SOUTH FLORIDA RESEARCH CENTER

REPORT SFRC-86/04

Aspects of the Population Dynamics & Biology of the Stone Crab (*Menippe mercenaria*) in EVER & BISC as Determined by Trapping

Everglades National Park, South Florida Research Center, P.O. Box 279, Homestead, Florida 33030

Aspects of the Population Dynamics and Biology of the Stone Crab (*Menippe mercenaria*) in Everglades and Biscayne National Parks as Determined by Trapping

Report SFRC-86/04

T. M. Bert, J. Tilmant, J. Dodrill, and G. E. Davis

National Park Service
South Florida Research Center
Everglades National Park
Homestead, Florida 33030

1986

Bert, T. M., Tilmant, J., Dodrill, J., and Davis, G. E. 1986. Aspects of the Population Dynamics and Biology of the Stone Crab (*Menippe mercenaria*) in Everglades and Biscayne National Parks as Determined by Trapping. South Florida Research Center Report SFRC-86/04.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES

ABSTRACT

Stone crabs (Menippe mercenaria) were trapped on a lunar cycle (full moon) from June 1979 to June 1980 to investigate the population biology and life history of the organism in south Florida marine waters managed by the National Park Service. Seventeen stations, located throughout the coastal regions of Everglades National Park and Biscayne National Park, were fished for an entire year. Five additional stations were fished the last nine months of the study. An array of morphometric and biological data was taken on each crab captured. Salinity, temperature, water clarity, principal fouling biota, and bottom type were recorded at each station during sampling.

Relative abundance, proportion of females, and number of juveniles were highest in Everglades National Park marine waters from Lostmans River northward. Also, mean size of both sexes was generally smallest in that region. Progressing southward along the Gulf of Mexico and east into Florida Bay, relative abundance of both adults and juveniles decreased, proportion of males increased, and mean size of both sexes became larger. Juveniles were never found at most stations sampled in Florida Bay. Biscayne National Park resembled Florida Bay in number and size of adults, proportion of males, and lack of juveniles. Juvenile distribution and abundance was directly correlated with relative abundance of adults and proportion of females in the trapped population. The primary source of adults in Florida Bay appears to be a very slow movement of crabs from the Gulf of Mexico progressively farther into Florida Bay. The stone crab population in Biscayne National Park may be dispersing from farther north along the Atlantic coast of Florida.

Temporal changes in relative abundance, sex ratio, and size class frequency of female stone crabs captured were strongly correlated to various aspects of reproductive activity. Changes in values of these parameters for males were related to changes in water temperature and female reproductive activity. Differences in relative abundance and mean size of both sexes also corresponded to commercial fishing season near the seaward limits of Everglades National Park in the Gulf of Mexico, and to the number, proportion, and mean size of males in commercially fished areas of Florida Bay. Because of the simultaneous occurrence of natural and artificial factors affecting the trapped population over time, it is difficult to attribute observed variations to any particular factor. As determined by trapping, changes in the population biology of stone crabs in Everglades and Biscayne National Parks occurring during the year are cyclic, and the population recovers to its initial state by the onset of the next year.

Female stone crabs produce eggs throughout the summer. Younger females peak in egg production in late summer and older females in late spring. Young females molt and possibly mate more frequently than older females, but egg production of the young segment of the female population is reduced. By age three, all females have apparently reached sexual maturity. Molting occurs from fall through spring in young females and molt frequency declines with increasing age until, at age four, females molt annually in the fall. Females increase in carapace width about 10 mm with each molt and can live to about age seven.

Male stone crabs may molt throughout the year, but most appear to have recently molted in November. Annual molt increment in males decreases dramatically at about 70 mm carapace width, and averages about 16 mm carapace width for crabs greater than that size. Molt increment in males shows twice as much variability as in females and decreases continuously with increasing size of crab. Males have a higher mortality rate than females, possibly due in part to their greater susceptibility to commercial fishing pressure. The majority of males mate in traps with females of their own age class, despite the discrepancy in size (males are larger). Evidence indicates that males reach sexual maturity at about 70 mm carapace width, and develop a legally harvestable claw at a slightly larger size.

INTRODUCTION

The stone crab (Menippe mercenaria) supports a commercial fishery by virtue of its huge and delectable claws. Only the claws are harvested; trapped crabs are declawed in the field and returned to the water. Although stone crabs are widely distributed in southeastern North America, by far the largest commercial fishery occurs in southwest Florida (Bert et al. 1978). About 80 percent of all U.S. annual landings come from the three southernmost counties in Florida (Dade, Monroe, and Collier), with Monroe and Collier counties having by far the highest production. In these three counties, stone crabs are the third most valuable commercial fish harvest after shrimp and spiny lobster (Prochaska and Cato 1974). Everglades National Park, spanning Monroe and Collier counties, forms the shorewardmost area of the large gulf fishery and may play an important role in maintaining the stock for that fishery (Figure 1). Biscayne National Park occupies approximately a fourth of Dade County's coastal waters and contributes to production in that county.

Commercial stone crab fishing has been allowed in Everglades National Park and Biscayne National Park since their creation. Recently, the fishery in Everglades National Park has shown signs of stock depletion. Trap catch per unit of fishing effort (g claws/trap night) fell from 113 g to 29 g from 1972 to 1977, and economic extinction of the fishery occurred after two-thirds of the fishing season had expired each year from 1974 to 1976. While catch rate fell, the number of stone crabbers fishing the park increased from 35 in 1970-71 to 60 in 1975-76.

Special park regulations governing the stone crab fishery at the time this study was undertaken prohibited harvest in all areas of Everglades National Park within 400 m of the coastline, and in the northern half of Florida Bay. Only males with a propodus (claw) length of 2.75 in (7 cm) could be taken in Everglades National Park. Outside of Everglades National Park, the state of Florida and the federal government allow the harvest of both sexes with this claw size (370.13 FL State Statutes; Fed. Reg. 44(65):19445-19496). Biscayne National Park allows harvest in accordance with state laws. Crabbers are limited to 400 traps in Everglades National Park and must have park permits in addition to their state permits. No trap limits are set for Biscayne National Park, state, or federal fishing grounds. Open season in the parks conforms with state and federal regulations (October 15 through May 15).

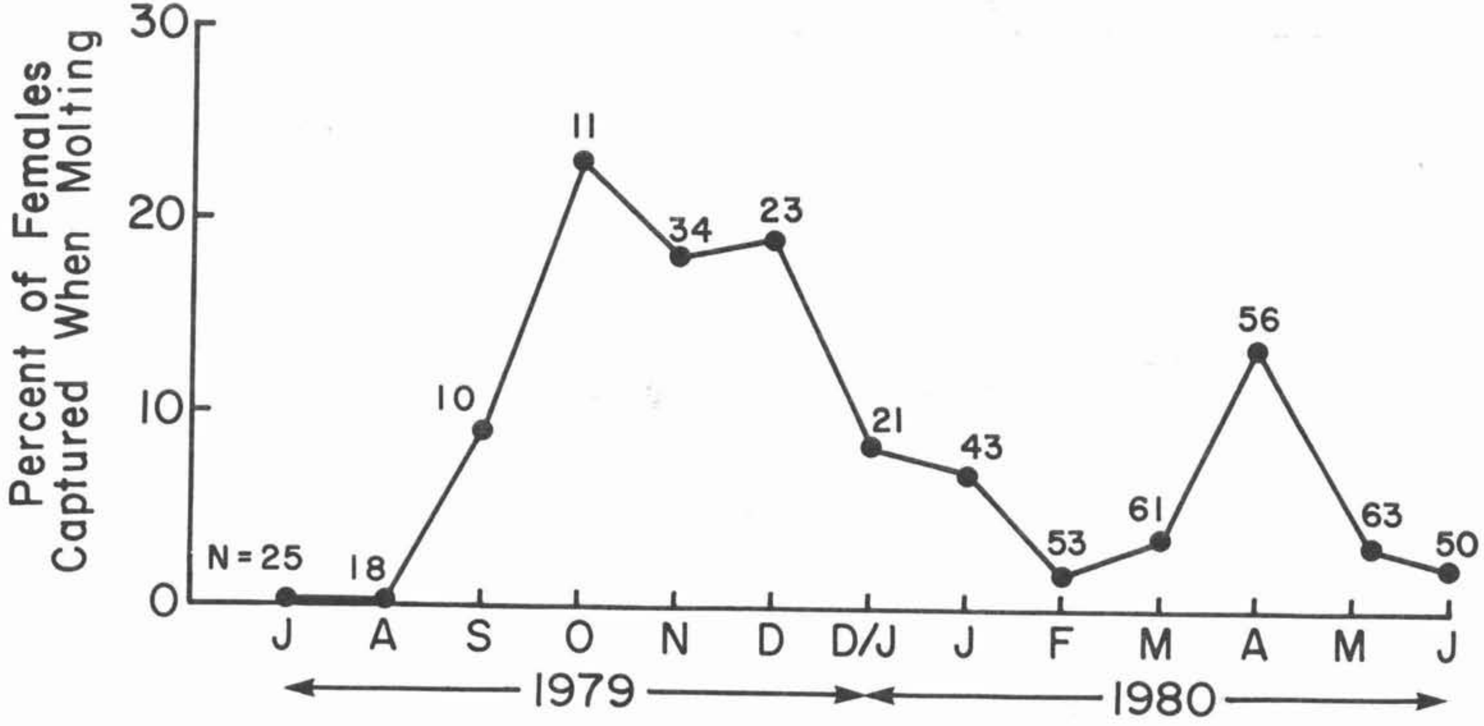


Figure 8. Proportion of females molting, by month (number of molting females/number of females captured). N equals number of females captured each sampling period.

Depth of the inland bays and lakes in this system usually does not exceed 2 m, whereas the major streams and rivers may reach depths of 4 m or more. Offshore near the seaward margin of the park, water depth increases from an average of 2 m at Everglades City to about 4 m at Cape Sable.

Rainfall averages 125-135 cm/yr (Thomas 1974) and is seasonally divided such that 60-65 percent falls from June to August and only 8-10 percent from December to February (Carter et al. 1973), creating seasonal salinity variations that can be detected to the seaward limit of the park (Davis 1940; Lindall et al. 1973). The fresh water of inland bays and streams becomes brackish during the dry season, and oceanic influences can be seen several kilometers inland (Carter et al. 1973). Salinity along the gulf coast ranges down to 10 ppt during the rainy season, and typically approaches oceanic values (30-33 ppt) at the close of the dry season in early spring. Tidal influences on coastal salinity cause variations of several parts per thousand (Carter et al. 1973), but are secondary to wind and rain generated seasonal differences. At the seaward margin of the park, variations in salinity are dampened by mixing and normally range from 25-34 ppt, depending on season. However, isolated pockets of abnormally low or high salinity water can be encountered (up to 10 ppt greater or less than ambient), probably due to incomplete mixing. Vertical salinity stratification is usually negligible throughout the area.

Water temperature drops to about 20 °C in winter, but may deviate substantially (Carter et al. 1973; present study), dependent upon the intensity of the season. Warmest temperatures are reached in July and August and coolest in December and January. The shallow waters of inland bays and streams begin to warm in February or March, earlier in the year than in the open gulf. Summer temperatures in July and August reach 30-33 °C, and are commonly 1-3 °C warmer inland and along the coast than offshore.

Normal tidal amplitude deviates ± 40-70 cm from mean sea level, varying with phase of the moon. Seasonal variations in level of the surrounding ocean (Marmer 1954), enhanced by predominant winds, greatly reduce the depths of inland, coastal, and offshore waters in winter and elevate them in late summer.

Large amounts of organic compounds and detritus, wind mixing, and tides reduce visibility to nearly zero throughout most of the year in all water masses. Inshore waters occasionally become clear, although deep brown in color, at the end of the dry season. Visibility rarely exceeds 2 m offshore.

Algal components of the coastal estuarine and marine flora are composed of *Garcilaria* spp., *Rhizoclonium hookeri* (Carter et al. 1973), and *Cladophora* spp. in soft-bottomed localities and *Udotea* spp., and *Batophora oerstedii* (Schmidt and Davis 1978) on firmer substrate. The oyster shell and foliacious red algae accumulating in the channels provide habitat for large numbers of small crabs (*Panopeus*, *Neopanope*, *Eurpaneopeus*, *Rithropanopeus*, and *Perilisthes* spp.) and snapping shrimp (*Alpheus* spp.).

Offshore, subtropical and warm temperate sponges and gorgonians are rooted to available hard substrate, interspersed with patches of turtle grass (Thalassia testudinum) and shoal grass (Halodule wrightii). Benthic filter feeders (barnacles, tunicates, sponges, worms, hydroids, and bryozoans) are very abundant and rapidly colonize any available substrate, forming dense, fast-growing colonies which shelter small mobile invertebrates, particularly juvenile Menippe mercenaria, isopods, and amphipods.

Florida Bay

Florida Bay, sandwiched between the upper Florida Keys and southern tip of mainland Florida, is a semi-enclosed triangular honeycomb of nearly emergent calcareous banks surrounding deeper (to 3 m) basins locally known as "lakes". Small islands of low elevation, called keys, appear at irregular intervals along the banks. Channels in the banks form avenues for water exchange between adjacent lakes. Water exchange with the open ocean is restricted except through channels between the upper Florida Keys and the broad banks forming the western border of the bay. As a result, tidal influences on water level are secondary to those generated by wind and seasonal fluctuations in ocean levels. Water level is generally higher in fall and winter, when north to northwest winds pile water into the bay and regional oceanic levels are higher, and lower in summer when south to southeast tradewinds blow water out of the bay (Ginsburg 1956; Tabb et al. 1961). Diurnal tidal variation of about 50 cm (McNulty et al. 1972) is superimposed on these seasonal factors in western Florida Bay. Tidal influence is gradually reduced eastward in the bay.

Florida Bay is underlain by Miami oolite (Cooke and Mossom 1929). Overlying sediments are chiefly fine-grained calcareous algal muds. Some transport of abiotic sediment occurs from the surrounding Gulf of Mexico into the western basins (Hoffmeister 1974). Sediment depth varies among basins and is generally greater in western and southern basins.

Salinity varies greatly both seasonally and spacially in Florida Bay. The salinity in basins of northern and central Florida Bay changes seasonally and annually under the influence of freshwater runoff primarily from Taylor Slough (Schmidt and Davis 1978). Central Florida Bay contains extensive areas of very shallow (less than 1 m) water with restricted flushing and becomes very hypersaline during years of low rainfall (Tabb et al. 1961; Turney and Perkins 1972). Values of up to 70 ppt have been recorded (Finucane and Dragovich 1959). Proximity to the open gulf prevents such extreme changes in salinity in southern and western Florida Bay. However, these areas commonly experience salinities of 40 ppt in summer despite greater flushing action.

Recorded water temperatures in Florida Bay have a wider range than those in the Gulf of Mexico, extending from 10 °C (present study) to 38 °C (Ginsburg 1956). In summer, temperatures are generally higher in shallow central Florida Bay and on mud banks than in the deeper basins of eastern and western Florida Bay. Restricted circulation and the shallow nature of the bay make it susceptible to large rapid drops in water temperature (to as low as 5 °C) during winter cold fronts (Tabb et al. 1961).

Certain portions of Florida Bay are virtually always highly turbid: 1) the northern sector of the bay receiving freshwater runoff; 2) individual basins lacking sediment stabilizing benthic flora, and; 3) some basins at the southern margin of the park affected by wind and tidal mixing.

Tabb et al. (1961) characterized the flora and fauna of Florida Bay as typical of the Carolinian biogeographic province. Benthic associations can vary substantially from basin to basin and range from vast seagrass communities to unconsolidated mud-dwelling complexes. Ginsburg (1956) and Turney and Perkins (1972) found notable differences in the molluscan and foraminiferan assemblages among the basins in the bay, and Turney and Perkins (1972) separated the bay into four subdivisions based on differences in the molluscan fauna.

Biscayne National Park

Biscayne National Park encompasses the southern half of Biscayne Bay and extends seaward to the edge of the continental shelf (Figure 1). The park contains essentially two water masses of approximately equal size, a shallow tropical lagoon and a typical Caribbean barrier reef extending to about 20 m depth (Schmidt and Davis 1978). Separating the two bodies of water are narrow islands of exposed Key Largo limestone. Several channels cutting between the islands connect the bay with the ocean. The deepest of these is about 3 m.

Southern Biscayne Bay

The lagoon of southern Biscayne Bay is a semi-enclosed basin having restricted exchange with other water masses. The bay is bordered on the east and west by land masses and on the north and south by nearly emergent submarine banks. Freshwater flow into the bay is limited and comes mainly from mosquito control ditches and water management canals on the mainland.

The western edge of the bay is lined by mangrove swamp. Seagrass flats, primarily turtle grass and shoal grass, extend seaward from the mangroves and give way to a sponge-gorgonian hard-bottomed community in places where the bedrock surfaces from beneath calcium carbonate biogenic sediments (Schmidt and Davis 1978). The deeper (to 3 m) eastern side of the bay is thickly overlain with calcium carbonate mud and contains sparse to dense beds of seagrasses mixed with calcareous green algae (Codiaceae).

Tides range from about 50 cm near the mainland to 60 cm near the barrier islands (Schneider 1969). Prevailing easterly winds generate an elevated sea level in the western part of the bay.

Salinity varies from nearly fresh to exceeding oceanic values within the bay, depending on season and location. During the rainy season, salinities can be much lower along the western shoreline. Severe rainstorms or prolonged heavy rains can lower salinity throughout the lagoon. For example, Voss et al. (1969) recorded a low of 5 ppt off Fender Point during October 1968 when salinity was lowered throughout the bay. In contrast, evaporation rate is very high, enhanced by east to southeast tradewind. Salinity in shallow portions of the bay occasionally reaches hypersaline values (Segar et al. 1971; Lee 1975).

Bay waters are also susceptible to atmospheric changes in temperature. Water temperatures in winter frequently decline to 13-15 °C and may fall rapidly in response to winter cold fronts. Summer water temperature usually ranges between 30-33 °C; de Sylva (1971) recorded an extreme of 41.7 °C near the mainland coast.

Bay waters are normally clear except near the intercoastal water channel which roughly bisects the bay from north to south. However, strong sustained winds occasionally resuspend the fine-grained sediment sand and reduce visibility to essentially zero throughout the bay.

Coral Reef Tract

Between the barrier islands and deep waters of the Florida Straits lies a characteristic West Indian coral reef tract. The discontinuous outer reef is nearly emergent at low tide and is primarily composed of elkhorn and staghorn corals (*Acropora* spp.), and brain and star corals (*Montastraea diploria* and *Siderastrea* spp.). Hawk Channel is a depression 5 to 10 m deep lying between the outer reef and islands. The channel is irregularly punctuated with patch reefs composed of heads of brain and star corals intermingled with staghorn coral and finger corals (*Porites* spp.) (Voss et al. 1969 lists the floral and faunal reef constituents). Sea feathers, whips, and fans (*Alcyonaria*) are frequently found topping the coral reef mass (Schmidt and Davis 1978). Turtle grass beds interspersed with occasional patches of barren sand fill in the space between reef patches. Between the channel and barrier islands, seagrass flats generally give way to extensive areas of rocky bottom with soft corals, calcareous algae (Codiaceae and Corallinaceae), sponges, and small corals (*Porites*, *Manicina*).

Proximity of the warm Gulf Stream ammeliorates summer and winter extremes in temperature on the reef tract. Temperature can be 5 °C warmer on the seaward side of the islands than near the mainland in winter (present study), and temperature near the islands has a greater seasonal range (about 18-32 °C) than farther offshore (20-30 °C) (Smith et al. 1950; Chew 1954; present study).

Open ocean circulation also stabilizes salinity. Smith et al. (1950) and Jones (1963) reported salinity values of 37 ppt with very little variation. However, salinity may drop slightly near the cuts between barrier islands where lagoon water mixes with offshore water.

Turbidity levels can be relatively high, particularly in winter and spring when strong northeast and east winds stir up bottom sediments. Visibility usually ranges between 10 m and 15 m.

PREVIOUS STUDIES ON THE STONE CRAB

Much of the early recorded information on the stone crab (*Menippe mercenaria*) is a documentation of its occurrence with some notes on variation in habitat with size and season (Rathbun 1884, 1887; Hay and Shore 1918; Schroeder 1924; Rathbun 1930; Behre 1950; Parker 1959; Tabb et al. 1961; Tabb and Manning 1961; Bullis and Thompson 1961; Finucane and Campbell 1968; Powell and Gunter 1968). The stone crab has been recorded from Cape Hatteras southward along the Atlantic coast, throughout the Gulf of Mexico, in several of the leeward islands of the Caribbean, and, interestingly, possibly in the Black Sea (Abolmasona 1970).

The species has recently been divided into two semi-species (Bert 1985), one ranging from the Florida panhandle through the northern and western Gulf of Mexico, and the other, in its pure form, through south Florida and into North Carolina. The two forms hybridize in northwest Florida and along the Atlantic from east central Florida into South Carolina. Four structural phenotypes and three hybrid phenotypes have been reported from Cuba, as determined by size and abundance of spots on carapace and claws (Ros et al. 1980).

By far, the greatest abundance of the species is on the continental shelf of southwest Florida, from Naples to Key West (Bert et al. 1978). Detailed information on local distribution and abundance has been accumulated for the coasts of northwest Florida (McRae 1950; Bender 1971), southwest Florida (Sullivan 1979), southeast Florida (Noe 1967), and central South Carolina (Wenner and Stokes 1983). These studies also included various aspects of the life history of the organism obtained from direct observation and capture-recapture data.

Six larval stages, five zoeal and one megalopal, were documented by Hyman (1925) and an occasional sixth zoeal stage by Porter (1960). Based on the number and morphology of larval stages, Scotto (1979) assigned the genus Menippe a primitive phylogenetic status, noting that the genus was more similar to cancrid crabs than to the Xanthidae.

Ong and Costlow (1970) and Costlow (1970) found that larval stone crabs metamorphose most rapidly in warm (25-30 °C) water of near oceanic salinity (30-33 ppt). Stone crab larvae respond to elevated salinity (40 ppt) by raising the levels of certain amino acids in the body (Tucker 1978). Anger et al. (1981) calculated an increase in reaction rates for duration of larval development and in survival time with increasing temperature. Stone crab larvae exhibit a positive photo-response in high light intensities, a negative response in low light intensities, and rapidly sink if their light source is abruptly extinguished (Forward 1977).

The energetics involved in larval growth were calculated by Mootz and Epifanio (1974). Larvae starved immediately after hatching exhibit a much greater negative effect (stunted growth, death) than those starved after 1-2 days of feeding (Anger et al. 1981). Feeding is critical at first hatching. Larvae reared on brine shrimp exhibited greater survival than those fed rotifers (Sulkin and van Heukelem 1980). Goy and Costlow (1980) determined the nutritional effects of feeding Artemia from different geographical locations. Details of the development and ontogeny of the mandibles and gastric mill (Factor 1980) and sex characteristics (Payen 1974) have been studied in both larval and postlarval stone crabs.

Bookhout, Costlow, and associates (Bookhout and Costlow 1972, 1974; Bookhout et al. 1972; Costlow 1979) found that sublethal doses of various pesticides and pollutants tend to increase the frequency of the sixth zoeal stage and reduce survivorship of the larvae.

Juveniles in northwest Florida inhabit upper intertidal rocks singly, each juvenile possessing its own territory (Hazlett 1979). Savage and co-workers (Savage and McMahan 1968; Savage 1971b; Savage et al. 1974; Savage and Sullivan ms.) and Manning (1961) looked at various aspects of growth and molting in juvenile and adult stone crabs including rates of growth and effect of varying salinity and temperature on these rates. Cheung (1969) elucidated the relationship between endocrine control of growth and reproduction.

Bender (1971), Perry et al. (1983), and Bert (1985) have documented general habitat usage by stone crabs in northwest Florida, Mississippi, and southwest Florida, respectively. Studies on stone crab reproduction have included: 1) detailed accounts of the internal (Binford 1918) and external (Savage 1971a) fertilization process and mechanisms of its physiological control (Cheung 1969); 2) investigations of seasonality and fecundity (Noe 1967 and Bender 1971); 3) verification of transmolt sperm retention (Cheung 1968); and 4) mating habitat usage (Hembree 1984). Noe (1967) also described ten stages of female gonadal maturation, and an efficient precise method of conducting egg counts for fecundity measurements was formulated by Ros and Rojas (1978).

An investigation of the respiration and osmoregulation of adult stone crabs submitted to salinity and temperature stress conditions was done by Karandieva and Silva Lee (1967). They found that stone crabs could withstand salinities of 6.0 to 7.5 ppt when gradually acclimated without additional oxygen consumption and could survive total oxygen deprivation for 17-21 hours. Bender (1971) also conducted studies on the relationship of temperature and salinity to osmoregulation. Stone crabs have a relatively low rate of oxygen consumption when compared to other crabs (Ayers 1938), a constant metabolic rate over a wide range of oxygen concentrations (Leffler 1973), and can withstand severe hypopia (Albert and Ellington, in press). Suarez and Diaz (1969, 1971) also conducted general physiological studies on stone crabs in Cuba.

Stone crabs, voracious feeders, are known to eat mollusks of all types (Powell and Gunter 1968; Bender 1971). The mechanism and behavior they exhibit in opening various types of mollusk shells was described by Vermeij (1978) and Merz (1979). Vermeij (1978) and Kent (1983) discuss adaptations in mollusk shells to inhibit such predation. The damage they can inflict upon oyster beds when feeding is well documented (Menzel and Hopkins 1956; Menzel and Nichy 1958). They have also been reported to feed upon quahog clams (Mercenaria mercenaria) occasionally (Whetstone and Eversole 1978). Suchenia and Claro Madruga (1967) studied adult stone crab feeding energetics and found that stone crabs could exist for up to two weeks after consuming a maximum of food.

The antagonistic disposition of the stone crab is well known among those who deal with the organism. Sinclair (1977), in the only behavorial study of the animal conducted to date, found a great deal of ritualism associated with intraspecific encounters, a common occurrence in agressive species. The primary weapons of the stone crab are its large and formidable claws. Brown et al. (1979) measured 14,000 p.s.i. pressure exertion at the tip of the pincer claw in an adult stone crab.

Stridulation, originally reported to be absent in the stone crab (Guinot-Dumortier and Dumortier 1960), has been observed and may serve an important function in territorial and mating behavior (Bender 1971; Bert et al. 1978).

Electrophoretic work on the stone crab has included a single interpopulational study of haemocyanin (Rodriquez 1975) and a comprehensive investigation of geographic variation throughout the range of the species in the USA (Bert 1985). Protein variation with differences in sex, size, missing chelae, water temperature, reproductive activity, and diet were considered in Rodriquez's study. Only degree of starvation produced significant differences in the basic electrophoretic pattern. A study of the oxidative metabolism of stone crabs (Mauro and Magnum 1982) found that the performance of the haemocyanin-oxygen transport system was maximized at 15 °C, and that the gill was incompletely oxidized at 25 °C.

The only microhistological study conducted on stone crabs has been an investigation of the photoreceptor microvilli, when Eguchi and Waterman (1973) compared a number of crabs.

Several studies have shown that several common crab parasites infest stone crabs. Chitinoclastic bacteria cause "black spot" on the exoskeleton (Iversen and Beardsley 1976). Fungal parasites invade the ova (Bland and Amerson 1975), and the goose-neck barnacle ectoparasite (Octolasmis muelleri) attaches to the gills of crabs in regions of hybridization (T. M. Bert, pers. observ.).

A commercial fishery is based upon the huge claws of the stone crab. If the crab survives the declawing process, it can regenerate its claws within one year (Sullivan 1979) or more. The nature of the fishery has generated much investigative interest in mortality and rates of regeneration associated with declawing. Davis et al. (1979) found that survivorship was greatly reduced when the basal-ischial declawing wound was greater than 14 mm in diameter; Schlieder (1980) found reduced survival after declawing following prolonged atmospheric exposure. Rates of claw regeneration have been documented for crabs of various sizes by Cheung (1973), Sullivan (1979), and Savage and Sullivan (1978). Claw removal at first crab stage has been shown to generate rapid growth (Rodriguez and Yang 1977). Cheung (1976), in a biostatistical study of the heteromorphic claws, deduced that "left handed" crabs (the term "handed" meaning the crusher claw) had developed from normal "right handed" crabs that had reversed crusher claws upon loss of the original right crusher claw. Recently, Simonson and Steele (1981) and Simonson (in press) have looked closely at claw reversal in all sizes of stone crabs. They believe that claw reversal occurs in young, but not necessarily in older, crabs.

The biology and Florida fishery of the stone crab were reviewed in detail by Bert et al. (1978) and again by Lindberg and Marshall (1983). The Cuban fishery was reviewed and evaluated by Ros and Perez Perez (1979). Several additional reports on the economics, methods, and extent of the U.S. fishery have been produced by Florida Sea Grant (Prochaska and Cato 1974, 1975; Prochaska 1976; Prochaska and Landrum 1981), the Florida

Department of Natural Resources (Savage et al. 1975; Sullivan 1979) and National Marine Fisheries Service (Zuboy and Snell 1980, 1982). A fishery management plan for federal waters in the Gulf of Mexico has been in effect since 1979 (Costello et al. 1979).

Mariculture efforts on stone crabs have met with very limited success. Among other problems in closed system stone crab culture, hydrozoans are reported to be significant pests (Sandifer et al. 1974). In the laboratory, stone crabs reared from eggs have reproduced successfully (Cook 1969; Lindner and Cook 1971; Yang 1971, 1972; Roberts 1975) and winter mating has been induced (McConaugha et al. 1980). Yang attempted a large-scale rearing experiment in outdoor tanks and ponds from egg to marketable adult (Yang and Krantz 1976). He experienced highly variable growth rates and very low survivorship. In essence, the stone crab is a high level cannabalistic carnivore with aggressive behavior and, thus, has food and space requirements which make the economic feasibility of mariculture questionable. Nevertheless, it has been incorporated into a program exploring closed system mariculture in both South Carolina (Sandifer and Smith 1974) and the Bahamas (Robert McConnaughey, Wallace Groves Aquaculture Foundation, Freeport, Bahamas, pers. comm.).

METHODS

Field Sampling

Sampling by trapping was conducted throughout the coastal waters of Everglades National Park and Biscayne National Park. Seventeen stations were located in Everglades and five in Biscayne (Figure 1). Table 1 lists the physical characteristics of each station. Five plastic commercial stone crab traps (Isle of Capri Fisheries, Naples, Florida) were set at each station. Traps were placed linearly approximately 100 m apart and baited with processed ground herring crab bait (Atlantic and Gulf Fishing Supply Co., Miami, Florida). Traps were pulled on a lunar cycle on the full moon for a one year period.

Traps were initially set at 16 of 22 stations during May and June 1979 (Table 1) for acclimation to the water. All traps were pulled (taken from the water), cleaned of captured crabs, baited, and replaced in June to begin the study. Six more stations were added to the study in October. Traps used at these stations were not presoaked. All traps were sampled through June 1980.

After a trap was pulled, an array of biological and morphological data was taken on each captured crab large enough to tag (about 30 mm carapace width, CW) (Table 2). The crab was then tagged with a sphyrion spaghetti tag (Floy Tag Co., Seattle, Washington) if not previously tagged, and released. Additional notes were taken on biotic fouling organisms on the trap and on number of juveniles too small to tag found on the trap. Small juveniles were collected by first searching the interior of the trap, followed by scraping the entire exterior clean of fouling organisms and systematically sorting through the debris for the juveniles. The traps were then rebaited, tied closed with 100 lb test monofilament fishing line, and replaced on site.

Surface, mid-water, and bottom salinity and temperature were taken with a salinometer, or surface salinity and temperature were taken with refractometer and thermometer.

Statistical Analysis

Except where noted, statistical tests used followed procedures found in Steele and Torrie (1960); Snedecor and Cochran (1967); Sokal and Rohlf (1969). Overall spatial and temporal relative abundance for both adults and juveniles was evaluated by non-parametric methods. The Friedman test for randomized blocks was used to test for significant differences among months. This analysis was followed by the Kruskal-Wallis test to detect differences among stations. The Wilcoxon-Mann-Whitney simultaneous test procedure (STP) was used to isolate differences when they did occur. Detailed analysis of relative abundance over time among individual stations or groups of stations was accomplished by completely random design analysis of variance and Student-Neuman-Kuel (SNK) range test for location of significant differences.

Where sample size was adequate or several stations could be logically pooled, the heterogeneity G-test was employed to investigate variations in sex ratio over time and space. The interactive capacity of this test allowed statistical comparisons to be made among stations and among months and enabled partitioning of homogeneous sets of replicates into significant groupings by the STP. In cases where sample size was too small for the G-test, actual probabilities were calculated or results were simply discussed.

Statistical analysis of size, molt frequency, mating, and spawning for spatial and temporal variation was done using completely random design analysis of variance or t-test for detection of significant differences and SNK range test for partitioning the differences. The data from several months or stations were frequently pooled for analysis in the most logical and statistically meaningful manner to compensate for the recurring problem of small sample size.

The Somerton (1980) method of estimating size of 50 percent sexual maturity was employed to estimate size of reproductive maturity in males. This method utilizes the shift in allometric proportions of two body dimensions that commonly occurs when crabs reach sexual maturity to estimate the size at which a randomly chosen individual has a 50 percent chance of being sexually mature.

Two methods of calculating annual mortality rate were used. The Hancock (1965) approach involves the calculation of an instantaneous mortality coefficient (Z) for crabs by using annual molt increment and numbers of crabs in small size classes within the molt increment. The slope of the least squares line generated by plotting size against the natural logarithm of numbers of crabs of that size is proportional to the total mortality rate ($N_t = N_o e^{-zt}$) over the range in which growth is effectively constant. In this case, mortality coefficients were calculated for each sex and each molt increment possible. Annual mortality rate was also calculated for each sex and molt increment using proportion of animals lost (or gained) between adjacent 2-mm size classes. The proportions were summed for all size classes within a molt increment to give estimates of percent of the population lost within that molt increment.

Temporal and spatial relationships among biological (relative abundance of adults and juveniles, sex ratio, spawning, molting) and physical (salinity, temperature) factors were investigated using multiple and simple correlations. Generally, three-factor multiple correlation was used to test one biological factor against either two other biological, or the two physical factors.

RESULTS

Seasonal Distribution

Relative Abundance

Adults: Because some stations were sampled for an entire year (13 samples) and others for only part of the study period (9 samples), overall differences in relative abundance were analyzed twice using the same statistical methods. Only the 16 stations sampled throughout the year were evaluated for the entire sample period, and all 22 stations were analyzed for the nine samples.

Both sampling groups showed highly significant differences among stations (p is less than .005). Rank analysis grouping stations with statistically similar means for the two periods (Table 3) showed that two stations sampled throughout the year (Northwest Cape and Sandy Key Channel) had a sufficiently lower mean number of crabs per trap line when only 9 months were averaged so as to change them to a grouping of lower relative abundance. Of the other stations sampled throughout the year, two (Pavilion Key and Outside Lostmans River) showed slight decreases, and six (Conchie Channel, Twin Key Basin, Lostmans River Channel, Pelican Bank, Inside Sands Cut, Tern Keys) showed slight increases, in mean relative abundance when averaged from only November to June. However, in no case was the magnitude of change great enough to change the grouping of any station.

No significant differences in relative abundance among months were detected for either group analyzed. To further investigate changes in relative abundance over time, individual stations were analyzed for changes in average number of crabs captured per trap per month. Only four stations showed significant variation in mean catch over time (Northwest Cape, p less than .05; Conchie Channel, p less than .01; Sandy Key Channel, p less than .01; Inside Sands Cut, p less than .001). Figure 2 illustrates mean catch per trap per month for each station. No overall patterns in catch rates over time were readily apparent, but several different trends were seen among the stations. Several stations had mean catch rates that were generally higher in summer and fall and lower in winter and spring (Outside Lostmans River, Northwest Cape, Sandy Key Channel, and Billys Point). Shark Point and Arsenicker Keys also appeared to follow this trend, with a delay factor of two months (however, these stations were not sampled in summer and early fall). A number of other stations showed a marked increase in relative abundance in spring and/or early summer over other times of the year (Chokoloskee Bay, Black Betsy Keys, Tern Keys, Blackwater Sound, and Outside Sands Cut). Bimodal peaks in catch rate occurred at several stations. Of the stations sampled throughout the year, Pavilion Key, Captain Key, and Pelican Bank had relatively high catch rates in fall and spring, while Lostmans River Channel, and Conchie Channel had winter and spring peaks. Chatham Bend and Twin Key Basin also had winter-spring peaks, but were not sampled during all fall months. Only six of the 21 stations at which stone crabs were captured did not show elevations in catch rates sometime between March and June (Shark Point, Sandy Key Channel, Arsenicker Keys, Captain Key, and Billys Point). Of the stations sampled throughout the year in the Gulf of Mexico, only Chokoloskee Bay and Lostmans River Channel did not show additional fall maxima.

Juveniles: Juvenile stone crabs were found on traps only at Gulf of Mexico stations and at Conchie Channel in Florida Bay, with the exception of one juvenile found in September at Billys Point in Biscayne Bay. The vast majority of juveniles were less than 5 mm CW. Thus, the number of juveniles found on the traps was taken to be representative of the number settling at about that point in time.

Similarly to the analysis of adults, spatial differences in relative abundance of juveniles were analyzed twice--once using only stations sampled throughout the year and once using all 22 stations for nine samples. Some stations were significantly different from others in both instances (p less than .001). No stations changed groupings, as they did for adults. A composite of similar stations was derived from the two analyses (Table 4). Stations in the high number category (the offshore Gulf of Mexico, north of the Shark River) had 86 percent of all juveniles captured. Thirteen percent of the juveniles came from the moderately low group (coastal gulf at the mouths of estuaries and offshore gulf, from the Shark River southward) and only one percent from all other stations (Lostmans River channel, Florida Bay channels and basins, and Biscayne National Park).

An obvious peak in settlement from September through November occurred at most stations where juveniles were found (Figure 3). Only Shark Point displayed a notably delayed peak in recruitment. The monthly number of juveniles settling was significantly greater during the three peak settlement months than during the rest of the year (p less than .01).

Sex Ratio

Spatial Differences

Overall, a significant deviation from a 1:1 sex ratio (p less than .001), was observed due to higher capture rates of males. The proportion of males also varied significantly among trapping locations (p less than .01). In northeast Florida Bay, overall sex ratios (male:female) were 1:1 at Black Betsy Key, 1:2 at Tern Keys, and 11:4 at Blackwater Sound. At

Conchie Channel, virtually only males were caught, while at some northern gulf and Florida Bay stations, sex ratios were not significantly different from 1:1 (Pavilion Key, Outside Lostmans River, and Captain Key). The stations clustered into two distinct groups (Table 5). A group with very high proportions of males was composed of stations in the Gulf of Mexico below Lostmans River (except Sandy Key Channel), Lostmans River channel, and Biscayne National Park. Stations with significantly more females were located in the Gulf of Mexico from Lostmans River northward, the basins of Florida Bay, and at Sandy Key Channel.

Temporal Variation

Sex ratios (male:female) differed significantly among months in the Gulf of Mexico and western Florida Bay (p less than .001), but not at other locations. A significantly higher percent of males was captured from late summer to early winter at these stations (p less than .001) (Figure 4). However, most of this monthly variation was due to changes at those stations falling into the statistical group with a relatively low proportion of males. Those stations showed an abrupt decrease in the proportion of males captured from March to July. The ratio again abruptly changed to very high proportions of males after July. The group of stations with relatively high proportions of males also differed seasonally (p less than .01), but the changes in sex ratio were not as distinctive. Only the month with the lowest sex ratio (February) was statistically different from the months with the highest ratios (August and December/January). However, the percent of males was somewhat lower from January through June than in the remainder of the year.

In northeast Florida Bay (Black Betsy Keys, Tern Keys, and Blackwater Sound), females were only captured in spring and summer. When present, the females greatly outnumbered males (April to August sex ratio, 3:14). Only males (n=8) were caught from late summer through winter (September to February). March was apparently a transition month with a M:F sex ratio of 5:1. No crabs were captured from October to January.

In Biscayne National Park, low catch success made determinations of sex ratio questionable. Only January had a sex ratio approaching 1:1. Sex ratios varied greatly for other months, and no seasonal trends were apparent. Few females were captured in Biscayne National Park over the entire study period, but pooling the monthly data according to the seasonal pattern seen in Everglades National Park resulted in a lower sex ratio from January through July than from August to January (male:female = 35:4 and 60:3, respectfully).

The greatest actual number of males per trap was captured from November through June at all stations in the Gulf of Mexico and channels leading from the gulf to Florida Bay, except at Northwest Cape and Sandy Key Channel, where number of males captured was highest in summer. The greatest number of males was captured in February and March in the basins of Florida Bay, and in December/January, March, and April in Biscayne National Park.

Size Composition

Mean Size

Size distribution of crabs (mm CW) captured followed a normal distributional curve. Therefore, the mean and standard deviation of size was used for statistical comparisons over time and space.

Mean size of both male and female stone crabs varied greatly among sites sampled (Figure 5). For males, all stations offshore in the Gulf of Mexico north of Shark Point, along with Lostmans River Channel had the smallest mean size and were statistically similar. The two remaining gulf stations located close to shore had small males, but significantly larger than the offshore stations. Northwest Cape had intermediate-sized males and did not fall into any group. All stations in Florida Bay and Biscayne National Park formed a group with large males. Northeast Florida Bay had substantially larger males than did the remainder of the bay. In Biscayne National Park, mean size of males increased from the coast to the reef.

Although groups of statistically similar size were not as clearly defined for females, inspection of the data revealed essential categories--a group with small females in the Gulf of Mexico and one with large females in Florida Bay and Biscayne National Park. Mean size of females generally increased with movement southward in the gulf and into Florida Bay. As with males, the largest females were found in northeast Florida Bay. Only a few females, of all sizes, were captured in Biscayne National Park.

Monthly comparison of mean size, where sample sizes were adequate, revealed significant differences at three stations for males and two stations for females (Figure 6). All offshore Gulf of Mexico stations and Conchie Channel showed a decline in mean size of males during winter. Shark Point, Northwest Cape, and Sandy Key Channel exhibited a reduction in mean size of males in spring and early summer. Conchie Channel had a decline in mean size of males in September, a pattern not seen elsewhere. Females in the offshore gulf from Lostmans River northward also showed a winter reduction in mean size. Shark Point had a decline in female mean size in spring and early summer, analogous to the situation for males at that station.

Size Class Frequency

Ten millimeter size class histograms were used to further investigate change in size of stone crabs during the study. Three criteria were used to group stations for histogram comparisons; 1) statistical similarity of overall mean size; 2) comparability of geographical location and habitat; and 3) similarity of seasonal variation in mean size. A station was omitted from the analysis if it could not be categorized by these standards. In cases where a station fell into two different groups, overall mean size and geographical location were given priority. Table 6 lists groups constructed for both sexes and characteristics of each group.

Males: Figure 7 presents size class frequencies by month for the station groups in Table 6 that had sufficient numbers of crabs to illustrate general trends. In the offshore Gulf of Mexico, modal size usually ranged between 90-100 mm CW. Notable increases in small size classes (less than 80 mm CW) were seen from fall to spring. The size of most crabs captured clustered around the mode from August through December, followed by a spread with all size classes more evenly represented through June. Largest size classes (greater than 120 mm CW) were found from February through June.

Except for December, modal size of males in the nearshore Gulf of Mexico was 100-110 mm CW from fall through winter. Size distribution was usually clustered tightly about the mode. Smaller size classes (less than 80 mm CW) were captured in relatively high frequencies in December, with a return to larger classes in January when the largest males were captured (to 140 mm CW). Modal size decreased to 90-100 mm CW in spring, influenced by a reduction in mean size of crabs captured at Shark Point.

Modal sizes in Florida Bay were large (110-130 mm CW) most of the year. A shift to smaller size classes occurred in September and October, when modal size dropped to 100-110 mm CW. Smaller size classes were also collected in January when only a few males of a broad range of size frequencies were caught. Highest proportions of large males (greater than 130 mm CW) were captured in February and April.

No distinct mode was usually apparent in Biscayne National Park males. However, many large males (greater than 120 mm CW) were taken in the December/January sample and all small males (less than 80 mm CW) were trapped from July through December.

Females: A distinct mode of 90-100 mm CW was observed in July and August for the offshore gulf (Figure 7). An increase in the proportion of smaller females (less than 70 mm CW) occurred from September to November, during which time no clearly definable modal size was present. Virtually all crabs collected in December and January were less than 100 mm CW and modal size dropped to 40-50 mm CW in January. In February, a shift back toward larger crabs began until modal size reached 80-90 mm CW in May and June.

A distinct modal size was not evident for the nearshore Gulf of Mexico, possibly due to low sample sizes. However, comparatively smaller crabs (all less than 90 mm CW) were obtained in March, whereas larger crabs were captured in February and April (all greater than 60 mm CW). No influx or efflux of any size class was apparent.

In Florida Bay, size frequencies could only be identified for February (90-100 mm CW) and March (100-110 mm CW) due to low catch rates. All females collected were less than 110 mm CW in the fall. Most females were more than 90 mm CW the remainder of the year, ranging to 130 mm CW in all months except January.

Growth and Mortality

Molting

Seven males and 33 females were molting at the time of sampling during this study. A crab was considered to be in the molting state if it had a soft exoskeleton (postmolt) or was beginning to emerge from its old exoskeleton which had separated at the molting suture lines (premolt).

Twenty-six molting females were found at the offshore Gulf of Mexico stations, five at nearshore gulf stations, and two in west Florida Bay. Four molting males were captured offshore and one nearshore in the Gulf of Mexico, one in west Florida Bay, and one in Biscayne National Park. All molting females were observed from September to June, with bimodal peaks in late fall and in spring (Figure 8). Males were found molting in July, September, January, March, and April. Analysis of variance and Student-Neuman-Kuel range test determined that mean size of females molting in the fall (Sept.-Nov.) ($x=87.3$; S.D.=16.8 mm CW; N=10) was significantly larger than that of females molting in winter (Dec.-Feb.) ($x=60.6$; S.D.=18.5 mm CW; N=10) or spring (Mar.-June) ($x=69.1$; S.D.=9.7 mm CW; N=13) (p less than .01).

Intermolt growth increments for four males and 12 females were available from capture of postmolt crabs and their exuviae at the time of sampling (Table 7). We recaptured no tagged crabs of either sex which had grown while at large. Growth of males, in both absolute change and percent increase in size, was greater than that of females. Model I linear regression of female growth showed that growth rate was constant over the size range available for testing (Figure 9). Curvilinear regression was tested by $x + 1$ and log x transformation, but linear regression gave the best fit to the data.

Mortality

Mortality coefficients were computed for adult stone crabs collected from the western Florida coast (Gulf of Mexico plus Florida Bay). Crabs were separated into 2-mm size classes for estimates of age class mortality (Figure 10). The size class captured in the greatest proportion was used as 100 percent trap retention length (102-104 mm CW, males; 94-96 mm CW, females). Molt increments of 16 mm CW for males (Everglades National Park, unpublished data) and 10 mm CW for females (Table 7) were used to define year classes, with the 100 percent retention length as the starting point. Molt frequency was assumed to be annual over the range for which mortality rates were calculated (Cheung 1969; Sullivan 1979; Everglades National Park, unpublished data).

Table 8 presents the results of the Hancock (1965) method of estimating mortality rate and shows a large discrepancy for both sexes in total annual mortality between the two age classes examined, with the older class undergoing the higher rate of mortality. In addition, mortality rate of females for both molt increments is substantially lower than that of males. Table 9 gives the total mortality estimate using a second method which assumes a constant recruitment level for all years. Results closely agree with those obtained using the Hancock method. These estimates indicate that about 99 percent of the males alive at the start of the 102-104 mm CW size class died within the following two molt increments. Approximately 83 percent of the females alive between

94-96 mm CW were lost by the time they reached 112-114 mm CW, also two molt increments.

Reproduction

Mating

Over the course of our field sampling, a number of pairs of stone crabs were trapped while in mating condition. A pair was classified as a mating pair if one or more of the following criteria were met:

1. The female was paired with a male defending her and she was in the premolt or postmolt condition.
2. The only female present in the trap was paired with her defending male and all other males had been killed.
3. The female and her defending male were spatially separated from other crabs in the trap, as identifiable when the mating pair would be found in the bait cup attached to the upper corner of the trap.

Although most stone crabs are typically aggressive to varying degrees, the type of aggressive behavior exhibited by a male defending an apparently sexually receptive female was easily distinguishable. When a stone crab of either sex is approached for removal from the trap, its avoidance behavior characteristics include both presentation of the claws and independent movement around in the trap. A defending male presents his claws and is usually aggressive but does not move. Rather he will remain above the unresponsive female trying to maneuver her under his walking legs. Once the male is removed, the female generally remains relatively unaggressive and attempts to hide rather than defend herself against the intruder. Savage (1971) noted similar behavior of mating pairs in burrows during field observation.

We found 34 mating pairs from September through June; 25 in the offshore Gulf of Mexico, 7 along the gulf coast, and 2 in western Florida Bay channels. The highest proportion of the population found mating was in the fall, notably October (Figure 11), with another lesser peak in April.

For statistical analysis of size of mating pairs vs. time of year, and size of crabs composing a mated pair, the size of mating females was standardized to postmolt carapace width where necessary by adding 10 mm to the premolt measurement. The mean size of mating crabs of both sexes in spring (March-June) (males: $x=89.4$, S.D.=12.0 mm CW; females: $x=71.9$, S.D.=8.5 mm CW; $n=23$) was significantly smaller (analysis of variance, p less than .01) than mean size in fall (Sept.-Nov.) (males: $x=106.5$, S.D.=9.4 mm CW; females: $x=87.4$, S.D.=16.0 mm CW; $n=11$). A highly significant correlation (p less than .01) existed in size of males and females composing a mated pair in the traps (Figure 12). The size of 50% reproductive maturity in males is 71 mm CW (Figure 13).

Spawning

Spawning females were observed only in Everglades National Park (Table 10). The largest number of gravid females was found along the gulf coast, but the highest relative proportion of gravid females was captured in northeast Florida Bay.

Mean size of ovigerous females in both the Gulf of Mexico and Florida Bay was significantly larger than mean size of all females (Table 11). This observation would be expected in the gulf, where large numbers of small females were captured. However, all females captured in Florida Bay were well above the average reported minimum size of spawning (about 40 mm CW). No statistically significant differences were found in mean size of gravid females among months in any area, due to the high variability in reproductive size. However, most crabs spawning in winter in the Gulf of Mexico were 10-20 mm CW smaller than the mean size of gravid females for all other months. The highest percentage of spawning females in the Gulf of Mexico occurred in mid-summer (Figure 14), with a lesser peak occurring in May.

Females from Everglades National Park were divided into age classes to further investigate the variation in proportion of females among reproductive stages with increasing size (Figures 15 and 16). Studies on growth of stone crabs have shown that females reach an average size of about 40-60 mm CW at age one, 60-80 mm at age two, and increase their carapace widths by about 10 mm per year after that (Savage and McMahan 1968; Cheung 1969; Yang and Krantz 1976; Savage and Sullivan 1978; Sullivan 1979; present study).

Females of age classes 1 and 2 were found to molt twice as frequently as older age females (Figure 15) and molted with equal frequency during all seasons in which females were found molting (Figure 16). Older females molted essentially only after the summer spawning season, and not in spring. The proportion of females of age 1 found mating was not significantly greater than that of older age classes, but age 2 females mated with significantly greater frequency (p less than .05) than age classes 4 through 7, and age 3 females mated with significantly greater frequency than ages 4 and 5 (Figure 15). Females more than 3 years old were only observed mating in the fall, whereas smaller females mated not only in the fall, but in winter and spring as well (Figure 16).

A relatively low proportion of females less than age 3 were found in the ovigerous condition (Figure 15). From age 3 to age 6, the proportion was consistently slightly under 30%. Most 7 year old females captured were gravid. Females of age groups 3 and older-than-3 contributed significantly greater proportions (p less than .01) of the spring spawning effort compared to that of the younger-than-3 age group (Figure 16). No spawning in any age group was observed in October and November, when 31 and 46 females were captured, respectively. Winter spawning in age groups 3 and older-than-3 was only observed in February; no females in these groups were found spawning from October through January.

DISCUSSION

Distribution and Abundance

Spatial Distribution

In general, the greatest number of adult stone crabs was found in the offshore Gulf of Mexico north of the Shark River and in the channels that connect Florida Bay to the gulf. The greatest number of juveniles and highest proportion of females were seen in the offshore Gulf of Mexico from Lostmans River northward. Also, stone crabs in that section of the gulf were smaller than those found elsewhere. Progressing southward along the gulf and east into Florida Bay, both adults and juveniles continuously declined in number, adults became larger, and the proportion of males generally increased. Like Florida Bay, Biscayne National Park had few, generally large, crabs, a high percentage of males, and no juveniles. With movement from the mainland coast to the reef, relative abundance dropped and average male size increased.

Of the biological and physical factors considered in this study (see Statistical Analysis section), the distribution and abundance of adults was correlated solely to the distribution and abundance of juveniles (p less than .05). As far as is known, no unique stone crab predators or competitors are present in areas of low relative abundance, and habitat and food do not seem to be limiting resources in at least some of these areas (T.M. Bert, pers. observ.). Similarly to this study, Bender (1971) trapped his greatest catches in offshore areas of the Cedar Keys.

Juvenile distribution and abundance was correlated with relative abundance of adults and also to proportion of females in the trapped population (p less than .05). There was a highly significant interactive component between the two factors in determining relative abundance of juveniles (p less than .005). Although a number of females was collected in the basins of Florida Bay, and spawning females were present, no juveniles were ever collected. Plenty of juvenile habitat was available on the fouled traps. The fouling community was, in most cases, similar to that seen in areas of high levels of juvenile settlement. Juveniles have been reported to be relatively common in west Florida Bay in the past (Manning 1961; Tabb et al. 1961). However, no juveniles were sighted in 230 man-hours of *in situ* searching by SCUBA in the basins of west Florida Bay during a concurrent study to be published elsewhere.

Environmental factors that may contribute to the absence of juveniles from some areas include seasonal extremes in salinity and temperature in Florida Bay and Biscayne Bay and rapid salinity fluctuations in coastal and inshore areas during the summer rainy season. Salinity and temperature (see Area Description) reach levels harmful or lethal to larvae and juveniles at these times (Ong and Costlow 1970; Bender 1971). Juvenile stone crabs utilize a wide variety of substrates for cover (Hay and Shore 1918; Powell and Gunter 1968; Bender 1971), and it is doubtful that substrate for settlement is limiting, particularly since some of the most extensive expanses of suitable substrate are found in areas where juveniles are rare or absent. It seems unlikely that larvae or juveniles would migrate from these areas. Extensive larval or juvenile migrations are not known for stone crabs.

The size of a stone crab, as with most other organisms, is indicative of its age. The significant difference in size of both sexes over the area encompassed in this study indicates that stone crabs may spatially segregate by age, or that fishing practices have gleaned the largest crabs from certain areas (T.M. Bert, unpublished data). Males reach an average size of about 40-60 mm carapace width at one year of age, 60-90 mm at two years, 90-110 mm at three years, 110-125 mm at four years, and 125-140 mm at five years (Savage and McMahan 1968; Cheung 1969; Yang and Krantz 1976; Savage and Sullivan 1978; Sullivan 1979; Everglades National Park, unpublished capture-recapture data on 67 males). Based on this size/age relationship in males, and on that of females previously discussed (see Spawning), stone crabs of both sexes are predominately two- to three-years old in the Gulf of Mexico. In Florida Bay, most males are four years of age in the western part of the bay and five years old in the eastern part; most females are four to five years and six-years old in these respective sections of the bay. Males range from two to seven years of age in Biscayne National Park, with the older age classes predominating seaward.

Temporal Variation

Several stations in the Gulf of Mexico and channels connecting Florida Bay to the gulf were lower in relative abundance of adults during the fishing season. One station south of the Shark River and one in a gulf-to-bay channel dropped significantly. No unusual variations in salinity or temperature occurred at these stations. If crabs moved from these sites, the movement was to waters farther offshore or to areas not sampled, because compensatory increases in relative abundance did not occur at other sites monitored within the park. Commercial fishing pressure has previously been attributed to the seasonal reduction of relative abundance (Sullivan 1979; Wenner and Stokes 1983) and mean size (Savage et al. 1975), and may contribute to the decrease in abundance of crabs at these stations.

Changes in relative abundance at other stations were related to a number of factors. The entry of females into traps seemed to be strongly influenced by seasonal molting and spawning. In the month preceeding spawning, a number of metabolic and physiological changes occur within the female (Noe 1967; Cheung 1969). These changes may have induced females to enter traps which, in turn, affected the sex ratio of crabs in the traps. The proportion of females in traps was correlated to percent of gravid females captured (p less than .05) when the latter factor was delayed by one month. The proportion of females trapped was negatively correlated to molting (p less than .05), and molting and spawning were interactive (p less than .05) in their influence on the ratio of females to males in traps. In the Gulf of Mexico, sex ratio was also highly correlated with salinity (p less than .01), but not with temperature. The correlation with salinity in the gulf may only be an autocorrelate since the rainy season and spawning season coincide and the rainy season strongly influences salinity along the open gulf coast.

The greatest number (but not necessarily highest proportion) of females was captured in spring in the gulf, when large females began spawning and smaller females molted and mated; some elevation in numbers occurred coincident with the fall molting peak in the coastal gulf and the basins of Florida Bay. Females do appear to enter traps in greater numbers during molting season. The negative correlation seen between molting and proportion of females trapped may be the result of the combined effect of the inverse relationship between molting and spawning (see Aspects of Biology), and the fact that trapped molting females probably attract males to traps so that the sex ratio reflects the disproportionate entry of males competing for receptive females. More crabs of both sexes entered traps during molting season, and the increase in number of males was greater than that of females. In previous studies, Noe (1967) and Sullivan (1979) also trapped the highest proportion and number of females during spawning season. Noe also noted a small increase in number of females in traps coincident with the fall molting season and drop in water temperature.

Both the proportion and number of males captured fell from January to June at most stations. The proportion of males could not be correlated to any obvious internal seasonal biological processes, as could females, but was negatively correlated to salinity (p less than .05). Here, as with other studies (Noe 1967; Bender 1971; Bert et al. 1978; Sullivan 1979), most males entered traps after a sudden drop in water temperature in winter, and when females also entered with greater frequency during their molting season.

In the gulf and gulf-to-bay channels, the decline in the proportion and number of males observed during winter was more noticeable at fished stations, probably due at least in part to the removal of males from the park by commercial fishermen (Bert et al. 1978). Also, in the gulf and adjacent channels, no spring peak in number of males captured was seen, contrary to the situation in both the basins of Florida Bay and Biscayne National Park. Many commercial traps were observed at the two stations where the decrease in abundance of males was statistically significant. More males were collected during the closed season (May 16 to October 15) at these stations than at any other time of the year. Noe (1967) and Bender (1971) had disproportionate numbers of female crabs throughout the year when stone crab fishing laws allowed only the taking of male crabs.

During the year, sex ratio changed more dramatically in the northern gulf coast area above the Shark River and in the basins of Florida Bay, than it did in the southern gulf and gulf-to-bay channels and Biscayne National Park. With the exception of Sandy Key Channel, stations that dramatically shifted in sex ratio fell into the low proportion of males group.

The winter-early spring decline in mean size of males and females in the gulf from Lostmans River northward could have been due to a number of factors. 1) The decline was highly correlated with temperature (males: p=.01; females: p less than .01). The decrease in temperature may have triggered a differential behavioral response among the age classes. Bender (1971) noted seasonal change in mean size of males in traps due to movement of different size classes into or out of an area. The increase in number of smaller males was also associated with a decline in proportion of males and/or relative abundance at several stations. Possibly small males are deterred from entering or remaining in traps stocked with large crabs. Size class frequency of males spread from the mode during this period, whereas females shifted modes and entire age classes disappeared. Large females may simply not enter traps during certain seasons. 2) Larger crabs may have been removed from the population through commercial harvest. The slight decline in CPUE seen concurrently with the decrease in mean size in this region supports this suggestion. The fact that females are affected similarly to males implies that either the influence of the commercial fishery harvest, conducted outside the park boundary, is seen within the park or, alternatively, that the change in mean size was not due to the fishery. 3) Smaller size classes may have molted to a size at which they were retained in traps, causing an influx of small crabs in the traps. Seasonal molting and the growth of year classes have been previously related to changes in mean size and size range during the year (Sullivan 1979). However, such an event should result in an increase in CPUE, contrary to the observed decline.

Aspects of Biology

Juveniles

Laboratory studies have shown that larval stone crabs proceed through development to settlement in 14 to 28 days, with most observations centering around 21 to 28 days (Ong and Costlow 1970; Bender 1971; Yang 1971; Mootz and Epifanio 1974; Yang and Krantz 1976). Our study indicates that stone crab larvae may have a longer pelagic life in nature than has been seen in the laboratory. Correlations between peak spawning and peak settlement months were highest (p less than .01) when a three-month delay was applied to spawning time. Allowing a mean of four to seven days for maturation of eggs (Binford 1918) and three to four weeks for molting to modal size of captured juveniles (about 3.5 mm CW) (Savage and McMahan 1968; Yang and Krantz 1976), the larval stone crabs would had to have spent an average of about eight weeks in the plankton.

Ong and Costlow (1970) and Bender (1971) reported a lengthening of time spent in the water column at temperatures and salinities below or above the optimum (30 °C; 30-35 ppt). Reduced salinities associated with the summer rainy season may have contributed to the longer settlement time we observed. Nearshore Gulf of Mexico stations, which showed delayed peak settlement when compared to offshore stations, also exhibited reduced salinities later in the year than did offshore stations.

Females

Molting in females is closely associated with reproduction since females can only mate when they molt and the exoskeleton is soft. However, molting apparently is not always an indicator of reproduction, particularly in younger crabs. Females begin to reach sexual maturity at about age one (McRae 1950; Powell and Gunter 1968; Cheung 1969; Bender 1971; Savage and Sullivan 1978; present study), but a substantial number may molt without mating. The low proportion of gravid females in this age class supports this idea. Similarly to age one females, females of age two also have a low proportion of gravid females despite equivalence in percentage of crabs molting and mating in that age class. Either these females have not matured enough to spawn (although they can mate), or they put forth fewer spawns during the season than do older crabs. Either the age at which females attain full reproductive maturity is highly variable, or reproductive maturation is a slow process in stone crabs.

Previous observations (Cheung 1969; Bender 1971; Sullivan 1979) have indicated that large stone crabs of both sexes molt once per year, and smaller females more frequently. Our data show that large females molt only in the fall, whereas smaller females molt in all seasons except summer. If the fall moltings of large females are indeed annual, the incidence of multiple ecdyses during the year sharply declines at age three. Only a small proportion of that age group molts or mates more than once per year. Beyond age three, females settle into a predictable pattern of molting and mating only once a year, in fall. The proportion of gravid females in the trapped population also doubles at this age and reaches the value held for most remaining age groups, suggesting that all females have reached reproductive maturity by this age.

Differences in timing of mating among age groups are reflected in peak spawning months of those groups. Bimodal peaks in April-May and August-September are seen when all ages are grouped. But different age groups contribute to those peaks. One- and two-year-old females mate in spring and subsequently contribute to the late summer spawning peak. They are the only age group to mate and spawn in mid-winter. Age three females have a greater proportion of females mating in fall and spawning in spring than younger crabs. Older age classes, mating in fall, exhibit a definite burst of spawning activity in spring. It is apparent that mating in fall promotes early synchronous spawning the following spring. Other researchers have also recorded similar bimodal spawning peaks for Florida stone crabs (Figure 17).

Since they may molt more than once between consecutive spawning seasons, young female stone crabs have an increased probability of becoming fertilized by more than one male per spawning season. The concurrent high incidence of mating in two- and three-year-old crabs indicates that they may in fact mate more than once a year. Trans-molt sperm retention has been documented in the species (Cheung 1968). Details of the storage of sperm from more than one male are currently being investigated (D. Wilber, Florida State Univ., pers. comm.).

The timing of molting and spawning necessarily oppose one another and the two processes are therefore negatively correlated (p less than .01, Noe 1967; p less than .05, present study) in the stone crab. Spawning acts to inhibit molting at the hormonal, physiological, and physical levels (Noe 1967 and Cheung 1969). Molting in crabs is also inhibited by cooler temperatures (Passano 1960). Thus, most molting is restricted to fall and spring when spawning is at low levels and water temperatures are not yet at yearly minimums.

The initiation and cessation of spawning activity are evidently regulated by external factors acting on hormonal controls (Cheung 1969). All studies on seasonality of spawning conducted to date have indicated that temperature is an important factor in determining spawning season (Noe 1967; Cheung 1969; Bender 1971; Sullivan 1979; present study (p less than .01)). However, neither the onset nor termination of spawning is controlled by a specific temperature, at least within the annual temperature range usually encountered in Florida. The incidence of gravid females increases notably at any time in spring (Figure 17). Temperatures recorded at the time of increased numbers of gravid females in past studies have ranged from 22-24 °C in March and April for Sullivan's and Noe's data, to 25-29 °C in May and June for Bender's study, and 25-29 °C in April and May for our study. When spawning activity decreases abruptly in October and November, temperatures recorded have ranged from 26-18 °C (Bender 1971) to 28-26 °C (present study). Cheung (1969) has suggested that light intensity plays an additional role in the control of spawning season.

Mating is also correlated to temperature (p less than .05) and, of course, to molting (p less than .05). However, molting is not correlated to temperature due to the high proportion of crabs undergoing ecdysis in early winter after water temperature has reached minimum values. The data suggest that a number of females molting late in the year may not be fertilized. Young stone crabs would presumably have another mating opportunity in spring, but older crabs would not and would be forced to rely on sperm retained after the molt for fertilization the following spawning season.

Stone crab claws are commercially harvestable at 70 mm propodus length. In females, this corresponds to a carapace width of approximately 87 mm (Sullivan 1979; present study). This size is within the same size class at which the female population reaches 100% sexual maturity (80-90 mm CW).

Males

Male stone crabs evidently lack seasonal regulatory controls on growth comparable with those found in females. Data is scanty, but our findings and those of others (Bender 1971; Sullivan 1979) suggest that males molt at any time of the year.

An Everglades National Park unpublished capture-recapture study suggests that incremental growth in males is both greater and more variable than that of females. In that study, time at large varied from 1 to 64 weeks (x=19 weeks). Molt increment did not significantly increase with time at large in any size class, with the exception of a single crab at large for 64 weeks (Figure 18). Thus, we might assume that only one molt occurred in these animals while they were at large. Data on the 67 males show an average variation of about 30 percent increase in size per molt for 10 mm size classes, and that increment of growth declines with increasing size (Table 12). Similar variation in females is about 15 percent (combining data from Sullivan 1979 and Table 7). The young males recaptured (less than 70 mm CW) grew a great deal more than did larger size classes. These males either molted more frequently or had disproportionately larger increases in size at molting. These males were at large from 13 to 26 weeks.

The notable reduction in growth shown by the Everglades National Park data occurring at about 70 mm CW suggests that males may undergo a shift in energy allocation at that size, possibly due to the onset of reproductive activity. The calculated size of 50% sexual maturity (71 mm CW) supports this idea (Fig. 13).

Males seem to have higher mortality rates and shorter life spans than do females. At least a portion of that difference could be attributable to commercial fishing. Trapping may capture disproportionate numbers of males. Males attain a larger size than females and have a proportionately larger claw size to body size ratio (Sullivan 1979). Both factors probably contribute to a greater retention of males in traps by reducing agility and mobility and the probability of successful escape. In addition, males enter the fishery at a smaller size than females (78 mm CW) (Sullivan 1979; present study) and are, therefore, subject to removal through fishing mortality, which may be quite high (Bert et al. 1978; Davis et al. 1979; Schleider 1980) at an age when females are still protected.

Males tend to mate with females of the same age class in traps. Two-thirds of the mating pairs observed were probably in the same age class, and all but three pairs were within plus or minus one age class. Circumstantial evidence (e.g. a higher incidence of male deaths in traps during mating season) indicates that males compete for females to serve as mates. Competition for mates may favor larger males (Bert 1985). Males were older than their mates in 75 percent of the mating pairs we collected with an age differential between mates.

About 65 percent of males had claws of minimum legal size that were involved in mating activity. Males reach harvestable size at age two, coincident with the beginning of most reproductive activity in both sexes. We found very few male crabs with claws below legal size that were mating.

CONCLUSIONS

Population Biology

The presence of relatively large numbers of young adults, newly settled juveniles, and a high proportion of females in traps are spatially varying population characteristics which seem to indicate the location of productive stone crab recruitment areas. Such an area exists in Everglades National Park marine waters from Lostmans River to the northern boundary of the park. High larval production apparently occurs from the relatively great numbers of females in this region. Juvenile settlement is successful, with good survivorship to adulthood.

The relative abundance of newly settled juveniles decreases with movement south along the gulf below Lostmans River and into Florida Bay until it reaches zero throughout much of the bay. Although gravid females are found throughout the bay, newly settled juveniles are found only in seaward channels of the bay. Mortality at either the egg or larval stage increases to 100 percent with movement south of Lostmans River and into Florida Bay. Two explanations are plausible. 1) Locally hatched larvae do not survive to metamorphosis in areas removed from the upper Gulf coast region of the park. Physiochemical or biological change in quality of the environment such as salinity and/or temperature extremes are likely contributing factors in the basins of Florida Bay, but would not account for the decrease in numbers of juveniles observed progressing southward in the gulf. Two major estuarine drainage systems flow into the gulf above Cape Sable. Moving southward, water characteristics become increasingly oceanic along the Gulf of Mexico and gulf-to-bay channels of Florida Bay. Alterations in environmental characteristics associated with remoteness from estuarine influences could reduce survival of larvae. 2) Hatching of eggs is unsuccessful outside of the recruitment area and larvae are transported south from this area along the gulf, around Cape Sable and into gulf-to-bay channels, where some settle. This case would suggest that some characteristic(s) of the environment present in the recruitment area and possibly associated with estuarine influences is necessary for egg maturation. However, we saw no overt indications of premature spawning or abnormal egg development in gravid females from areas where newly settled juveniles were rare or absent.

Either case implies that the primary source of stone crabs in Florida Bay is dispersal of adults from the more northern Gulf of Mexico recruitment ground. Rather than a single-year migration, the movement of a stone crab progressively farther into Florida Bay may take years and would be difficult to monitor in capture-recapture studies (e.g. Sullivan 1979). (Unpublished data from Everglades National Park on 46 male crabs from a one-year capture-recapture study conducted in west Florida Bay showed movement of males into the basins of the bay without compensatory movement back into the Gulf of Mexico.)

Biscayne National Park, like Florida Bay, appears to lack a local juvenile recruitment source. Adult or juvenile stone crabs do not seem to move to the east coast of Florida in significant numbers from either the open Gulf of Mexico or Florida Bay. The nearest known concentration of juvenile stone crabs north of the bay is in the vicinity of Indian River in east central Florida. Possibly a slow movement of crabs southward from the Indian River area accounts for a percentage of the Biscayne population, analogous to the situation in Florida Bay.

Although it is possible that older age classes have been removed from the offshore Gulf of Mexico by years of intensive fishing, park waters close to shore in the gulf and in much of Florida Bay have been protected from fishing of both sexes, and females have always been protected throughout both parks. Therefore, it is doubtful that the overall pattern of regional distribution and abundance observed in this study could solely be an artifact of commercial fishing.

Temporal changes in sex ratio occur primarily due to large shifts in number of females entering traps and are therefore most noticeable in Everglades National Park north of the Shark River and in the basins of Florida Bay, locations where the greatest proportion of females are found. The number and size of females entering traps is, in turn, evidently strongly influenced by their reproductive cycle. Greater numbers of females enter traps throughout molting (=mating) and spawning seasons.

Mean size of females in traps tends to be largest in fall, when older females molt, and smallest in winter, when only very young females molt.

Male entry into traps may be affected by female molting season. Greater numbers of males are found in traps when large females are also abundant in traps during their fall molting season. Males also enter traps in noticeably greater numbers during the cold season, particularly after a sudden drop in temperature.

Superimposed on the physical and biological factors relating to the movement of stone crabs into traps is the influence of the commercial fishing season. Apparently, the fishing season considerably affects the number, sex ratio, and size of crabs of both sexes entering traps. Traps near the Gulf of Mexico border of the park experience decreased catch rates in legal-sized crabs of both sexes during fishing season, possibly reflecting their proximity to commercial fishery grounds governed by the state, where both sexes can be harvested. Larger size crabs increase in frequency during spring, at least in part because sublegal crabs molt and replenish those size classes. Commercially fished stations in Florida Bay, remote from the recruitment ground, exhibit declines in proportion of males as the fishing season progresses. Stations that are intensely fished can become essentially devoid of males. At the time this study was conducted, males had to be removed from park waters to be declawed, due to the nature of the laws governing the fishery, and were not available for trapping if they survived the declawing process.

Previous and concurrent studies have shown that the segment of the population seen in traps may or may not be representative of the true population structure at that time. A complex interactive array of biological, physiological, and social factors enters into the observed seasonal change in number, sex, and size of stone crabs entering traps. Therefore, it is difficult to determine whether the changes in these characteristics of population biology as seen in traps actually reflects populational shifts occurring in nature. Even assuming that changes in population parameters in traps are indicative of the natural situation, one cannot attribute an observed change to a particular factor because the various influences occur simultaneously over time.

Life History

Sufficient information has been amassed from this study and others conducted in south Florida to synthesize a view of the life history of stone crabs in the region. In south Florida, most stone crabs are hatched in mid-summer (July through September), spend one to two months as larvae in the pelagic mode of life, undergo metamorphosis, and settle as very small (1.5-2.0 mm carapace width) juveniles in the fall (September through November). These crabs molt frequently and reach a size of about 30-40 mm carapace width by the following fall (age one) and can be easily differentiated sexually.

At age one, females molt and some mate during the winter. They may molt and mate again the following spring. The proportion of females that are capable of spawning is low at this time, or if all females are capable of spawning, they spawn less frequently than older females. Those that spawn do so primarily in late summer (August and September). Most females reach a size of about 60-70 mm carapace width with the fall molt at the beginning of their second year and many mate. Winter molting and mating still occur, but is not prevalent as in the first year. Most females molt and mate again in spring and peak in spawning activity during late summer. A greater percentage, but not all, are mature enough to spawn in the summer of their second year or, alternatively, spawning frequency increases. The majority of females are about 70-80 mm carapace width after the fall molt at the onset of their third year, and most mate during the molting season. Very few, if any, females molt in the winter of their third year, but some molt and mate the following spring. Age-three females probably spawn throughout summer and all are sexually mature. Possibly those who successfully mated the previous fall did not molt in spring and were early spawners. Female stone crabs molt to about 90-100 mm carapace width and mate again in fall at the close of their third year. They are then available to the commercial fishery. The winter and spring molts are virtually eliminated by the beginning of the fourth year. At that age, the animals fall into a synchronous reproductive pattern which is sustained for the remainder of their lives. They annually molt and mate in fall, retain and store the sperm throughout the winter, and spawn the following spring through summer. Peaks in spawning activity occur around May and August. Females four-years old and beyond increase in size (carapace width) an average of approximately 10 mm per year and can live to be about seven years old.

Male stone crabs below 70 mm carapace width (age one) apparently grow at least twice as rapidly as those greater than that size, annually increasing that body dimension by about 35 mm or more. Annual increase in carapace width for crabs larger than 70 mm ranges from approximately 19 mm for crabs 70-80 mm carapace width (age two) to 15 mm or less in crabs greater than 110 mm carapace width (age four). Growth in male stone crabs is both greater and more variable than in females. Males molt at any time of year, but primarily in late fall. Aging a male by his size is undoubtedly subject to greater error than aging a female. Male stone crabs below 70 mm carapace width apparently rarely or never mate. This fact, together with the substantial reduction in annual growth increment and allometric shift in body proportions that occurs at about that size, suggests that size at which a male has a 50 percent chance of being reproductively mature is near 70 mm carapace width (beginning age two). Males tend to mate with females of their own age class in traps and rarely mate with females as large or larger than themselves. Males enter the commercial fishery shortly after most have reached sexual maturity, at a smaller size than females, and at least as a partial consequence, have a higher mortality rate. Males live to be about six-years old.

ACKNOWLEDGEMENTS

This research would not have been possible without the strong support of many individuals from the various divisions of Everglades National Park. In particular, we thank the park rangers at the Everglades City, Flamingo, and Key Largo stations for outstanding cooperation and logistical assistance. We are also deeply grateful to the maintenance personnel in the park for assistance in the mechanics of keeping the equipment functional, and to our fellow researchers for providing field assistance when needed. A project of this scale cannot be successful without the cooperation of many individuals.

We appreciate the skillful assistance of Catherine Sikkema, Diane Peebles, and David Williams for drafting and photographing the figures, and Jessie Brundige and Barbara Blair for typing and editing many drafts of the manuscript. Finally, we thank John Stevely, Florida Sea Grant Program and Harriet Perry, Gulf Coast Research Laboratory for critically reviewing the manuscript.

LITERATURE CITED

Albert, J. L., and Ellington, W. R. Patterns of energy metabolism in the stone crab, Menippe mercenaria, during hypoxia and subsequent recovery. J. Expt. Zool. In press.

Abolmasona, G. I. 1970. Size weight characteristics of some Black Sea crabs. Gidrobiol. Zh. 6(1):85-90.

Anger, K., Dawirs, R. R., Anger, V., and Costis, J. D. 1981. Effects of early starvation periods on zoeal development of Brachyuran crabs. Biol. Bull. 161(2):199-212.

Ayers, J. C. 1938. Relationship of habitat to oxygen consumption by certain estuarine crabs. Ecol. 19:523-527.

Behre, E. H. 1950. Annotated list of fauna of the Grand Isle region. Occasional paper--Marine Laboratory. Louisiana State Univ. Publ. 6:1-66.

Bender, E. S. 1971. Studies of the life history of the stone crab, Menippe mercenaria (Say), in the Cedar Key area. Master's Thesis, Dept. of Biology. Gainesville, FL: Univ. of FL.

Bert, T. M., Warner, R. E., and Kessler, L. D. 1978. The biology and Florida fishery of the stone crab, Menippe mercenaria (Say), with emphasis on southwest Florida. FL Sea Grant Tech. Report No. 9. Gainesville, FL: Univ. of FL, Fl Sea Grant Program.

Bert, T. M. 1985. Geographic variation, population biology, and hybridization in Menippe mercenaria and evolution in the genus Menippe in the southwestern North Atlantic Ocean. Ph.D. Dissertation, Dept. of Biology. New Haven, CT: Yale University.

Binford, R. 1918. The germ-cells and the process of fertilization in the crab, Menippe mercenaria. Journ. Morph. 24(2):148-202.

Bland, C. E., and Amerson, H. V. 1975. Occurrence and distribution in North Carolina USA waters of Lagenidium callinectes, a fungal parasite of blue crab ova. Chesapeake Sci. 15(4):232-235.

Bookhout, C. G., and Costlow, J. D., Jr. 1972. Effects of pollutants on larval development of crabs. Proc. Int. Congr. Zool. 17(4):1-13.

Bookhout, C. G., Wilson, A. J., Jr., Duke, T. W., and Lowe, J. I. 1972. Effects of Mirex^R on the larval development of two crabs. Water, Air, Soil Pollut. 1(2):165-180.

Bookhout, C. G., and Costlow, J. D., Jr. 1974. Crab development and effects of pollutants. Thal. Jugosl. 10(1/2):1-11.

Brine, C. J., and Austin, P. R. 1981a. Chitin variability with species and method of preparation. Comp. Biochem. Physiol. 69B(2):283-286.

Brine, C. J., and Austin, P. R. 1981b. Chitin isolates: species variation in residual amino acids. Comp. Biochem. Physiol. 70B(2):173-178.

Brown, S. C., Cassuto, S. R., and Loos, R. W. 1979. Biomechanics of chelipeds in some decapod crustaceans. J. Zool. (London) 188:143-159.

Bullis, H. R., Jr., and Thompson, J. R. 1965. Collections by the exploratory fishing vessels *Oregon*, *Silver Bay*, *Combat*, and *Pelican* made during 1956 to 1960 in the southwestern North Atlantic. Special Sci. Report, Fisheries No. 510. Washington, D.C.: U.S. Fish & Wildlife Service.

Carter, M. R., Burns, L. A., Cavinder, T. R., Dugger, K. R., Fore, P. L., Hicks, D. B., Revells, H. L., and Schmidt, T. W. 1973. Ecosystems analysis of the Big Cypress Swamp and estuaries. EPA 904/9-74-002 N.P. Atlanta, Ga.: U.S. Environmental Protection Agency, Reg. IV.

Cheung, T. S. 1968. Trans-molt retention of sperm in the female stone crab, *Menippe mercenaria* (Say). Crustaceana 15(2):117-120.

Cheung, T. S. 1969. The environmental and hormonal control of growth and reproduction in the adult female stone crab, *Menippe mercenaria* (Say). Biol. Bull. 136:327-346.

Cheung, T. S. 1973. Experiments on the simultaneous regeneration of claws in the aged male stone crab, *Menippe mercenaria* (Say), with special reference to the terminal molt. Bull. Inst. Zool. Acad. Sinica 12(1):1-11.

Cheung, T. S. 1976. A biostatistical study of the functional consistency in the reversed claws of adult male stone crabs, *Menippe mercenaria* (Say). Crustaceana 3(2):137-144.

Chew, F. 1954. Physical oceanography of Key West Harbor and approaches. Univ. Miami Report p. 54-13. Miami, FL: Marine Lab, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami.

Cook, H. L. 1969. Larval culture. U.S. FWS Circ. 325:5-6.

Cooke, C. W., and Mossom, S. 1929. Geology of Florida. Florida Geol. Survey 20th Ann. Report, p. 29-288.

Costello, T., Bert, T. M., Cartano, D. G., Davis, G., Lyon, G., Rockwood, C., Stevely, J., Tashiro, J., Trent, W. L., Turgeon, D., and Zuboy, J. 1979. Fishery management plan for the stone crab fishery in the Gulf of Mexico. Fed. Reg. 44(65):19445-19496.

Costlow, J. D., Jr. 1979. Effect of Dimilim^{R} on development of larvae of the stone crab *Menippe mercenaria*, and the blue crab, *Callinectes sapidus*. *In* Marine Pollution: Functional Responses. Vernberg, W. B., Thurberg, F. P., Calabrese, A., and Vernberg, F. J., eds. New York: Academic Press.

Costlow, J. D., Jr. 1970. The effect of salinity and temperature on the larval development of the stone crab, Menippe mercenaria (Say), reared in the laboratory. Texas A & M Report 11(1):16-29.

Davis, G. E., Baughman, D. S., Chapman, J. D., MacArthur, D., and Pierce, A. C. 1979. Mortality associated with declawing stone crabs, Menippe mercenaria. SFRC Report T-552. Homestead, FL: Everglades N.P., South Florida Research Center.

Davis, J. H., Jr. 1940. The ecology and geologic role of mangroves. Carnegie Inst. Wash. Publ. 213, Pap. Tortugas Lab. 9:307-409.

deSylva, D. 1971. Ecology and distribution of post larval fishes of southern Biscayne Bay, Florida. Progress Report to the Division of Water Quality Research, Water Quality Office, EPA. Contract FWQA 18050 Div.

Eguchi, E., and Waterman, T. H. 1973. Orthogonal microvillus pattern in the eighth rhabdomere of the rock crab, Grapsus. Z. Zellforsch Mikrosk. Anat. 137(29):145-157.

Factor, J. R. 1980. Development of the mandibles and gastric mill of the stone crab, Menippe mercenaria. Amer. Zool. 20(4):843.

Factor, J. R. 1981a. Unusually complex basement membranes in the mid gut of two decapod crustaceans, the stone crab, Menippe mercenaria, and the lobster, Homårus americanus. Anat. Rec. 200(3):253-258.

Factor, J. R. 1981b. Complex basement membranes in the mid gut of several decapod crustaceans. Amer. Zool. 21(4):1002.

Finucane, J. H., and Campbell, W. 1968. Ecology of American oysters in old Tampa Bay, Florida, USA. Quart. J. FL Acad. Sci. 31(1):37-46.

Finucane, J. H., and Dragovich, A. 1959. Counts of red tide organisms, Gymnodinium breve, and associated oceanographic data from Florida west coast 1954-1957. U.S. FWS Sci. Report, Fish. No. 289:202-295. Washington, DC: U.S. FWS, Office of Biological Services.

Forward, R. B., Jr. 1977. Occurrence of a shadow response among brachyuran larvae. Mar. Biol. 39(4):337-341.

Ginsburg, R. N. 1956. Environmental relationships of grain size and constituent particles in some south Florida carbonate sediments. Bull. Amer. Assoc. Pet. Geol. 40(10):2384-2427.

Goy, J. W., and Costlow, J. D. 1980. Nutritional effects of Artemia from different geographical strains on larval development of decapod crustaceans. Amer. Zool. 20(4):888.

Guinot-Dumortier, D., and Dumortier, B. 1960. Le stridulation chez les crabs. Crustaceana 1(2):117-155.

Gunter, G. 1950. Seasonal population changes and distribution as related to salinity of certain invertebrates of the Texas coast, including the commercial shrimp. Univ. of Texas: Publ. Inst. Mar. Sci. 1:1-5.

Hancock, D. A. 1965. Yield assessment in the Norfolk fishery for crabs (Cancer picerus) (Rapp). Reun. Cons. Perm. Int. Explor. Mer. 159:81-94.

Hay, W. P., and Shore, C. A. 1918. The decapod Crustacea of Beaufort, North Carolina, and the surrounding region. Bull. U.S. Bur. Fish. 35:369-475.

Hazlett, B. A. 1979. Biotic aspects of the distribution of the crabs Panopeus herbstii and Mithrax sculptus. Bull. Mar. Sci. 29(4):576-580.

Hembree, D. E. 1984. The offshore migration of stone crabs and temperature's effect on locomotor activity. Master's Thesis, Dept. of Biological Science. Tallahassee, FL: FL State Univ.

Hoffmeister, J. E. 1974. Land from the sea: the geologic story of South Florida. Coral Gables, FL: Univ. of Miami Press.

Hyman, O. W. 1925. Studies on the larvae of crabs of the family Xanthidae. Proc. U.S. Nat. Mus. 67(3):1-22.

Iversen, E. S., and Beardsley, G. L. 1976. Shell disease in crustaceans indigenous to South Florida, USA. Prog. Fish Cult. 38(4):195-196.

Jones, J. A. 1963. Ecological studies of the southeastern Florida patch reefs. Part 1. Diurnal and seasonal changes in the environment. Bull. Mar. Sci. 13(2):282-307.

Karandieva, O. G., and Silva Lee, A. 1967. Intensity of respiration and osmoregulation of the commercial crab, Menippe mercenaria (Say), from Cuban coastal waters. Acad. de Ciencias de Cuba. Estudios 2(1):5-19.

Kent, B. 1983. Patterns of coexistence in busyconine whelks. J. Exper. Mar. Biol. Ecol. 66:257-283.

Lee. T. N. 1975. Circulation and exchange processes in southeast Florida's coastal lagoons. T.R. 75-3. Miami, FL: Rosenstiel School of Marine and Atmospheric Sciences, Univ. of Miami.

Leffler, C. W. 1973. Metabolic rate in relation to body size and environmental oxygen concentration in two species of Xanthid crabs. Comp. Biochem. Physiol. 44A(4):1047-1052.

Lindall, W. N., Jr., Hall, J. R., Fable, W. A., Jr., and Collins, L. A. 1973. Fishes and commercial invertebrates of the nearshore and estuarine zone between Cape Romano and Cape Sable, Florida. In South Florida Ecological Study, Appendix E, Estuarine-Dependent Marine Fishes. St. Petersburg, FL: Natl. Mar. Fish. Serv., Gulf Coast Fish. Cent., pt. III, sect. II.

Lindberg, W. J., and Marshall, M. J. 1983. Species profiles: life histories and environmental requirements (South Florida)-stone crab. U.S. FWS Div. Biol. Serv. FWS/OBS-82-11. Washington, DC: U.S. Army Corps of Engineers, TR EL-82-4.

Lindner, M. J., and Cook, H. L. 1971. Progress in shrimp mariculture in the USA. FAO Fish Report 71(2):157-162.

Manning, R. B. 1961. Some growth changes in the stone crab, Menippe mercenaria (Say). Quart. J. FL Acad. Sci. 23(4):273-277.

Marmer, H. A. 1954. Tides and sea level in the Gulf of Mexico. In Gulf of Mexico: Its origin, waters, and marine life. Bull. U.S. FWS 55(89):115-116.

Mauro, N. A., and Magnum, C. P. 1982. The role of the blood in the temperature dependence of oxidative metabolism in decapod crustaceans. II. Interspecific adaptations to latitudinal changes. J. Exp. Zool. 219:189-195.

McConaugha, J. R., McNally, K., Goy, J. W., and Costlow, J. D. 1980. Winter induced mating in the stone crab, Menippe mercenaria. Proc. World Maricult. Soc. 11.

McNulty, J. K., Lindall, W. N., Jr., and Sykes, J. E. 1972. Cooperative Gulf of Mexico estuaring inventory and study, Florida: Phase I, area description. NOAA Tech. Report NMFS CIRC-368. Miami, FL: NMFS, SEFC.

McRae, E. D., Jr. 1950. An ecological study of the Xanthid crabs in the Cedar Key area. Master's Thesis. Gainesville, FL: Univ. of FL.

Menzel, R. W., and Hopkins, S. H. 1956. Crabs as predators of oysters in Louisiana. Proc. Natl. Shellfish Assoc. 46:107-184.

Menzel, R. W., and Nichy, F. E. 1958. Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. Bull. Mar. Sci. Gulf Carib. Fish. Inst. 8(2):125-145.

Merz, R. A. 1979. A study of the behavioral and biomechanical defense of Strombus alatus, the Florida fighting conch. Master's Thesis. Gainesville, FL: Univ. of FL.

Mootz, C. A., and Epifanio, C. E. 1974. An energy budget for Menippe mercenaria larvae fed Artemia nauplii. Biol. Bull. 146:44-55.

Noe, C. D. 1967. Contribution to the life history of the stone crab, Menippe mercenaria (Say), with emphasis on the reproductive cycle. Master's Thesis. Miami, FL: Univ. of Miami.

Ong, K. S., and Costlow, J. D., Jr. 1970. The effect of salinity and temperature on the larval development of the stone crab, Menippe mercenaria (Say), reared in the laboratory. Ches. Sci. 11(1):16-29.

Parker, R. H. 1959. Macro-invertebrate assemblages of central Texas coastal Bays and Laguna Madre. Bull. Amer. Assoc. Pet. Geol. 43:2100-2166.

Passano, L. M. 1960. Low temperature blockage of molting in Uca pugnax. Biol. Bul. 118:129-136.

Payen, G. 1974. Sexual morphogenesis in cyclomelopa crabs during embryonic larval and post larval development. Bull. Mus. Natl. Hist. Nat. Zool. 139:210-262.

Perry, H., Stuck, K. C., and Reissig, D. S. 1983. Menippe mercenaria: the potential for development of a fishery. Annual Report to Mississippi Sea Grant, 1983. Ocean Springs, MS: Gulf Coast Research Lab.

Porter, H. J. 1960. Zoeal stages of the stone crab, Menippe mercenaria (Say). Ches. Sci. 1(3/4):168-177.

Powell, E. H., Jr., and Gunter, G. 1968. Observations of the stone crab, Menippe mercenaria (Say), in the vicinity of Port Aransas, Texas. Gulf Res. Reports 2(3):285-299.

Prochaska, F. J. 1976. Florida commercial marine fisheries: Growth, relative importance, and input trends. FL Sea Grant Report No. 11. Gainesville, FL: FL Sea Grant Program, Univ. of FL.

Prochaska, F. J., and Cato, J. C. 1974. Landings, values, and prices in commercial fisheries for the Florida Keys region. FL Sea Grant Publ. SUSF-SG-74-004.

Prochaska, F. J., and Cato, J. C. 1975. Landings, values, and prices in commercial fisheries for the Florida west coast. FL Sea Grant Publ. SUSF-SG-75-003.

Prochaska, F. J., and Landrum, P. D. 1981. Spiny lobster, stone crab, and secondary fishery costs and revenues in the Florida Keys, 1978-79 season. FL Sea Grant Report No. 42. Gainesville, FL: FL Sea Grant Program, Univ. of FL.

Rathbun, M. J. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atcelecyclidae, Cancridae, and Xanthidae. U.S. Natl. Mus. Bull. 152.

Rathbun, R. 1884. The stone crab, Menippe mercenarius, Gibbes. In The fisheries and fishery industries of the United States, Sect. 1, Pt. 5. S. B. Goode, ed. pp.772-774.

Rathbun, R. 1887. The crab, lobster, crayfish, rock lobster, shrimp, and prawn fisheries. In The fisheries and fishery industries of the United States, Sect. 5, Vol. 2, Pt. 21. G. B. Goode, ed. pp. 650-669.

Roberts, M. H., Jr. 1975. Culture techniques for decapod crustacean larvae. In Culture of marine invertebrate animals, W. L. Smith and M. H. Chanley, eds. New York: Plenum Press. 209-220.

Rodriguez, G. A., and Yang, W. T. 1977. Regeneration of chelae and growth in the first crab stage (Menippe mercenaria) (S.) under laboratory conditions. In National Oceanographical Congress; Guaymas, Mexico, 22-25 Oct. 1974; vol. 5:565-579. Instituto Technologico y le Estudios Superiores do Monterrey, Guaymas (Mexico). Escuela de Ciencias Maritimas y Alimentarias.

Rodriguez, G. A. 1975. Electrophoretic patterns of blood serum from stone crabs Menippe mercenaria (Say), (Crustacea: Decapoda) held under laboratory conditions. Master's Thesis. Miami, FL: Univ. of Miami.

Ros, R. M., and Perez Perez, D. 1979. Fishing for the stone crab, Menippe mercenaria, in Barabano, Cuba. Cienc. Ser. 8 Invest. Mar. No. 44:1-32. (Havana).

Ros, R. M., Perez Perez, D., and Arboleya, Z. 1980. Polychromatism in the stone crab, Menippe mercenaria (Say 1818). Rev. Invest. Mar. 1(2-3):175-196.

Ros, R. M., and Rojas, R. M. 1978. A method for determining fecundity in decapod crustaceans with external roe. Cienc. Ser. 8 Invest. Mar. No. 40:1-20 (Havana).

Sandifer, P. A., and Smith, T. I. J. 1974. Development of a crustacean mariculture program at South Carolina's Marine Resources Research Institute. Proc. Annual Meet. World Maricult. Soc. 5:431-439.

Sandifer, P. A., Smith, T. I. J., and Calder, D. R. 1974. Hydrozoans as pests in closed system culture of larval decapod crustaceans. Aquaculture 4(1):55-59.

Savage, T. 1971a. Mating of the stone crab, Menippe mercenaria (Say) (Decapoda, Brachyura). Crustaceana 20(3):315-317.

Savage, T. 1971b. Effect of maintenance parameters on growth of the stone crab, Menippe mercenaria (Say). Spec. Sci. Report No. 28, Contr. 175. St. Petersburg, FL: Florida Dept. of Natural Resources, Mar. Res. Lab.

Savage, T., and McMahan, M. R. 1968. Growth of early juvenile stone crabs, Menippe mercenaria (Say, 1819). Spec. Sci. Report No. 21. St. Petersburg, FL: Florida Bd. Conserv., Mar. Res. Lab.

Savage, T., Sullivan, J. R., and Kalman, C. E. 1974. Claw extraction during molting of the stone crab, Menippe mercenaria (Decapoda, Brachyura, Xanthidae). FL Mar. Res. Publ. No. 4. St. Petersburg, FL: Florida Dept. of Natural Resources, Mar. Res. Lab.

Savage, T., Sullivan, J. R., and Kalman, C. E. 1975. An analysis of stone crab, Menippe mercenaria, landings on Florida's west coast, with a brief synopsis of the fishery. FL Mar. Res. Publ. No. 13. St. Petersburg, FL: Florida Dept. of Natural Resources, Mar. Res. Lab.

Savage, T., and Sullivan, J. R. 1978. Growth and claw regeneration in the stone crab, *Menippe mercenaria* (Say). FL Mar. Res. Publ. No. 32. St. Petersburg, FL: Florida Dept. of Natural Resources, Mar. Res. Lab.

Schlieder, R. A. 1980. Effects of dessication and autospasy on egg hatching success in the stone crab, *Menippe mercenaria*. Fish. Bull. 77(3):395-700.

Schmidt, T. W., and Davis, G. E. 1978. A summary of estuarine and marine water quality information collected in Everglades National Park, Biscayne National Monument, and adjacent estuaries from 1897 to 1977. SFRC T-519. Homestead, FL: Everglades N.P., South Florida Research Center.

Schneider, J. J. 1969. Tidal relations in the south Biscayne Bay area, Dade County, Florida. Open File Report. Tallahassee, FL: U.S.G.S., Water Resources Division

Schroeder, W. C. 1924. Fisheries of Key West and the clam industry of southern Florida. Appendix II, U.S. Fish Comm. Report 1923.

Scotto, L. E. 1979. Larval development of the Cuban stone crab, *Menippe nodifrons* (Brachyura, Xanthidae) under laboratory conditions, with notes on the status of the family Menippidae. Fish. Bull. 77(2):359-386.

Segar, D. W., Gerchakov, S. M., and Johnson, T. 1971. Chemistry. *In*: An Ecological Study of South Biscayne Bay and Card Sound, Florida, Pt. IV. Progress Report to the U.S. Atomic Energy Comm. and Florida Power and Light Co. Miami, FL: Univ. of Miami, RSMAS.

Simmons, E. G. 1957. An ecological survey of the upper Laguna Madre of Texas. Univ. Texas: Publ. Inst. Mar. Sci. 4(2):156-200.

Simonson, J. L., and Steele, P. 1981. Cheliped assymetry in the stone crab, *Menippe mercenaria*, with notes on claw reversal and regeneration. Northeast Gulf Sci. 5(1):21-30.

Simonson, J. Handedness, reversal, growth, and claw stridulation pattern in the stone crab, *Menippe mercenaria* (Say) (Crustacea, Xanthidae). J. Crust. Biol, in press.

Sinclair, M. E. 1977. Agnostic behavior in the stone crab, *Menippe mercenaria* (Say). Anim. Behav. 25:193-207.

Smith, F. G. W., Williams, R. H., and Davis, C. 1950. An ecological survey of the subtropical inshore waters adjacent to Miami. Ecol. 31(1):119-140.

Snedecor, G. W., and Cochran, W. G. 1967. Statistical Methods. Ames, Iowa: Iowa St. Univ. Press.

Sokal, R. R., and Rohlf, F. J. 1969. Biometry. San Francisco, CA: W. H. Freeman & Co.

Somerton, D. A. 1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci. 37:1488-1494.

Steel, R. G. D., and Torrie, J. H. 1960. Principles and procedures of statistics. New York, New York: McGraw-Hill.

Suarez, A. G., and Diaz, R. X. 1969. Physiological aspects of some marine invertebrates of commercial interest in Cuba. FAO Fish. Report 71(1):155.

Suarez, A. G., and Diaz, R. X. 1971. Physio-ecologic aspects of some marine invertebrates of commercial importance to Cuba. FAO Fish. Report 73(2):279-281.

Suchenia, L. M., and Claro Madruga, R. 1967. Quantitative regularities of feeding and their connection with the balance of energy of the commercial crab, Menippe mercenaria (Say). Academia de Ciencias de Cuba. Estudios 2(1):75-97.

Sulkin, D. S., and Van Heukelem, W. F. 1980. Ecological and evolutionary significance of nutritional flexibility in planktotropnic larvae of the deep sea red crab, Geryon quinquedens, and the stone crab, Menippe mercenaria. Mar. Ecol. Prog. Ser. 2(2):91-95.

Sullivan, J. R. 1979. The stone crab, Menippe mercenaria, in the southwest Florida fishery. FL Mar. Res. Publ. No. 36.

Tabb, D. C., DuBrow, D. L., and Manning, R. B. 1961. The ecology of northern Florida Bay and adjacent estuaries. Tech. Ser. No. 39. Miami, FL: Univ. of Miami, Inst. Mar. Sci., Mar. Lab.

Tabb, D. C., and Manning, R. B. 1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July 1957 through September 1960. Bull. Mar. Sci. Gulf Carib. 11(4):552-649.

Thomas, T. M. 1974. A detailed analysis of climatological and hydrological records of south Florida with reference to man's influence upon ecosystem evolution. In Environments of South Florida: Present and Past. P. J. Gleason, ed. Mem. 2, Miami Geol. Soc. p. 82-122.

Tucker, R. K. 1978. Free amino acids in developing larvae of the stone crab, Menippe mercenaria. Comp. Biochem. Phys. 60A(2):169-172.

Turney, J., and Perkins, B. 1972. Molluscan distribution in Florida Bay. Sedimenta III. Miami, FL: Univ. of Miami, RSMAS, Comparative Sedimentology Lab, Div. Mar. Geol. & Geophy.

Vermeij, G. J. 1978. Biogeography and Adaptation: Patterns of marine life. Cambridge, Mass.: Harvard Univ. Press.

Voss, G. L., Bayer, F. M., Robins, C. R., Gomon, M., and Laroe, E. T. 1969. The marine ecology of the Biscayne National Monument. A report to the National Park Service, Dept. of Inter. Miami, FL: RSMAS, Univ. of Miami.

Wass, M. L. 1955. The decapod crustaceans of Alligator Harbor and adjacent inshore areas of northwestern Florida. Q. Journ. FL Acad. Sci. 18(3):129-176.

Wenner, E. L., and Stokes, A. D. 1983. Preliminary observations on the distribution and abundance of the stone crab, *Menippe mercenaria*, in South Carolina waters. South Carolina Marine Resources Center Tech. Report No. 55. Charleston, SC: Marine Resources Research Inst., South Carolina Wildlife and Marine Resources Dept.

Whetstone, J. M., and Eversole, A. G. 1978. Predation on hard clams, *Mercenaria mercenaria*, by mud crabs, *Panopeus herbstii*. Proc. Natl. Shellfish Assoc. 68:42-48.

Whitten, H. L., Rosen, H. F., and Hedgepeth, J. W. 1950. The invertebrate fauna of Texas coast jetties; a preliminary survey. Univ. of Texas: Publ. Inst. Mar. Sci. 1:53-87.

Williams, A. B. 1965. The decapod crustaceans of the Carolinas. U.S. Fish. Bull. 65(1):1-298.

Yang, W. T. 1971. Preliminary report of the culture of the stone crab, *Menippe mercenaria* (Say), reared from eggs. Proc. 3rd Ann. Workshop, World Maricult. Soc. 3:183-184.

Yang, W. T. 1972. Notes on the successful reproduction of stone crabs, *Menippe mercenaria* (Say), reared from eggs. Proc. 3rd Ann. Workshop, World Maricult. Soc. 3:183-184.

Yang, W. T., and Krantz, G. E. 1976. "Intensive" culture of the stone crab, *Menippe mercenaria*. Sea Grant Tech. Bull. No. 35. Coral Gables, FL: Univ. of Miami, Sea Grant Program.

Zuboy, J. R., and Snell, J. E. 1980. Assessment of the Florida stone crab fishery. NOAA Tech. Mem. NMFS-SEFC-21. Miami, FL: NMFS-SEFC.

Zuboy, J. R., and Snell, J. E. 1982. Assessment of the Florida stone crab fishery. NOAA Tech. Mem. NMFS-SEFC-79. Miami, FL: NMFS-SEFC.

Table 1. Physical characterization of stations in Everglades National Park and Biscayne National Park used in this study. (See Figure 1 for location of stations.)

Station[1,2]	Salinity(ppt) x(SD)/Range	Temp (°C) x(SD)/Range	Depth (m)	Turb[3]	Bottom Type	Predominant Benthos	Locality[4]
AREA: GULF OF MEXICO							
Chokoloskee Bay (CKB)[1]	26(5)/18-34	26(5)/18-32	0.7	high	soft mud	oysters	inshore, in bay
Indian Key (INK)[2]	29(5)/20-35	16(5)/18-33	1.2	high	hard sand, small rocky outcroppings	sponges, soft corals	offshore, near seaward, edge of park
Chatham Bend (CTB)[2]	25(8)/19-35	26(6)/18-34	2.0	high	oyster shell	oysters	close to shore, mouth of estuary
Pavillion Key (PVK)[1]	30(3)/26-34	25(5)/18-34	3.0	high	hard sand, small rocky outcroppings	sponges, soft corals of park	offshore, near seaward edge[4]
Lostman Second Bay (LSB)[1]	11(7)/2-22	26(6)/18-33	1.0	high	soft mud	algae	inshore, in bay
Lostmans River Channel (LMI)[1]	24(4)/17-33	26(6)/17-34	1.7	high	oyster shell	oysters	close to shore, in river channel
Outside Lostmans River (LMO)[1]	31(4)/20-34	25(5)/18-31	2.0	high	hard sand, small rocky outcroppings	sponges soft corals	offshore, near seaward edge of park[4]
Shark Point (SPT)[2]	20(4)/26-36	25(5)/18-31	1.2	high	hard mud	barren	close to shore, mouth of estuary*

Table 1 continued.

Station[1,2]	Salinity(ppt) x(SD)/Range	Temp (°C) x(SD)/Range	Depth (m)	Turb[3]	Bottom Type	Predominant Benthos	Locality[4]
Northwest Cape (NWC)[1]	33(3)/28-38	25(5)/18-31	3.5	mod. high	hard sand, small rocky outcroppings	sponges, soft corals of park	offshore, near seaward edge[4]
AREA: FLORIDA BAY							
Conchie Channel (CCH)[1]	35(3)/31-40	25(4)/19-31	3.0	high	soft sand	unknown	west bay, channel to Gulf of Mexico
Sandy Key Channel (SKC)[1]	35(2)/32-38	25(4)/19-32	3.0	mod. high	hard sand, rocky outcroppings	sponges, algae of Mexico	west bay, channel to Gulf[4]
Arsenicker Keys (ASK)[2]	34(1)/33-37	25(6)/14-31	2.3	mod. low	soft sand, rocky outcroppings	sponges, soft corals	basin, west bay[4]
Twin Key Basin (TKB)[1]	35(2)/32-39	25(6)/14-31	2.0	low	soft sand, rocky outcroppings	seagrass, sponges	basin, west bay[4]
Captain Key (CPK)[1]	35(4)/26-42	25(5)/16-31	1.2	mod.	soft sand	barren	basin, west bay[4]
Black Betsy Keys (BBK)[1]	32(6)/26-42	25(6)/15-31	1.5	mod. high	soft mud	barren	basin, northeast bay

Table 1 continued.

Station[1,2]	Salinity(ppt) x(SD)/Range	Temp (°C) x(SD)/Range	Depth (m)	Turb[3]	Bottom Type	Predominate Benthos	Locality[4]
Tern Keys (TNK)[1]	36(5)/30-45	25(6)/15-32	1.2	mod. low	hard sand	barren	basin, northeast bay
Blackwater Sound (BWS)[1]	33(3)/29-38	25(5)/14-30	2.0	low	soft sand	seagrass	basin, northeast bay
AREA: BISCAYNE BAY							
Pelican Bank (PLB)[1]	31(6)/20-36	24(6)/13-31	1.5	low	soft sand, small rocky outcroppings	sponges, soft corals	mainland side of lagoon
Billys Point (BLP)[1]	34(2)/31-36	24(6)/13-31	2.0	low	soft sand	sponges, soft corals	shoreward side of barrier islands[4]
Inside Sands Cut (SCI)[1]	34(2)/32-36	25(6)/14-31	2.5	low	soft sand	seagrass	shoreward side of barrier islands[4]
AREA: BISCAYNE REEF							
Outside Sands Cut (SCO)[2]	34(2)/32-36	25(5)/18-30	1.5	low	hard sand, small rocky outcroppings	seagrass, sponge, algae	seaward side of barrier islands[4]

Table 1 continued.

Station[1,2]	Salinity(ppt) x(SD)/Range	Temp (°C) x(SD)/Range	Depth (m)	Turb[3]	Bottom Type	Predominant Benthos	Locality[4]
Sands Cut Reef (SCR)[2]	34(1)/32-36	25(3)/20-29	5.0	low	soft sand, coral reef	seagrass, corals	offshore, patch reef[4]

*commercially fished very late in the season

[1] stations sampled from June 1979 to June 1980

[2] stations sampled from October 1979 to June 1980

[3] turbidity is a qualitative judgement based on average color and clarity of the water

[4] stations in zone open to commercial fishing

Table 2. Outline of biological and morphological data recorded on stone crabs captured in this study.

- I. Biological Data
  - A. Capture Category
    - 1. New capture
    - 2. Recapture
    - 3. Dead
    - 4. Molt
  - B. Sex
  - C. Claw Type
    - 1. Crusher
    - 2. Pincer
    - 3. Regenerated crusher
    - 4. Regenerated pincer
  - D. Molt state
  - E. Degree of fouling and principal fouling organisms
  - F. Reproductive status (females only)
  - G. Injuries
- II. Morphological Data
  - A. Carapace width
  - B. Carapace length
  - C. Propodus width
  - D. Propodus length
  - E. Dactyl length

Table 3. Stations with statistically similar mean numbers of stone crabs captured per trap as determined by the Wilcoxon-Mann-Whitney simultaneous test procedure. Statistical differences among stations were determined by Kruskal-Wallis test (H=149.2**, 15 df, for stations sampled throughout the year; H=43.57**, 21 df, for stations sampled October through June). (Note: The Wilcoxon-Mann-Whitney procedure is a rank analysis test and does not necessarily imply that stations in the various groups are all significantly different from each other in the parametric sense.)

Dates Sampled	High Relative Abundance[1]	Moderate Relative Abundance[2]	Low Relative Abundance[3]	Zero Relative Abundance[4]
June 1979-June 1980	Pavilion Key Outside Lostmans River Northwest Cape Conchie Channel Sandy Key Channel	Lostmans River Channel Twin Key Basin Captain Key	Chokoloskee Bay Blackwater Sound Black Betsy Keys Tern Keys Pelican Bank Billys Point Inside Sands Cut	Lostmans Second Bay
Oct. 1979-June 1980	Indian Key Chatham Bend Pavilion Key Outside Lostmans River Shark Point Conchie Channel	Lostmans River Channel Northwest Cape Sandy Key Channel Twin Key Basin Arsenicker Keys Captain Key	Chokoloskee Bay Blackwater Sound Tern Keys Black Betsy Keys Pelican Bank Billys Point Inside Sands Cut Outside Sands Cut	Sands Cut Reef Lostmans Second Bay

[1] From June 1979 - June 1980, "high" ranged from means of 10-21 crabs per trap line; from Oct. 1979 - June 1980, "high" ranged from means of 18-26 crabs per trap line.

[2] From June 1979 - June 1980, "moderate" ranged from means of 6-8 crabs per trap line; from Oct. 1979 - June 1980, "moderate" ranged from means of 6-9 crabs per trap line.

[3] From June 1979 - June 1980, "low" ranged from means of 1-4 crabs per trap line; from Oct. 1979 - June 1980, "low" ranged from means of 1-5 crabs per trap line.

[4] From June 1979 - June 1980, "zero" equaled 0 crabs per trap line; from Oct. 1979 - June 1980, "zero" ranged from means of 0-1 crabs per trap line.

Table 4. Stations with statistically similar numbers of juveniles settling on traps, based on simultaneous test procedure analysis of number of juvenile stone crabs per 5-trap line per month among stations. Kruskal-Wallis nonparametric analysis for significant differences among stations was highly significant (H=132.8**, 21 df).

Stations	High Number of Juveniles (35-46 per trap line)	Moderately low Number of (4-10 per trap line)	Few or no Juveniles (0-3 per trap line)
Gulf of Mexico			
Outside Lostmans River	X		
Indian Key	X		
Pavilion Key	X		
Chatham Bend		X	
Shark Point		X	
Northwest Cape		X	
Lostmans River Channel			X
Lostmans Second Bay			X
Chokoloskee Bay			X
Florida Bay			
Conchie Channel			X
Sandy Key Channel			X
Twin Key Basin			X
Arsenicker Keys			X
Captain Key			X
Black Betsy Keys			X
Tern Keys			X
Blackwater Sound			X
Biscayne Bay			
Pelican Bank			X
Inside Sands Cut			X
Billys Point			X
Biscayne Reef			
Outside Sands Cut			X
Sands Cut Reef			X

Table 5. Trapping stations having statistically similar sex ratios (as determined by simultaneous test procedure) in the Gulf of Mexico, west Florida Bay, and Biscayne National Park (all stations summed) tested for goodness of fit to 1:1 sex ratio (male:female) by G-test (G_H=38.28**, 13 df). (Note: The STP is a non-parametric rank analysis test, see note on Table 1).

	Station	% male
Stations with relatively high proportion of males	Conchie Channel	95.5
	Biscayne National Park	92.8
	Arsenicker Keys	91.4
	Northwest Cape	88.8
	Shark Point	83.2
	Lostmans River Channel	80.0
Stations with relatively low proportion of males	Sandy Key Channel	78.0
	Twin Key Basin	70.7
	Chatham Bend	64.4
	Indian Key	61.0
	Captain Key	58.9
	Outside Lostmans River	51.3
	Pavilion Key	46.9

Table 6. Characteristics of station groups used for size class frequency analysis. Stations were grouped on basis of similarity in annual mean size, seasonal variations in mean size, and habitat at the station location. See Table 1 for station names.

Station Group	Group Characteristics
Offshore Gulf of Mexico	
Males (INK, PVK, LMO)	No significant difference in mean size. Located offshore in Gulf of Mexico; same habitat characteristics.
Females (INK, PVK, LMO)	No significant difference in mean size. Located offshore in Gulf of Mexico; same habitat characteristics. Same seasonal trends in variation in mean size.
Nearshore Gulf of Mexico	
Males (CTB, SPT)	No significant difference in mean size. Located on Gulf of Mexico at mouth of fresh water outflow; same habitat characteristics.
Females (CTB, LMI, SPT)	No significant difference in mean size. Located in Gulf of Mexico at mouth of fresh water outflow. Some similarity in seasonal variation in mean size.
Florida Bay	
Males (CCH, SKC, TKB, ASK, CPK, BBK, TNK, BWS)	No significant difference in mean size. Located in Florida Bay; some similar habitat characteristics.

Table 6 continued.

Station Group	Group Characteristics
Females (SKC, ASK, TKB, CPK, BBK, TNK, BWS)	No significant differences in mean size. Located in Florida Bay; some similar habitat characteristics. No seasonal trends in variation in mean size seen at any station. Few female crabs at each station.
Biscayne National Park	
Males (PLB, BLP, SCI, SCO, SCR)	No significant differences in mean size. Located on the Atlantic Ocean; geographically separated from gulf stations.

Table 7. Growth of male and female stone crabs (mm carapace width, CW) from capture of molting crabs and their exuvia during this study. Females are divided into 10 mm size classes. Males are individually listed. Standard deviation in parentheses.

Sex & Size (mm)	Number	Change in CW (mm)	% Increase in CW
Males			
79.0	1	12.0	15.2
81.4	1	17.5	21.5
90.2	1	18.3	20.3
91.8	1	20.0	21.8
Average:		17.0 (3.0)	19.7 (2.7)
Females			
50-60	2	8.5 (0.6)	14.8 (0.6)
60-70	5	11.8 (2.1)	18.8 (3.4)
70-80	3	9.0 (0.8)	12.0 (0.9)
80-90	1	11.3	13.9
90-100	1	6.8	7.5
Average:		10.1 (2.2)	15.0 (4.2)

Table 8. Estimation of instantaneous mortality coefficient (Z) and total annual mortality rate ($N_t=N_oe^{-zt}$) for male and female stone crabs from Everglades National Park, using the average annual grown increment method of Hancock (1965).

Sex	Size Group (mm CW)	N	Z	e^{-zt}	Total Annual Mortality
Male	102-117.9	357	0.76	0.468	54.3%
	118-133.9	181	1.47	0.230	77.0%
Female	94-103.9	87	0.35	0.704	29.6%
	104-113.9	41	0.70	0.498	50.2%

Table 9. Estimation of stone crab mortality rate in Everglades National Park, using proportion of stone crabs lost from the population within annual molt increments (calculated from percent lost or gained between adjacent 2 mm carapace width size class intervals).

Sex	Size Interval	N	% Lost	Sex	Size Interval	N	% Lost
Male	102-103.9	62		Female	94-95.9	22	
	104-105.9	54	13		96-97.9	18	18
	106-107.9	48	10		98-99.9	17	5
	108-109.9	46	3		100-101.9	14	14
	110-111.9	48	-3		102-103.9	16	9
	112-113.9	37	18				
	114-115.9	33	6	Total:			28%
	116-117.9	29	11				
Total:			58%				
Male	118-119.9	34		Female	104-105.9	11	
	120-121.9	31	9		106-107.9	10	9
	122-123.9	26	15		108-109.9	3	64
	124-125.9	20	18		110-111.9	12	-81
	126-127.9	27	-20		112-113.9	5	63
	128-129.9	24	9				
	130-131.9	14	32	Total:			55%
	132-133.9	6	20				
Total:			83%				

Table 10. Proportion of females that were found to be in gravid condition by area of capture within Everglades National Park.

Area	Number Females Captured	Percent Total of Females Captured	Percent Gravid	Number Gravid	Percent Total Gravid Females
Gulf of Mexico	394	83.8	16.8	66	80.7
Western Florida Bay	67	14.3	16.4	11	12.0
Northeast Florida Bay	9	1.9	66.7	6	7.2

Table 11. Size of gravid females in relation to that of all females captured by area within Everglades National Park.

Area	Class	Mean Size	SD	Range	N
Gulf of Mexico	gravid	89.5***	(12.9)	48.4-112.4	66
	all	80.9	(19.3)	33.4-116.3	394
Florida Bay	gravid	107.3*	(12.0)	83.1-123.9	17
	all	99.4	(14.4)	76.7-126.2	58

*Significantly larger than all (p less than .05).
***Significantly larger than all (p less than .001).

Table 12. Growth of male stone crabs (from an unpublished capture - recapture study conducted in Everglades National Park from March 1978 to March 1979). Standard deviation in parentheses.

Premolt Size Range (mm CW)	N	Weeks at Large	Mean Change In Size (mm CW)	Mean Percent Increase in Size
60-70	3	13-26	37.6 (2.9)	56.8 (2.1)
70-80	6	8-30	19.2 (6.1)	24.8 (8.4)
80-90	15	2-52	18.7 (5.1)	21.4 (6.3)
90-100	16	2-34	19.7 (5.0)	20.4 (4.7)
100-110	21	1-54	16.8 (5.8)	15.8 (5.5)
110-120	5	7-56	15.0 (4.0)	13.3 (3.5)
120-130	1	9	10.6	7.5
Total (all crabs):			19.2 (7.2)	20.9 (10.3)

Figure 1a. Location of sampling stations in Everglades National Park. See Table 1 for names of stations.

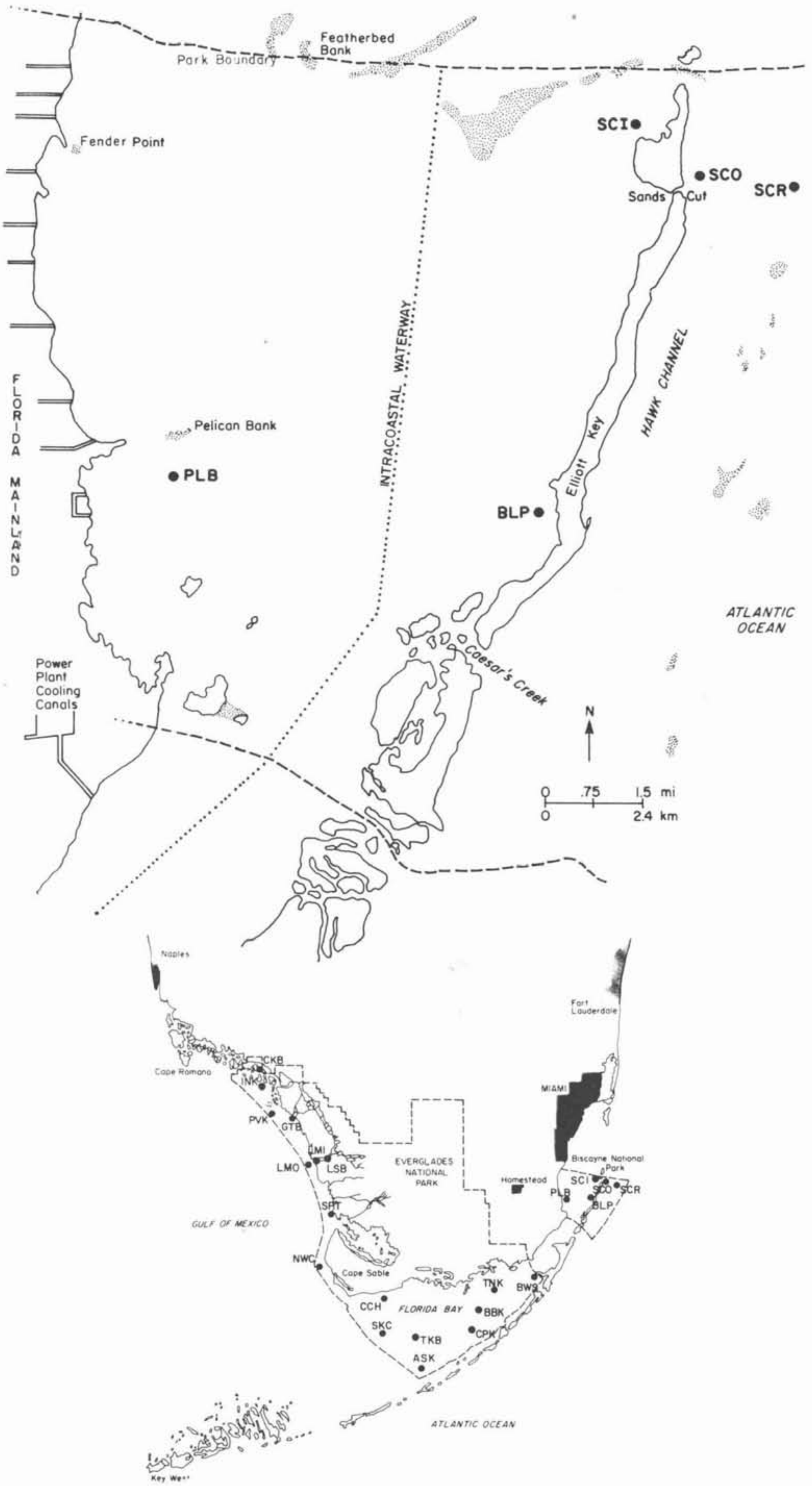


Figure 1b. Location of sampling stations in Biscayne National Park. See Table 1 for names of stations.

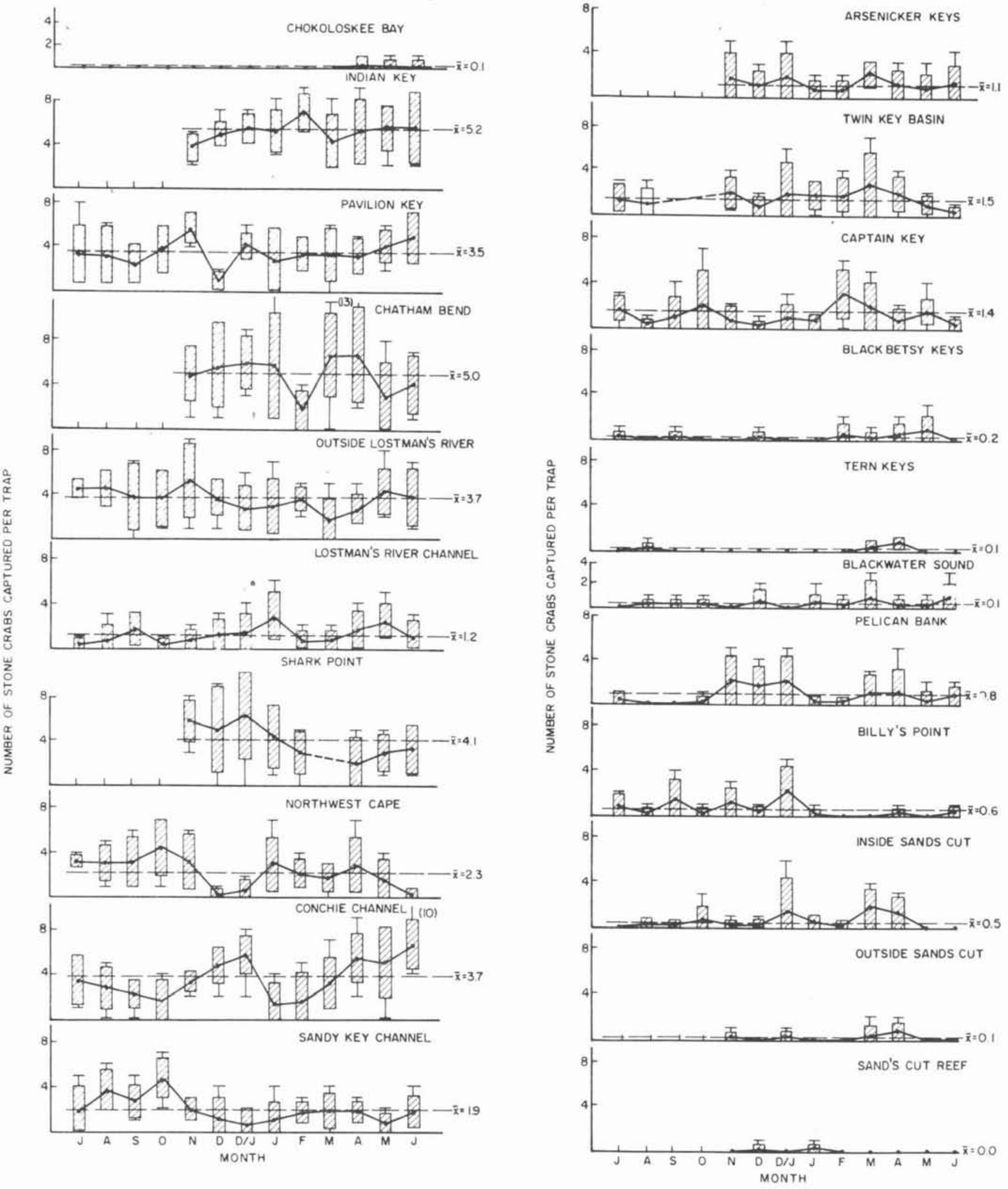


Figure 2. Mean number of stone crabs captured per trap in monthly samples by station. Bars and lines show standard deviation and range, respectively. No crabs were ever captured at station LSB.

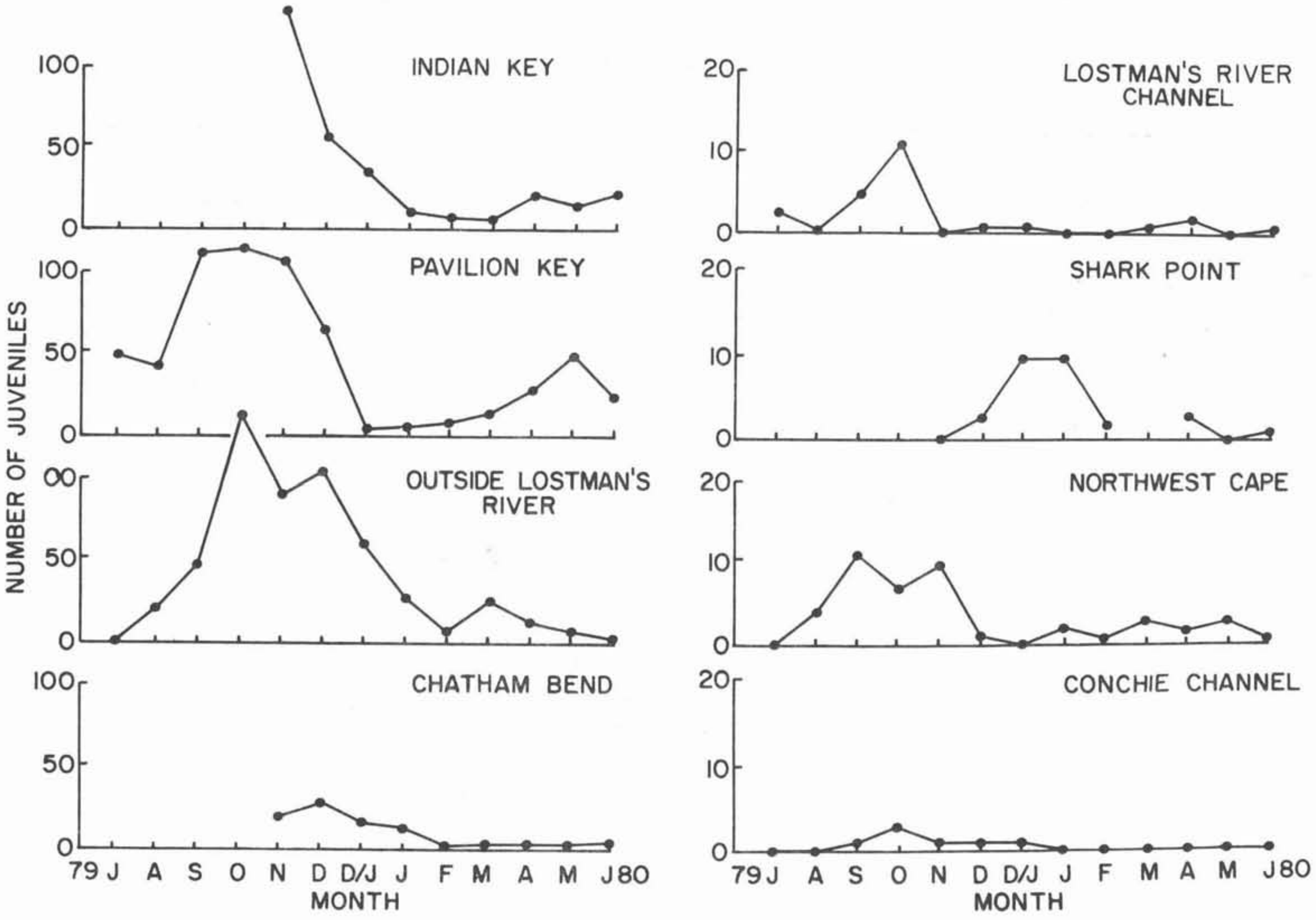


Figure 3. Number of juvenile stone crabs found on adult stone crab traps, by month. Each data point represents number of juveniles per 5-trap line. NOTE: change of scale in graphs in last four stations.

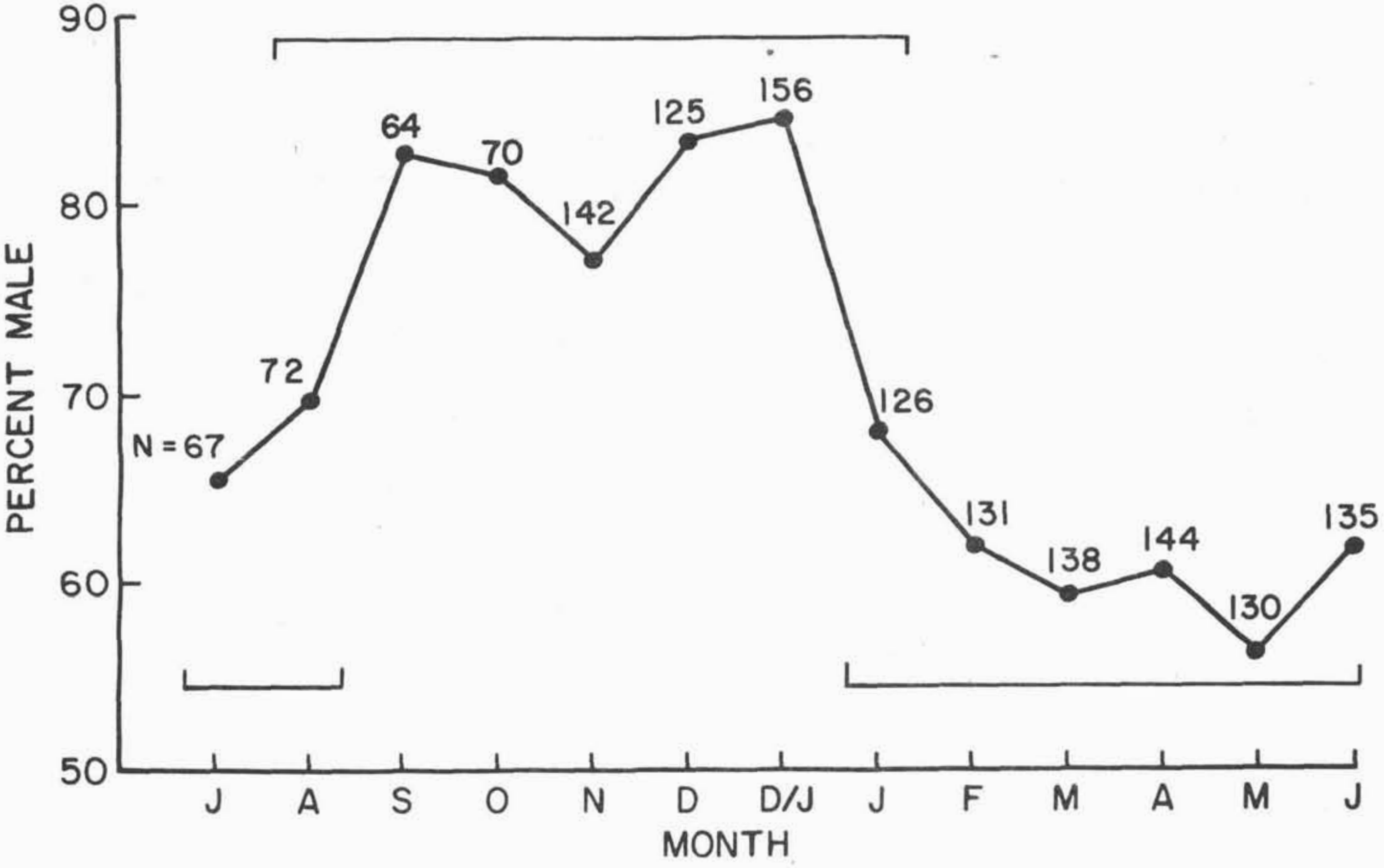


Figure 4. Proportion of total catch comprised of male stone crabs, by month, for the Gulf of Mexico and western Florida Bay. Statistical differences in sex ratio (male:female) among months were established by G-test (GH=76.56**,12 df). Statistically similar groups of months (illustrated) were determined by simultaneous test procedure. N=total number of crabs captured each sampling interval.

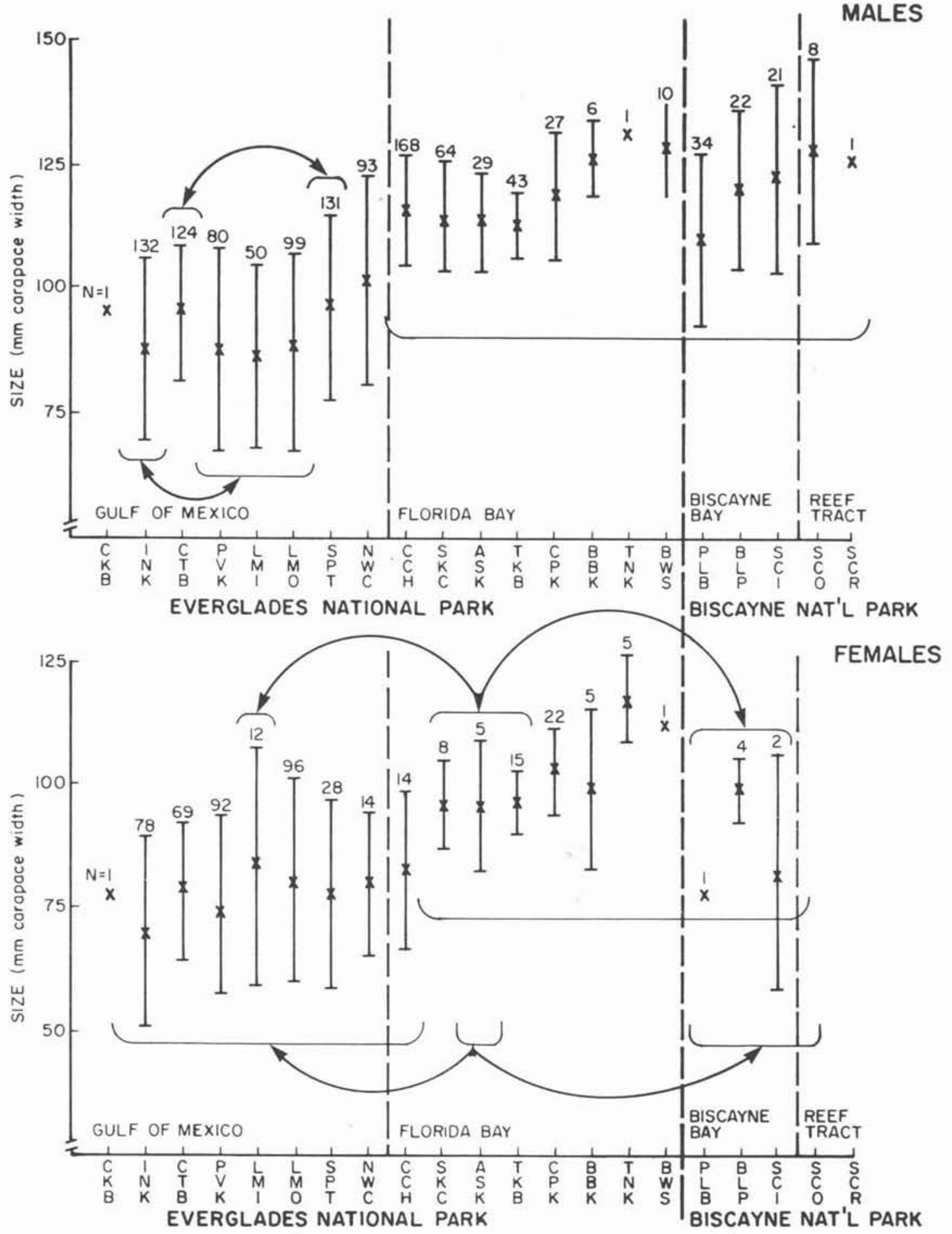


Figure 5. Mean size (and standard deviation) of male and female stone crabs for each station at which crabs were captured. Statistically similar stations, as determined by analysis of variance and Student-Neuman-Kuel rank analysis, are illustrated.

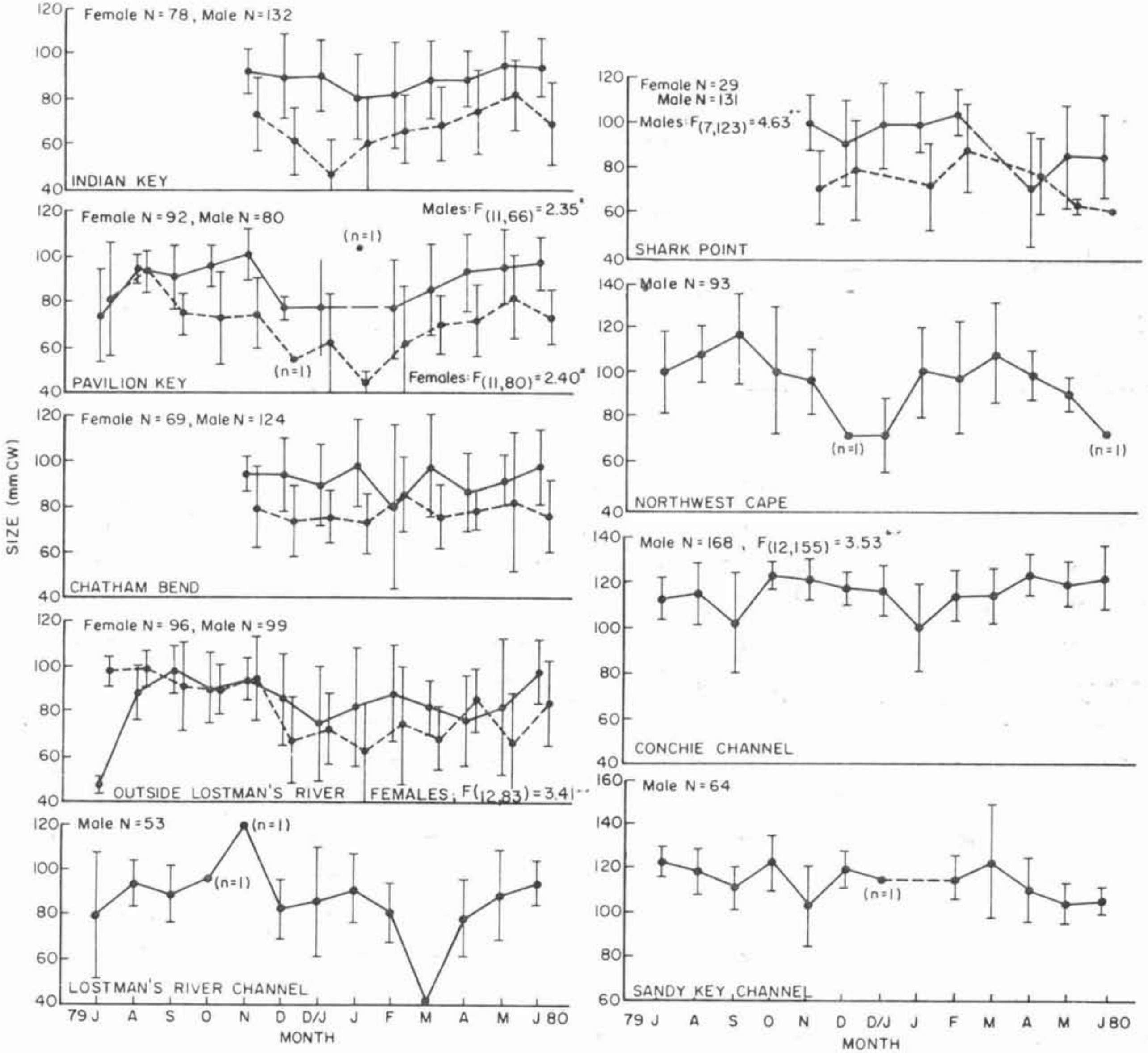


Figure 6. Mean size (mm carapace width and standard deviation) of male (solid lines) and female (dashed lines) stone crabs at individual stations over time. Only those stations with sufficient numbers of crabs of either sex were included. F values are given for stations shown by analysis of variance to be significantly different in mean size of one or both sexes over time.

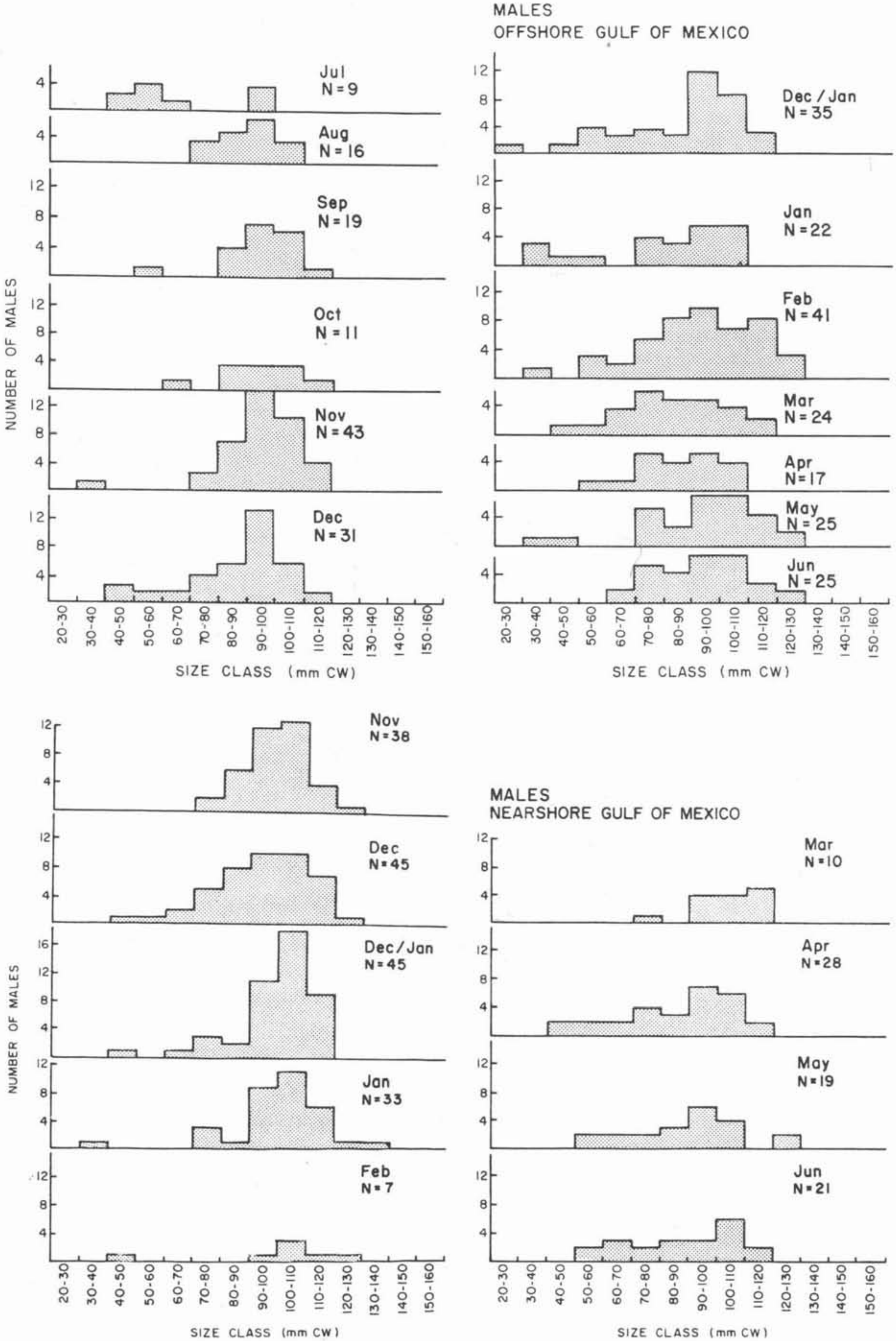
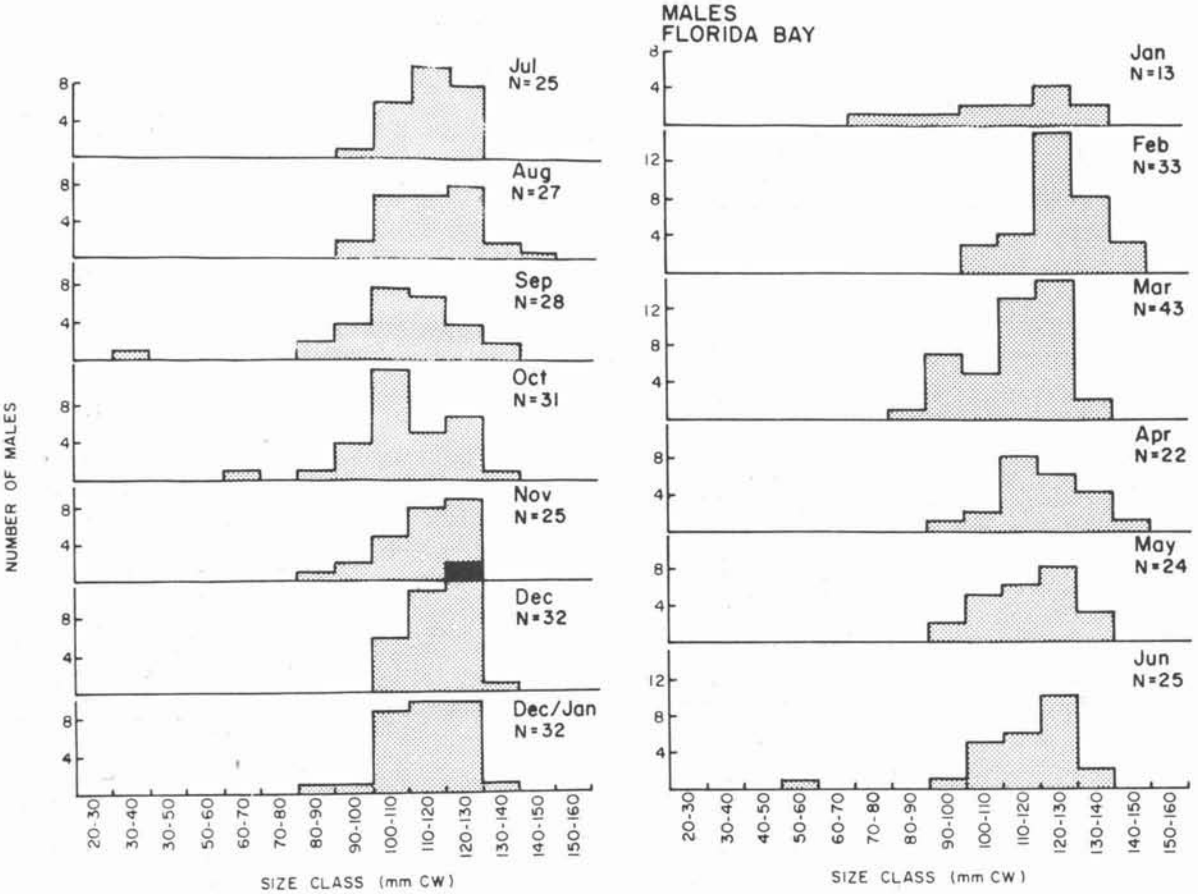


Figure 7. Ten millimeter size class frequencies (carapace width) of stone crabs by month. Stations were grouped according to criteria discussed in the text. Station groups, and characteristics of each group, are listed in Table 6. Station groups with insufficient numbers of crabs of one or both sexes are not shown.


MALES
FLORIDA BAY

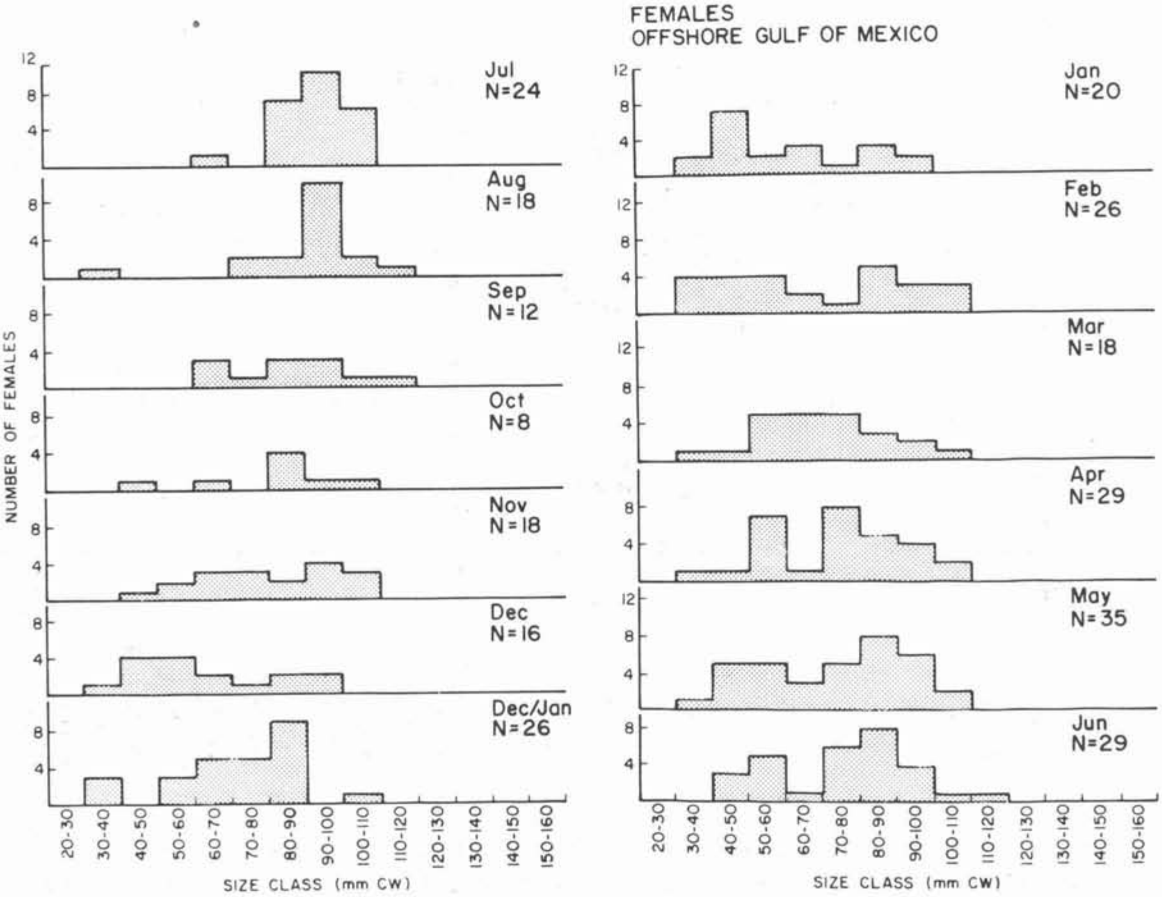

FEMALES
OFFSHORE GULF OF MEXICO

Figure 7 continued.

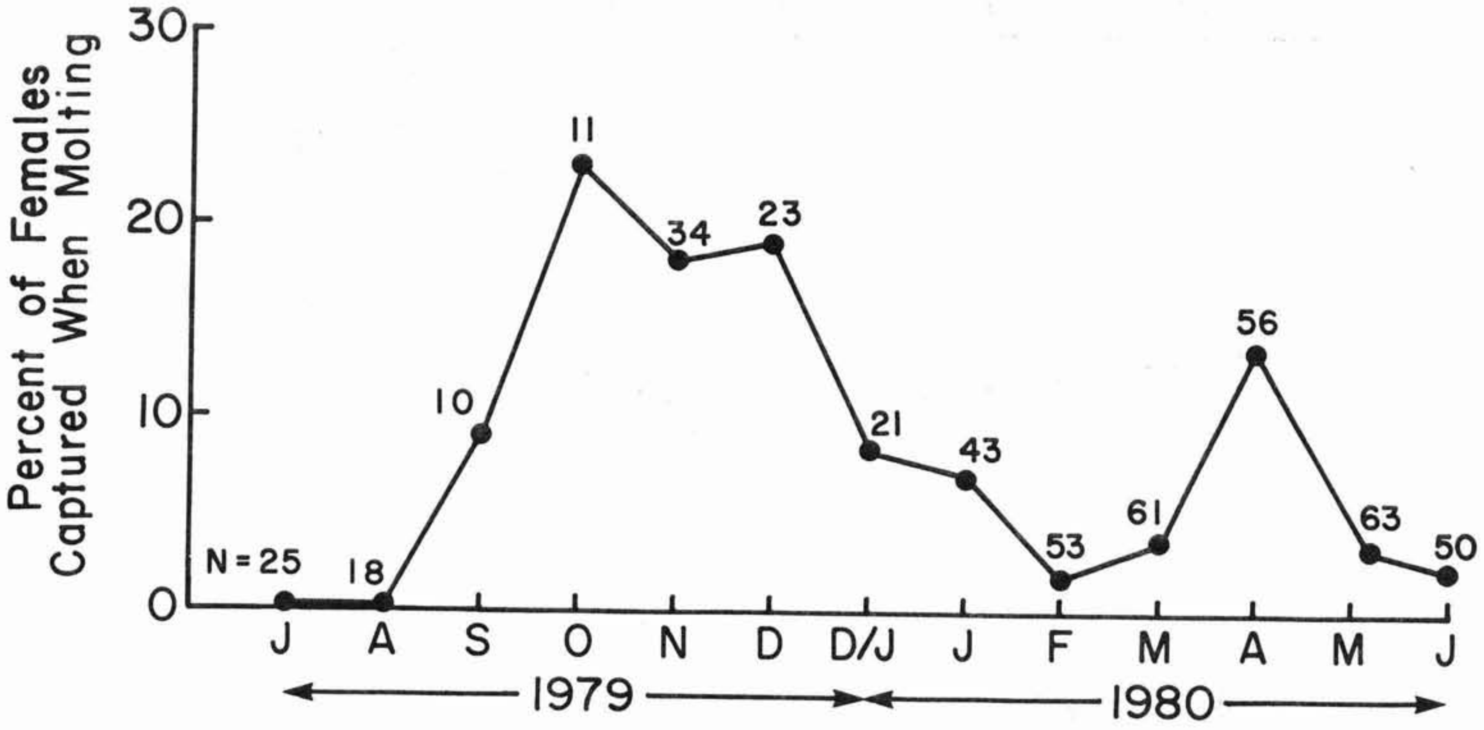


Figure 8. Proportion of females molting, by month (number of molting females/number of females captured). N equals number of females captured each sampling period.

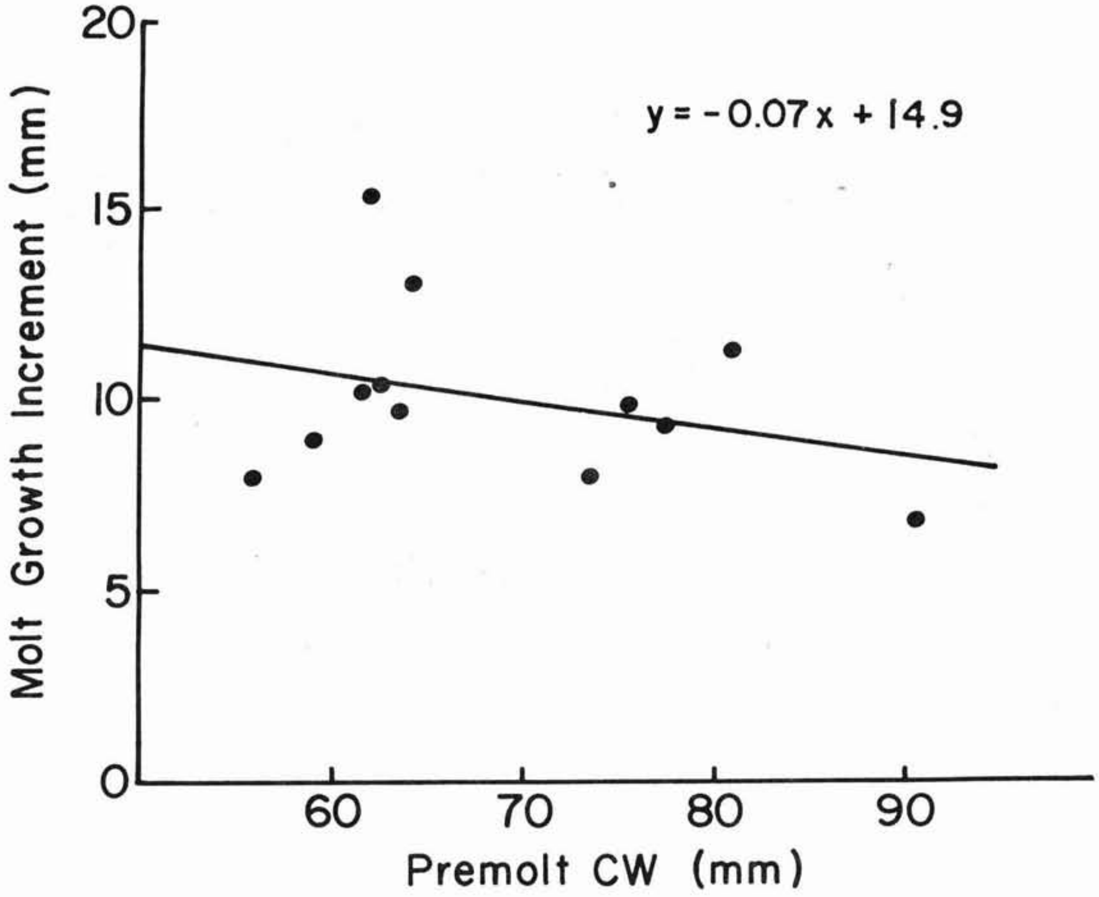


Figure 9. Regression (Model I) of female size (premolt mm carapace width) on growth increment. The line generated did not differ significantly from a line with a slope of zero.

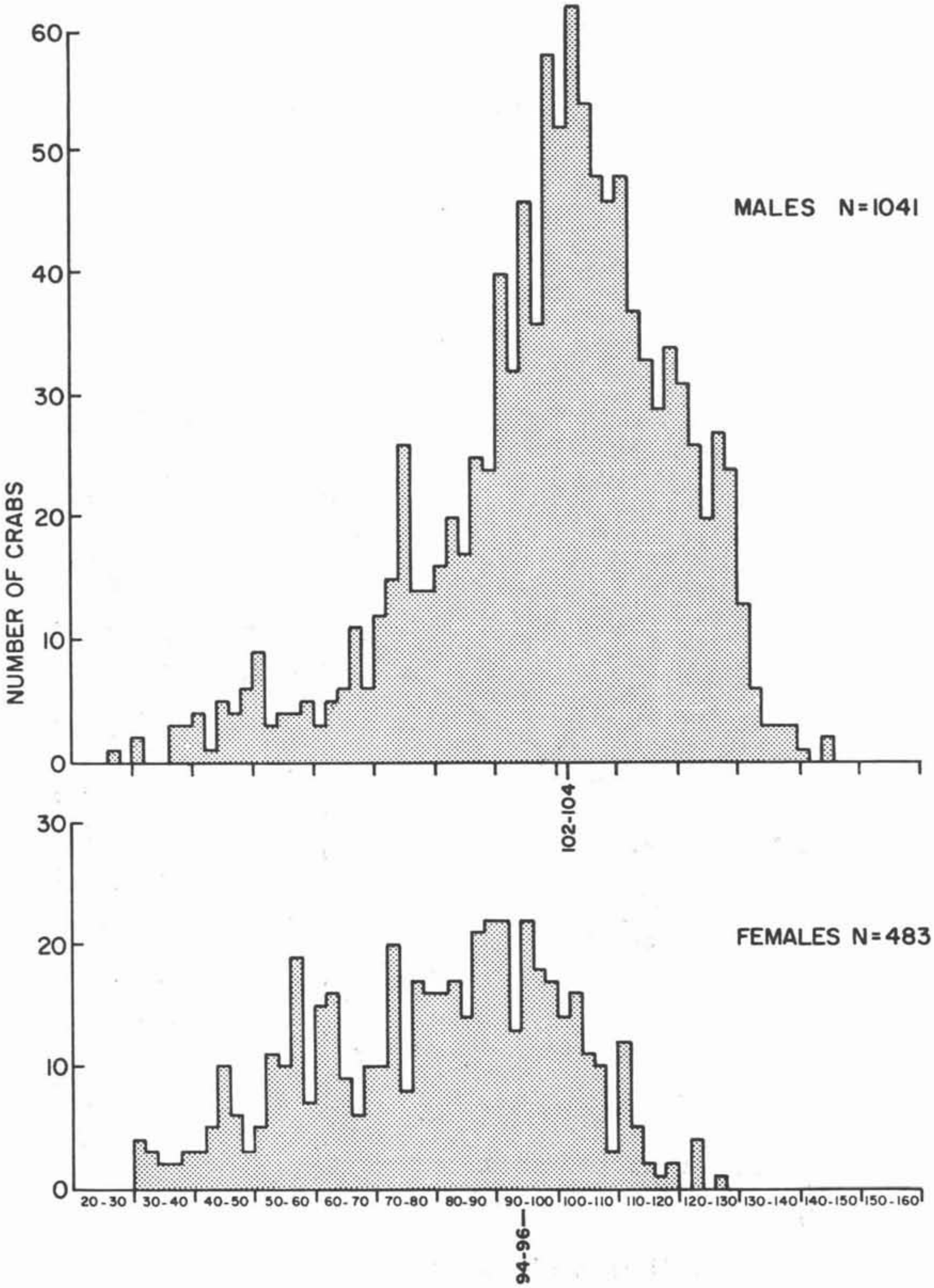


Figure 10. Number of crabs per 2 mm size increment captured in nearshore southwest Florida in this study (Gulf of Mexico and Florida Bay). One hundred percent retention size increments used in calculation of mortality coefficients are shown.

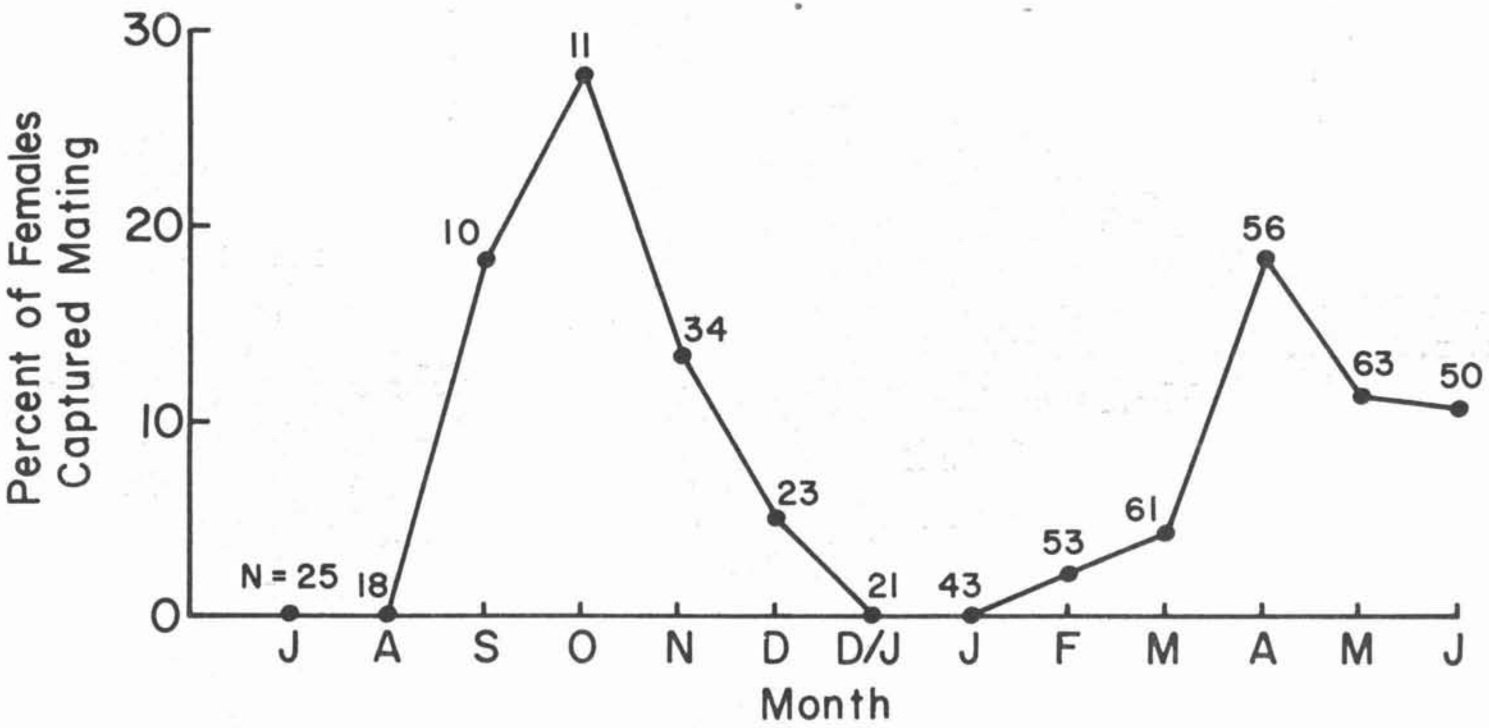


Figure 11. Proportion of the female population found mating, by month, in the Gulf of Mexico and western Florida Bay. Females were used as the indicator of proportion of the population mating, since males were always in excess in traps (see Sex Ratio) and assumed to be in sufficient supply for mating purposes. N = total number of females captured each month.

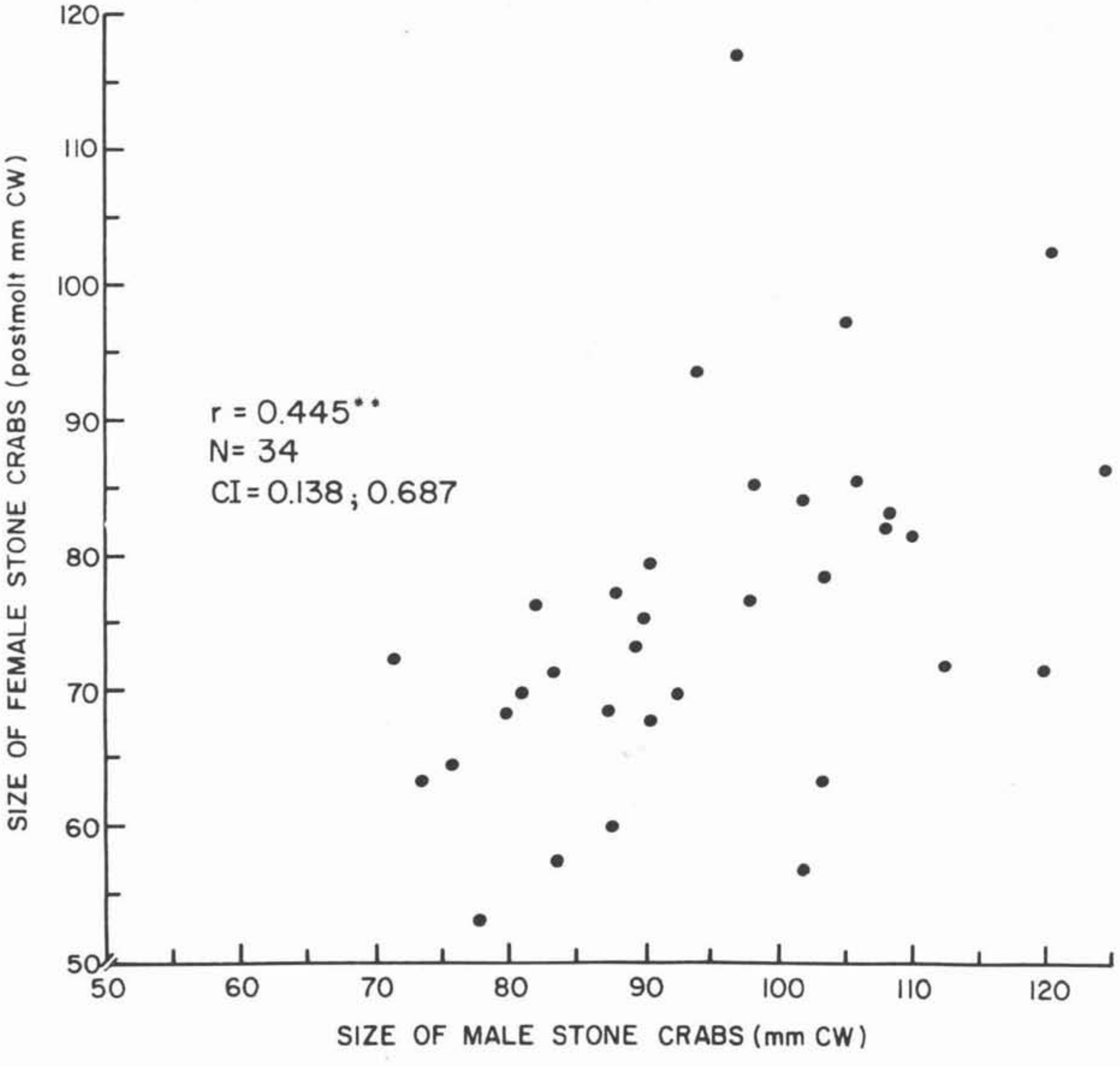


Figure 12. Correlation between size of male and female stone crabs composing a mated pair.

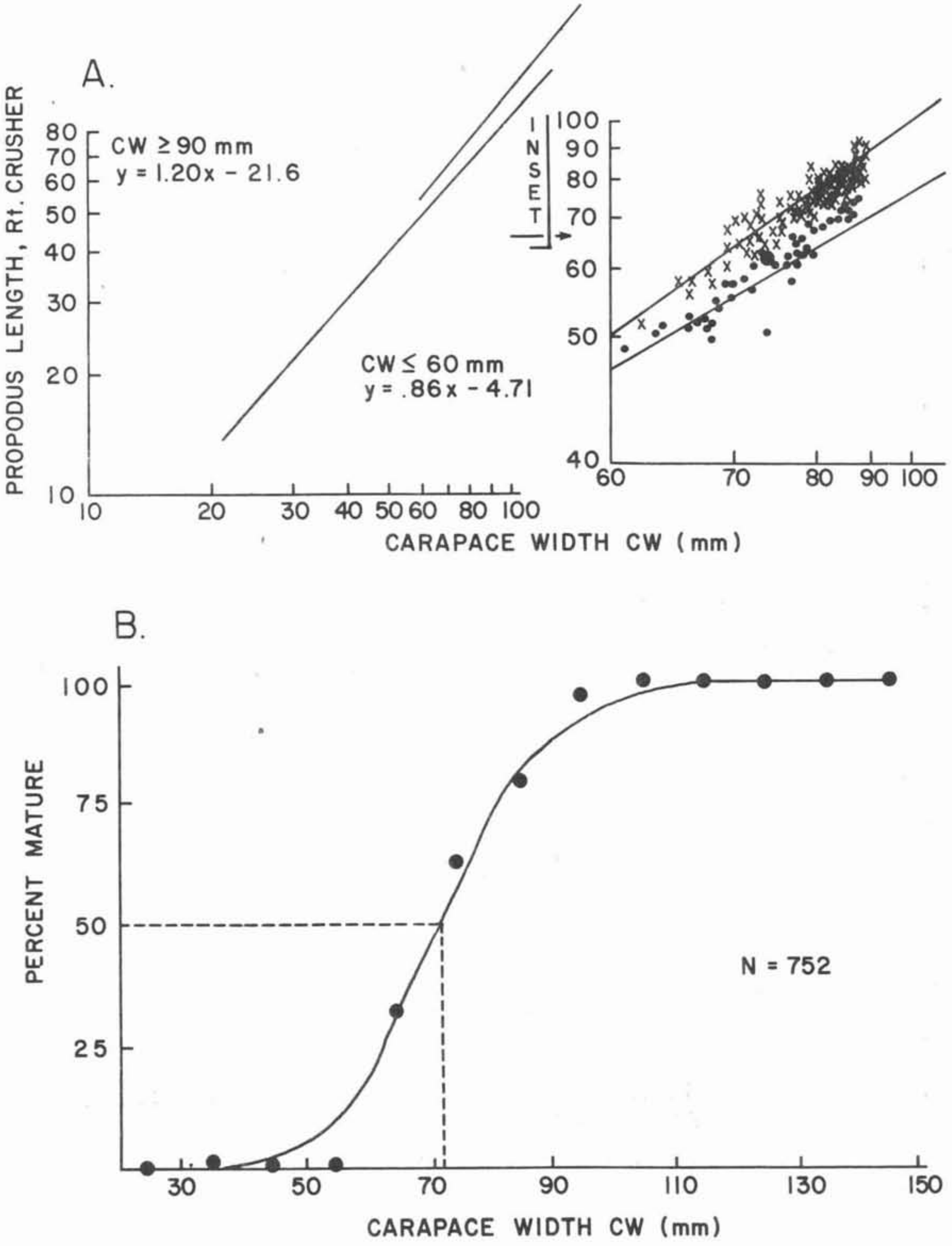


Figure 13. Size of 50% maturity of male stone crabs, according to the method of Somerton (1980). Figure A represents the regression line of adult and juvenile male crabs, as determined by non-heirarchial cluster analysis. The size of 50% maturity (Figure B) is estimated by using non-linear regression to fit a logistic function to percent maturity and size estimates. Only males with unregenerated (original) right crusher claws were used in the analysis.

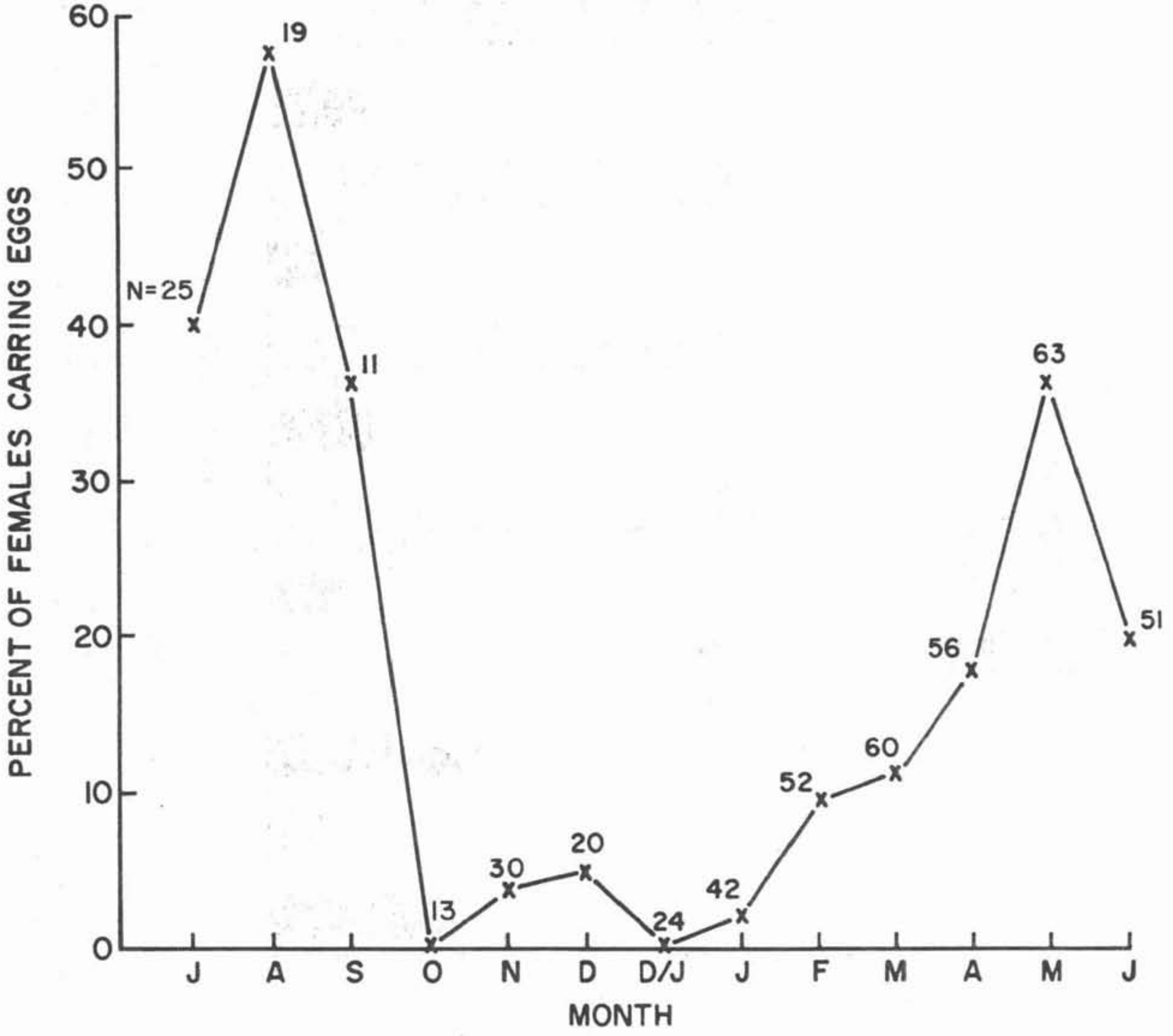


Figure 14. Monthly variation in proportion of females in reproductive state (ovigerous) in Everglades National Park. N = total number of females captured.

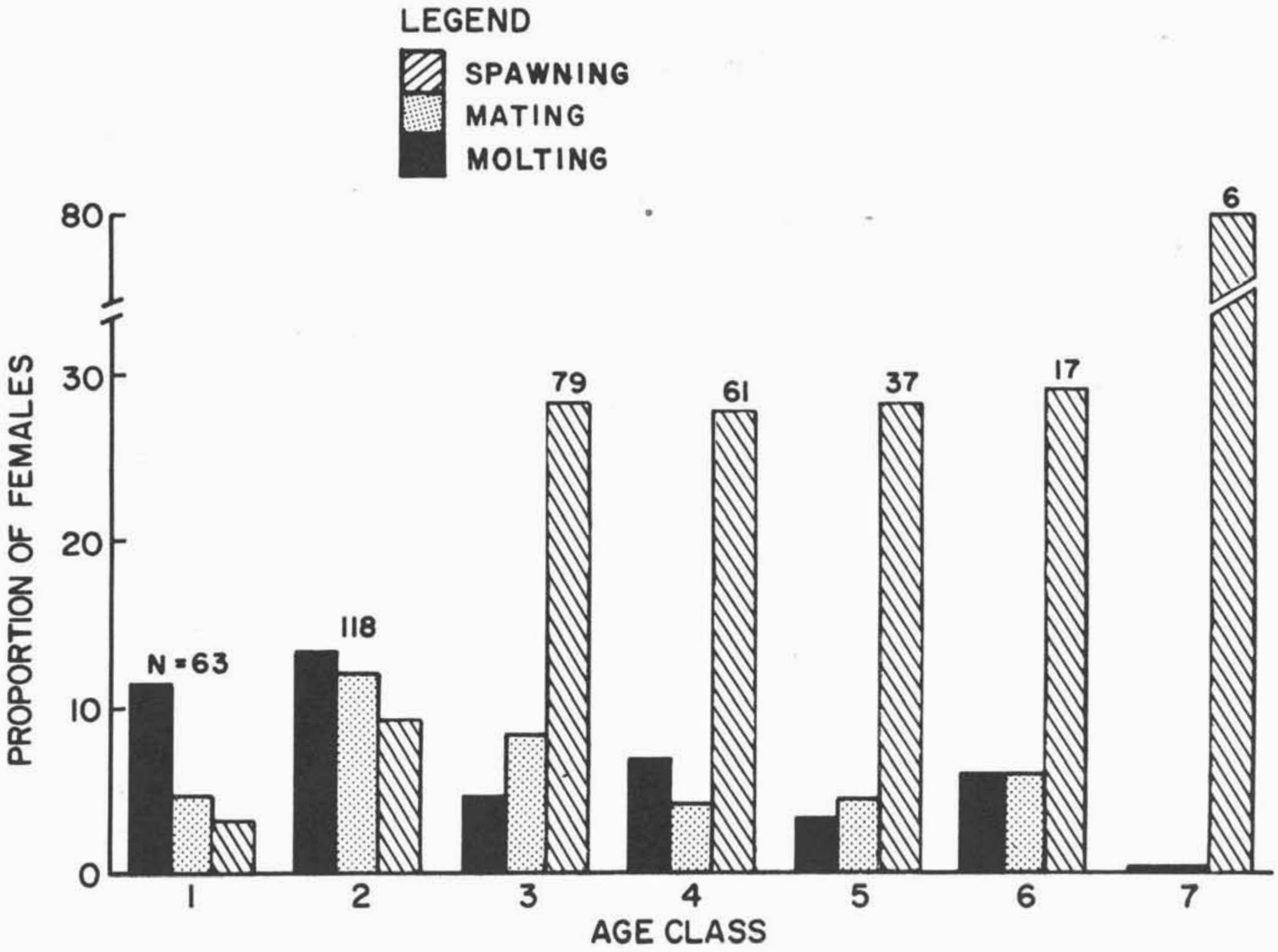


Figure 15. Proportion of females molting, mating, and spawning, by age class (number in specified state/total number within age class), in Everglades National Park. Age classes are defined in the text. No females considered to be less than one year of age (less than 40 mm CW) were collected in any of these three character states. N = total number of females in each age class.

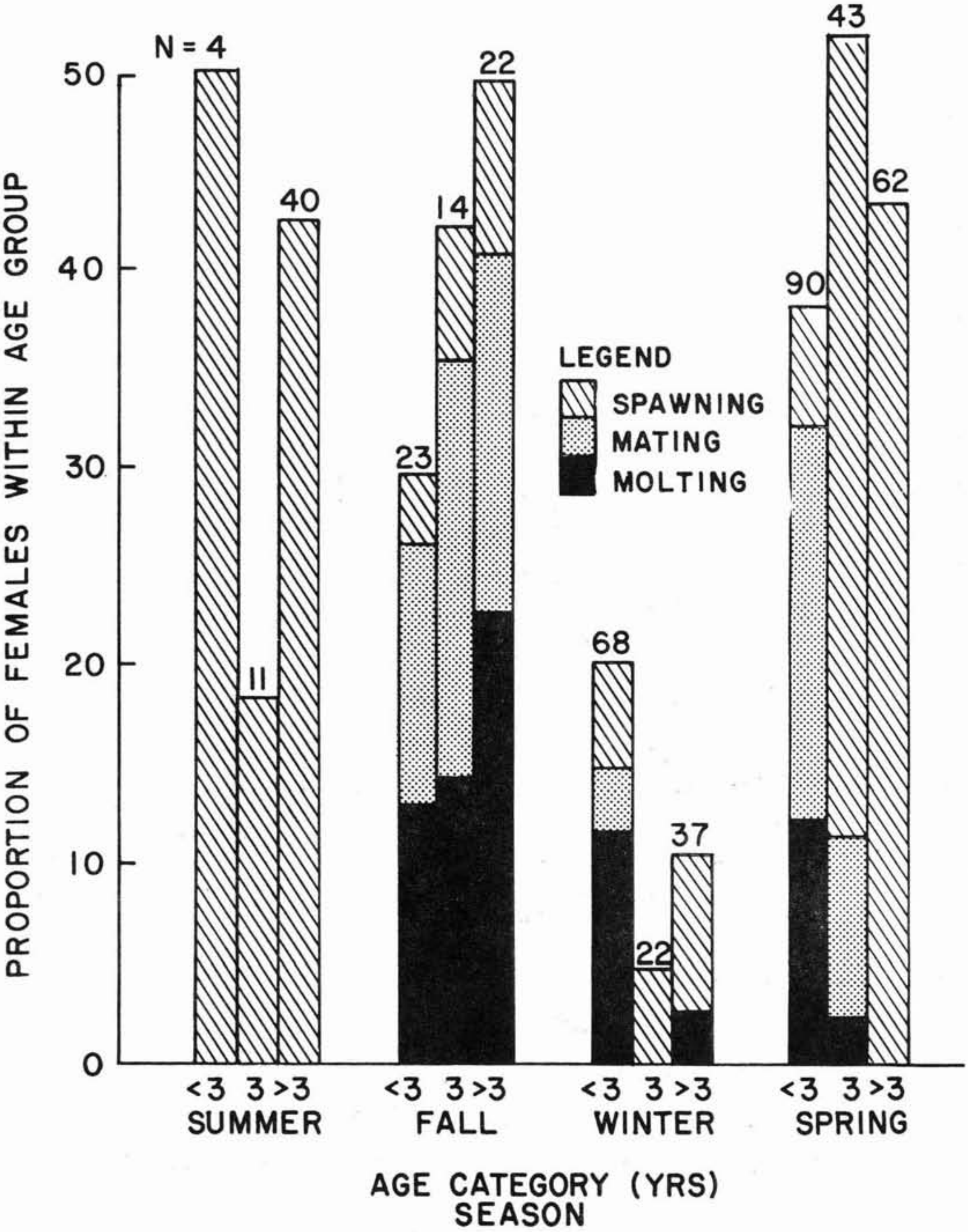


Figure 16. Seasonal variation in proportion of females in three age categories found molting, mating, and spawning in Everglades National Park. N = total number of females captured in each age category. The seasons are defined as follows: summer--July-Aug; fall--Sept.-Nov.; winter--Dec.-Feb.; spring--Mar.-June.

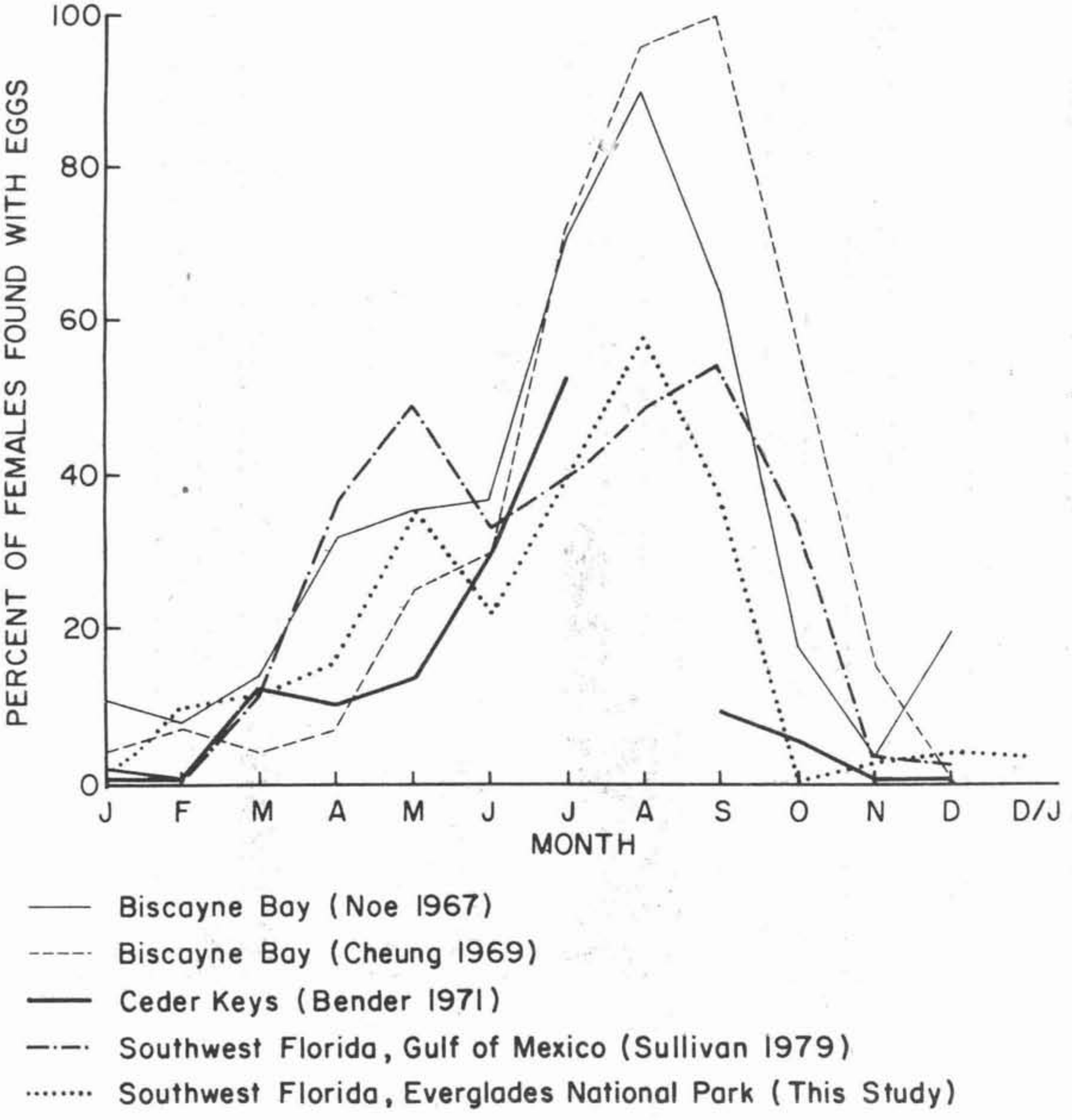


Figure 17. Composite of percent of total trapped female stone crabs with eggs, by month, from all studies conducted in Florida.

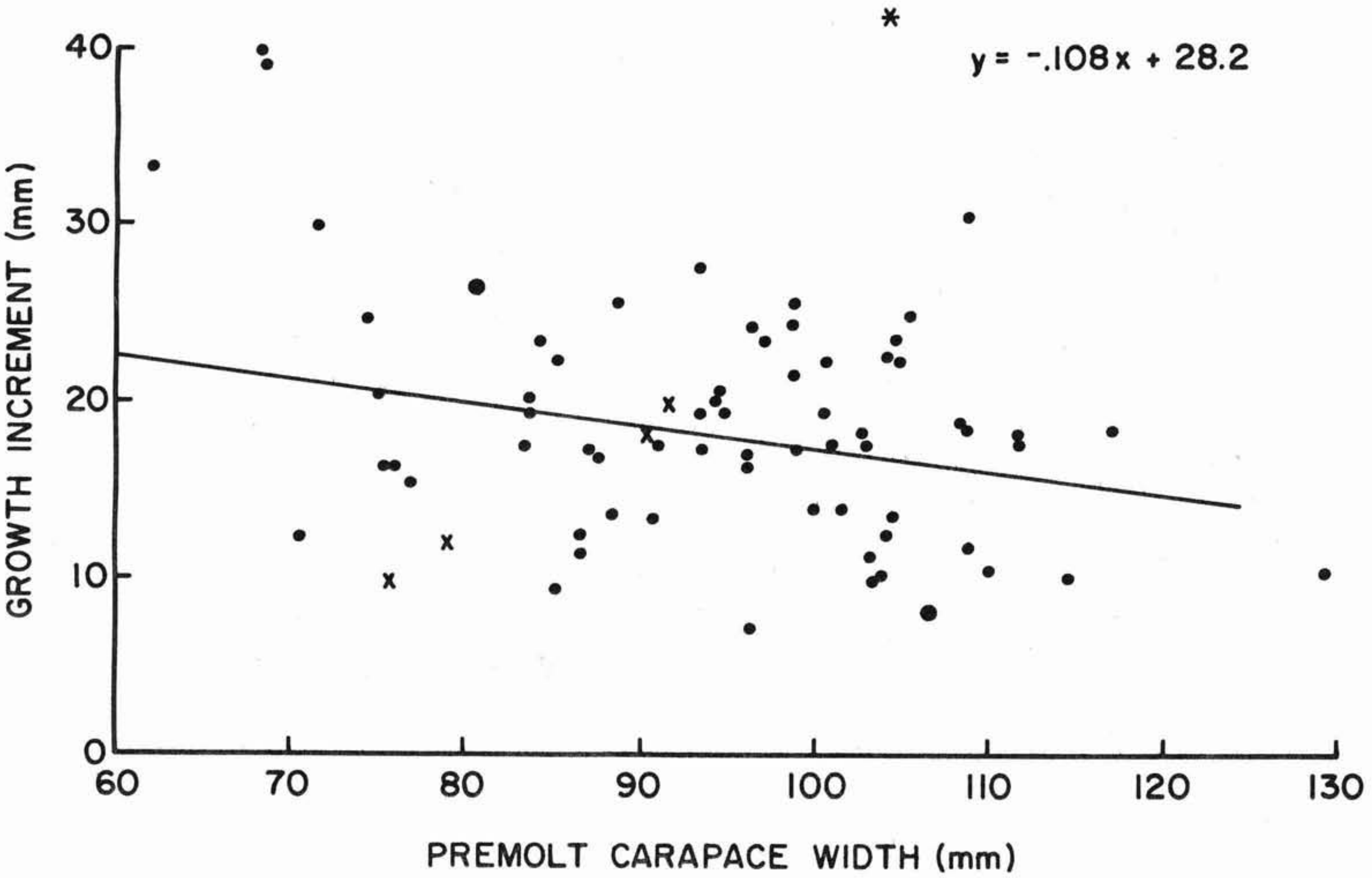


Figure 18. Regression of growth increment on premolt carapace width in male stone crabs greater than 70 mm carapace width. Dots represent capture-recapture data from an unpublished study conducted by Everglades National Park personnel in western Florida Bay from March 1978 to March 1979. X's represent data from crabs captured while molting during this study. The regression line generated is not significantly different from a line with a slope of zero (t=1.86, 60df). The starred point deviates significantly (t=3.56, 60 df; p less than .001) from the line and may represent a crab that molted twice while at large. (This crab was at large longer than all other crabs.) Crabs less than 70 mm carapace width were omitted from calculation of the regression equation due to obvious differences in growth increment.