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CHELIPED ASYMMETRY IN THE STONE CRAB, *Menippe mercenaria*, WITH NOTES ON CLAW REVERSAL AND REGENERATION

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ABSTRACT: Stone crabs (*Menippe mercenaria*) were reared in the laboratory to determine natural handedness. Claws of feral juvenile crabs were autotomized to test for reversal and to determine stridulatory pattern sequences. All crabs less than 4 mm carapace width were right-handed (side bearing the crusher claw). Eighty-eight percent of juvenile crabs with autotomized crushers showed signs of handedness reversal after the first regenerative molt. Stridulatory sequences indicated that a normal pattern was attained after two regenerative molts. Dockside claw surveys and trap sampling programs involving several Florida stone crab populations reveal an approximate 80:20 right:left-handed ratio in adult crabs through largest sizes trapped. This indicates that adults do not reverse as readily as juveniles.

Stone crabs, *Menippe mercenaria* (Say), possess two large claws of unequal size and appearance. Major (crusher) claws, equipped with large basal teeth on the dactyl, are used for holding and crushing; minor (pincer) claws, with numerous small teeth, are used for cutting. Crab "handedness" is determined by the side bearing the major claw. Approximately 80% of adult crabs are right-handed in commercially exploited populations. Major claws reach legal size (propodus length $\geq$ 70 mm) more rapidly than minor claws and constitute 60% of fishery landings (Sullivan, 1979). One-third of harvested crabs yield only major claws. Major claws outweigh minor claws of the same propodus length. Normally, both claws constitute approximately one-half of adult body weight (Sullivan, 1979). Claws are the only legally harvested portion. Proper claw removal allows return of the crab to the fishery with potential for regenerating claws and contributing to the spawning stock. Regeneration has been demonstrated by Savage and Sullivan (1978). Sullivan (1979) reported a tagged crab which regenerated two legal size claws within one year of harvest.

Claw reversal has been hypothesized for stone crabs when the crusher alone is removed. Early regenerative claws resemble pincers, regardless of previous claw type (Savage *et al.,* 1974). Consequently, autotomized crushers are replaced with pincers. If reversal occurs. unmolested pincers opposite removed crushers will differentiate into more commercially desirable crusher claws. This study was designed to quantify natural claw handedness and establish direct evidence for reversal of handedness after claw loss.

The phenomenon of claw reversal has been described by numerous investigators. Przibram (1901, 1931), Wilson (1903), and Darby (1934) documented claw reversal in pistol shrimp, *Alpheus* spp., following crusher removal. Lewis (1969) described reversal in the box crabs, *Calappa* spp. Lang et al. (1978) found that if either claw was autotomized during early juvenile stages of the American lobster (*Homarus americanus*), the opposite claw always developed into a crusher. Studies conducted by Atwood (1963, 1968), Atwood and Dorai Raj (1964) and Lang et al. (1977a, 1977b) also deal with the physiochemical mechanisms behind development of asymmetry in crustaceans.

Cheung (1976) presented statistical

evidence for claw reversal in stone crabs through comparison of propodus length to carapace width for right and left crusher and pincer claws. He suggested that left crushers are formed through claw reversal following autotomy of right crushers. Savage and Sullivan (1978) obtained feral adult stone crabs missing a crusher claw, but observed no claw reversal after one molt.

Stone crab claws possess raised striae on the inner surface of the propodus (Figure 1) which function as a stridulatory organ when rubbed against the anterior carapace margin (Guinot-Dumortier and Dumortier, 1960). The normal striae pattern consists of transverse, unbroken lines (Figure 1d). Savage et al. (1975) described three patterns associated with claw regeneration which they identified as dotted (Figure 1a), dashed (Figure 1b), and beaded-normal (Figure 1c). Dotted and dashed patterns have been used to identify regenerated claws in dockside landing surveys. Savage et al. (1975) hypothesized that crabs bearing regenerative patterns again produced claws with normal patterns after molting. They found regenerative patterns on approximately 10 percent of

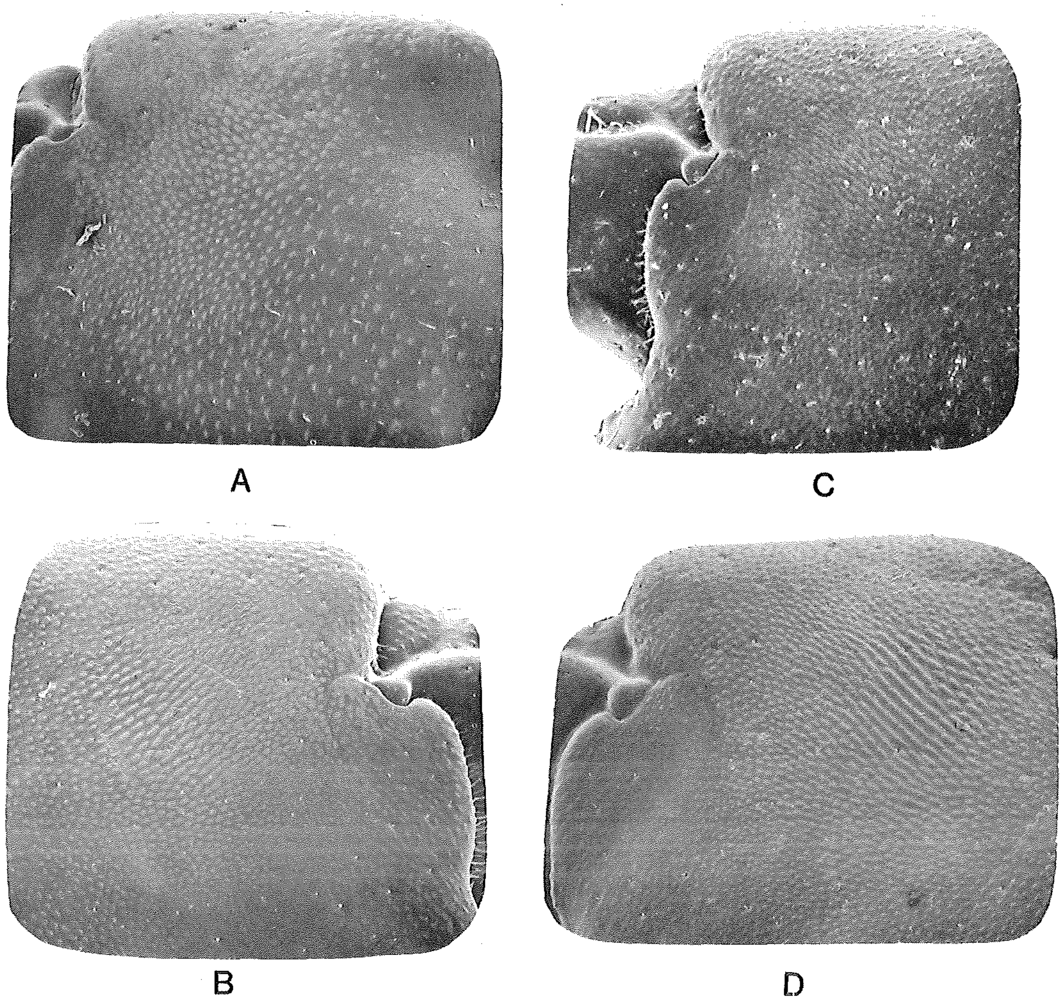

Figure 1. Scanning electron micrographs of stridulatory patterns on inner surface of stone crab claws: A. Dotted; B. Dashed; C. Beaded-Normal; D. Normal.

commercially landed claws, but this may reflect only a portion of the total contribution of regenerated claws to the fishery if regenerated claws can possess a normal pattern. Identification of "normal pattern" regenerated claws in dockside landings would add support to present fishery management practices of releasing crabs alive following claw removal.

METHODS AND MATERIALS

Juvenile and adult stone crabs were collected in the Tampa Bay area of west central Florida, from May to August, 1979, using commercial plastic crab traps (41 x 41 x 33 cm). Traps were covered with hardware cloth (6 mm mesh) to retain juvenile crabs. Juvenile crabs < 20 mm carapace width were retained for laboratory autotomy and regeneration experiments. A few gravid females were kept for larval rearing experiments.

Each crab was examined for sex, handedness, claw type and pattern. Measurements included carapace width (CW), propodus length (PL) and depth (PD), and lower dactyl length (DL) and depth (DD) (Figure 2). Measurements of juvenile crabs were made with a dissecting microscope equipped with an ocular micrometer. Large crabs were measured with dial vernier calipers. Ratios of dactyl depth:length (DD:DL) were derived to quantify claw shape and change in dentition, and to permit comparisons between claws of different sizes. When changes in shape of regenerated claws were compared to those of normal claws, reversal could be quantified. All pictures of crab claws and claw patterns were produced with an HHS-2R Hitachi scanning electron microscope, following coatings with carbon and gold paladium.

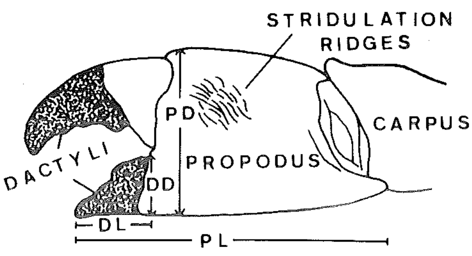

Figure 2. Morphology of a stone crab claw showing inner aspect of right crusher with measurement locations: propodus length (PL); propodus depth (PD); dactyl length (DL); dactyl depth (DD).

Natural Handedness Experiments

Crabs were reared from eggs to determine initial handedness. Larval rearing techniques for *Menippe mercenaria* were based on those of Porter (1960), Savage and McMahan (1968), Ong and Costlow (1970), Yang (1970), Yang and Krantz (1976), and Schlieder (1980). Gravid females were placed in separate compartments within laboratory holding tanks as illustrated by Schlieder (1980). When eggs hatched in 7-9 days, larvae were removed by water flow through a stand pipe drain into a larval collecting tank. First stage zoeae were transferred to a larval rearing system consisting of 100-l fiberglass cones where saltwater mixed from Instant Ocean sea salts was recirculated and filtered through crushed coral. Salinity and temperature were maintained at 30-35‰ and 27-30°C. Tanks were cleaned daily to remove solid waste and insure low levels of NH_3 and NO_2. A 14L:10D photoperiod was provided by overhead flourescent bulbs.

Initial stocking density in each cone was 50 zoeae per liter; densities decreased to approximately five zoeae per liter by day 15. Zoeae were fed newly hatched *Artemia* nauplii at densities of 5-10 nauplii per ml. Average duration of the larval period (five zoea stages and one megalopa stage) was 18 days. Yang (1970) recorded a similar larval rearing period for *M. mercenaria*. Settling screens were added when megalopae developed, at which time ground frozen shrimp replaced *Artemia* as food. Upon reaching first crab stage, individuals were transferred to laboratory holding tanks.

Claw Regeneration Experiments

Feral juvenile crabs (6-10 mm CW) were isolated in submerged, open-topped glass jars (500 ml) containing a substrate of clam shell fragments within laboratory holding tanks. Crabs were identified by a numbered glass slide in each jar. Saltwater (30-33 ‰) was kept at a depth of 20 cm within each holding tank by a stand pipe drain and water flow was maintained at approximately 68·l per min. Water was monitored twice weekly for changes in NH_3 and NO_2 levels and corrected when necessary by partial water exchange. Water temperature ranged between 27-32° C. Natural lighting was provided by numerous windows and occasionally augmented by overhead fluorescent bulbs. Crabs were fed chopped frozen shrimp, and jars were examined for molts twice daily.

Ninety crabs were maintained for an adjustment period of one week prior to experimental manipulation. Forty-four crabs served as controls and were not autotomized. Autotomy was induced in 46 crabs by insertion of a probe through the arthrodial membrane between merus and carpus segments of the crab claw (Figure 3). Of the 46 crabs (single claw autotomy), 20 survived at least one molt, providing regenerative data for 16 crabs with autotomized crushers and 4 crabs with autotomized pincers. Claws on experimental crabs were categorized as "regenerating" (following single-claw autotomy) or "stressed" (claw opposite autotomized claw). The term "stressed" was used because it was expected that the remaining claw would grow differently than if both claws were present. The stressed claw must assume the burden of defense and feeding. Dactyl depth: length (DD:DL) ratios were calculated from measurements at times of capture and first laboratory molt. Crusher claws normally have greater DD:DL values than pincer claws. Claw reversal was recognized by an enlargement of basal teeth on the pincer claw in subsequent molts. An increase in pincer DD:DL values provided numerical evidence of development of crusher-like dentition and general morphology.

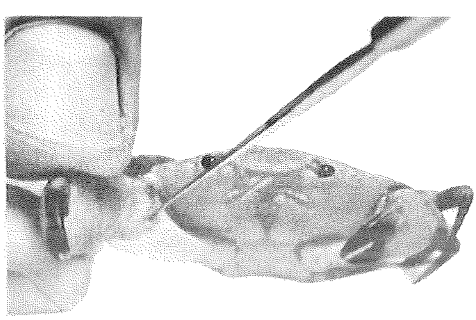

Figure 3. Probe inserted into arthrodial membrane between merus and carpus segments of stone crab claw to induce autotomy.

RESULTS

Natural Handedness Experiments

Stridulatory patterns of laboratory-reared first stage crabs developed from random dots into a normal configuration through successive molts (Table 1). Pattern development lacked sharply defined stages, resulting in varied pattern sequences before normal striations developed. However, the order of pattern appearance was never inverted (e.g., normal molting did not produce a beaded-normal, dotted, normal stridulatory pattern sequence). All crabs had normal or beaded-normal claws by 6 mm CW, and normal patterns by 10 mm CW. Therefore, crabs larger than 6 mm CW would not possess a dotted or dashed claw without claw loss and regeneration.

Twenty-five crabs less than 4 mm CW (≤ third molt) were measured for initial claw characteristics (Table 2). Thirteen of

Table 1. Stridulatory pattern development of laboratory-reared stone crabs through sequential molts. Patterns: 1 = dotted; 2 = dashed; 3 = beaded-normal; 4 = normal.

Molt Sequence							
1	2	3	4	5	6	7	N
1	1	1	2	3			4§
1	1	1	3	3	4		1
1	1	2	2	3	3	4	1
1	1	1	2	3	3	4	4
1	1	1	2	3	4		9

§ Crabs died before pattern completion.

16 laboratory-reared crabs possessed a longer right PL and three had claws of equal length. Seven of nine feral crabs possessed a longer right PL, while two crabs had claws of equal length.

Fourteen of 16 laboratory crabs possessed a greater right PD and two had claws of equal depth. All nine feral crabs had a greater right PD. Paired measurements indicated a longer or deeper right claw on 24 of 25 crabs and measurements were equal on the remaining crab, suggesting that all crabs initially were right-handed.

Table 2. Carapace widths (CW), propodus lengths (PL), and propodus depths (PD) of 16 laboratory reared and 9 feral stone crabs less than 4 mm CW.[1]

Source	Crab #	CW	Right PL	Left PL	Right PD	Left PD
Lab	265	1.6	1.15§	1.10	0.65	0.65
Lab	238	2.4	1.50§	1.30	0.80§	0.70
Lab	260	2.4	1.45§	1.35	0.75§	0.65
Lab	267	2.5	1.50§	1.45	0.75§	0.70
Lab	231	2.5	1.60§	1.48	0.80§	0.74
Lab	244	2.5	1.65§	1.50	0.83§	0.70
Lab	256	2.5	1.55§	1.43	0.85§	0.80
Lab	243	2.6	1.50	1.50	0.75	0.75
Lab	246	2.6	1.70§	1.50	0.85§	0.80
Lab	263	2.7	1.55	1.55	0.87§	0.80
Lab	271	2.7	1.70§	1.60	0.85§	0.75
Lab	250	2.8	1.70	1.70	0.85§	0.80
Lab	272	2.8	1.75§	1.70	0.90§	0.85
Lab	251	2.8	1.68§	1.50	0.85§	0.80
Feral	39	2.9	1.75	1.75	0.94§	0.88
Lab	236	3.0	1.80§	1.72	0.88§	0.80
Feral	220	3.0	1.81§	1.69	1.00§	0.94
Lab	276	3.0	1.80§	1.65	0.90§	0.80
Feral	41	3.3	1.94	1.94	1.13§	0.94
Feral	311	3.4	1.65§	1.60	1.05§	0.90
Feral	68	3.6	2.19§	2.00	1.19§	0.94
Feral	34	3.7	2.35§	2.15	1.25§	1.05
Feral	218	3.8	2.25§	2.09	1.25§	1.06
Feral	320	3.8	2.19§	2.13	1.13§	1.06
Feral	49	3.8	2.25§	2.13	1.31§	1.13

[1] All measurements in mm.
§ Greater measurement.

Claw Regeneration Experiments

Dotted and dashed stridulatory patterns of small crabs did not differ greatly. Table 3 presents data on 20 juvenile crabs which molted at least once following autotomy of a normal-patterned claw (14 right crushers, two left crushers, four left pincers). Eighteen crabs exhibited a dashed pattern on the first regenerated claw; two crabs displayed a dotted pattern. Nine crabs molted a second time and each regenerated claw regained a normal pattern. Figure 4 illustrates the regenerative sequence from normal (autotomized claw) through dotted to normal (regenerated claw).

Table 3. Changes in claw stridulatory patterns through successive regenerative molts of laboratory-maintained juvenile stone crabs. First entry of molt sequence is the autotomized claw pattern. Patterns: 1 = dotted; 2 = dashed; 4 = normal.

Molt Sequence			
1	2	3	N
4	1		1
4	1	4	1
4	2		10
4	2	4	8

The mean DD:DL ratio of crushers was greater than that of pincers for normal-patterned double-clawed crabs under 20 mm CW (Table 4). Data sets (right crusher-left pincer, left crusher-right pincer) were tested for normality with the Shapiro-Wilk W-statistic and found to be non-normal ($P = 0.05$). Transformations failed to normalize all data sets, so the nonparametric Wilcoxon paired-sample test was used. Crusher DD:DL values were significantly greater than corresponding pincer values for both crab handedness data sets (P =

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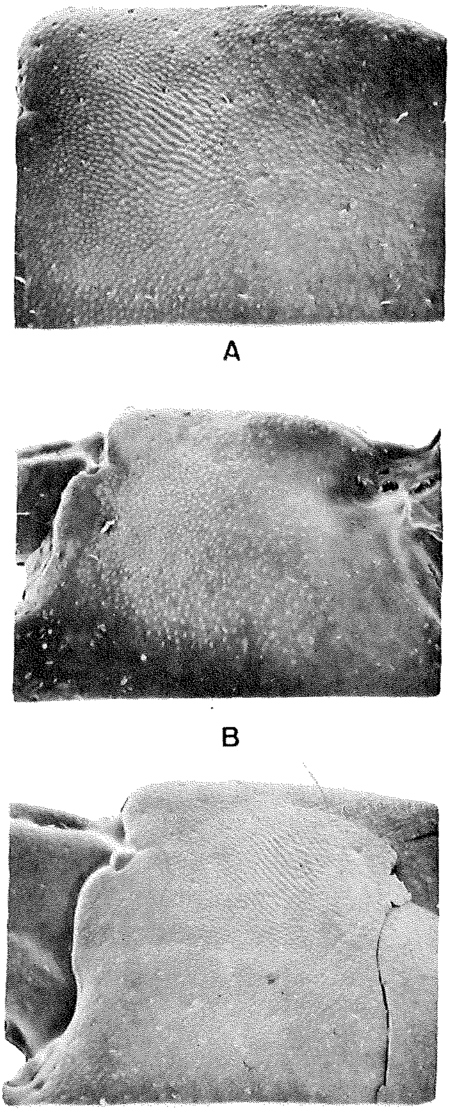

A B C

Figure 4. Scanning electron micrographs of pre- and post-autotomy stridulatory patterns from sequential molts of one laboratory-maintained juvenile crab, showing normal-dotted-normal sequence: A. Normal pattern — autotomized claw (x24); B. Dotted pattern — first regenerative molt (x18); C. Normal pattern — second regenerative molt (x24).

0.01). Experimental crabs did not exceed 20 mm CW prior to their second regenerative molt, so the DD: DL ratio could be used to examine pre-autotomy and post-regenerative changes in claw morphometry.

Table 4. Comparison of dactyl depth: dactyl length (DD:DL) ratio for crushers and corresponding pincers of normal-patterned double-clawed stone crabs less than 20 mm CW. Data tested with non-parametric one-tailed Wilcoxon paired-sample test.

Claw Type	DD:DL Mean	Std. Dev.	N	T'
Rt. Crusher	0.776	0.073	44	
Left Pincer	0.603	0.051	44	1979**
Left Crusher	0.710	0.029	12	
Right Pincer	0.639	0.064	12	276**

** P = 0.01

Fourteen of 16 crabs (6-10 mm CW) with autotomized crushers (14 right, two left) showed indications of claw reversal of the stressed claw upon first regenerative molt (Table 5). None of four crabs with autotomized pincers exhibited signs of reversal in the stressed crushers. Three of 44 control crabs exhibited accelerated growth of the pincer claw without cor-

Table 5. Results of autotomy experiments performed on juvenile stone crabs. Dactyl depth:dactyl length (DD:DL) ratios of stressed claws (opposite autotomized claws) listed for each crab before autotomy and following the first regenerative molt.[1]

Stressed Claw	Crab #	DD:DL of Stressed Claw A. Before Autotomy	B. Following Regenerative Molt
Left Pincer	8	0.48	0.71§
	10	0.60	0.70§
	12	0.65	0.67§
	16	0.60	0.69§
	322	0.51	0.66§
	25	0.66	0.73§
	45	0.65	0.69§
	47	0.59	0.76§
	52	0.57	0.57
	53	0.65	0.76§
	54	0.59	0.62§
	61	0.64	0.60
	63	0.59	0.75§
	82	0.69	0.71§
Right Pincer	48	0.60	0.63§
	23	0.68	0.84§
Right Crusher	9	0.74	0.75
	15	0.80	0.74
	19	0.77	0.73
	44	0.83	0.75

[1] All measurements in mm.
§ Reversal indicated: (B-A) > 0.01

responding growth of the crusher, but this could not be verified as claw reversal.

Mean differences between DD:DL values of successive molts of control and experimental crabs are presented in Table 6. Data were tested for normality with the Shapiro-Wilk W-statistic and found to be normal. DD:DL values decreased (differences were negative) for all claw types except stressed pincers, which increased (differences were positive). The mean change in DD:DL values for stressed pincers was significantly greater than that of control crushers and pincers, regenerating claws (previously crusher or pincer), and stressed crushers (one-tailed student's t-test: P = 0.1). This increase in DD:DL values of stressed pincers provides quantitative support for observed development of crusher-like dentition and overall morphology (Figure 5). Although the 0.1 probability level does not permit a strong statistical statement, results support claw reversal. Only first laboratory molts were used for analyses. Claws in all categories continued to become proportionally more narrow (DD:DL decreased) through several regenerative molts except for stressed pincers, which developed the typical large basal tooth and crusher proportions.

DISCUSSION

Stridulatory pattern development of stone crabs roughly follows a dotted, dashed, beaded-normal, normal sequence through 6 or 7 successive molts. The normal configuration is developed by 10 mm CW. The order of pattern appearance is only inverted during claw regeneration. Very young crabs regain a normal pattern upon the second regenerative molt regardless of whether the intermediate pattern is dotted or dashed. This differs from the regenerative pattern sequence followed by adult crabs, where at least two successive non-normal patterns occur (Savage and Sullivan, 1978; Sullivan, 1979).

Each of 25 small stone crabs (< 4mm CW) in our study possessed either a longer right propodus (80%) or had claws of equal length. The absence of any crabs with a longer left claw suggests that crabs are initially right-handed.

Claw reversal following crusher removal is documented in this study for juvenile crabs between 6 and 10 mm CW. Savage and Sullivan (1978) observed no reversal in the remaining pincer claw of laboratory-held adult stone crabs regenerating a missing crusher. A few cases of claw reversal in adult stone

Table 6. Mean differences between dactyl depth:dactyl length (DD:DL) claw ratios of successive molts of control (non-autotomized) and experimental (autotomized) stone crabs.

Claw Categories	Mean (DD:DL Ratio Diff.)	Std. Dev.	N	t	df
Control Crusher	-0.015	0.074	42	1.356†	56
Control Pincer	-0.024	0.075	42	1.456†	56
Regenerating Claw (previously crusher)	-0.245	0.091	16	4.012**	30
Regenerating Claw (previously pincer)	-0.022	0.045	4	1.559†	18
Stressed Crusher	-0.022	0.054	4	1.530†	18
Stressed Pincer	0.084	0.072	16		

** P = 0.01
† P = 0.10

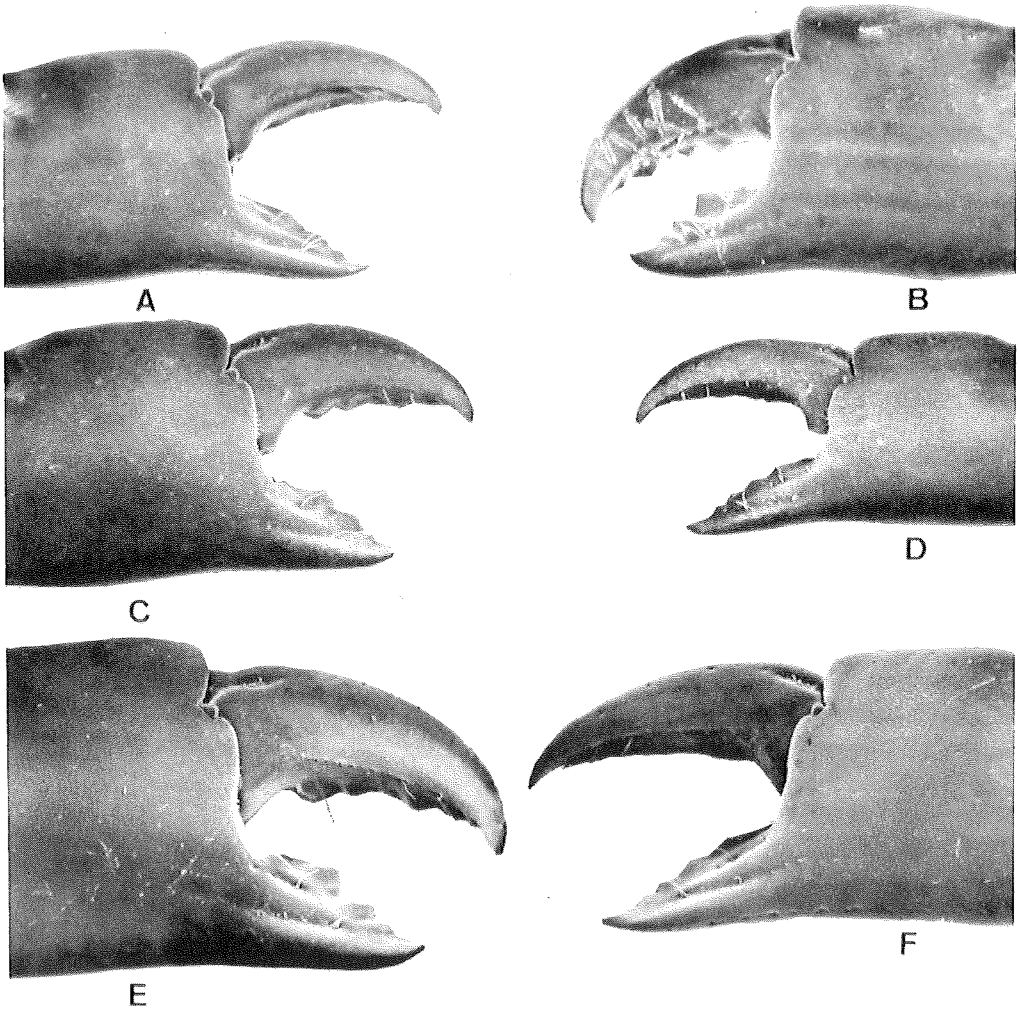

Figure 5. Scanning electron micrographs of paired claws from successive molts of one experimental crab showing reversal sequence of claw proportions and dentition: A. Left pincer (x15); B. Autotomized right crusher (x15); C. Stressed pincer after first molt (x12); D. Regenerating claw after first molt (x12); E. Left crusher after second molt (x12); F. right pincer after second molt (x12).

crabs have been reported by G.E. Davis (National Park Service, 1980, personal communication).

Hamilton *et al.* (1976) studied claw handedness of the blue crab, *Callinectes sapidus*. They found crabs less than 5 mm carapace length (CL) possessed right crushers and left pincers only. The proportion of right crushers decreased gradually with increasing CL until 55 mm CL, after which only 75-80% right crushers were found. Figure 6 illustrates the percentage of right-handed stone crabs through the entire size range, based on this study and data from Sullivan (1979). Only crabs less than 4 mm CW are 100% right-handed. Values decrease rapidly, leveling off around 80% by 40 mm CW.

An 80:20 right:left crusher ratio is attained well before the stone crab fishery has any effect on the population; significant fishery impact first occurs around 80 mm CW. This ratio is maintained through largest crabs trapped. Small juveniles losing a crusher experience immediate claw reversal and rapidly regain a normal pattern on the regenerating claw. If adults reversed as readily as juveniles, the handedness ratio should continue to increase with increasing CW, but

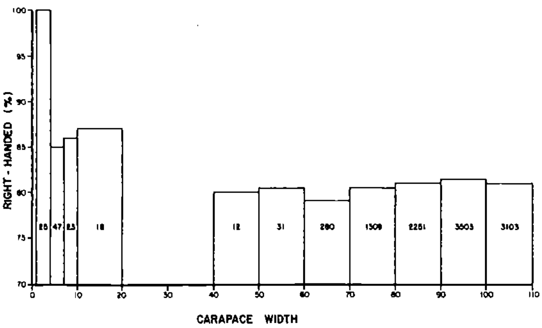

Figure 6. Percentage of right-handed, normal patterned, double-clawed stone crabs from this study (1-50 mm CW) and from Sullivan (1979) (50-110 mm CW). Sixteen of the 25 crabs less than 4 mm CW were reared from gravid females in the laboratory. Numbers within bars represent total crabs in each size class.

it does not. The constancy of the 80:20 right:left-handed ratio indicates that reversals are rare in adult crabs.

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