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REVERSAL OF HANDEDNESS, GROWTH, AND CLAW STRIDULATORY PATTERNS IN THE STONE CRAB *MENIPPE MERCENARIA* (SAY) (CRUSTACEA: XANTHIDAE)

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ABSTRACT

All 103 stone crabs reared from eggs of one left-handed and two right-handed female crabs were initially right-handed (side bearing crusher claw), but 88% of laboratory-reared juveniles whose crushers were removed reversed handedness on the first regenerative molt. Eight of 12 (67%) feral adult or pre-adult crabs reversed handedness on third or fourth molt following crusher loss, but only 5% (1 of 19) and 6% (1 of 16) reversed on the first and second molts, respectively. Reversal of handedness following claw loss by young juveniles is the most likely cause of the change from 100% initial right-handedness to 80% among older juveniles and sublegal (carapace width < 80 mm) adults in natural populations. The ratio is not altered in fished populations, probably because natural death occurs before most legal crabs can complete the number of molts (3 or more) required for adult claw reversal. No adult crab regained a normal stridulatory pattern on a regenerated claw, even after five postregenerative molts. Therefore, most, if not all, claws regenerated following initial claw harvest by the fishery should be recognizable as such in subsequent landings. Growth averaged 20% carapace width increase per molt for 94 laboratory molts of adult crabs; this was comparable to field growth increments in other studies.

The Florida fishery for the stone crab *Menippe mercenaria* (Say) is unique in that only claws are harvested and crabs are returned alive to the water. It is presumed that survivors can regenerate claws and reproduce. Legal claws (propodus length ≥ 70 mm) are produced by males at about 80 mm carapace width (CW), and by females at about 90 mm CW (Savage and Sullivan, 1978). Sullivan (1979) reported a tagged crab that regenerated two legal claws within one year of harvest.

Stone crabs have a crusher claw with an enlarged basal tooth on the pollex and a smaller pincer claw with numerous small teeth used for cutting. Crab "handedness" is determined by the side bearing the crusher claw. Reversal of handedness occurs when a crusher is removed and the remaining pincer differentiates into a crusher after molting. A lost crusher is always replaced by a regenerated pincerlike claw. Barnwell (1982) noted that most crabs with functionally dimorphic feeding claws reverse handedness following crusher loss, since a pincer can develop into a crusher in a single molt. Simonson and Steele (1981) showed that reversal was quite frequent (88%) on the first molt following crusher loss among small juvenile stone crabs.

Under present fishery regulations, both claws may be harvested if of legal size. However, recently suggested changes in stone crab regulations have included various schemes for taking only one claw from a crab, both to enhance survival of the declawed crabs and potentially to increase availability of larger, more valuable claws. As a practical consideration to facilitate enforcement, only one claw type (right or left, crusher or pincer) could be legally harvested under such regulation. Crushers are heavier than pincers of the same size and are a more desirable product for commercial harvest. To minimize economic impact, proponents have proposed that either right claws (80% crushers) or crusher claws

would be the initially designated legal claw type, the presumptions being that crabs losing right crushers would subsequently produce left crushers, and removal of any crusher would prompt enlargement of the opposite pincer. Thus, the incidence of development of crushers from pincers following crusher loss (reversal of handedness) in adult stone crabs has considerable implication for fishery management.

Although harvest has increased steadily for at least the last decade (Zuboy and Snell, 1982), sampling of stone crab populations throughout Florida via trapping and dockside surveys has consistently shown approximately 80% right handedness among all legal size claws (Savage *et al.,* 1975; Sullivan, 1979; personal observations), indicating that reversals are rare in adult crabs. Among adult stone crabs that are missing crushers when initially captured, Savage and Sullivan (1978) observed no transformation of pincers into crushers following one laboratory molt. They hypothesized that adult stone crabs required several molts to complete reversal, unlike the immediate reversals observed among juvenile stone crabs and most other crustaceans known to reverse handedness. Occurrence of claws intermediate between crusher and pincer also suggested a gradual reversal requiring several molts (Savage and Sullivan, 1978; Sullivan, 1979). A study encompassing several molts per individual adult crab was needed to determine whether such gradual reversal of handedness actually occurs.

Claws of stone crabs have a distinctive pattern of parallel ridges and bumps on the inner surface of the propodus that function as a stridulatory organ when rubbed against the anterior carapace margin (Guinot-Dumortier and Dumortier, 1960). The normal pattern consists of unbroken lines, but regenerated claws have dotted and dashed patterns which may be used to identify such claws in landing surveys. Simonson and Steele (1981) found that juvenile stone crabs < 15 mm CW regained a normal pattern on the second regenerative molt. However, no adult crabs recaptured during a tagging/regeneration study by Sullivan (1979) had a normal pattern on a regenerated claw, even though several had molted twice. Sullivan (1979) hypothesized that regenerated claws of adult crabs regain a normal pattern following several molts. If adult crabs do regain a normal pattern on regenerated legal claws, those claws would not be identified in landing surveys and thus would not reflect the total contribution of regenerated claws to fishery landings.

The present study was designed to test the hypotheses that adult stone crabs reverse handedness following crusher loss and can regain a normal stridulatory pattern on a regenerated claw. Results of additional studies to determine initial crab handedness, frequency of reversal of handedness in juvenile stone crabs, and growth in adult crabs are also reported.

Methods and Materials

Stone crabs were collected in Tampa Bay, Florida, during 1980 and 1981 using commercial plastic crab traps. Gravid females were kept for larval rearing experiments to determine initial crab handedness. Small juvenile crabs reared from eggs (carapace width < 15 mm), and feral pre-adult (25–50 mm CW) and adult (CW > 50 mm) crabs were retained for laboratory autotomy and regeneration experiments.

Crabs were examined for sex, handedness, claw type, and stridulatory pattern. Measurements included carapace width (CW), propodus length, pollex length (PL), and pollex depth (PD) (Fig. 1). Measurements of laboratory-reared crabs were made with a Zeiss dissecting microscope equipped with an ocular micrometer. Larger crabs were measured with dial vernier calipers. Measurements of CW were used in growth analyses. A ratio of pollex depth:length (PD:PL) was calculated as a measure of claw dentition to quantify changes between molts, since crusher PD:PL values exceed those of opposing pincers on unregenerated crabs by approximately 10%.

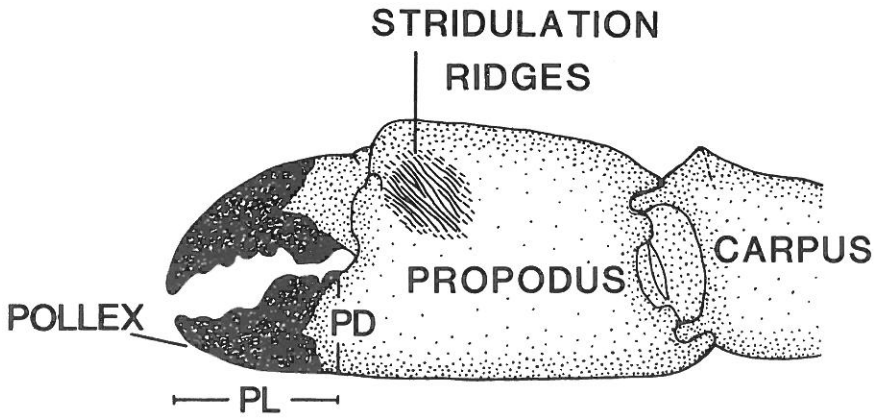

Fig. 1. Morphology of a stone crab (*Menippe mercenaria*) claw showing inner aspect of right crusher with measurement locations: pollex length (PL); pollex depth (PD).

Handedness Experiments

Eggs of stone crabs were hatched and larvae reared following procedures described by Simonson and Steele (1981). One left-handed and two right-handed gravid crabs were placed in separate compartments within laboratory holding tanks (see Schlieder, 1980, fig. 1). Eggs hatched in 7–9 days, and average duration of the larval period (five zoea stages and one megalopa stage) was 19 days. Megalopae and first stage crabs were placed in separate numbered compartments of three floating habitats constructed from 65 mm diameter by 80 mm long polyvinyl chloride (PVC) pipe sections, with 450-μm mesh nylon screen base and styrofoam floats. Shell fragments were placed in each compartment, since Lang *et al.* (1978) found that juvenile American lobsters, *Homarus americanus,* need a coarse substrate to develop handedness. Crabs were fed once and checked twice daily for molt or accidental claw loss; molts were recorded and preserved. When crabs exceeded 8 mm CW, the most recent molt was examined and measured. Handedness was determined by differences in propodus length, pollex depth, and basal tooth development.

Claw Regeneration: Juvenile Crabs

One hundred and three reared stone crabs that never lost a claw were randomly apportioned into four groups: (1) control, no autotomy; (2) crusher autotomized; (3) pincer autotomized; and (4) both claws autotomized. Crabs were maintained in floating habitats on a diet of shrimp, fish, and squid. Autotomy was induced by inserting a probe through the arthrodial membrane between merus and carpus of the claw, causing the crab to drop its claw at the natural fracture plane between coxa and basi-ischium, which minimized damage to the crab (see Simonson and Steele, 1981, fig. 3).

Claws were categorized as "control" (neither claw autotomized), "regenerating" (new claw), or "stressed" (claw remaining after single autotomy). The term "stressed" was used because the remaining claw must assume the entire tasks of defense, feeding, and grooming. Claw reversal was visually recognized by an enlargement of basal teeth on the remaining pincer claw in subsequent molts. An increase in pincer PD:PL ratio values was used to document development of crusher dentition from pincer dentition.

Claw Regeneration: Adult Crabs

Crushers and pincers of feral adult or pre-adult crabs were autotomized for claw regeneration experiments; stridulatory patterns on all claws were initially normal. In order to minimize intermolt periods, most crabs were 30–50 mm CW when experiments began. Savage and Sullivan (1978) reported that a few stone crabs were sexually mature at 40 mm CW, and almost all were adults by 60 mm CW. Almost all (92%) crabs in the present study exceeded 40 mm CW by first laboratory molt and would expectedly complete two or three additional regenerative molts as pre-adults or adults within a year. However, large adult crabs bearing legal claws (CW > 80 mm; see Savage and Sullivan, 1978) may require a year or more between molts.

Crabs were maintained separately in compartments (30 × 30 × 45 cm) with clamshell substrate. Salt water (32–34‰) was kept at a depth of 20 cm by standpipe drains; water flow was maintained at

approximately 10 l per min. To enhance molting, overhead full-spectrum lighting provided summer photoperiod schedules (14L:10D), and water temperatures were maintained at summer levels (27–32°C). Crabs were fed whole fresh shrimp, small whole fish, chopped squid, and oysters.

Autotomy was induced as in juvenile crabs. Crabs caught with regenerated claws (dotted or dashed stridulatory pattern) were also maintained, since use of such crabs decreased laboratory time necessary to observe stridulatory pattern sequences through several successive molts and increased the probability of observing a return to a normal pattern. PD and PL were measured to 0.1 mm, with a maximum ratio error of 4%. Laboratory molts were measured and preserved for comparisons. Reversal was indicated when a stressed pincer developed crusher dentition and the PD:PL value increased by at least 10%, the amount that normal crusher PD:PL values exceeded those of opposing pincers on crabs with unregenerated claws.

Results

Handedness Experiments

Each of 103 laboratory-reared crabs examined for initial handedness determinations had a right claw whose PD and propodus length values equaled or exceeded those to the left. Thirty-five crabs were offspring from a left-handed female, and 35 and 33 were from two right-handed females. Crabs were 8–11 mm CW when measurements were taken. Wilcoxon values for propodus length and PD differences between claws in all three brood groups showed that the right claws were significantly larger than opposing left claws ($T = 0.00^{**}$, $P < 0.01$, for each of six tests). This indicates that *Menippe mercenaria* is initially right-handed, regardless of parentage, and supports the results of Simonson and Steele (1981) obtained from a sample of 25 crabs.

Claw Regeneration: Juvenile Crabs

Of the original 103 crabs, 23 with autotomized claws died before a regenerative molt, 9 lost a claw or died during molting, 11 had damaged molts, and 3 gave erroneous data. Fifty-seven crabs were used in analyses: 18 as controls, 15 with crusher removed, 10 with pincer removed, 14 with both claws removed.

Juvenile crabs were 10–15 mm CW when claws were autotomized. PD:PL ratios for crushers and pincers of juvenile stone crabs were tested separately with a modified Kolmogorov-Smirnov normality test (Helwig and Council, 1979), and found to be normal at $P < 0.05$ (crusher: $D = 0.1211$ n.s., pincer: $D = 0.1267$ n.s.). A paired-sample Student's t-test was used to compare ratios between claws prior to experimentation. Crusher PD:PL values were significantly greater than corresponding pincer values ($t = 12.12^{**}$, 103 = d.f.), so this ratio was used to examine changes in basal tooth development. Changes in PD:PL were calculated as the difference between initial PD:PL value and ratio of first experimental molt. Mean differences between PD:PL values of successive molts of control and experimental crabs are presented in Table 1. No control pincers developed crusher dentition. Of 15 crabs with autotomized crushers, 13 stressed pincers had increased PD:PL values and developed a more pronounced, crusherlike basal tooth. This 87% incidence of reversal is almost identical to the 88% incidence of reversal found by Simonson and Steele (1981) among 16 laboratory-reared juveniles. Regenerated claws (particularly crushers) were proportionately narrower than the claws they replaced (PD:PL decreased), whereas ratios of stressed pincers increased considerably more than any other category. Simonson and Steele (1981, fig. 5) illustrated a reversal of handedness sequence for the paired claws of one juvenile stone crab.

Data were tested for normality with the Shapiro-Wilk W-statistic at $P < 0.05$. Control crusher and pincer, stressed pincer, and regenerated crusher data sets were

Table 1. Mean differences between pollex depth : pollex length (PD:PL) of successive molts of control (nonautotomized) and experimental (autotomized) juvenile stone crabs *Menippe mercenaria*. The nonparametric Wilcoxon's two sample test was used to compare stressed pincers with remaining categories. * = means significantly different at $P < 0.05$.

Claw category	Experimental category	PD:PL difference ($\bar{x} \pm$ SD)	N	T
Control crusher	No autotomy	0.017 ± 0.054	18	192*
Control pincer		−0.006 ± 0.049	18	170*
Regenerating claw (previously crusher)	Double claw autotomy	−0.130 ± 0.047	14	105*
Regenerating claw (previously pincer)		−0.050 ± 0.28	14	109*
Stressed crusher	Pincer autotomy	0.008 ± 0.052	10	92*
Regenerating claw (previously pincer)		−0.013 ± 0.044	9	62*
Regenerating claw (previously crusher)	Crusher autotomy	−0.121 ± 0.041	14	105*
Stressed pincer		0.056 ± 0.045	15	

normally distributed. However, remaining data sets were not normal, and could not be normalized by transformations. Therefore, the nonparametric Wilcoxon two sample test (Steel and Torrie, 1960) was used to compare stressed pincers with each of the other categories at $P < 0.05$. The mean change in PD:PL values of stressed pincers ($\bar{x} = 0.056 \pm 0.045$) was significantly greater than corresponding values for controls, stressed crushers, and each of the other five categories (Table 1). The significantly greater increase in PD:PL values of stressed pincers in comparison with other experimental and control claws provides quantitative support for observed development of crusher dentition and general morphology, indicating reversal of handedness in small juvenile crabs.

Adult Crabs: Growth

Growth data were recorded from sequential laboratory molts of 35 experimental and 15 control pre-adult and adult crabs used in regeneration studies. All but four crabs exceeded 40 mm CW on or before the first laboratory molt, nearing adult size. Intermolt days and percentage of CW growth were summarized by 20 mm premolt CW groups (Tables 2, 3). Data were tested for normality and equality of variance, and all means were compared with a one-tailed Student's t-test at $P < 0.05$ for unpaired data sets with equal variance (Steel and Torrie, 1980).

Twenty-three crabs molted two or more times, averaging 53 days for 94 intermolt periods. Mean intermolt days increased significantly ($P < 0.05$) with increasing premolt CW from 36.5 days (25–44.5 mm premolt CW) to 64.6 days (65–84.5 mm premolt CW) (Table 3). Forty-nine crabs averaged 31.8 ± 15.8 days to the first laboratory molt (range: 4–78 days). Twenty-four of these crabs averaged 31.9 ± 15.1 days to the first laboratory molt following single claw autotomy; 25 with no claw removal averaged 31.7 ± 16.8 days. However, since mean size differed between groups and dates of last molt prior to capture or claw removal were not known, it was not possible to test for effects of claw autotomy on intermolt length.

Table 2. Average percentage carapace width (CW) increase in experimental laboratory-maintained stone crabs *Menippe mercenaria* by 20 mm premolt CW groups. Means are compared with a one-tailed Student's *t*-test for unpaired data sets with equal variance, at $P < 0.05$. * = means significantly different.

Group	Premolt CW (mm)	Percentage growth ($\bar{x} \pm$ SD)	N	Student's *t*-test		
				Test	d.f.	t
1	25.0–44.5	26.1 ± 4.79	22	1 versus 2	58	2.423*
2	45.0–64.5	22.8 ± 5.24	38	2 versus 3	65	1.817*
3	65.0–84.5	20.5 ± 4.71	29	1 versus 3	49	3.085*

Growth ranged from 10% to 36% CW increase, with a mean increase of 20% for 94 molts. Mean growth decreased significantly ($P < 0.05$) with increasing size from 26.1% (25–44.5 mm premolt CW) to 20.5% (65–84.5 mm premolt CW) (Table 2).

Adult Crab Regeneration: Claw Patterns

One or more regenerative molts was produced by each of 35 pre-adult and adult crabs which had a regenerated claw at capture or had a normal claw autotomized. Table 4 presents the varied pattern sequences of regenerated claws. Twenty-six crabs autotomized a normal-pattern claw; following the first regenerative molt of these crabs, 19 claws had a dotted pattern and seven were dashed. Six crabs captured had a dotted claw, eight had a dashed claw. Seventeen dotted claws became dashed on the next molt and three remained dotted. Once a regenerated claw developed a dashed pattern it retained this pattern through every subsequent laboratory molt. Twelve regenerated claws retained abnormal patterns through three molts, six through four molts, and one through five molts (Table 4). No crab regained a normal pattern on a regenerated claw. An illustration of a typical adult molt series (Fig. 2) shows a dotted-dashed-dashed sequence on the regenerated claw. In contrast, Simonson and Steele (1981, fig. 4) illustrated a typical dotted-normal sequence on the regenerated claw of a juvenile stone crab.

Adult Crab Regeneration: Reversal of Handedness

PD:PL ratios were calculated for the stressed pincers of 19 adult crabs with autotomized crushers (Table 5). Three crabs attained PD:PL increases more than 10% greater than pre-autotomy values without developing crusher dentition. Percentage of reversal was calculated as the number of crabs completing reversal of handedness on a given molt, divided by the total number of crabs completing

Table 3. Average intermolt days in experimental stone crabs *Menippe mercenaria* maintained in the laboratory at summer temperatures, by 20 mm premolt carapace width (CW) groups. Means are compared with a one-tailed Student's *t*-test for unpaired data sets with equal variance at $P < 0.05$. * = means significantly different. n.s. = not significant.

Group	Premolt CW (mm)	Intermolt days ($\bar{x} \pm$ SD)	N	Student's *t*-test		
				Test	d.f.	t
1	25.0–44.5	36.5 ± 22.8	23	1 versus 2	59	2.610*
2	45.0–64.5	54.1 ± 26.9	38	2 versus 3	66	1.514 n.s.
3	65.0–84.5	64.6 ± 30.5	30	1 versus 3	51	3.697*

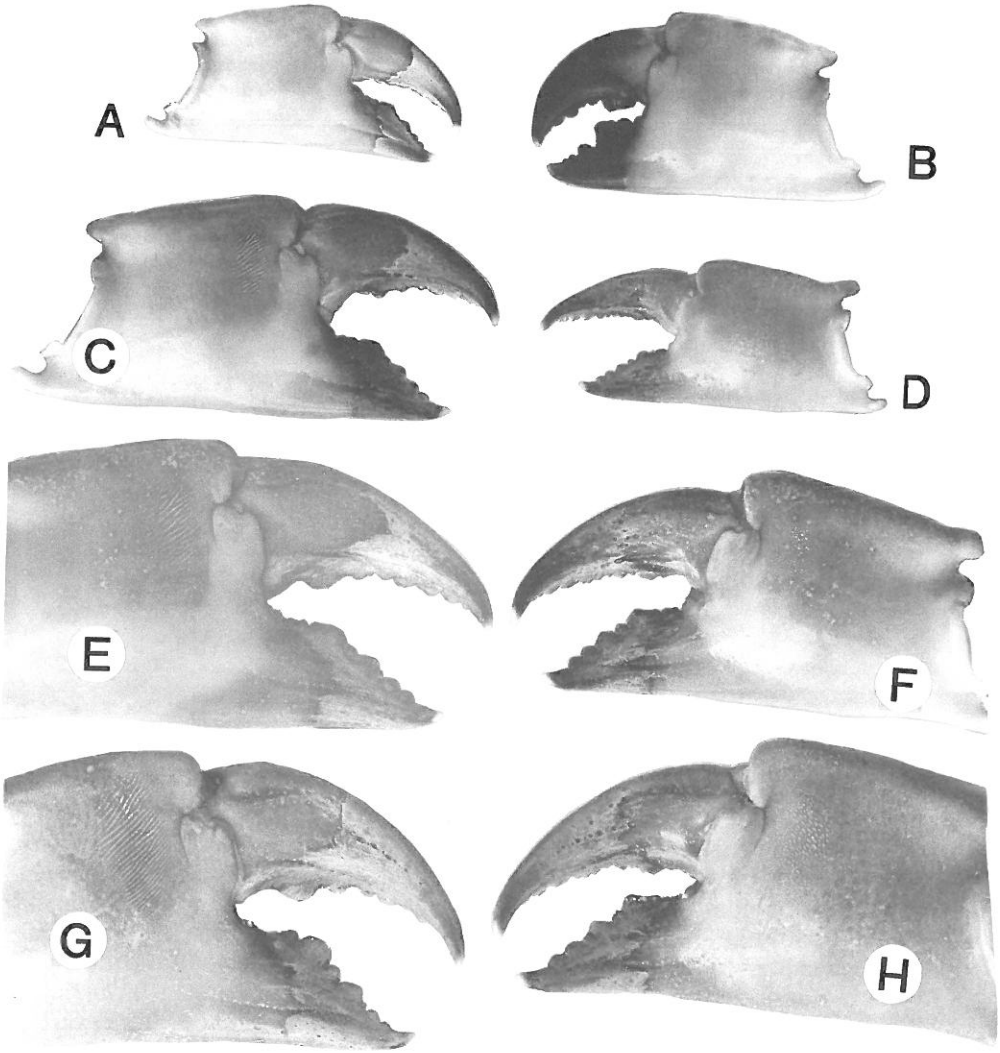

Fig. 2. Inner aspects of paired claws of *Menippe mercenaria* from successive molts of one adult experimental crab showing reversal of handedness sequence and stridulatory patterns: A, left pincer, normal pattern; B, autotomized right crusher*, normal pattern; C, stressed pincer after first molt; D, regenerated claw after first molt, dotted; E, stressed intermediate claw after second molt; F, regenerated claw after second molt, dashed; G, left crusher after third molt (reversal); H, regenerated claw after third molt (pincer), dashed. Claws are actual size. *Autotomized crusher (B) is very similar to claw lost from this sequence, but from a different crab; claw included for comparison only.

that molt which had not previously reversed. Most of 10 crabs that reversed handedness did so on their third or fourth molt following crusher loss (Table 5; Fig. 3). This trend suggests that, with sufficient number of molts, adult crabs can reverse handedness. Figure 2 illustrates a typical reversal sequence.

Mean PD:PL ratio differences between initial and first molt of control (non-autotomized) and experimental (crusher autotomized) crabs were calculated. The nonparametric Wilcoxon two sample test was used to compare intermolt changes

point of initial divergence coincides with approximate size of female sexual maturity. These analyses indicate that the increasing PL:CW variance observed by Sullivan (1979) was principally due to increasing differences related to sexual dimorphism, not to the presence of normal-pattern regenerated claws.

None of 17 crabs completing three to five regenerative molts during the present study regained a normal stridulatory pattern on any regenerated claws. Therefore, it appears that regenerated claws of adult stone crabs do not regain a normal pattern over time, and all claws regenerated following harvest may be discernible in fishery landings.

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