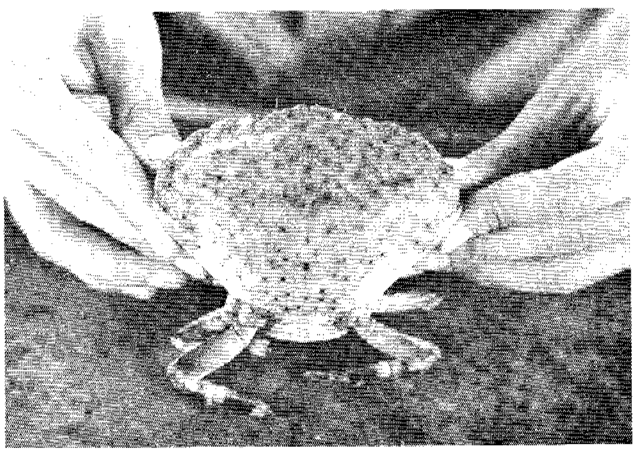

Figure 6. Typical photograph of carapace for identification purposes.

Figure 8. Most successful, least damaging method of inducing claw autotomy.

TABLE 2. MORPHOMETRIC CHARACTERISTICS OF MALE AND FEMALE STONE CRABS.

Sex	Type Regression	Equation	r^2	N
A. Carapace Width (x) *vs.* Carapace Length (y)				
Male	Linear	y = 0.76865 + 0.68730x	.99598	47
Female	Linear	y = 0.17468 + 0.70302x	.97860	72
B. Carapace Width (x) *vs.* Major Claw (y)				
Male	Power curve ($\log_e$)	$y = 0.23836x^{1.30128}$	.98580	62
Female	Power curve ($\log_e$)	$y = 0.34246x^{1.18576}$	.96755	108
C. Carapace Width (x) *vs.* Minor Claw (y)				
Male	Power curve ($\log_e$)	$y = 0.27502x^{1.22803}$	.98774	60
Female	Power curve ($\log_e$)	$y = 0.43440x^{1.09438}$	.96188	108

our Laboratory's Hourglass collections contained an ovigerous female with CW = 36.9 mm.

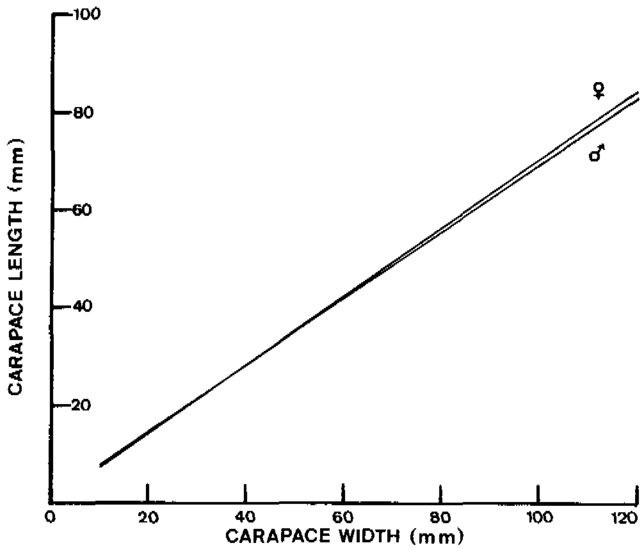

Figure 9. Carapace width vs. length relationship of 47 normal male and 72 normal female stone crabs.

CARAPACE WIDTH VS. CLAW SIZE RELATIONSHIPS

The stone crab fishery is unique in that only the claws are marketed; crabs are released after claw harvest. Consequently, fishery regulations deal only with sizes of claws and not with crab body sizes. Since carapace width is the standard measurement used to denote size class frequencies, onset of sexual maturity, and other size-related biological parameters of brachyuran crabs, it is advantageous to know the relationships between stone crab carapace widths and claw sizes.

Only normal crabs were used in these $\log_e$ transformed regression analyses for reasons stated in the previous section. Major claws attained commercially legal size (≥ 70 mm) at a smaller CW than did minor claws (Figure 10). Major claws of males achieved legal size at a smaller CW (79.5 mm) than did those of females (89.0 mm). Minor claws reached legal proportions in males at 91.5 mm CW and in females at 103.2 mm CW. When slopes of these lines were tested at the 95% confidence level, there was no significant difference noted between slopes of lines denoting female major and male minor claws. However, testing relationships between other slopes revealed significant differences summarized in Table 3. Relationships of major and minor claws of both sexes are virtually equivalent below approximately 35 mm CW (Figure 10), but diverge greatly above this size, further suggesting female sexual maturity at about 35 mm CW, and also indicating male maturity at approximately the same size.

GROWTH

NATURAL CARAPACE WIDTH AND CLAW GROWTH

These data were recorded from field observations of the Pinellas Point intertidal population and serve as a basis for comparison with results of laboratory investigations. Results of the examination of normal

TABLE 3. SIGNIFICANCE TESTS OF SLOPES.

A. Carapace Width *vs.* Carapace Length
$t = 3.50^*$, d.f. = 115

B. Carapace Width *vs.* Claw Size

	Female Minor	Female Major	Male Minor
Male Major	$t = 7.18^*$, d.f. = 166	$t = 4.01^*$, d.f. = 166	$t = 2.69^*$, d.f. = 118
Male Minor	$t = 5.55^*$, d.f. = 164	$t = 1.52$ns, d.f. = 164	
Female Major	$t = 2.68^*$, d.f. = 212		

*95% confidence level.

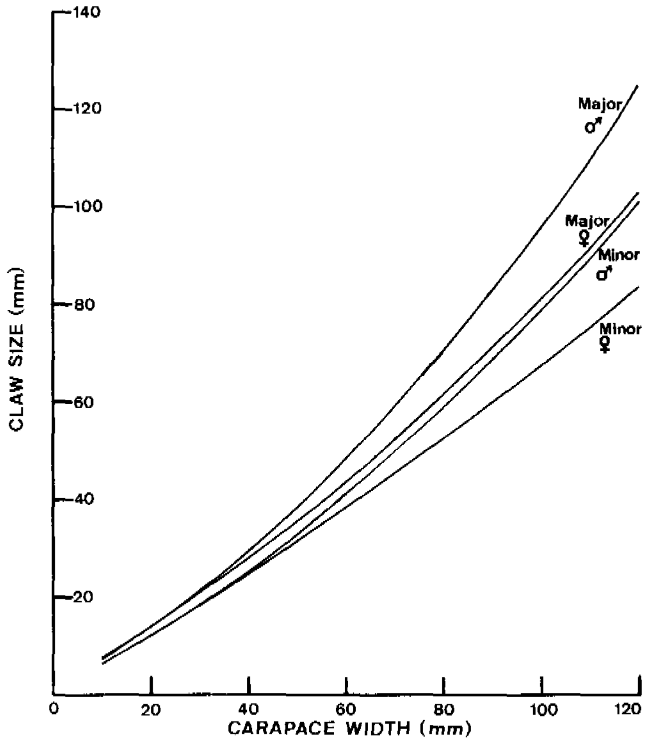

Figure 10. Curvilinear representation of carapace width vs. claw size relationships:
CW/major claw size, 62 normal males, 105 normal females;
CW/minor claw size, 60 normal males, 108 normal females.

carapace width growth in the field is presented in Table 4. Males in the 51-60 mm CW size category increased their CW sizes by the greatest average increment (13.6 mm) of all crabs examined. Of 40 total crabs in all size categories, 18 males increased their CW sizes by a greater average increment (12.1 mm) than did 22 females (10.5 mm). Overall average growth increment, regardless of size, was 11.1 mm; overall percent growth decreased at each molt with increasing size above the 21-30 mm CW size group.

Males also displayed greater average claw growth increments for both major (11.5 mm) and minor (10.3 mm) chelae than did females (8.2 mm and 7.2 mm, respectively) (Table 5). Percent growth for both major and minor claws generally decreased with increasing size. Overall average percent growth was virtually identical for both major (23.3%) and minor (23.2%) claws.

Carapace width incremental growth was also recorded for 14 females possessing at least one regenerated claw (Table 6). Ten crabs possessed one normal and one regenerated claw; their average CW growth increment was 9.7 mm. The four remaining crabs possessed two regenerated claws; their CW sizes increased an average of 7.5 mm per molt. Percent growth generally decreased with increasing size. These 14 crabs displayed smaller incremental CW growth than did normal females. Incremental growth data on regenerated claws was too sketchy and incomplete to be analyzed.

LABORATORY CARAPACE WIDTH AND CLAW GROWTH

This study phase involved monitoring of large control and experimental crabs retained in the circular, habitat tanks. Control crabs were not subjected to induced claw autotomy, while experimental crabs were. Numbers and sizes of crabs examined do not necessarily reflect tendencies for survival in captivity nor indicate normal population ratios, but simply convenience of size and abundance at collection.

Forty-nine normal control crabs, of which 41 were females, provided carapace width growth data (Table 7). Because of the disproportionate number of males, only two size classes were represented for male CW growth, making comparison between field and laboratory growth of males tentative at best. Hence, comparative emphasis will be directed toward female growth. Females displayed a less variable growth pattern than did their field counterparts, ranging from 8.0 mm per molt in the 51-60 mm CW size class to 10.0 mm per molt in the 71-80 mm category. This uniformity of growth probably reflects the more controlled environment of the laboratory as compared to natural environmental conditions. Females possessed a larger average growth increment (9.6 mm) than did males (8.9 mm), contrary to field results wherein males achieved

TABLE 4. CARAPACE WIDTH GROWTH FROM FIELD MOLTS OF NORMAL CRABS.

	Pre-exuvial CW Size (mm)						
	21-30	31-40	41-50	51-60	61-70	71-80	Avg.
Males							
Average growth increment (mm)	8.0	12.0	10.6	13.6	13.0	12.0	12.1
Individuals examined	1	1	5	6	4	1	
Females							
Average growth increment (mm)	6.0	—	12.9	10.8	10.7	9.9	10.5
Individuals examined	1		2	6	6	7	
Average percent growth, sexes combined	26.4%	30.8%	24.6%	21.7%	18.1%	13.3%	20.1%

TABLE 5. CLAW GROWTH FROM FIELD MOLTS OF NORMAL CRABS.

	Pre-exuvial Claw Size (mmm)					
	21-30	31-40	41-50	51-60	61-70	Avg.
Male Major Claw						
Average growth increment (mm)	6.3	11.1	18.6	—	—	11.5
Individuals examined	1	4	1			
Female Major Claw						
Average growth increment (mm)	13.0	—	10.0	5.8	9.5	8.2
Individuals examined	1		2	4	1	
Average percent growth, sexes combined	33.7%	30.7%	26.5%	10.3%	15.1%	23.3%
Male Minor Claw						
Average growth increment (mm)	7.0	12.5	—	—	—	10.3
Individuals examined	2	3				
Female Minor Claw						
Average growth increment (mm)	9.6	7.6	6.9	6.3	—	7.2
Individuals examined	1	1	3	2		
Average percent growth, sexes combined	28.2%	31.0%	15.5%	11.8%	—	23.2%

greater carapace width growth than did females. However, percent growth generally decreased with increasing size for all crabs under both field and laboratory conditions.

Although males possessed smaller incremental CW growth, they possessed greater average growth in both major (10.7 mm) and minor (9.7 mm) claws than did females (8.6 mm and 8.2 mm, respectively) (Table 8). Average growth increment for the 49 crabs examined was 9.0 mm per molt for major claws and 8.4 mm per molt for minor claws. Average percent growth generally decreased with increasing size for both claw types. Overall percent growth was nearly equal for both major and minor claws (17.2% and 17.5%, respectively).

In addition to these normal control crabs, 29 crabs with at least one regenerated claw were monitored. Twenty-four of these possessed one regenerated claw and one normal claw (Table 9). Carapace width growth within the four size classes was fairly uniform, ranging from 9.5 mm per molt in the 61-70 mm CW category to 11.0 mm per molt in the 81-90 mm class, averaging 9.9 mm per molt. The five remaining crabs, each possessing two regenerated claws, grew by an average CW increment of 8.0 mm. Average growth for all 29 crabs was 9.6 mm per molt, nearly identical to the average increment for 49 normal crabs (9.5 mm). Average percent growth decreased with increasing size.

TABLE 6. CARAPACE WIDTH GROWTH FROM FIELD MOLTS OF FEMALE CRABS POSSESSING REGENERATED CLAWS.

	Pre-exuvial CW Size (mm)			
	39-50	51-60	61-71	Avg.
One Regenerated Claw				
Average growth increment (mm)	11.7	9.3	7.3	9.7
Individuals examined	4	3	3	
Two Regenerated Claws				
Average growth increment (mm)	—	6.0	9.0	7.5
Individuals examined		2	2	
Average percent growth, sexes combined	27.2%	14.9%	11.7%	17.3%

Data on incremental increases of regenerated claws from laboratory control animals (Table 10) is more complete than is that from field molt retrieval because of field methodology. Laboratory crabs possessing one normal and one regenerated claw were analyzed with regard to major and minor claw regeneration. Average growth of regenerated major claws was 11.7 mm per molt. Three males of varying sizes averaged 14.0 mm per molt while eight females averaged 10.9 mm per molt. Growth of minor regenerated claws averaged 8.9 mm per molt. Five males averaged 11.0 mm per molt for various sizes while nine females averaged 7.8 mm per molt. No growth data were available for crabs possessing two regenerated claws.

Twenty-eight experimental crabs whose claws were caused to be autotomized for claw regeneration analyses molted. Nine of these were single claw autotomies while 19 were double claw autotomies (Table 11). Crabs that were singly autotomized grew an average of 7.7 mm CW per molt, almost two millimeters less per molt than did normal, non-autotomized laboratory crabs. Doubly autotomized crabs grew even less (6.5 mm per molt), three millimeters less than did laboratory controls. Average CW growth increment for these 28 crabs was 6.9 mm per molt. Percent growth per molt again decreased with increasing size.

TABLE 7. CARAPACE WIDTH GROWTH FROM LABORATORY MOLTS OF NORMAL CRABS.

	Pre-exuvial CW Size (mm)						
	41-50	51-60	61-70	71-80	81-90	91-100	Avg.
Males							
Average growth increment (mm)	12.0	—	—	8.4	—	—	8.9
Individuals examined	1			7			
Females							
Average growth increment (mm)	—	8.0	9.5	10.0	8.7	9.5	9.6
Individuals examined		1	6	23	9	2	
Average percent growth, sexes combined	27.3%	13.0%	14.4%	12.6%	10.2%	10.2%	12.6%

FIELD-LABORATORY COMPARATIVE GROWTH

Incremental CW growth for all types of claw condition is summarized in Table 12. Normal field crabs had the highest growth rates (11.1 mm per molt) while normal laboratory control crabs averaged considerably less (9.5 mm). Captivity apparently has a depressing effect upon carapace width growth of normal crabs, especially in larger crabs, even though food was readily available. Males were especially affected, attaining greater growth increments than females in the field but smaller increments in the laboratory. It is possible that laboratory feeding regimes satisfactorily provided basic requirements for smaller crabs but were less adequate for larger specimens.

Normal crabs possessed the greatest incremental CW growth while doubly autotomized crabs displayed the least. Apparently, normal CW growth is sacrificed when claws must be regenerated (Hughes and Mathiessen, 1962). Some of the energy usually spent on normal growth must be diverted into the regenerative process of claw recovery. Another more important factor in the growth tendency imposed by claw loss may be the altered diet feral crabs must assume after such loss. Without claws, crabs can not crush their usual staples of oyster, scallop, clam and conch, and may not receive enough of their basic dietary requirements to accomplish normal growth. Loss of other appendages probably causes additional deviation from normal growth. This is supported by the fact that crabs with previously regenerated claws provided intermediate growth rates between normal and autotomized crabs.

Normal field claw growth closely paralleled normal laboratory growth for both major and minor claws (Table 13). As previously noted (Tables 5, 8) field and laboratory normal males increased their claw sizes by greater average increments than did normal females. Average laboratory major and minor claw increment increases were nearly equivalent (9.0 mm and 8.3 mm, respectively); field growth increments were similar for minor claws, but were greater for major claws (Table 13). Curiously, average growth increments of regenerated claws from laboratory

TABLE 8. CLAW GROWTH FROM LABORATORY MOLTS OF NORMAL CRABS.

	Pre-exuvial Claw Size (mm)					
	31-40	41-50	51-60	61-70	71-80	Avg.
Male Major Claw						
Average growth increment (mm)	10.0	—	10.5	11.0	—	10.7
Individuals examined	2		2	5		
Female Major Claw						
Average growth increment (mm)	—	7.8	8.5	9.1	8.0	8.6
Individuals examined		4	19	14	3	
Average percent growth, sexes combined	27.5%	16.7%	15.3%	15.3%	11.0%	17.2%
Male Minor Claw						
Average growth increment (mm)	8.5	11.0	9.8	—	—	9.7
Individuals examined	2	1	6			
Female Minor Claw						
Average growth increment (mm)	7.0	7.4	9.4	6.0	—	8.2
Individuals examined	2	21	16	1		
Average percent growth, sexes combined	25.4%	16.1%	17.9%	9.5%	—	17.5%

TABLE 9. CARAPACE WIDTH GROWTH FROM LABORATORY MOLTS OF CRABS POSSESSING REGENERATED CLAWS.

	Pre-exuvial CW Size (mm)				
	51-60	61-70	71-80	81-90	Avg.
One Regenerated Claw					
Average growth increment (mm)	10.5	9.5	9.6	11.0	9.9
Individuals examined	2	4	13	5	
Two Regenerated Claws					
Average growth increment (mm)	—	—	9.5	7.0	8.0
Individuals examined			2	3	
Average percent growth, sexes combined	18.8%	13.6%	12.7%	11.2%	12.8%

controls were considerably greater than increments for normal major claws and slightly higher than for normal minor claws.

TECO investigators studying stone crab CW growth in elevated water temperatures obtained results (Table 14) similar to our results obtained in ambient temperatures (Table 7). In both studies, average percent growth decreased with increasing size. Unfortunately, TECO investigators did not examine claw stridulatory patterns, and consequently some of their specimens may have been undergoing claw regeneration with resultant alteration on normal CW growth. Still, it is safe to conclude that the thermal effluent did not change the relationship of increasing age and decreasing size increment at ecdysis. Additionally, thermal effluent did not appear to influence the size of the growth increment as might be expected of the higher metabolic rate inferred from higher temperatures.

AGE PREDICTION

Because of the commercial importance of stone crabs, it would be useful to know the periods of time necessary to attain various stages in the crab's life history. A hypothetical growth plot constructed from incremental growth data of four normal male stone crabs maintained in the laboratory is presented in

TABLE 10. CLAW GROWTH FROM LABORATORY MOLTS OF CRABS POSSESSING REGENERATED CLAWS.

	Pre-exuvial Claw Size (mm)			
	31-40	41-50	51-60	Avg.
Male Major Claw				
Average growth increment (mm)	—	14.0	14.0	14.0
Individuals examined		1	2	
Female Major Claw				
Average growth increment (mm)	14.0	11.0	9.0	10.9
Individuals examined	1	5	2	
Average percent growth, sexes combined	46.7%	27.2%	19.8%	27.0%
Male Minor Claw				
Average growth increment (mm)	14.0	9.0	10.7	11.0
Individuals examined	1	1	3	
Female Minor Claw				
Average growth increment (mm)	—	7.8	7.7	7.8
Individuals examined		6	3	
Average percent growth, sexes combined	40.0%	18.1%	17.1%	19.2%

Figure 11. Three millimeters was chosen as the initial CW size for the growth plot because it is the smallest crab that provided good growth data (Savage, 1971b). Size at first crab stage may be at least 1.6 mm smaller than our starting size because Savage and McMahan (1968) reported a 1.4 mm female juvenile. However, this and other similar small crabs experienced poor growth and will not be used in this estimation. Time involved in growing from 1.4 mm to 3.0 mm can not be of such magnitude as to invalidate our estimation scheme based on a starting size of 3.0 mm.

The first two crabs used in the estimate, providing information on growth up to CW = 43.0 mm, were reported in Savage's (1971b) maintenance parameters study. The remaining two crabs were taken from the present study. These four crabs, displayed in order of increasing size, depict the approximate number of molts and estimated time required to reach given sizes. These crabs had similar molting time so occurrences of ecdyses could be synchronized within two months to account for seasonal growth differences.

TABLE 11. CARAPACE WIDTH GROWTH FROM LABORATORY MOLTS OF AUTOTOMIZED CRABS.

	Pre-exuvial CW Size (mm)						
	51-60	61-70	71-80	81-90	91-100	101-110	Avg.
Single Autotomy							
Average growth increment (mm)	—	—	8.0	7.5	7.0	—	7.7
Individuals examined			4	4	1		
Double Autotomy							
Average growth increment (mm)	5.0	8.2	6.0	6.6	5.8	6.5	6.5
Individuals examined	2	2	2	6	1	6	
Average percent growth, sexes combined	10.4%	12.5%	10.1%	8.1%	6.6%	6.2%	8.3%

TABLE 12. COMPARISON OF AVERAGE CARAPACE WIDTH GROWTH FROM LABORATORY-MAINTAINED AND FERAL CRABS.

Pre-exuvial CW Size	Growth Increment Per Molt							
	Normal Crabs		Crabs w/regenerated Claws				Autotomized Crabs	
	Field	Laboratory	Field		Laboratory		Laboratory	
			one	two	one	two	one	two
≤ 50 mm	10.5	12.0	11.7	—	—	—	—	—
Individuals examined	10	1	4					
51-80 mm	11.5	9.6	8.3	7.5	9.7	9.5	8.0	7.8
Individuals examined	30	37	6	4	19	2	4	3
≥ 81 mm	—	8.8	—	—	11.0	7.0	7.4	6.6
Individuals examined		11			5	3	5	13
Average growth increment	11.1	9.5	9.7	7.5	9.9	8.0	7.7	6.7
Individuals examined	40	49	10	4	24	5	9	16

Two important aspects revealed are approximate ages when sexual maturity and legal size are reached. Legal size is not achieved in males (≥ 80 mm) until approximately 2½ years have elapsed, whereas sexual maturity is probably attained sometime near the end of the first year. Females have been shown to grow incrementally slower than males, but even with this difference they should mature in about one year. Females metamorphosing in summer (the most prevalent time of larval production) may be sexually mature and producing eggs by the following summer.

TABLE 13. COMPARISON OF AVERAGE CLAW GROWTH PER MOLT FROM LABORATORY MAINTAINED AND FERAL CRABS.

Pre-exuvial Claw Size	Growth Increment Per Molt		
Major Claws	Normal Crabs		Crabs w/regenerated major claws
	Field	Laboratory	Laboratory
≤ 50 mm	11.3	8.5	11.5
Individuals examined	9	6	6
> 50 mm	6.5	9.1	11.5
Individuals examined	5	43	4
Average growth increment	9.6	9.0	11.5
Individuals examined	14	49	10

Minor Claws	Normal Crabs		Crabs w/regenerated minor claws
	Field	Laboratory	Laboratory
≤ 50 mm	8.8	7.5	8.7
Individuals examined	10	26	8
> 50 mm	6.3	9.3	9.2
Individuals examined	2	23	6
Average growth increment	8.4	8.3	8.9
Individuals examined	12	49	14

They also can spawn in the next summer (third year) before entering the fishery (≥ 90 mm CW). State regulations allowing females of a commercially important crustacean species to spawn in at least two seasons before entering the fishery reflects sensible fishery management and a reassuring safeguard against over-exploiting the species.

Several weaknesses are inherent in this type of approximation. The time lag between molting of different crabs, the fact that crabs were used from two separate studies, and natural variability in growth can all cause considerable fluctuation. Assumptions of similar laboratory and field growth also lend themselves to error. Even growth and intermolt duration

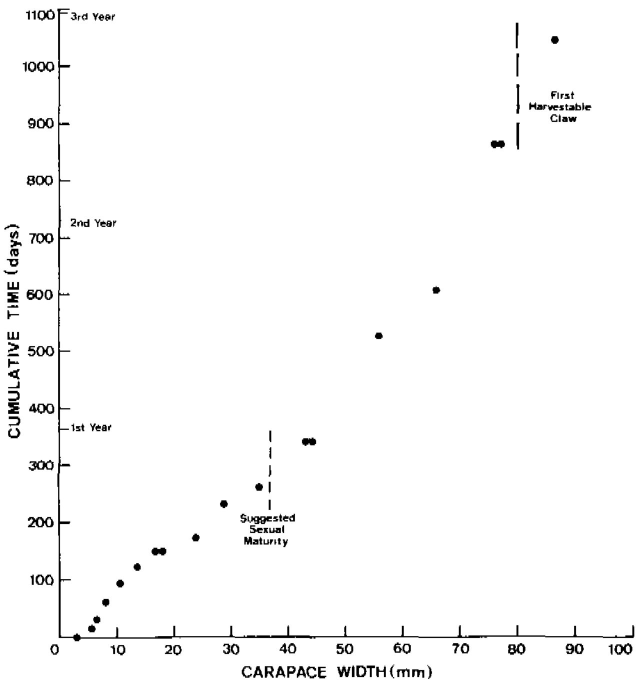

Figure 11. Hypothetical growth plot constructed from incremental growth of four normal male stone crabs.

TABLE 14. CARAPACE WIDTH INCREMENTAL GROWTH FROM TECO MARINE LABORATORY.

	Pre-exuvial CW Size (mm)						
	41-50	51-60	61-70	71-80	81-90	91-100	Avg.
Males							
Average growth increment (mm)	—	—	10.0	10.4	—	—	10.3
Individuals examined			1	2			
Females							
Average growth increment (mm)	—	—	9.5	9.0	8.1	7.2	8.6
Individuals examined			1	6	5	1	
Average percent growth, sexes combined	—	—	14.2%	12.5%	9.0%	7.4%	11.3%

displayed in Figure 11 can be lengthened or shortened by varying laboratory conditions. Yang (1970) produced a legal-size crab (91 mm CW) in seven months (10 molts) from hatching, indicating a promising future for stone crab culture. However, Yang and Krantze (1976) reported disappointing results when this operation was converted to pond culture. Only 1.7% of 2,000 crabs released into the pond were harvested, and these only after arduous work to extract them from their burrows. It appears that stone crabs can be successfully reared at accelerated levels in the laboratory but not yet on a large-scale, commercial basis.

CLAW REGENERATION

Without successful claw regeneration, there is little biological justification for a fishery based on the harvest of claws only. Savage et al. (1975) demonstrated that approximately 10% of stone crab claws landed on Florida's west coast are regenerated claws. These figures represent only legal-sized claws, however, and do not provide a complete picture of claw regeneration in the total population. To understand the regenerative process in stone crabs, it is necessary to know the sequence of events that occurs to a crab following loss of its claws.

When an appendage is lost through either natural or experimentally-imposed means, a process is initiated insuring minimal haemolymph loss and subsequent regeneration of that appendage. Because most crustacean groups maintain the same fundamental pattern of autotomy, Paul's (1915) description of anatomical mechanisms (presented in Hiatt, 1948) making autotomy and regeneration possible in hermit crabs is also applicable to stone crabs. "At the fracture plane the sclerotized strata of the integument are continuous for a part of the circumference of the appendage. The columnar epithelical cells are greatly enlarged at this point and possess processes which extend inward, meeting those of the opposite side. These fibers mat together to form the diaphragm. The appendicular artery passes through a foramen, which it completely fills; but the foramen for the nerve is a funnel-like prolongation of the diaphragm which fits loosely about the nerve, thereby affording the venous blood a return passageway." Hiatt continues: "Paul has demonstrated that upon severance of the appendage both the artery and nerve retract from the diaphragm, and blood extravasates from the ruptured distal end of the artery. The increased pressure in the haemocoelic space forces together the funnel-like flaps which completely occlude the foramina. Actually, some blood does pass to the outside of the diaphragm at autotomy because a layer of clotted blood covers the developing papilla for several days in *Pachygrapsus crassipes*, and has likewise been reported in other species."

Stages of the regenerate(s) following autotomy and leading to regeneration of a new claw, not previously described for *M. mercenaria*, are presented herein. The initial injury (Figure 12a) is hereafter referred to as the wound and, for our purposes, is considered to terminate at onset of the first regenerative claw stage. The previously mentioned layer of blood corresponds to the scab condition (Figure 12b), here considered the first regenerating claw stage. The developing papilla (Figure 13), which will grow and gradually differentiate into a new claw, is referred to as the limb bud after it fractures the scab. A cuticular sheath encases this limb bud throughout its papillary development (Figure 14). As podomeric differentiation of the limb bud continues, a miniature replica of the crab's massive claw is formed (Figure 15). Just prior to molting, the claw regenerate undergoes rapid inflation, such that the pliable, protective sheath is stretched and bulged outward (Figure 16). A final, additional inflation of the claw occurs as the crab discards its old exuvia. Figure 17 illustrates a crab regenerating a single claw. The claw emerging through the exuvia several minutes later is considerably larger than the inflated claw seen previously; a final filling-out is accomplished until the paper shell condition is achieved.

GROWTH OF THE CLAW REGENERATE

Although decapod crustaceans possess the ability to regenerate lost appendages, they can not immediately regenerate these appendages to normal

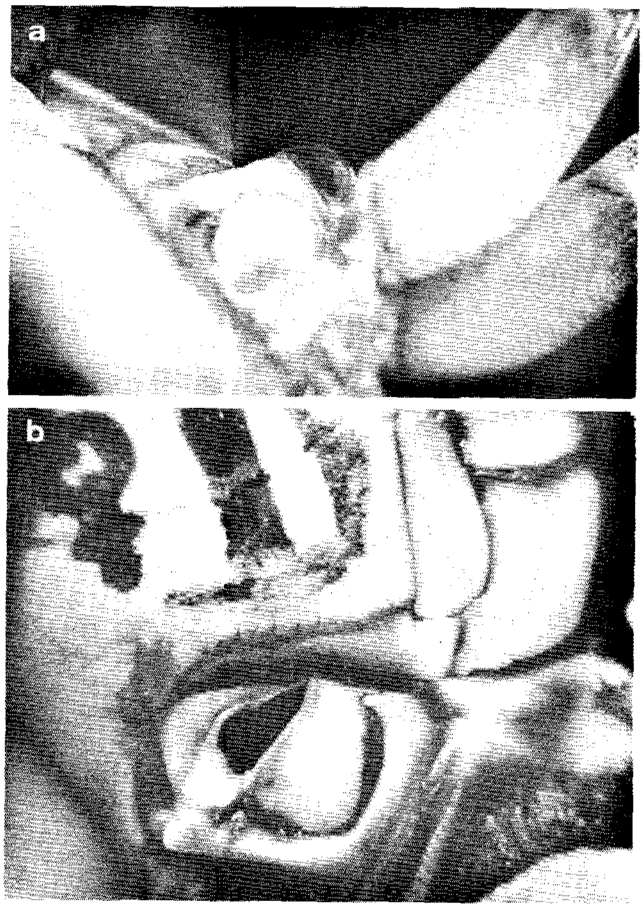

Figure 12. Wound condition (a) which appears immediately after claw loss; scab condition (b), showing blackened layer of clotted blood completely covering claw stump.

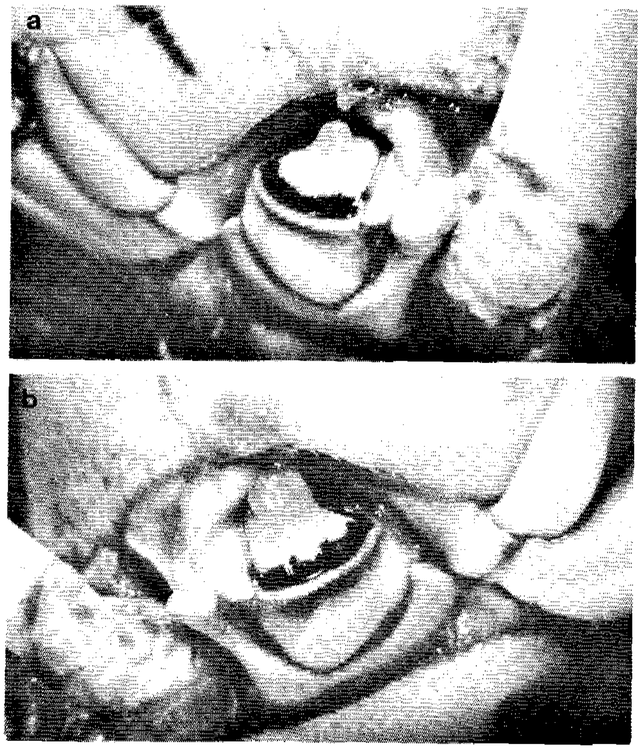

Figure 13. Limb bud condition (a), resulting after developing papilla fractures scab; more advanced bud condition (b).

sizes. Regenerating appendages of a spiny lobster, *Panulirus interruptus*, attain two-thirds of their original size after the first regenerative molt (MacGinitie and MacGinitie, 1949). Emmel (1907) reported greater recuperative powers in *Homarus americanus*. Juvenile walking leg replacements represented approximately 85% of the normal size after the regenerative molt; adults averaged somewhat less (76%). Bennett (1973) reported that the claw regenerate of the brachyuran, *Cancer pagurus*, is functional and approximately one-half the size of a similar unregenerated claw. Skinner and Graham (1972) found that walking leg regenerates of *Gecarcinus lateralis* are approximately two-thirds the size of their corresponding limb on the opposite side of the animal. When excessive appendage loss (> 6 legs) is experienced, the regenerate limb is only half as large as a normal leg. Hiatt (1948) described a high regenerative capability in *Pachygrapsus crassipes*, wherein the leg regenerate size was approximately three-quarters of the size of a normal leg. Generally, two or three molts are required before the regenerate appendage recovers to the same size as its opposite counterpart.

In our studies, claw regenerates of minor chelae realized greater recovery (73.5% of pre-autotomized sizes) after the initial regenerative molt than did regenerates of major claws (68.6%) (Table 15). Legal-sized chelae (≥ 70 mm) within these two claw categories displayed lower recovery percentages than did sub-legal chelae.

Twenty percent of the experimental crabs molted twice after autotomization. Three of these were used for the following analyses (Table 16). Regenerates of autotomized minor chelae possessed a greater percent-

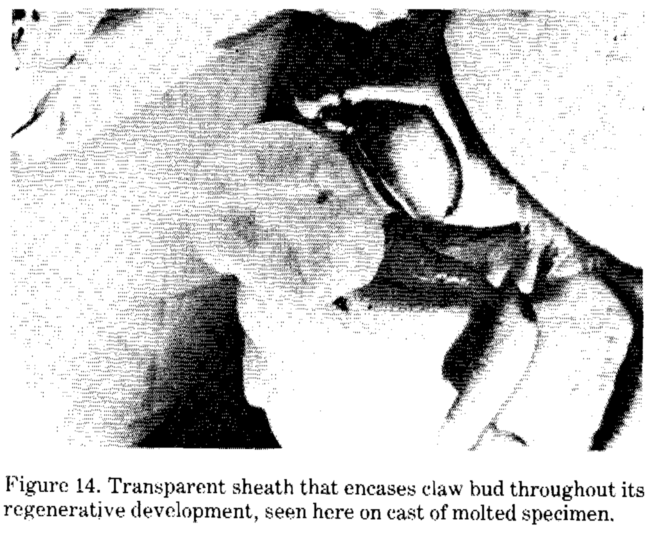

Figure 14. Transparent sheath that encases claw bud throughout its regenerative development, seen here on cast of molted specimen.

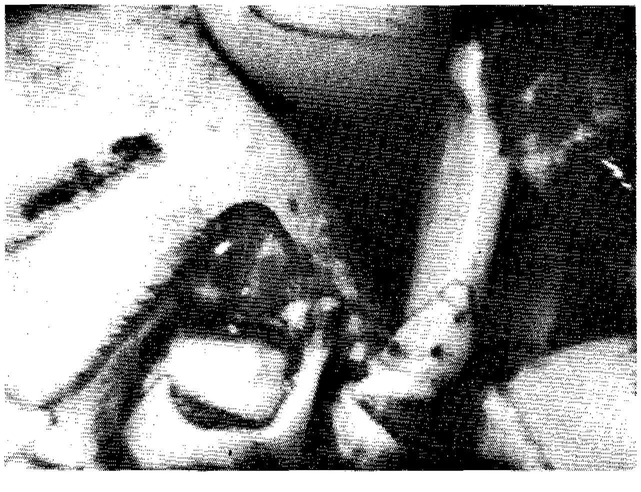

Figure 15. Miniature replica of what is to become a massive claw; merus, carpus and propodus all visible at this stage.

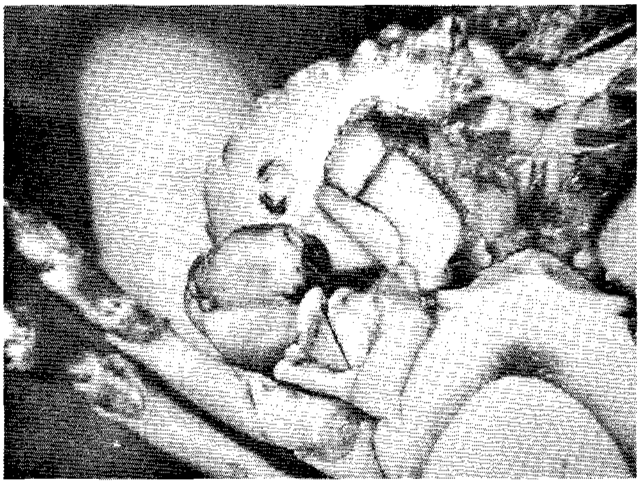

Figure 16. Inflated condition just prior to molting; developing claw is two to four times larger than claw bud shown in Figure 13.

age of recovery to pre-autotomized sizes after two regenerative molts (96.5%) than did major claw regenerates (89.0%). Two of these crabs, BM 25 and CR 10, had 100% recovery of regenerating minor claws to pre-autotomized sizes after two regenerative molts. The major claw of BM 25 was 87% of pre-autotomized dimensions after the second regenerative molt and likely would have had 100% recovery after its next molt. Crab CR 10 regenerated its major claw to 88% of original size after the first regenerative molt but subsequently lost that claw to injury while still soft following the second regenerative molt. It could not be accurately measured due to damage but appeared to be 100% of its pre-autotomized size.

A percentage estimate of regenerated claw size to normal claw dimensions can be approximated based on previous morphometric analyses. Knowing the original claw type, present regenerate claw size, and carapace width of the crab possessing this claw, and comparing these with the size that this type claw would normally be for a crab with corresponding carapace width, will allow determination of percent size recovery. For example, claws of crab BM 25 under normal conditions would have measured approximately 61 mm and 52 mm for major and minor claws, respectively, at 76.6 mm CW (size after first regenerative molt) (Table 16). The major and minor regenerated claws measured 35.3 mm and 39.9 mm, representing 58% and 75% recovery to normal claw dimensions after the first regenerative molt. The second regenerative molt produced a major claw measuring 48.9 mm, a minor claw of 49.9 mm, and a CW of 84.6 mm. Expected claw size of a crab with such CW would be 68 mm for a major claw and 59 mm for a minor claw. Thus, major claw recovery is 72%, and minor claw regenerate recovery is 85%. Results of computations performed in the same manner on other autotomized crabs successfully regenerating one or both claws are contained in Table 17.

Data reported in a summarized general history of an "aged" male stone crab (Cheung, 1973) is similar to that presented in Table 16. Both regenerated claws were restored to pre-autotomized sizes after two molts. Major and minor claws recovered 74% and 83% after the first molt. The crab, autotomized in October, 1965, required 294 days for complete restoration of claws. Claws of our crab BM 25 were removed in January, 1970 and required 328 days for full minor claw recovery and 87% major claw restoration. Crab CR 10 was autotomized in April, 1972 and required only 237 days to completely regenerate its minor claw. Other crabs autotomized in spring and summer months attained the first regenerative molt significantly sooner than specimens autotomized in colder months (Table 18). Eleven captives autotomized during winter months required an average of 158 days to regenerate their claws, while 11 other crabs autotomized during spring and summer months needed only an average of 72 days to reach the first molt following autotomy.

Claw regeneration after autotomy was also investigated by the TECO marine laboratory (Anonymous, 1972). One crab (60.4 mm CW at autotomy) molted twice after double autotomy, regenerating both major and minor claws to pre-autotomized dimensions in 82 days, 246 days less than our crab BM 25 utilized to completely regenerate its minor claw and 87% of its major claw, and 155 days less than crab CR 10 utilized to regenerate 100% of its minor claw. Because of their similar sizes, each crab's respective intermolt period should not have played a part in these considerable discrepancies. Elevated temperatures utilized by TECO may have significantly reduced the time required for regeneration of autotomized claws by reducing the intermolt period. Several FDNR crabs also kept in tanks with elevated temperatures had shorter intermolt periods than did crabs of similar sizes retained in ambient temperatures. Higher tempera-

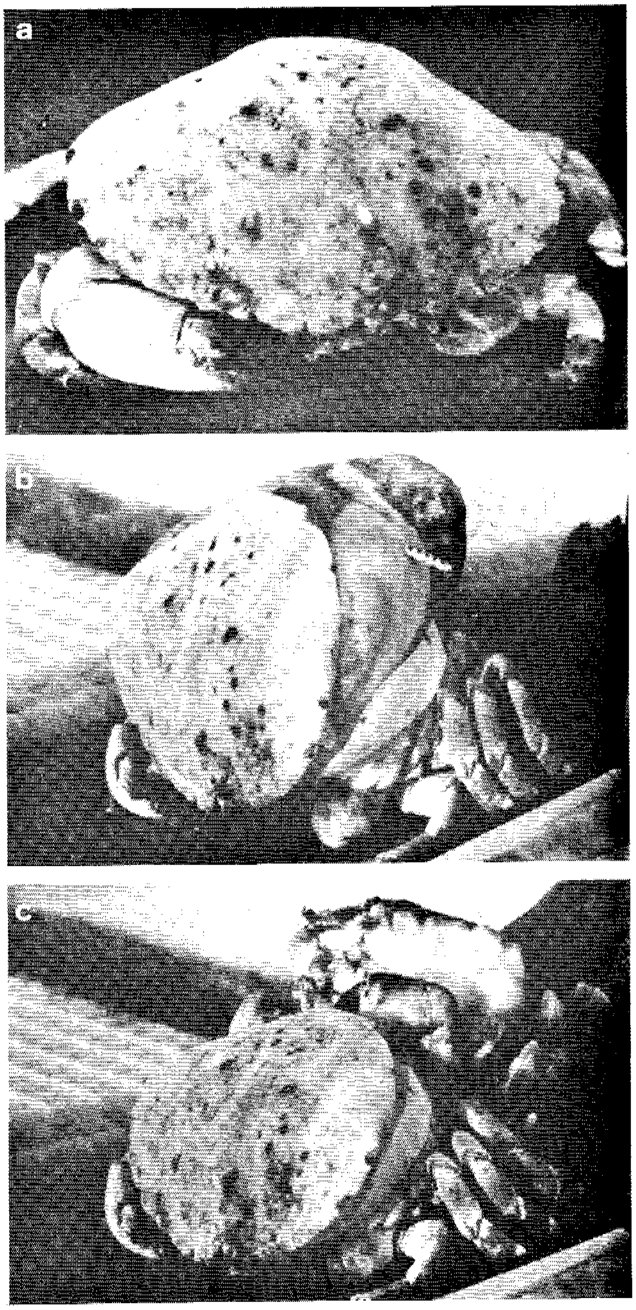

Figure 17. Initial stages of ecdysis in specimen regenerating left claw: a. immediately before ecdysis; b. same during early ecdysis; c. seconds after completing ecdysis,

tures in both cases simulated summer conditions, when most molting occurs.

EFFECTS OF CLAW REGENERATION ON GROWTH

Although cold water molt inhibition has been well documented in brachyurans by Passano (1960), Savage (1971a), and others, reports of inhibition of growth

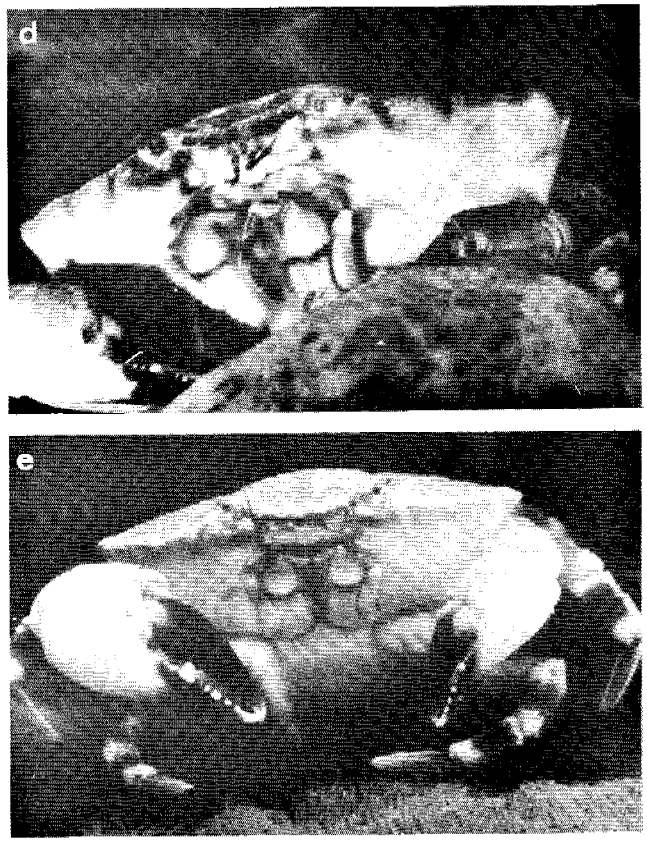

Figure 17 (continued). d. frontal view of same animal (note disparity in size of unregenerated right pincer claw and newly regenerated left claw); e. sixteen hours after ecdysis, in papershell condition.

associated with regeneration are rare. Claw regeneration is a particularly important process for stone crabs because each claw contributes to the general welfare of the crab. The major chela crushes conchs, oysters, and

TABLE 15. CLAW RECOVERY EXPRESSED AS PERCENT OF PRE-AUTOTOMIZED CLAW SIZE FOLLOWING FIRST REGENERATIVE ECDYSIS.

Pre-autotomized Claw Size (mm)	Individuals Examined	Average Percent Recovery
Major Chelae		
40-49	2	77.5%
50-59	3	77.7%
60-69	5	66.0%
70-80	3	68.0%
81-90	5	62.6%
< 70	10	71.8%
≥ 70	8	64.7%
Minor Chelae		
30-39	2	79.5%
40-49	3	80.0%
50-59	3	71.8%
60-69	4	70.2%
70-80	3	69.0%
< 70	12	74.5%
≥ 70	3	69.0%

TABLE 16. EXPERIMENTAL REGENERATIVE SEQUENCE FOR THREE AUTOTOMIZED CRABS.

	CW	Major Claw	(Expected Size)	Minor Claw	(Expected Size)
BM 25—Female					
Original Dimensions Claws autotomized 1/11/70	69.2 mm	56.4 mm	—	49.0 mm	—
1st Regenerative Ecdysis (6/15/70)	76.6 mm	35.3 mm		38.9 mm	
1. Recovery to Pre-autotomized sizes		62.6%		79.4%	
2. Recovery to Expected normal sizes		57.9%	(61.0 mm)	74.8%	(52.0 mm)
2nd Regenerative Ecdysis (12/5/70)	84.6 mm	48.9 mm		49.9 mm	
1. Recovery to Pre-autotomized sizes		86.7%		101.8%	
2. Recovery to Expected normal sizes		71.9%	(68.0 mm)	84.6%	(59.0 mm)
CR 09—Male					
Original Dimensions Claws autotomized 4/10/72	81.0 mm	70.0 mm	—	60.0 mm	—
1st Regenerative Ecdysis (6/20/72)	89.0 mm	51.0 mm		46.0 mm	
1. Recovery to Pre-autotomized sizes		72.9%		76.7%	
2. Recovery to Expected normal sizes		63.8%	(80.0 mm)	67.6%	(68.0 mm)
2nd Regenerative Ecdysis (01/9/73)	99.0 mm	64.0 mm		58.0 mm	
1. Recovery to Pre-autotomized sizes		91.4%		96.7%	
2. Recovery to Expected normal sizes		66.7%	(96.0 mm)	72.5%	(80.0 mm)
CR 10—Male					
Original Dimensions Claws autotomized 4/10/72	63.0 mm	49.0 mm	—	42.0 mm	—
1st Regenerative Ecdysis (6/16/72)	72.0 mm	43.0 mm		34.0 mm	
1. Recovery to Pre-autotomized sizes		87.8%		81.0%	
2. Recovery to Expected normal sizes		69.4%	(62.0 mm)	66.7%	(51.0 mm)
2nd Regenerative Ecdysis (12/3/72)	83.0 mm	*		45.0 mm	
1. Recovery to Pre-autotomized sizes				107.1%	
2. Recovery to Expected normal sizes				73.8%	(61.0 mm)

*Claw lost after ecdysis completed and before measurement could be made.

other bivalves, and the minor claw assists in tearing the food into edible proportions; both claws render defense. Expeditious regeneration of claws is survival-oriented; without chelae, the crab must alter its diet to consume soft invertebrates, animal detritus, algae, and grasses (Bender, 1971).

Early regenerative claws resemble minor claws (Savage et al., 1974), regardless of previous claw type. Consequently, neither claw can function as a crusher tool, but both can probably assist in defense and in tearing food. Additionally, clawless laboratory crabs were routinely observed eating oysters growing on holding tank walls by prying them open with their powerful, pointed walking legs. If other bivalves can be opened in a similar manner, loss of a major claw could be compensated for until regeneration is accomplished.

If the crusher claw is essential for survival, it would be expected that stone crabs would have evolved the mechanism of immediate claw-type reversal exhibited by the pistol shrimp genus *Alpheus* (Przibram, 1901; Wilson, 1903) and the brachyuran crab *Calappa* (Lewis, 1969). Kiortsis-Trampusch (1965)

TABLE 17. RECOVERY OF AUTOTOMIZED CLAWS TO NORMAL SIZE DIMENSIONS.

	Major Claws	Minor Claws
1st Regenerative Ecdysis		
Average Percent Recovery	60.8%	67.0%
Specimens Investigated	16	12
Percentage Range	51.4%– 70.0%	60.7%– 75.0%
Carapace Width Range	63.0 mm– 106.7 mm	63.0 mm– 106.7 mm
2nd Regenerative Ecdysis		
Average Percent Recovery	69.5%	76.3%
Specimens Investigated	2	4
Percentage Range	67.0%– 72.0%	73.0%– 85.0%
Carapace Width Range	72.0 mm– 89.0 mm	72.0 mm– 93.0 mm

reported that "the pincer chela is phylogenetically more primitive than the partner crusher, so that the latter is liable to regenerate through a pincer stage in any case. Equally, perhaps, a normal pincer is liable to go on to the crusher grade if conditions ever become propitious." Laboratory stone crabs have not demonstrated the ability to achieve immediate claw-type reversal. Although a separate study was not designed to investigate this, enough control crabs missing a crusher claw were received from the field to facilitate a cursory investigation. None of these crabs exhibited immediate claw-type reversal upon molting. Figure 17 demonstrates typical regeneration of a left major claw. Although laboratory efforts have been unable to maintain crabs long enough to observe thoroughly such a phenomenon, it is possible that claw-type reversal is achieved after several molts. Cheung (1976) demonstrated statistically that claw reversal must occur in nature. The claw survey of Savage et al. (1975) indicates that approximately 10% of Florida west coast landings are comprised of claws exhibiting features intermediate between crushers and pincers. Such claws could be either regenerating major claws proceeding through the more primitive minor claw appearance or normal pincer claws undergoing claw-type reversal.

TABLE 18. SEASONAL VARIATION IN INTERMOLT LENGTH OF LABORATORY CRABS SUBJECTED TO INDUCED CLAW AUTOTOMY.

Crab	Sex	Pre-molt CW (mm)	Autotomization Date	1st Molt Date	Elapsed Time (days)	2nd Molt Date	Elapsed Time (days)
Spring Autotomy							
CR 10	Male	63.0	4/10/72	6/16/72	67	12/03/72	170
CR 6	Female	70.0	4/10/72	6/12/72	63		
CR 4	Female	74.0	4/10/72	6/06/72	57		
CR 9	Male	81.0	4/10/72	6/20/72	71	1/09/73	203
CR 1	Female	81.0	4/10/72	6/27/72	78		
CR 11	Male	87.0	4/10/72	6/30/72	81		
CR 5	Female	91.0	4/10/72	7/04/72	85		
Average time to first molt following spring autotomy: 72 days							
Summer Autotomy							
MP 6	Male	64.0	8/28/69	10/14/69	47		
PP 6	Female	66.0	7/08/69	8/25/69	48		
PP 1	Male	69.0	7/08/69	9/24/69	78		
SB 5	Female	76.7	6/04/70	9/25/70	113	4/02/71	189
Average time to first molt following summer autotomy: 72 days							
Winter Autotomy							
BM 25	Female	69.2	1/11/70	6/15/70	155	12/05/70	173
BM 41	Female	78.0	1/15/70	5/31/70	140		
BM 26	Female	80.6	1/11/70	7/20/70	189		
BM 28	Female	85.0	12/23/69	5/27/70	136		
BM 46	Female	86.8	1/15/70	7/12/70	177	12/20/70	161
BM 6	Male	91.3	12/17/69	7/01/70	196		
C 13A	Female	101.0	2/17/71	7/31/71	163		
C 11	Female	102.2	2/17/71	7/12/71	145		
C 9A	Female	103.3	2/17/71	7/15/71	148		
C 4B	Female	104.1	2/17/71	8/02/71	166		
C 10A	Female	106.2	2/17/71	6/16/71	118		
Average time to first molt following winter autotomy: 158 days							

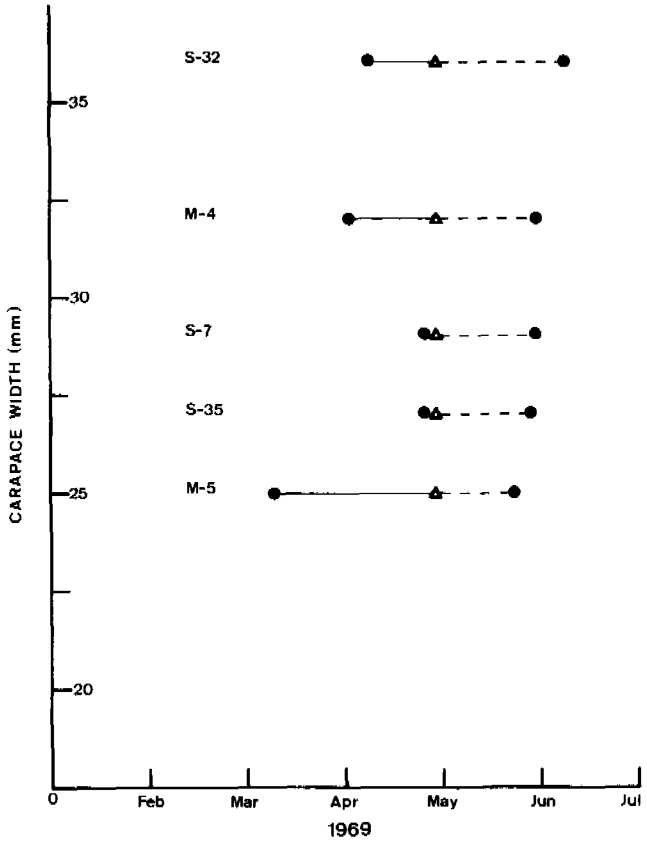

Figure 18. Effect of induced claw autotomy on normal intermolt cycle of five juvenile crabs; ● = ecdysis, Δ = induced autotomy.

EFFECT OF CLAW REGENERATION ON THE INTERMOLT INTERVAL

Eighteen intact crabs provided the data for this analysis (Table 19). Intermolt interval increased with larger pre-ecdysial CW size. Crabs in the smallest size category (60-69 mm CW) required the least time between ecdyses, averaging 107 days, while animals in the largest category (90-99 mm CW) had the longest average intermolt period, 159 days.

Length of the normal intermolt interval is the result of an animal's physiological response to physical environmental conditions. Other influences, such as claw harvest and claw regeneration that insues from such harvest, can be expected to interrupt the normal progress of intermolt duration. Sather (1966) stated that "...regeneration of an appendage...may significantly alter the duration of a molt stage." Hughes and Mathiessen (1962) speculated that "replacement of such a relatively large structure as a claw might inhibit the overall rate of growth." Bender (1971) reported that the length of the stone crab intermolt interval increases when claw(s) are being regenerated. On the other hand, Bliss (1956) suggested that multiple appendage regeneration in otherwise normal crabs can lead to ecdysis even though the crabs are experiencing unfavorable environmental conditions.

To analyze effects of claw loss on length of the normal intermolt period, it is necessary to know the date of each crab's molt prior to autotomization. Since data on the molt prior to capture was not known for autotomized crabs in this study, an heretofore unperformed analysis was made on data for experimental crabs from Savage's (1971b) earlier study in which such information was known. Five crabs with similar CW sizes were selected to reasonably insure approximately equivalent intermolt period lengths (Figure 18). Two crabs (S-7, S-35) forced to autotomize both claws immediately after ecdysis molted 30 days later, each crab successfully regenerating two new claws. The other three crabs were in various stages of their respective intermolt periods at the time they were induced to autotomize their claws. The smallest crab (M-5) required the least time to achieve ecdysis after claw loss (24 days) but also experienced the longest elapsed intermolt time prior to claw loss. The largest crab (S-32) required the longest time (40 days) after autotomy to molt and regenerate a new claw but was also autotomized after the shortest period following previous ecdysis. Since larger crabs normally possess longer intermolt intervals, it seems logical that larger crabs should require longer intervals to regenerate new claws. Apparently, the period required for crabs with carapace widths near 30 mm to develop two new claws is approximately one month, regardless of elapsed time prior to claw autotomy. This 30 day increment to regenerate a new claw is added to the number of days already spent in the intermolt period. Hence, the length of a normal intermolt interval may be shortened by inducing claw autotomy just after ecdysis or extended by inducing autotomy later in the intermolt cycle. For example, inducing autotomy in claws of a hypothetical crab (CW = 30 mm; intermolt period = 60 days) 10 days after ecdysis should shorten the length of the intermolt interval by 20 days [60 – (10 + 30) = 20 days]. Conversely, inducing autotomy 40 days after ecdysis in the same crab should lengthen the intermolt interval by 10 days [(40 + 30) – 60 = 10 days]. There is a time late in the intermolt cycle when the molting process can not be suppressed, even when both claws are lost (Hiatt, 1948). In such instances, the molting process occurs without regeneration of claws. This happened on several occasions in previous FDNR studies and during the present study. Claws were subsequently regenerated on those crabs that molted again.

There is also some indication from our observations of stone crabs in captivity that regenerating more than one appendage will not significantly affect the percentage duration of each regenerating stage, providing the appendages are lost at the same time and that limb loss is not severe. However, limb loss subsequent to a previous loss in the same intermolt

TABLE 19. INTERMOLT INTERVAL FOR NORMAL LABORATORY CONTROL CRABS MAINTAINED AT AMBIENT TEMPERATURES.

Crab	Sex	CW (mm)	Molt Date	Subsequent Molt Date	Intermolt Period (days)
Pre-molt CW 60-69 mm					
PP 72	Female	60	6/30/70	9/01/70	63
M 56	Female	66	12/03/69	5/03/70	151
			Average intermolt period—107.0 days		
Pre-molt CW 70-79 mm					
PP 84	Female	72	7/27/70	10/30/70	95
27	Female	73	4/29/72	7/23/72	86
10	Female	75	6/09/72	11/11/72	155
M 56	Female	77	5/03/70	10/27/70	175
PP 80	Female	79	7/09/70	12/03/70	147
6	Female	79	6/17/72	1/02/73	199
			Average intermolt period—142.8 days		
Pre-molt CW 80-89 mm					
15	Female	80	5/31/72	9/30/72	122
35	Male	80	6/01/72	11/27/72	179
51	Female	80	5/27/72	11/22/72	179
9	Female	85	6/06/72	10/06/72	122
24	Female	85	5/28/72	10/06/72	131
32	Male	86	6/14/72	11/19/72	158
60	Male	86	5/31/72	11/16/72	169
2	Female	87	5/21/72	1/01/73	224
34	Male	89	7/06/72	11/11/72	128
			Average intermolt period—156.8 days		
Pre-molt CW 90-99 mm					
14	Female	92	6/01/72	11/11/72	163
16	Female	92	6/01/72	11/03/72	155
			Average intermolt period—159.0 days		

period appears to lengthen the percentage duration of the stage that previously regenerating appendages are experiencing at the time of the new loss.

Duration of each regenerating claw stage for two (M-4, M-5) of the five aforementioned juvenile stone crabs was recorded. During the claw regenerative progression of these two crabs, the injured claw stump (wound) healed over (scab condition) during the first days immediately following induced autotomy. The first tissue claw bud did not appear until a week after claw loss. A miniature claw was apparent one week later, and the inflated condition appeared six to ten days subsequently. Ecdysis occurred within a week following the last phase.

Because a large crab may spend more time in one regenerative stage than a small crab spends in its entire intermolt period, attempts to describe the duration of each regenerating stage should express each as a percentage of the total intermolt time (Figure 19). In this form, our previous juvenile data can be compared with similar information gained more recently during a laboratory study to test tag retentivity. Ten adults ranging in size from 55 to 92 mm CW were routinely observed during regeneration of walking legs removed to aid in identification. Developmental stages were not as closely monitored for these adults as for the two juveniles. Each adult crab did not necessarily contribute a percentage for each regenerative stage because stages were often completed between checks. Still, there appears to be a comparable pattern between the times spent by both groups of crabs in each regenerating stage.

Frequency of feeding during intermolt stages was also casually monitored during the preliminary tagging study. Smaller crabs ceased eating one to two weeks prior to ecdysis, while larger crabs stopped two to three weeks prior to molting. Feeding resumed coincident with hardening of the new exoskeleton. Largest crabs required approximately one week to accomplish this, while smaller crabs needed less time. Passano (1960), in his table on brachyuran intermolt stages, estimated that these "negative" feeding stages represent approximately 20% of the entire intermolt period, agreeing with our observations.

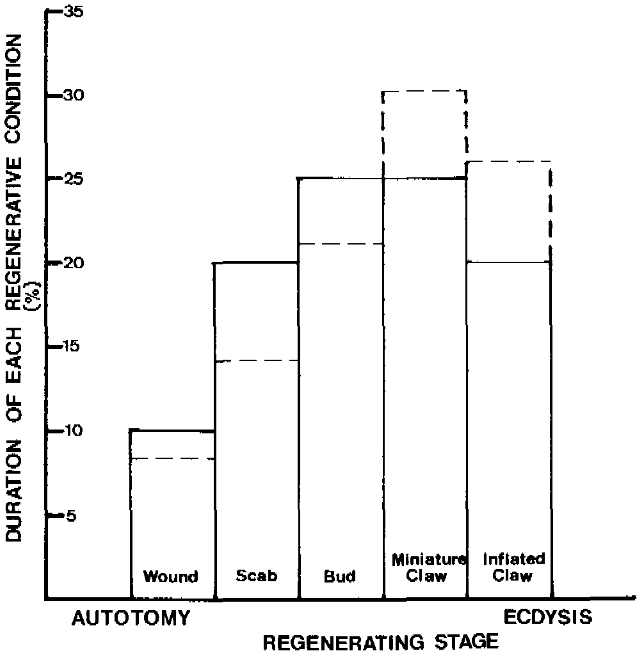

Figure 19. Percent duration of each regenerating appendage stage for two juvenile crabs (—) and ten adult crabs (---).

Passano (1960) further stated that "hibernation, ovarian maturation, and the carrying of developing eggs by females are the only interruption in [their] series of periodical molts." Our observations indicate that regeneration following either natural or induced appendage loss, especially claw loss, should also be considered an important influence on the normal intermolt cycle of stone crabs of both sexes.

SUMMARY

1. Laboratory-maintained and feral crabs were observed for incremental growth of carapace width and claws. Claw loss and regeneration were examined for effects on growth.
2. Field experiments were conducted at Pinellas Point in Tampa Bay. Crabs from various west Florida sites were maintained at ambient temperature in large, outdoor, circular tanks and smaller indoor, fiberglass tanks. Success of various marking techniques used during the experiments are discussed.
3. Normal morphometric relationships of carapace width (CW) against carapace length and against sizes of major and minor claws were derived from intact male and female crabs. Slopes of all lines were significantly different except those for male CW *vs*. minor claw and female CW *vs*. major claw.
4. Normal, feral male crabs showed greater average growth increments for carapace width and both claws than did normal females at similar sizes. Laboratory crabs displayed more uniform but overall reduced growth patterns than those of feral crabs. Normal laboratory females possessed larger average carapace width growth increments than did normal males, but incremental growth of claws was greater for laboratory males.
5. Incremental growth of carapace width was reduced in feral females possessing one or two regenerated claws. In the laboratory, growth of crabs with regenerated claws was similar to that for comparably maintained normal crabs but was less than growth of feral crabs with regenerated claws. Average carapace width growth at first molt for singly or doubly autotomized males was considerably less than growth of any other group. Crabs which regenerated two claws had average carapace width growth of three millimeters less per ecdysis than normal crabs.
6. A hypothetical growth plot constructed from incremental growth of several animals provided estimates of ages at sexual maturity (ten months) and commercial size (30 months).
7. Regenerated minor chelae possessed greater percentages of recovery to pre-autotomized sizes after both one and two regenerative molts than did major claw regenerates. After two molts, minor claws nearly regained pre-autotomized sizes, but had regained only 70-80% of dimensions expected for normal claws after two such additional molts. Investigators utilizing power plant thermal effluent achieved similar percent recovery data but in far less time because intermolt duration was reduced.
8. The concept of claw-type reversal is discussed, but such reversals were not evident on crabs completing two molts in the laboratory.
9. Claw regenerative stages are described. Duration of each stage is apparently independent of intermolt length.
10. Claw regeneration affects duration of the normal intermolt period. The period is reduced if claws are autotomized early in the cycle, or extended if claws are removed late in the cycle.

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