BULLETIN OF MARINE SCIENCE, 52(3): 873–885, 1993

GROWTH OF POSTSETTLEMENT JUVENILES OF THE FLORIDA STONE CRAB, *MENIPPE MERCENARIA* (SAY) (DECAPODA: XANTHIDAE), IN THE LABORATORY

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ABSTRACT

We combined relevant data from three laboratory studies to define molt increment and intermolt period of postsettlement (<10.5-mm carapace width [CW]) juveniles of the Florida stone crab, *Menippe mercenaria.* Regression of postmolt CW on premolt CW yielded a linear relationship. Mean growth (proportional increase in CW) per molt was 18%, but variation among individuals was high. Molt increment increased significantly and linearly as size of the crab increased. Intermolt period increased significantly with increasing crab size in a log-linear relationship. We attempted to define biologically meaningful size classes (instars) by using mean size-at-instar of individuals raised from the megalopal stage and size-at-molt of individuals who completed eight or more molts in the laboratory. Three determinants (mean, median, and maximum of intermolt period) and two techniques (one based on observed complete intermolt periods and one based on estimates of intermolt period) were used to predict age-at-size of instar-12 juveniles (>10.4 mm CW). Within a size class, estimates of mean, median, and maximum intermolt periods generally were not significantly different from corresponding values for the three determinants calculated using the observed intermolt periods. However, summing the size-specific intermolt period values to calculate age resulted in disparities among the six estimates of age at the end of instar 11. Nevertheless, our analyses suggest that under normal salinity and temperature conditions in Florida, postsettlement juvenile *M. mercenaria* may require up to 12 months to complete growth to approximately 10 mm CW.

As in all crustaceans, growth in crabs is a discontinuous function. Although small increases in size may occur during intermolt stages, when the arthrodial membranes extend (Kurata, 1962; Hartnoll, 1983), size increases dramatically only immediately following ecdysis, through uptake of water (Passano, 1960; Hartnoll, 1982, 1983). Because the integument is shed at each molt, no permanent record of growth remains. Thus, methods of age determination typically used for vertebrates are unsuitable for estimating growth in crabs; age is commonly calculated from observations of molt increment and intermolt period.

Laboratory studies of growth have been conducted on many species of crabs. The degree of success in elucidating growth pattern has varied among these studies, principally because laboratory conditions may affect both molt increment and intermolt period (Kurata, 1962; Hartnoll, 1982). Generally, as the size of the organism increases, molt increment increases and percentage increment (growth factor; Kurata, 1962) decreases (Kurata, 1962; Hartnoll, 1982), but the percentage increment is highly variable both within and among species (Hartnoll, 1982). Intermolt period also generally increases as size of the organism increases (Kurata, 1962; Hartnoll, 1983), and variation in both molt increment and intermolt period increases as the organism ages (Tagatz, 1968; Chittleborough, 1976; Restrepo, 1989).

Quantitative descriptions of growth in commercially valuable marine species are particularly important. A thorough understanding of the growth rates of these species in all life stages can be important for projecting yield per recruit, for determining the length of time required to reach legal size, and for estimating other parameters essential for management of the fishery. Growth studies, in conjunction with recruitment and population studies, provide the basis for fishery management.

The stone crab *Menippe mercenaria* (Say, 1818) is an important commercial species in Florida (Bert et al., 1978; Lindberg and Marshall, 1984), and a number of studies related to growth of this species have been conducted. Larval development in the laboratory has been described (Ong and Costlow, 1970; Field, 1989; Brown et al., 1992). Growth increments and growth rates of large juveniles and adults have been derived from both laboratory and field studies (Savage and McMahan, 1968; Savage, 1971; Yang, 1972; Yang and Krantz, 1976; Savage and Sullivan, 1978; Sullivan, 1979; Bert et al., 1986), but sample sizes in these studies were small. Also, holding conditions were highly variable and inconsistent both within and among the laboratory studies, and information from the field studies was largely anecdotal. In addition, many laboratory studies describing aspects of growth have focused on the role of claw regeneration (Savage et al., 1975; Savage and Sullivan, 1978; Sullivan, 1979; Simonson and Steele, 1981; Simonson, 1985) because in the stone crab fishery, only the claws are harvested. Despite the differences in methodologies and the emphasis on claw regeneration, laboratory studies of growth in *M. mercenaria* have elucidated the general qualitative relationships of molt increment and intermolt period for subadults and adults. Although substantial inter- and intra-individual variation exists, larger crabs generally have larger molt increments (Savage, 1971), smaller percentage increments (Savage and McMahan, 1968; Bert et al., 1986; Restrepo, 1989), and longer intermolt periods (Savage and McMahan, 1968; Savage and Sullivan, 1978) than do smaller crabs. Quantitative assessments of the components of growth of stone crabs in Florida have been made only for larger juvenile and adult males (Restrepo, 1989). Similar analyses are lacking for females of a comparable size range and for postsettlement juveniles.

We described the growth of postsettlement (metamorphosis to 10.5-mm carapace width [CW]) juvenile *M. mercenaria* utilizing the relevant data gleaned from three independent studies in which postsettlement juvenile stone crabs were reared in the laboratory. We analyzed both the molt increment and intermolt period of postsettlement juvenile *M. mercenaria,* and we estimated age at approximately 10.5 mm CW using three determinants (mean, median, and maximum of intermolt period) and two methods of calculating age-at-size (using observed intermolt period, using partial intermolt period).

METHODS AND RESULTS

Data Available.—Our values for molt increment and intermolt period were obtained from postsettlement juvenile *Menippe mercenaria* that had molted at least once in one of three laboratory studies. In two of the experiments (studies A and B), variations in temperature and salinity were controlled and photoperiod was constant (light : dark = 12h : 12h); in the third study (study C), variations in temperature, salinity, and photoperiod were not controlled. In study A (Florida Marine Research Institute, unpubl.), each juvenile was held in water of 27°C, 30‰ (ambient summer conditions) for 1 week. Then, depending upon the experimental treatment, water temperature was abruptly decreased by 3°C, 5°C, or 7°C for either 4 or 8 days. Following the treatment, water temperature was returned to 27°C for the duration of the experiment; total experimental time was 7 weeks. Two groups of juveniles (controls) were held at 27°C throughout the experiment. Study B (Brown et al., 1992) was a factorial experiment in which each juvenile was held in a specific water temperature-salinity combination for 7 weeks. Temperature

Table 1. Results of analysis of covariance comparing least-square regressions of postmolt carapace width on premolt carapace width for three data sets used to define growth parameters of postsettlement juvenile *Menippe mercenaria* (see text for definitions of data sets). A. Study A versus Study B. B. Study B versus Study C. C. Study A versus Study C. ns: not significant, *: significant at $\alpha \leq 0.05$ with sequential Bonferroni adjustment (Rice, 1989)

Source	df	SS	MS
A.			
Sum of groups	253	40.487	0.160
Pooled within	254	41.208	0.162
Total	255	41.583	0.163
F_{slope} = 4.508 ns		$F_{elevation}$ = 2.309 ns	
B.			
Sum of groups	351	44.686	0.127
Pooled within	352	44.946	0.128
Total	353	46.485	0.132
F_{slope} = 2.041 ns		$F_{elevation}$ = 12.053*	
C.			
Sum of groups	444	73.378	0.165
Pooled within	445	73.819	0.166
Total	446	75.006	0.168
F_{slope} = 2.664 ns		$F_{elevation}$ = 7.156*	

and salinity conditions in the factorial array ranged from 5°C to 35°C and 10‰ to 40‰, in 5°C and 10‰ increments. In both studies A and B, each juvenile was held separately in 100–150 ml of artificial seawater (Instant Ocean®), and the water was changed on alternate days. In study C (Florida Marine Research Institute, unpubl.), juvenile stone crabs were collected sporadically from October 1965 through September 1969 and held for various lengths of time in large outdoor tanks of natural seawater, permitting the temperature, salinity, and photoperiod to vary with ambient conditions (temperature and salinity ranges: 15°–30°C, 23‰–35‰). In each study, ample food (usually molluscan muscle) was provided on alternate days.

Because the temperature and salinity conditions in which the crabs were held differed among studies, our initial steps in the analysis were to determine the useful component of the data on molting within each study and to test the validity of combining the useful data from the three experiments into a single data set. First, crabs with missing appendages were eliminated from each data set. In study A, goodness-of-fit G-tests (Sokal and Rohlf, 1981) established that no significant differences in the percentage of crabs surviving or in molt frequencies occurred between controls and treatments; therefore, all data on molting were pooled and used in our analysis (N = 175). In study B, Brown et al. (1992) determined that low temperatures (≤10°C) or salinities (≤15‰) affected both survival and molting rates of postsettlement juvenile *M. mercenaria*; therefore, from that study only growth data from juveniles held in temperature-salinity combinations of 15°C, 20‰ or higher (N = 82) were included in our analyses. From study C, growth data were used from all individuals that were within our defined size range (N = 273) because the temperature and salinity conditions recorded for that study were never below the critical levels defined by Brown et al. (1992).

To examine the feasibility of combining the three data sets into a single data set, least-squares regressions of postmolt CW on premolt CW generated separately for each study were compared to each other in pairwise regressions. The variances of the data sets were homogeneous, allowing us to use analysis of covariance

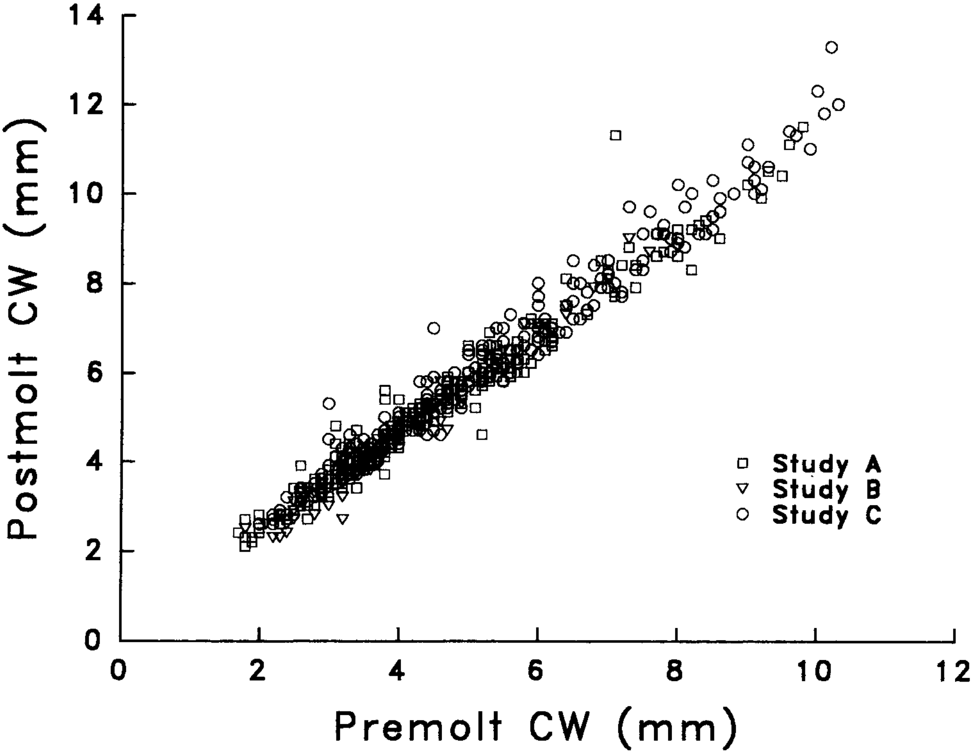

Figure 1. Scatterplot of postmolt carapace width (CW) vs. premolt CW for all data used for analyzing growth of postsettlement juvenile *Menippe mercenaria*. Studies are defined in the text.

(ANCOVA; Snedecor and Cochran, 1969) for the analyses. The sequential Bonferroni technique (Rice, 1989), a statistical adjustment for determining the significance of multiple tests of a single hypothesis, was used to determine the tablewide significance of each ANCOVA category. The slopes of all lines were homogeneous, but Study C differed significantly from studies A and B in elevation (Table 1). The homogeneity of slopes indicated that growth increment in the three studies was similar, and a scatterplot of the data confirmed that the data points from the three studies were thoroughly intermingled (Fig. 1). Therefore, all data were combined for further analyses.

Molt Increment.—We wished to use each molt as an independent data point for the analysis of growth. However, because some juveniles used from studies A and B had molted as many as three times in the laboratory, and many juveniles used from study C had molted numerous (up to 11) times in the laboratory, it was first necessary to evaluate whether the length of time these crabs were held in the laboratory affected molt increment. We grouped the data by laboratory molt number (1–9; sample sizes were inadequate for molts 10 and 11) and computed the linear regression for growth (postmolt CW on premolt CW) separately for each molt number through the ninth laboratory molt. All regressions had high r^2_{adj} values (0.95–0.99; N = 10–375), indicating that growth, as described by each molt number, fit a linear model. This similarity in pattern of growth among molts allowed us to compare the nine molt-specific regression lines in all pairwise combinations using ANCOVA; table-wide significance of each ANCOVA category

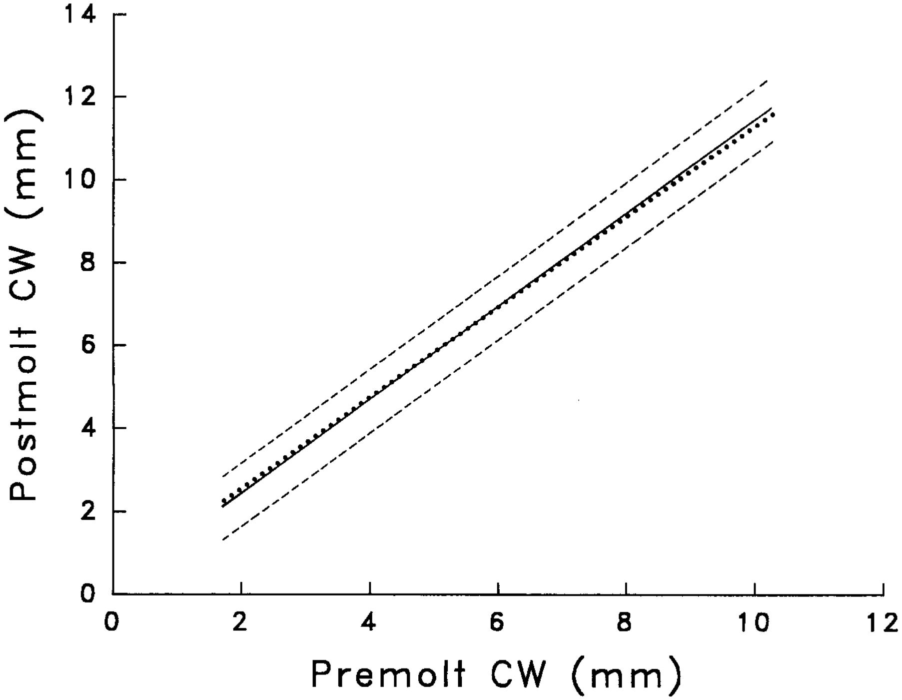

Figure 2. Regression lines for molt increment of laboratory-reared postsettlement juvenile *Menippe mercenaria*. Solid line: calculated using values for all molts recorded ($Y = 1.13X + 0.16$, $N = 530$); dashed lines show 95% confidence interval. Dotted line: calculated using only first laboratory molts ($Y = 1.12X + 0.22$, $N = 301$). CW: carapace width.

(slope and elevation) again was determined using the sequential Bonferroni technique (Rice, 1989). We found no significant differences in the slopes or elevations of any pairwise combination of lines, indicating that the length of time the crabs were held in the laboratory did not significantly affect molt increment. Therefore, we considered each molt in the data set to be an independent data point and combined information from all molts to describe growth. For postsettlement juvenile *M. mercenaria,* growth can be modeled by the equation

$$Y = 1.13X + 0.16 \qquad (1)$$

($r^2_{adj} = 0.97$; $P \ll 0.001$), where Y = postmolt CW and X = premolt CW (Fig. 2).

To further check for possible effects of laboratory holding time on growth, we used ANCOVA to compare the regression line generated using all molts (Equation 1) to a regression line generated using only the first laboratory molt (the molt presumed to be least affected by laboratory holding time). The lines were virtually identical (Fig. 2), further supporting the idea that laboratory holding time had no discernible effect on molt increment and the validity of using every laboratory molt in our analysis of growth.

To define the relationship between molt increment (postmolt CW minus premolt CW) and crab size, a regression line was generated, yielding the model

$$Y = 0.13X + 0.17 \qquad (2)$$

($r^2_{adj} = 0.28$), where Y = molt increment and X = premolt CW (Fig. 3A). Although the variance was high, as indicated by the relatively low r^2_{adj} value, molt increment

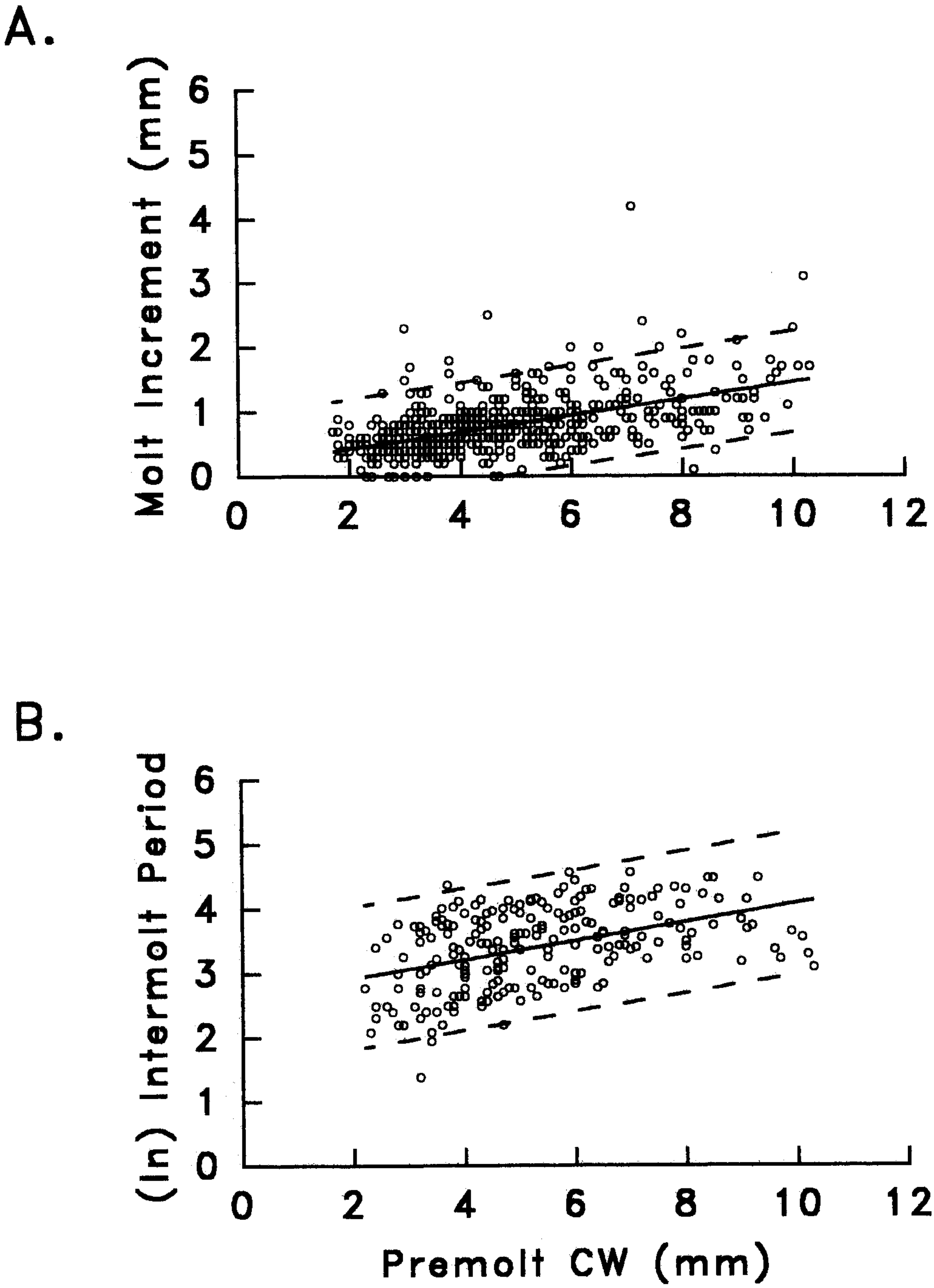

Figure 3. Relationship of growth parameters to crab size (premolt carapace width [CW]) for laboratory-reared postsettlement juvenile *Menippe mercenaria*. Dashed lines define 95% confidence intervals. A. Molt increment. Solid line: $Y = 0.13X + 0.17$, $N = 530$. B. Intermolt period (days). Solid line: $\ln Y = 0.14X + 2.64$, $N = 213$.

Table 2. Size (mean [x̄] and standard deviation [SD] of carapace width [mm CW]) of postsettlement juvenile *Menippe mercenaria* at each crab instar. Definitions of data sets used for determining size-at-instar and size-at-molt are presented in the text

	Size-at-instar (N = 5)		Size-at-molt (N = 10)		Size classes (N = 15)	
Instar	x̄ CW	SD	x̄ CW	SD	CW	Range
1	2.2	(0.2)	—	—	1.9–2.4	0.8
2	2.8	(0.3)	2.7	(0.4)	2.5–2.9	0.5
3	3.4	(0.5)	3.2	(0.6)	3.0–3.5	0.6
4	3.8	(0.6)	3.8	(0.7)	3.6–4.1	0.6
5	4.3	(0.6)	4.5	(0.7)	4.2–4.8	0.7
6	5.1	(0.9)	5.2	(0.9)	4.9–5.5	0.7
7	5.8	(0.9)	5.8	(0.9)	5.6–6.3	0.8
8	—	—	6.7	(1.1)	6.4–7.3	1.0
9	—	—	7.7	(1.5)	7.4–8.3	1.0
10	—	—	8.7	(1.7)	8.4–9.3	1.0
11					9.4–10.4	1.1

increased significantly ($P \ll 0.001$) as CW increased. Mean percentage of growth per molt was 18% (SD = 0.08) over the entire size range and was not related to size.

Intermolt Period.—Intermolt period (number of days between molts) typically increases as the size of the organism increases. We used regression analysis to determine the relationship of the length of intermolt period to the size of the crab (Fig. 3B). The relationship was best described by the equation

$$\ln Y = 0.14X + 2.64 \tag{3}$$

($r^2_{adj} = 0.18$; $P < 0.001$), where Y = intermolt period and X = premolt CW. Throughout the size range of the crabs in our study, intermolt period increased logarithmically as CW increased. Consequently, we grouped the data into size classes to evaluate size-at-age.

Rather than simply divide the data into uniform size-class increments, our objective was to establish size classes that presumably had biological relevance. We attempted to define size classes that reflected the sizes of crab instars by calculating the mean and standard deviation of crab size (mm CW) separately at each molt using two subsets of the data. The first data subset consisted of values for the intermolt periods of crabs raised from megalopae ($N = 5$); from this subset we calculated mean size-at-instar for each of the first seven instars. The second data set, from which we obtained size-at-molt, was composed of the values for intermolt period of crabs that had been brought into the laboratory at a size of ≤3.2 mm CW (the size of the largest instar-2 crab in the first data subset) and that had molted at least eight times in the laboratory ($N = 10$). We presumed that these crabs had molted only once prior to collection and were therefore initially in the second crab stage. The means and standard deviations of size-at-instar (calculated using data subset one) and size-at-molt (calculated using data subset two) agreed closely (Table 2). Therefore, we used the combined subset data to construct size classes that presumably reflect the size of postsettlement stone crabs at instars 1–10 (Table 2). Estimates for size class 11 were made by averaging the size of all crabs ≥9.0 mm CW ($N = 8$).

Within each defined size class, the data consisted of values for the intermolt periods of crabs that had been held in the laboratory for various lengths of time using the means and medians derived from the observed lengths of intermolt period. Error is inherent in each estimate of intermolt period; when intermolt periods for individual size classes are used for projecting long-term growth, summing intermolt periods to predict age-at-size compounds the effect of the error component.

Predictions of age-at-size from our equations of molt increment and intermolt period suggest that approximately one year is required to attain 10-mm carapace width. Our growth model is consistent with the minimum rate of growth of postsettlement juveniles inferred from data collected in Tampa Bay, Florida, (Florida Marine Research Institute, unpubl.) but these field studies suggest that rapidly growing juveniles may grow to 10-mm CW in the field within six months. Order-of-magnitude growth differences in juvenile Florida stone crabs have been found in a mariculture system that simulated natural conditions (Yang and Krantz, 1976), and considerable variation could also be expected in nature. Nevertheless, the growth rates we established for postsettlement juvenile *M. mercenaria* may have important implications for management of the Florida stone crab fishery. Slow-growing individuals may require two years to reach the larger juvenile size classes (e.g., 30–35 mm CW). Previous studies (Savage, 1971; Yang, 1971, 1972; Savage and Sullivan, 1978) may have underestimated the time required for *M. mercenaria* to progress through the postsettlement period and consequently may have underestimated the time required to grow to adulthood. Studies of growth for all life-history stages of other commercially important crabs (Tagatz, 1968; Orensanz and Gallucci, 1988) and evidence presented here suggest that a thorough survey of growth in all life stages of *M. mercenaria* is needed to understand the time required for this species to attain reproductive maturity and legal size.

ACKNOWLEDGMENTS

We thank H. Cruz-Lopez, J. Risser, D. Romero and P. Steele for field and laboratory assistance and D. Camp for statistical assistance. We also thank T. Perkins and G. Bruger for reviewing the manuscript. This research was funded by grants from the Department of Commerce, National Oceanographic and Atmospheric Administration (P.L. 99-659 [Project 2-IJ-2]) and from the Florida Sea Grant College Program (Project R/LR-B-24), and by the State of Florida, Department of Natural Resources, Florida Marine Research Institute.

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DATE ACCEPTED: May 11, 1992.

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