

A Profile of the Western Gulf Stone Crab,
Menippe adina



Gulf States Marine Fisheries Commission

January 1995

No. 31

A PROFILE OF
THE WESTERN GULF STONE CRAB, *Merippe adina*

by

The Gulf States Marine Fisheries Commission
TCC Crab Subcommittee

edited by

Vince Guillory
Harriet M. Perry
Richard L. Leard

published by

Gulf States Marine Fisheries Commission
P.O. Box 726
Ocean Springs, Mississippi 39566-0726

January 1995

Number 31

A publication of the Gulf States Marine Fisheries Commission pursuant to National Oceanic and Atmospheric Administration Award Number NA26FI0026-03. This paper is funded by a grant from the National Oceanic and Atmospheric Administration. The views expressed herein are those of the author(s) and do not necessarily reflect the views of NOAA or any of its sub-agencies.



Acknowledgements

The GSMFC, TCC Crab Subcommittee gratefully acknowledges the support for and technical critique of the profile by Dr. Theresa Bert (Florida Department of Environmental Protection). We also thank Ms. Christine Trigg (Gulf Coast Research Laboratory [GCRL]) for supplying physiological data and technical review, Mr. Charles Dugas (Louisiana Department of Wildlife and Fisheries [LDWF]) for morphometric data from the fishery, Mr. Lee Usie (National Marine Fisheries Service [NMFS]) for landings data, and Mr. Walter Brehm (Clinical Research Laboratory, Keesler Air Force Base) for statistical analysis of data. We are also grateful for editorial review by Ms. Marjorie Williams (GCRL), Mr. Paul Prejean (LDWF), and Mr. Martin Bourgeois (LDWF). Special appreciation is extended to Mr. Dave Donaldson (GSMFC) for preparation of graphics and to Ms. Cindy Yocom for her special attention and dedication to the quality of this document.

Table of Contents

Page

1.0 Introduction	1-1
2.0 Biological Description	2-1
2.1 Classification	2-1
2.2 Morphology	2-2
2.2.1 Larvae	2-3
2.2.2 Juveniles	2-3
2.2.3 Adults	2-3
2.3 Age, Growth, and Maturation	2-5
2.3.1 Larvae	2-5
2.3.2 Juveniles	2-6
2.3.3 Adults	2-7
2.3.3.1 Size at Maturity	2-7
2.3.3.2 Age at Maturity	2-7
2.3.3.3 Growth and Molting	2-7
2.3.3.3.1 Seasonality	2-8
2.3.3.3.2 Effects of Size	2-8
2.3.3.3.3 Effects of Autotomy and Declawing	2-8
2.3.3.3.4 Variations by Sex	2-8
2.3.3.4 Claw Regeneration/Handedness	2-9
2.4 Reproduction	2-9
2.4.1 Sex Ratios	2-9
2.4.2 Mating and Fertilization	2-10
2.4.2.1 Mating	2-10
2.4.2.2 Fertilization	2-10
2.4.3 Gonadal Development	2-11
2.4.4 Spawning	2-11
2.4.5 Fecundity	2-14
2.5 Pathology/Parasitology	2-14
2.6 Trophic Relationships	2-14
2.6.1 Larval Food Habits	2-14
2.6.2 Juvenile Food Habits	2-15
2.6.3 Adult Food Habits	2-15
2.6.4 Predator-Prey Relationships	2-16
2.7 Movement and Migration	2-16
2.8 Recruitment	2-17
2.9 General Behavior	2-18
3.0 Geographic Distribution and Habitat	3-1
3.1 Geographic Distribution	3-1
3.2 General Habitat Conditions	3-1
3.2.1 Larvae	3-1
3.2.2 Juveniles	3-1
3.2.3 Adults	3-1
3.2.4 Community Interrelationships	3-2
3.3 Environmental Tolerances	3-2
3.3.1 Temperature and Salinity	3-2
3.3.1.1 Larvae	3-3
3.3.1.2 Juveniles	3-4

3.3.1.5 Adults	3-4
3.3.2 Dissolved Oxygen	3-6
3.3.3 Pollutants/Toxicants	3-6
4.0 Description of the Fishery	4-1
4.1 Commercial Fishery	4-1
4.1.1 Texas	4-1
4.1.2 Louisiana	4-5
4.2 Recreational Fishery	4-5
4.3 Fishery-Related Population Characteristics	4-5
4.3.1 Texas	4-9
4.3.2 Louisiana	4-9
4.3.3 Mississippi	4-13
4.4 Fishery-Related Population Characteristics of <i>M. adina</i>	4-15
4.4.1 Morphometric Relationships	4-15
4.4.2 Biological Population Characteristics	4-16
4.4.3 Implications for Management	4-17
4.5 Potential for Directed Fishery Development	4-18
4.5.1 Texas	4-18
4.5.2 Louisiana	4-18
4.5.3 Mississippi	4-19
4.6 Mariculture	4-19
5.0 Rules and Regulations	5-1
5.1 Florida (State Waters)	5-1
5.2 Alabama, Mississippi, and Louisiana	5-1
5.3 Texas	5-2
5.4 Federal	5-2
5.4.1 Size Restrictions	5-2
5.4.2 Harvest Practices	5-2
5.4.3 Seasons	5-3
5.4.4 Closed Areas	5-3
5.4.5 Gear Restrictions	5-3
5.4.6 Vessel Enumeration	5-3
5.4.7 Statistical Reporting	5-3
5.4.8 Amendments	5-3
5.4.8.1 Amendment 1	5-3
5.4.8.2 Amendment 2	5-3
5.4.8.3 Amendment 3	5-4
5.4.8.4 Amendment 4	5-4
6.0 Literature Cited	6-1

1.0 INTRODUCTION

The western Gulf stone crab (*Menippe adina*) ranges in coastal waters from northwest Florida around the Gulf of Mexico to the state of Tamaulipas, Mexico. Currently, *M. adina* supports small, directed commercial fisheries in Louisiana and Texas. In Mississippi and Alabama, the fishery exists as a limited, seasonal bycatch component of the blue crab (*Callinectes sapidus*) fishery. High dockside value of stone crab claws and an apparently unsatisfied market demand have created interest in further development of commercial fisheries for stone crabs (Bert 1992).

The Gulf of Mexico Stone Crab Fishery Management Plan (Costello et al. 1979) reviewed the stone crab resource throughout the Gulf with management recommendations applicable to the exclusive economic zone (EEZ) (9 to 200 nautical miles offshore), particularly off the west coast of Florida and the Florida Keys. Because *M. adina* and the hybrid forms were not recognized at the time of plan development, some of the biological and ecological data used to characterize *Menippe mercenaria* may refer to these other taxa. In addition, discrepancies in the literature may be the result of ecological differences among the taxa. With the exceptions of Florida and Texas, the western Gulf stone crab fishery is essentially unregulated in the Gulf of Mexico.

The goal of this document is to provide a data base for use in development of management measures. The objectives are to summarize available literature, data, and regulations pertaining to the western Gulf stone crab and to describe the fishery.

2.0 BIOLOGICAL DESCRIPTION

Information on life history, population dynamics, and ecology of *M. adina* will be utilized in this document where available; however, where the data are deficient, references to *M. mercenaria* will be used to provide supplemental information. Stuck and Perry (1992) concluded that biological and ecological differences in *M. adina* and *M. mercenaria* may be sufficiently distinct as to warrant management of these two species as separate stocks and that specific life history information available for *M. mercenaria* may not be directly applicable to *M. adina*. Bert (1985) cautioned against extrapolation of historic survey data on *Menippe* from the hybrid zone to either true form.

Relatively little research has been conducted on the biology and life history of *M. adina*, however, there have been a number of recent surveys to assess population abundance and distribution in northern Gulf of Mexico estuaries. A symposium addressing the biology and fishery for stone crab taxa was held April 25-26, 1986, at the Mote Marine Laboratory in Sarasota, Florida.

2.1 Classification

The classification of Crustacea and Reptantia in particular is unsettled, and a diversity of taxonomic groupings has been proposed (Bowman and Abele 1982, Schram 1986). The following classification of Schram (1986) is a compromise that incorporates some recent taxonomic advances:

Phylum: Crustacea
Class: Malacostraca
Subclass: Eumalacostraca
Order: Decapoda
Suborder: Reptantia
Infraorder: Brachyura
Section: Heterotremota
Family: Xanthidae

The genus *Menippe* in the Gulf of Mexico has been subjected to recent taxonomic revisions. Bert (1986) noted that stone crabs ranging from northwest Florida to Mexico differed from those found from northwest Florida to North Carolina. Williams and Felder (1986) later described the western Gulf of Mexico form as *M. adina*. Bert and Harrison (1988) and Cline et al. (1992) presented data on hybridization, evolutionary history, and general taxonomy of *M. adina*.

Bert (1986) used variations in proteins and color morphology to determine the evolutionary relationships of *Menippe* in the southeastern United States. *Menippe mercenaria, sensu lato*, was shown to contain two distinct forms that exhibited broad geographic areas of great homogeneity in allozymes and coloration. Bert (1986) concluded that the two forms were sufficiently distinct to warrant taxonomic recognition at the semispecies level but not at the species level (a semispecies may exhibit distinct morphological and genetic characteristics, but extensive interbreeding occurs). She suggested that the two forms probably evolved as a consequence of allopatric subdivision of the parental stock by major glacial and tectonic events perhaps 2.9 to 3.2 million years BP.

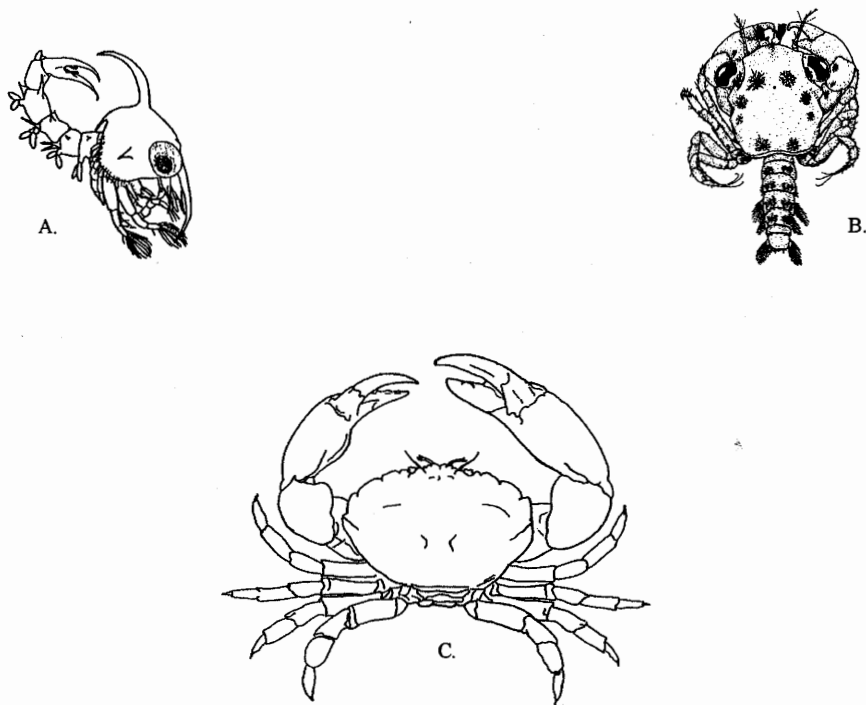
Williams and Felder (1986) evaluated color, stridulatory patterns, and morphology of *M. mercenaria, sensu lato*, throughout the Caribbean and Carolinian Provinces of the western North Atlantic. They identified two morphologically distinct populations with narrowly overlapping geographic ranges. The peninsular Florida form was delineated as *M. mercenaria, restricted*. The western Gulf form, recognized by Bert (1986), was described as a new species, *M. adina*. The specific name '*adina*' was derived from the Greek word '*adinos*' (meaning close or crowded) and refers to the patch of closely crowded striae on the inner palmer surface of the major chela. According to the taxonomic synonymy by Williams and Felder (1986), the following literature references were attributed to *M. adina*: *Menippe mercenarius* - Rathbun (1884, 1887); *Menippe mercenaria* - numerous references from the Florida panhandle westward; and *Menippe nodifrons* - Rathbun (1930), Scotto (1979).

The western Gulf form (maroon-brown) ranges from Texas to Cape San Blas, Florida; the peninsular Florida form (spotted/banded) is found from northwest Florida eastward (Bert 1986). Bert (1986) noted the presence of unique disjunct areas of clinal variation in allele frequencies and color patterns in both the Gulf of Mexico and Atlantic Ocean. She identified a zone of introgressive hybridization between *M. adina* and *M. mercenaria* in the Apalachee Bay area of Florida situated at the junction of the present ranges of the two parental forms. Crabs resembling *M. mercenaria* in both genotype and phenotype were most common in the hybrid zone; however, the full range of phenotypic hybrids occurred at the center of the hybrid zone with *M. adina* becoming more prominent in the Florida panhandle and *M. mercenaria* being more dominant down the peninsula. In the panhandle counties of Franklin and Wakulla, Wilber (1987) performed a discriminant function analysis on certain *Menippe* taxonomic characteristics and found that 46.6% were *M. adina*, 21.5% were hybrids, and 31.8% were *M. mercenaria*. At Cedar Key, stone crabs were predominantly phenotypic intermediates and *M. mercenaria*-like hybrids with few *M. adina* or *M. adina*-like hybrids (Lindberg et al. 1990).

In contrast to the findings of Bert (1986) and Bert and Harrison (1988), the data of Cline et al. (1992) did not suggest the presence of hybrids in northwest Florida. Their data supported the recognition of separate species of *Menippe*.

2.2 Morphology

Figure 2.1 shows typical life history stages of *Menippe*.



- A - Zoea (Porter 1968)
- B - Megalopa (Martin et al. 1988)
- C - Adult

Figure 2.1. Typical life history stages of *Menippe*.

2.2.1 Larvae

Wear (1970) reviewed xanthid larval development. Porter (1960) noted that *M. mercenaria* larvae differed from other xanthid genera by attaining five or six zoeal stages while other xanthid larvae had only four. Hyman (1925), Porter (1960), and Kurata (1970) also described the larvae of *M. mercenaria*. *Menippe nodifrons* and *M. rumphii* larvae were characterized by Scotto (1979) and Kakati (1977), respectively.

Zoeal stages of *M. adina* have not been formally described. Martin et al. (1988) described and illustrated the megalopal stage of *M. adina* and compared it to *M. nodifrons*, *M. rumphii*, and *M. mercenaria*. In general, megalopal characters of *M. adina* were similar to those described for *M. mercenaria*, however, some specific differences between the two species were noted:

- Ventral dactylar spines on the posterior walking legs of *M. mercenaria* are less serrate than in *M. adina* and are sometimes armed with only two or three large spinules rather than the numerous spinules seen in *M. adina*.
- Most *M. mercenaria* have four (rather than three) long serrate setae on the dactylus of the fifth pereopod.

2.2.2 Juveniles

No detailed morphological descriptions were found for juvenile *M. adina*. Bert (1986) and Lindberg and Marshall (1984) described small juvenile *M. adina* as being greenish or bluish gray to gray or dark tan with small dark spots on the dorsal carapace and chelae.

Manning (1961) and Wass (1955) pointed out the resemblance of young *M. mercenaria* to *Panopeus herbstii* and *Eurytium limosum*. Manning (1961) described juvenile *M. mercenaria* as having banded legs and a carapace color of black or deep maroon with light dots.

2.2.3 Adults

Williams (1965, 1984) listed recognition characters of the genus *Menippe* as:

"Carapace transversely oval, approximately 2/3 as long as wide, convex, nearly smooth to unaided eye, minutely granulate and punctate; anterolateral border divided into four lobes: first two wide, third wide but dentiform, fourth much narrower and dentiform; front with median notch and broad trilobulate lobe on each side; orbital border thick, fissures indistinct; chelipeds large and heavy, unequal, nearly smooth; inside surface of hands with patch of fine, oblique, parallel striae serving as a stridulating organ and adapted for playing against thick edge of second and third anterolateral teeth and outer suborbital tooth; dactyl of major chela with large basal tooth, and fixed finger with large subbasal tooth; fingers of minor chela with numerous small teeth; walking legs stout, hairy distally."

Differences in color and morphology between *M. adina* and *M. mercenaria* were tabulated by Williams and Felder (1986) and Bert and Harrison (1988) (Table 2.1).

Stone crabs have a crusher claw with an enlarged basal tooth on the pollex and a small pincer claw with numerous small teeth used for cutting (Simonson 1985, Simonson and Steele 1981). Laterality in *Menippe* and other crustaceans was also discussed by Davis (1987). Chela morphology in temperate and tropical *Menippe* was compared by Blundon (1988). The morphology of the stridulatory apparatus was described for *M. mercenaria* by Dumortier (1963).

TABLE 2.1. Morphological and color differences between *Menippe adina* and *M. mercenaria* according to Williams and Felder (1986) and Bert and Harrison (1988).

Structure	<i>M. mercenaria</i>	<i>M. adina</i>
Williams and Felder (1986)		
Color		
Carapace	Poorly defined light yellow spots on broken pattern of reddish-orange to reddish-violet, and often with additional dark spots; latter ocellated and near black in young.	Light yellow spots or flecks on broken pattern of reddish-orange to reddish-violet; spots edged with darker pigment in young.
Chelipeds	Frontal surface of major dactyl having border between light area at base and dark distal part usually with light area extended below punctate groove as broad tongue; often nearly vertical.	Frontal surface of major dactyl having border between light area at base and dark distal part usually with light area extended along punctate groove as narrow point; rarely almost vertical.
Legs	Carpi and propodi distinctly banded with reddish-brown to orange (some bands maroon); ground color lighter (more broken mottling) between dark bands; without broken line of light spots at midwidth of merus 5.	Carpi and propodi lacking distinct bands; ground color reddish-orange to wine; pale yellow spots in longitudinal broken line at midwidth of merus 5.
Morphology		
Anterolateral tooth 3	Almost always broader than 4, rarely equal to.	Usually broader than 4, but often narrower than and sometimes equal to.
Anterolateral tooth 5	Weakly prominent, somewhat blunt; anterior margin shallowly concave, tip directed more laterally than anteriorly.	Strong, prominent, fairly acute; anterior margin rather strongly concave, tip directed more anteriorly than laterally.
Posterolateral margin of carapace	Usually weakly convex in anterior 1/3.	Usually straight to concave in anterior 1/3.
Setae on legs 2-5	Dorsal margin of meri usually with few if any; sparse on propodus 5, restricted distally.	Dorsal margin of meri usually with well defined row; dense along most of ventral margin on propodus 5.

Table 2.1. Continued

Structure	<i>M. mercenaria</i>	<i>M. adina</i>
Bert and Harrison (1988)		
Dorsal carapace/claw color	Tan to light or medium gray.	Deep chocolate-brown to deep maroon-brown.
Ventral carapace/claw color	Creamy to white.	Golden to golden brown.
Carapace, claw markings	Black spotted, spots large or small (usually small), but uniform in size.	Occasional mottling of light to golden brown on dorsal posterior carapace: frequently solid with little or no mottling.
Legs	Dark brown, distinct white bands at junction of segments.	Solid deep chocolate-brown to maroon-brown.

Fishery-related morphometric relationships for *M. mercenaria* were described by Sullivan (1979). Similar data for *M. adina* are presented in Section 4.4.1.

2.3 Age, Growth, and Maturation

Growth is defined as the relationship between size (length or weight) and age. Determination of growth rates for decapod crustaceans is difficult (Cobb and Caddy 1989). Age must be indirectly determined by the construction of an age-size key based on data from modal analysis or tagging experiments. Because size increases only at ecdysis, the measured growth rate is made up of two components: (1) size increase at molting (growth increment) and (2) interval between molts (intermolt interval). Difficulties are compounded by the pronounced variability in growth increment and intermolt interval associated with fluctuations in salinity, water temperature, and food availability.

2.3.1 Larvae

Larval growth of *M. adina* involves metamorphosis through five, sometimes six, zoeal stages and one megalopal stage (Field 1989, Chen et al. 1990). Zoeae are planktonic. Megalopae are semi-planktonic, becoming more benthic near the end of the megalopal stage. It is not until metamorphosis to the first crab stage that a true benthic stage is reached.

Larval growth of *M. adina* under laboratory conditions was described by Field (1989) and Chen et al. (1990). At water temperatures of 25°-28°C, salinities of 30‰-34‰, and a photoperiod of 12 hours light to 12 hours dark, Chen et al. (1990) reported that the typical five zoeal stages averaged 14.6 days and that the megalopal stage averaged 6.8 days. Stuck and Perry (1992) indicated that (based on unpublished data) the megalopal stage lasted from 4-7 days.

Mean times to each larval stage of *M. adina* as reported by Chen et al. (1990) were similar to *M. mercenaria* at corresponding temperatures and salinities (Ong and Costlow 1970). Field (1989), however, compared developmental times of larval *M. adina* and *M. mercenaria* and found that larval developmental time varied significantly between species. Under all test conditions and over all developmental stages, *M. mercenaria* developed approximately twice as fast as *M. adina*.

Duration of larval stages of hybrid-zone *Menippe* and *M. mercenaria* was presented by Porter (1960), Ong and Costlow (1970), Bender (1971), Yang (1971), Mootz and Epifanio (1974), and McConaughy et al. (1980). Mootz and Epifanio (1974) noted that larval growth of *M. mercenaria* was exponential during zoeal stages but decreased during the megalopal stage.

In general, development time of *M. adina* to each stage decreased as water temperature increased (Field 1989). Similar effects of temperature on *M. mercenaria* or hybrid-zone larvae were reported by Porter (1960), Ong and Costlow (1970), Brown (1990), and Brown et al. (1992). Effect of salinity on developmental time of larval *M. adina* varied with stage and temperature but was shortest for all stages at 30°C and 20‰ (Field 1989). Ong and Costlow (1970) and Field (1989) observed a faster development rate of *M. mercenaria* at higher salinities [35‰ (Field 1989)]. Duration of larval stages of *M. mercenaria* was also impacted by diet (Mootz and Epifanio 1974).

Artificial laboratory conditions may also influence developmental times of *M. adina*. Brown (1990) noted that megalopal development time of *M. mercenaria* may have been an artifact of laboratory conditions or unsuitable settlement substrates. Bert et al. (1986) suggested that *M. mercenaria* larval stages may persist longer in the wild than in the laboratory with the duration of larval stages averaging eight weeks.

2.3.2 Juveniles

According to Lindberg and Marshall (1984), juvenile *Menippe* range from 3.5 to 35.0 mm carapace width (CW). Growth increments and intermolt intervals were determined for juvenile *M. mercenaria* in the laboratory. An average intermolt interval of approximately 40 days and a trend for longer intermolt periods with increasing size was documented by Savage and McMahan (1968). The incremental increase in carapace width per molt averaged about 15% of the pre-exuvial dimension for crabs >10 mm. Savage (1971a) documented a 20%-40% incremental increase at each molt, which is a rate comparable to growth increments verified in the field.

Chen et al. (1990) presented data on early juvenile stages (C1-C5) of *M. adina* held in glass petri dishes. Average growth was 0.124 mm/day. There was a trend toward increased intermolt periods with age. Intermolt period, carapace width, and percent increase in size for early crab stages were as follows:

Stage	Intermolt Period (days)	CW (mm)	Percent Increase
C1	5.7	2.28	32.0
C2	8.6	3.01	27.6
C3	11.0	3.84	26.8
C4	14.3	5.08	32.3
C5	--	7.21	41.9

Chen et al. (1990) also determined growth rates of juveniles held in a 200 liter, small-scale culture system for 188 days. The average growth rate was 0.186 mm/day.

Growth rates of juvenile *Menippe* have been shown to be influenced by water temperature. Hybrid zone *Menippe* exhibited greater growth rates at 30°C than at 20°C (Bender 1971). Molting frequency of *M. mercenaria* increased with water temperature to a maximum value above which no further increase was observed (Brown 1990). Growth of postsettlement (metamorphosis to 10.5 mm carapace width) juvenile *M. mercenaria* was described by Tweedale et al. (1993) utilizing data from three independent studies in which juvenile stone crabs were reared in the laboratory. They analyzed the molt increment and intermolt period and estimated age at approximately 10.5 mm CW (1 year old) using three determinants (mean, median, and maximum of intermolt period) and two methods of calculating age-at-size (observed intermolt period and partial intermolt period).

Age and size at sexual maturity are important variables for fisheries biologists because they not only mark the initiation of reproductive activity but also suggest an appropriate minimum legal size for retention. This type of regulation is frequently used in decapod fisheries (Cobb and Caddy 1989). No data on age-related mean sizes are available for *M. adina*. *Menippe mercenaria* males are thought to reach an average size of about 40-60 mm CW at one year of age, 60-90 mm CW at two years, 90-110 mm CW at three years, 110-125 mm CW at four years, and 125-140 mm CW at five years (Yang and Krantz 1976, Savage and Sullivan 1978, Sullivan 1979, Bert et al. 1986). Females are thought to range from about 40-60 mm CW at age one, 60-80 mm CW at age two, and to increase in carapace width by about 10 mm per year thereafter (Bert et al. 1986). Maximum reported ages of male *M. mercenaria* are thought to be VII (Bert et al. 1986) and VIII (Restrepo 1989a).

Allometric growth is the increase or decrease in size of an organ or body part in relation to the growth of a reference part or organ (Teissier 1960). *Menippe*, like many other crustaceans, exhibits allometric growth between the sexes and between juveniles and adults. Propodus lengths of *M. adina* and *M. mercenaria* differ between the sexes. Males have proportionally longer propodi than females (Sullivan 1979, Boslet 1989, Perry et al. 1995); consequently, males reach harvestable size at smaller carapace widths than females. Limited allometry is present between the carapace width and carapace length of juveniles and adults of *M. adina* (Powell and Gunter 1968) and *M. mercenaria* (Manning 1961). Longer carapace length for a given carapace width for female *M. mercenaria* was documented by Savage and Sullivan (1978) and Sullivan (1979).

2.3.3.1 Size at Maturity

Reported minimum sizes of ovigerous *M. adina* are as follows: 33.8 mm CW (Powell and Gunter 1968); 49 mm CW (C. Dugas unpublished data); 40-49 mm CW (Stuck and Perry 1992); and 60-69 mm CW (Bert 1985, Boslet 1989). These minimum sizes at maturity for *M. adina* are similar to those documented for *M. mercenaria* by Noe (1967), Cheung (1969), Savage and Sullivan (1978), Sullivan (1979), and Caldwell (1986). Bert (1985) suggested that while *M. adina* females may reach sexual maturity at a small size, on the average spawning begins at a size comparatively larger than for *M. mercenaria*. Perry et al. (1995) estimated size at 50% sexual maturity for female *M. adina* to be 73 mm CW, a size larger than the 63 mm estimated for *M. mercenaria* by Restrepo (1989b).

Little information is available on sexual maturity of male *Menippe*. Bert et al. (1986) suggested that 50% of *M. mercenaria* males are sexually mature at approximately 71 mm CW. Using morphometric data from Mississippi and Louisiana and methodology described by Somerton (1980), Perry et al. (1995) estimated that 50% of *M. adina* males would be sexually mature at 71 mm CW.

2.3.3.2 Age at Maturity

Female *Menippe* may reach sexual maturity at about age I (Savage and Sullivan 1978, Bert et al. 1986) but in low numbers. Bert et al. (1986) also found a low proportion of ovigerous age II females (under 10%). Numbers of ovigerous females in their study increased to approximately 30% at age III and remained at that level for most remaining age groups. At age VII, almost all females captured were ovigerous.

2.3.3.3 Growth and Molting

Numerous factors including size, sex, diet, temperature, salinity, light, and declawing affect the molt cycle (Passano 1960, Noe 1967, Savage 1971a, Savage and Sullivan 1978). Limited growth increment data are available for *M. adina*. The percentage increase in carapace width and number of individuals examined (in parentheses) have been determined as follows: Stuck and Perry (1992) - 19.7% (26), Stuck (1987) - 17% to 35% (2), and C. Dugas (unpublished data) - 9.2% to 14.6% (2).

2.3.3.3.1 Seasonality

Timing of female molting and spawning necessarily oppose one another, and the two are negatively correlated (Bert et al. 1986). In the Mississippi Sound, molting or recently molted *M. adina* males and small females were collected during spring and autumn; however, large, molting females were found only from September to November, apparently after the spawning season (Stuck 1987, Stuck and Perry 1992). In contrast, adult female *M. mercenaria* molted both before and after the spawning season (Bert et al. 1986).

2.3.3.3.2 Effects of Size

Based on casual observations, Powell and Gunter (1968) noted that molt intervals of *M. adina* and the duration of the soft-shelled phase increased with crab size. Intermolt intervals of *M. mercenaria* were quantified by Cheung (1969), Savage and Sullivan (1978), Simonson (1985), and Restrepo (1989a,b). In the laboratory, an increase in average intermolt interval was observed with increasing premolt carapace width: 107.0 days for 60-69 mm, 142.8 days for 70-79 mm, 156.8 days for 80-89mm, and 159.0 days for 90-99 mm (Savage and Sullivan 1978). Simonson (1985) also found that mean intermolt days increased significantly with increasing premolt carapace width from 36.5 days (25-44.5 mm) to 54.1 days (45-64.5 mm) to 64.6 days (65-84.5 mm SW). Utilizing both laboratory and field data, Restrepo (1989b) calculated intermolt periods of male *M. mercenaria* and used these intervals to construct growth curves. He estimated that male stone crabs reached harvestable size at an average age of 2.25 years, an estimate consistent with the data of Savage and Sullivan (1978) and Bert et al. (1986).

Growth per molt data for *M. mercenaria* are available from several studies. In both laboratory and field studies, the percentage size increase at molting decreased with increasing premolt carapace width. Savage and Sullivan (1978) reported the following percent increases for laboratory held specimens: 14.4% for 61-70 mm, 12.6% for 71-80 mm, 10.2% for 81-90 mm, and 10.2% for 91-100 mm. Data from a mark-recapture study (Bert et al. 1986) showed the following percent increases for male crabs: 56.8% for 60-70 mm, 24.8% for 70-80 mm, 21.4% for 80-90 mm, 20.4% for 90-100 mm, 15.8% for 100-110 mm, 13.3% for 110-120 mm, and 7.5% for 120-130 mm. They suggested that the observed reduction in growth as male crabs exceeded 70 mm CW may be due to a shift in energy allocation associated with reproductive activities. Simonson (1985) found that the percentage size increase at molting ranged from 10% to 36% CW with mean growth decreasing from 26.1% in 25.0-44.5 mm CW crabs to 20.5% for 65.0-84.5 mm CW crabs. Restrepo (1989b) quantified the postmolt-premolt size relationships for adult male *M. mercenaria*. He found that crabs 63 mm CW or smaller that molted in the laboratory grew more per molt relative to their carapace width than did larger crabs. Hembree (1984) calculated a regression line depicting molting increments and found that subadult stone crabs from the hybrid zone with a carapace width >44 mm will molt to the adult size class.

2.3.3.3.3 Effects of Autotomy and Declawing

Powell and Gunter (1968) reported that the rate of regeneration of lost appendages for *M. adina* was proportional to molt interval. Autotomy or removal of a cheliped by fishery practices altered both the incremental increase in carapace width and the intermolt interval of *M. mercenaria* (Savage and Sullivan 1978). Average carapace width growth at first molt for singly and doubly autotomized crabs was much less than for intact controls. Length of the intermolt period was dependent upon the time within the interval that the claw was removed. If a claw was removed early in the intermolt period, the interval was shortened. If the claw was removed near the end of the intermolt period, the interval was extended.

2.3.3.3.4 Variations by Sex

Sex-related growth differences have been documented in adult *M. mercenaria*. Bert et al. (1986) observed an average of 19.7% and 15.0% increase in carapace width of molting male and female crabs, respectively. Savage and Sullivan (1978) and Sullivan (1979) also found greater growth increments in males than in females. In addition, intermolt periods were shorter in males than in females; consequently, males attained a larger carapace width size and larger propodi than did females. Inhibition of molting by females during spawning could contribute to an overall

size difference between males and females (Lindberg and Marshall 1984). In general, males were also heavier and gained weight faster than non-ovigerous females of the same carapace width (Sullivan 1979).

2.3.3.4 Claw Regeneration/Handedness

The claws of *Menippe* are asymmetrical with a larger crusher or major claw and a smaller pincher or minor claw. Handedness is defined by the presence of the major chela on either the right or left side. Handedness of *M. mercenaria* with respect to age and growth and regeneration of claws was evaluated by several researchers (Cheung 1973, 1976; Rodriguez and Yang 1977; Simonson and Steele 1981; Simonson 1985). *Menippe* are initially right-handed, but the presence of right-handed crabs decreases rapidly to about 80% by 40 mm CW and then remains relatively constant with age. Stuck and Perry (1992) found that 93.1% of the juvenile *M. adina* for which handedness could be determined were right handed. This percentage was highest in the smaller size classes and decreased with increasing crab size.

A left-handed crab occurs after a left minor chela redevelops into a larger crusher form as a result of loss of the right major chela. In general, claw regeneration occurs faster in smaller individuals. Simonson (1985) found that some juvenile crabs (<15 mm CW) reversed handedness on the first molt following pincher loss while larger pre-adults (>25 mm CW) required up to three or more molts for reversal. Simonson (1985) estimated that fewer than 5% of legal *M. mercenaria* would survive long enough to complete reversal of handedness.

Handedness of *M. adina* was compiled from several studies. Right-handed crabs dominated in harvestable adults with reported right- to left-handed ratios of 3:1 (Perry et al. 1984, Horst and Bankston 1986) and 4:1 (Boslet 1989). A 4:1 ratio for *M. mercenaria* was documented by Simonson and Steele (1981).

2.4 Reproduction

2.4.1 Sex Ratios

Generalizations about sex ratios in decapods should be viewed with caution because local variation from a 1.0:1.0 ratio may be due to differential mortality, migration, or habitat selection. In addition, trap-caught *Menippe* yield biased sex ratios. According to Bert et al. (1986), a complex interactive array of biological, physiological, and social factors affect the sex ratio of crabs entering traps.

Adult female to male sex ratios of trap-caught *M. adina* were documented in several studies: 4.0:1.0 (Boslet 1989), 2.5:1.0 (Landry 1992), 1.9:1.0 (Horst and Bankston 1986), 1.3:1.0 (C. Dugas unpublished data), and 1.8:1.0 (Stuck and Perry 1992). Stuck and Perry (1992) found seasonal variations in the sex ratios of trap-caught *M. adina*. In August, only 5% of the individuals captured were males; however, by October the female to male ratio was near 1.0:1.0. A predominance of trap-caught *M. mercenaria* females during the summer was reported by Noe (1967), Sullivan (1979), and Bert et al. (1978).

Spatial variations in sex ratios of male and female *M. adina* in traps were documented by Stuck and Perry (1992). The relative proportion of females increased with salinity, and the sex ratios approached 1.0:1.0 along the deeper channels. Adult female to male ratios in the hybrid zone differed between intertidal and subtidal habitats (Wilber 1987). Intertidal reefs were occupied primarily by males (1.0:5.0) in the summer while adult females were predominant at subtidal reefs (9.0:1.0). Sex ratios were more uniform in the fall in both intertidal and subtidal habitats.

2.4.2 Mating and Fertilization

2.4.2.1 Mating

Copulation in *Menippe* takes place after molting when the female is soft (Binford 1913). In contrast, other xanthids such as *Neopanope sayi* mate while the female exoskeleton is hard (Swartz 1978). Available data suggest that mating in *M. adina* takes place in the fall (Stuck 1987, Stuck and Perry 1992). The occurrence of males in multiple mating pairs at different reefs (Wilber 1987) is consistent with the transient-mate searching strategy exhibited by blue crabs (Teytaud 1971).

Mating sites of *M. adina* have not been verified. Wilber (1986), however, suggested that oyster reefs may be an important mating habitat in the hybrid zone.

Mating behavior of *Menippe* was described by Binford (1913), Savage (1971b), Yang (1972), and Wilber (1987, 1989b, 1992). Pairing typically occurs after a male crab encounters a premolt female. Precopulatory guarding of premolt females lasts an average of 30 hours. Copulation lasts from 6 to 20 hours with an average of 13 hours. "Contact guarding," where males stand on the tips of their walking legs and keep the females positioned beneath them continues 1-2 days or until the exoskeleton hardens. "Noncontact guarding" occurs when females are sequestered in the den while males remain at the entrance.

Wilber (1987) found no obvious differences in the guarding and copulatory behaviors among the *Menippe*-complex forms in the hybrid zone. Mating among the various forms of stone crabs in the hybrid zone was random and included every possible pair-wise combination; however, nonuniform distribution of crabs between intertidal and subtidal habitats may result in nonrandom mating in the hybrid zone as a whole (Wilber 1989b, 1992).

The presence of postcopulatory mate guarding in *Menippe* (Hartnoll 1969) suggests that males do not remate immediately. A conservative estimate of mating frequency for large male *Menippe* was provided by a tagged male that was sighted guarding four different females within 30 days (Wilber 1987).

2.4.2.2 Fertilization

In *M. mercenaria*, masses of spermatozoa are transferred within spermatophores and are stored within the chitin-like seminal receptacle of the female. Fertilization of eggs takes place within the ovary lumen (Binford 1913). Female stone crabs may be polygamous or may store sperm from copulations at different molts (Cheung 1968). A single copulation can provide sperm for fertilization of eggs during an entire spawning season. Spawnings from a single copulation were reported to be four (Porter 1960), six (Binford 1913), and up to thirteen (Cheung 1969). Storage of spermatozoa for periods of up to six months prior to fertilization has been suggested for *M. mercenaria* and *Menippe* from the hybrid zone because mating transpires primarily in the fall and spawning occurs during the summer (Noe 1967, Cheung 1969, Wilber 1992). Female *Menippe* may also retain sperm through a molt (Cheung 1968, Wilber 1992).

Wilber (1987) suggested that males with sperm levels greater than 70 million will transfer the most sperm. These crabs transferred approximately 10% of the sperm content per mating. The sperm to egg expenditure ratio is not known for *Menippe* although Binford (1913) observed seven instances where from 28 to 73 sperm and one instance where 679 sperm pierced the outer layer of individual eggs. Wilber (1987) found that recently mated females contained an average of 7.6 million sperm.

2.4.3 Gonadal Development

Developmental stages of *Menippe* ovaries were classified by Noe (1967) and Caldwell (1986). The following description of developmental stages in ovarian tissue of adult *M. mercenaria* is taken directly from Noe (1967):

- Stage I - small and inconspicuous, gelatinous ovaries, ovarian index (i.e., ovarian width/carapace width x 100) 2-4, transparent to opaque color;
- Stage II - slightly larger ovary, ovarian index 4-5.5, white color and firmer;
- Stage III - ovary walls bulging, ovarian index 5.5-7, yellow color;
- Stage IV - greatly swollen, ovarian index 7-11, orange color;
- Stage V - very large, ovarian index 12-16, red color, individual ova easily separated and visible; and
- Stage VI - spent flaccid ovary, ovarian index 6-7, pale yellow to orange color.

Noe (1967) cautioned, however, that since ovarian maturation is a continuous process and repeated spawnings occur, eggs at all levels of development may be present. Consequently, these ovarian stages only signify overall ovarian maturity.

Caldwell (1986) identified four morphologically and histologically distinct ovarian stages in *M. mercenaria*: early developing, white color; intermediate, tan color; mature, orange color; and redeveloping, yellow color.

Spermatozoa of *M. mercenaria* are spherical and present year round in the vas deferentia (Caldwell 1986). Binford (1913) described *M. mercenaria* sperm and changes that occurred as the sperm penetrates the egg's surface within the ovary lumen. Only the white, anterior portions of the vas deferens contain mature sperm packaged in spermatophores (Wilber 1987).

The amount of sperm produced did not differ significantly between the *Menippe*-complex forms (Wilber 1987). Number of sperm ranged from approximately 10 million to 100 million. Among all *Menippe* forms in the fall, sperm number and body size were positively correlated for males. Wilber (1987) suggested that the baseline sperm content for intermolt adult males is 20-30 million sperm. Males engaged in pre-copulatory male guarding averaged 90-100 million sperm.

2.4.4 Spawning

After fertilization and ovarian development, *Menippe* eggs are deposited in an external mass or sponge. At this time, females are termed ovigerous. The extruded egg mass was described by McRae (1950) and Field (1989). The color of the sponge ranges from bright-orange initially to light-brown or tan and finally to grey-black or dark-brown as yolk absorption occurs and development of prezoae progresses. Wilber (1987) classified orange eggs as newly deposited, orange-brown eggs as intermediate in development, and brown eggs as well developed.

Hatching occurs within seven to eighteen days after egg extrusion (Binford 1913, Porter 1960, McConaughy et al. 1980, Wilber 1987). McConaughy et al. (1980) provided data on the time between mating and egg extrusion in *M. mercenaria*. Two females produced egg masses 82 and 109 days after mating, and one produced a second egg mass without further mating 45 days after the initial sponge.

Spawning in *M. mercenaria* was described by Binford (1913). The fertilized eggs are released into a basket formed by the female's extended abdomen and the exopods. Eggs are attached to the hairs on the endopods of the pleopods. The egg shells and stalks are later scraped off the endopod setae by the female.

The spawning season of *M. adina* was delineated by the incidence of ovigerous females in traps in Mississippi Sound (Stuck and Perry 1992), Barataria Bay (Horst and Bankston 1986, C. Dugas unpublished data), and Galveston Bay (Boslet 1989) (Table 2.2). Ovigerous females were found from March through September, although highest numbers were usually observed from May through July. Highest occurrences of ovigerous females

by study were 0/70 in June (Stuck and Perry 1992), 50% in May (Horst and Bankston 1986), 56% in April (C. Dugas unpublished data), and 16% in June (Boslet 1989).

In the northwest Florid hybrid zone, Wilber (1987) found that 75%-100% of adult female *M. adina* were ovigerous in May and June with a decline in July and early August (60%-75%), a peak again in August (80%), and another decline in September and October. Elsewhere in the hybrid zone, Bender (1971) and McRae (1950) collected ovigerous *Menippe* females from March through October and from April to September, respectively.

The spawning season of *M. mercenaria* lengthens in duration southward (Noe 1967, Sullivan 1979, Bert et al. 1986). Ovigerous females are found throughout the year in south Florida, but the principal reproductive season ranges from March to October.

A bimodal spawning peak (April-May and August-September) of *M. mercenaria* in south Florida was documented by Sullivan (1979) and Bert et al. (1986). Bert (1985) indicated that *M. adina* exhibits a similar bimodality.

Table 2.2. Incidence (% of total number of females) of ovigerous *Menippe adina* females by month.

Month	A	B	C	D
March	0	<1%	0	--
April	34%	27%	56%	--
May	55%	50%	38%	--
June	67%	--	15%	16%
July	50%	--	31%	15%
August	9%	--	36%	5%
September	20%	--	--	2%

A = Stuck and Perry (1992)

B = Horst and Bankston (1986)

C = Charles Dugas (unpublished)

D = Boslet (1989)

-- = no sample taken

The initiation and cessation of spawning activity is evidently regulated by external factors acting on hormonal controls (Cheung 1969). Temperature is an important factor influencing the spawning season in *Menippe* (Noe 1967, Cheung 1969, Bender 1971, Sullivan 1979, Stuck and Perry 1992). In Mississippi, ovigerous *M. adina* females were not collected in water temperatures below 18°C, and most were collected at water temperatures greater than 22°C (Stuck and Perry 1992). Water temperatures recorded in conjunction with increasing numbers of ovigerous females have ranged from 22°-24°C in March and April (Noe 1967, Sullivan 1979); 25°-27°C in May and June (Bender 1971); and 25°-29°C in April and May (Bert et al. 1986). When spawning activity decreases abruptly in October and November, water temperatures range from 28°-18°C (Bender 1971, Bert et al. 1986). Bert et al. (1986) suggested that neither the onset nor termination of spawning in *M. mercenaria* was controlled by a specific temperature, at least within the annual temperature range usually encountered in Florida. Light intensity may play an additional role in the control of spawning seasons (Cheung 1969).

The spawning habitat of *M. adina* has not been delineated; however, general spawning areas have been suggested based upon the occurrence of ovigerous females. Ovigerous females of *M. mercenaria* and possibly *M. adina* aggregate in specific habitat types (Bert 1985). Boslet (1989) calculated catch rates (number/48 hours) of ovigerous *M. adina* by habitat type: channel - 0.10, nonreef/channel - 0.05, and oyster reef - <0.01. Powell and Gunter (1968) noted that ovigerous females of *M. adina* were rarely found in intertidal habitats. Hembree (1984) also noticed the lack of ovigerous and large mature females in intertidal habitats and suggested that spawning takes place offshore in the hybrid zone. Wilber (1989b) noted that environmental requirements of ovigerous females in the hybrid zone were not found in intertidal habitats. Bert (1985) found that ovigerous *M. mercenaria* preferred excavations under rock or sponge within the mixed seagrass/emergent rock habitat, and Noe (1967) found high numbers on subtidal seagrass flats.

The number and percentage of ovigerous *M. adina* females in trap samples (Boslet 1989, Stuck and Perry 1992, C. Dugas unpublished data) by 10 mm carapace width size groups are tabulated in Table 2.3. Ovigerous females ranged in size from 40-49 to 110-119 mm CW. Stuck and Perry (1992) found highest percentages, and Boslet (1989) found highest numbers of ovigerous females in the 80-89 mm CW size interval. Charles Dugas (unpublished data) found the highest percentage in the 70-79 mm CW size group. The proportion of ovigerous females in these studies decreased with increasing size at carapace widths above 100 mm. Assuming no size-dependent sampling bias, Stuck and Perry (1992) suggested that the peak spawning activity by 80-89 mm CW females indicated that they had reached reproductive maturity and/or maximum reproductive output. Based upon sperm storage, the 60-69 mm CW size class was the smallest hybrid zone *Menippe* in which a substantial number of females had mated (Wilber 1992).

Table 2.3. Incidence (% of total number of females) of ovigerous *Menippe adina* females by size group.

Size Group (mm CW)	A Number	A Percent	B Number	B Percent	C Number	C Percent
40-49	1	16	1	11	0	0
50-59	2	9	3	8	0	0
60-69	11	19	8	11	3	14
70-79	31	30	22	26	18	10
80-89	47	43	6	11	51	13
90-99	64	38	1	3	30	9
100-109	59	28	0	0	11	19
110-119	26	24	0	0	0	0

A = Stuck and Perry (1992)

B = Charles Dugas (unpublished)

C = Boslet (1989)

Average size of ovigerous *M. adina* and *M. mercenaria* differs seasonally depending upon locality. Ovigerous *M. adina* in Texas and Mississippi were larger in August or September than during earlier months (Boslet 1989, Stuck and Perry 1992). The reverse, however, was found for *M. adina* in Barataria Bay (C. Dugas unpublished data). In southwest Florida, larger *M. mercenaria* spawn first (Bert 1985); whereas in South Carolina females from a wide range of sizes spawned consistently from May to August (Caldwell 1986).

The size of ovigerous females, relative to all females, is also variable. The mean sizes of *M. adina* ovigerous females and all females were not significantly different in Mississippi Sound (Stuck and Perry 1992) but were significantly different in Galveston Bay, Texas (Boslet 1989). Sullivan (1979) showed that mean size of ovigerous females did not differ from mean size of all females. Bert et al. (1986), however, found ovigerous *M. mercenaria* females to be significantly larger than all females.

2.4.5 Fecundity

Fecundity is a measure of the reproductive potential of a population. Reproductive potential is dependent upon batch fecundity (i.e., number of eggs per spawn), the number of spawns per year, and proportion of individuals of each size class or population that spawns. No estimates of batch fecundity or number of spawns are available for *M. adina*. Batch fecundity estimates of *M. mercenaria* by study are as follows: 500,000-1,000,000 (Binford 1913); 160,000-350,000 (Noe 1967); and an average of 280,000 (McRae 1950). Batch fecundity increases with size of *Menippe* (Noe 1967, Ros et al. 1981).

Spawning frequency of *M. mercenaria* was documented in several studies: 4 (Porter 1960), 6 (Binford 1913), 10 (Yang 1971), and an average of 4.5 (Cheung 1969). The interval between hatch of 1 brood and oviposition of the next was estimated at 2-3 days (Yang 1971), 1 day to 3 weeks with a mean of about 8 days (Binford 1913), and 1 week (Porter 1960).

2.5 Pathology/Parasitology

The parasitic fauna of xanthid crabs of the genus *Menippe* have been virtually ignored, although the species is a potential host to numerous ectoparasites and endoparasites. In his review of parasites, diseases, and symbionts of crustaceans, Iversen (1986) listed only one reference specific to *Menippe*.

The only documented parasites of *M. adina* or hybrids are ectoparasitic acorn barnacles, *Chelonibia patula*, tube worms (Powell and Gunter 1968); and the goose-neck barnacle, *Octolasmis muelleri* (Bert et al. 1986). Powell and Gunter (1968) noted that stone crabs were rarely found with external calcareous growths.

Some references exist on parasites and diseases of *M. mercenaria*. The barnacle, *Octolasmis lowei*, was reported by Humes (1941) and Wells (1966). A protozoan parasite of the family Parosporidae, *Nematopsis prytherchi*, was recorded by Sprague (1949), Sprague and Orr (1955), and Sprague and Couch (1971). In Florida, shell disease caused by several species of chitinoclastic bacteria was documented by Iversen and Beardsley (1976). This nonlethal disease produced dark-spotted areas on the exoskeleton and reduced the market appeal of claws.

2.6 Trophic Relationships

2.6.1 Larval Food Habits

The natural diet of *M. adina* or *M. mercenaria* zoeae and megalopae has not been described, but meroplanktonic larvae and permanent zooplankton are probably their preferred prey (Lindberg and Marshall 1984). Under laboratory conditions *M. mercenaria* larvae were vigorous carnivores of *Artemia* (Mootz and Epifanio 1974). Food consumption peaked at the megalopal stage and declined before metamorphosis.

Growth and survival of cultured *M. mercenaria* fed different food items have been documented in several studies. Larvae thrived on young brine shrimp, *Artemia* (Porter 1960, Mootz and Epifanio 1974). Larvae maintained on a diet of rotifers or algae instead of *Artemia* displayed increased mortality (Porter 1960, Sulkin and van Heukelem 1980). These data suggest that *Menippe* larvae have specific dietary requirements met only by certain types of planktonic animals.

The feeding rate and efficiency of food conversion for larval *M. mercenaria* fed brine shrimp were investigated by Mootz and Epifanio (1974). Individual larvae consumed up to 91 brine shrimp nauplii (equivalent to 0.502 calories) per day. They also determined a cumulative energy budget from hatching to first crab and found

that of the total energy ingested, 30.17% was used for growth, 20.57% for respiration, 0.07% for production of exuvia, and 36.7% was eliminated through egestion and excretion.

Resistance to starvation in early larval stages of *M. mercenaria* was documented by Anger et al. (1981a, 1981b). Anger et al. (1981a) found that sublethal effects of transitory prey shortage on later survival and development were at least as strong as those exerted by salinity and temperature variations.

Factor (1982) noted that megalopae have more advanced mandibles and cardiac stomachs than zoeae indicating a change in diet corresponding to the shift from planktonic to benthic life.

2.6.2 Juvenile Food Habits

The natural diet of juvenile *Menippe* species has not been determined, although they have been classified as opportunistic carnivores (Bert et al. 1978). Oysters, acorn barnacles, conchs, sea anemones, flatworms, boring clams, cabbage head jellyfish, blue crabs, hermit crabs, common mussels, and vegetative matter were ingested by juveniles, adults, or both stages of *M. adina* in laboratory studies conducted by Powell and Gunter (1968). Juvenile hybrid zone *Menippe* ate polychaetes, small bivalves, oyster drills, and each other while in captivity (Bender 1971). *Menippe mercenaria* in aquaria ate fish flesh, beef liver, and chicken parts (Savage and McMahan 1968).

2.6.3 Adult Food Habits

Costello et al. (1979) characterized adult *Menippe* as omnivorous. Adult *menippe* in captivity and in the natural environment have been reported to consume oysters, oyster-shell parasites, boring clams, acorn barnacles, conchs, flatworms, grapsoid crabs, blue crabs, hermit crabs, cabbage-head jellyfish, and carrion (Gunter 1955, Powell and Gunter 1968, Bender 1971). Shellfish of all kinds were described as the staple food of adult *M. adina* (Powell and Gunter 1968). *Menippe* in the hybrid zone fed primarily on gastropods, bivalves, echinoderms, annelids, and other crustaceans (Wilber and Herrnkind 1986, Lindberg et al. 1990).

Menippe has been shown to incidentally ingest vegetative matter. Based on its habit of picking up diatom-laden materials and the observance of vegetable matter in the gut, Powell and Gunter (1968) suspected that algae constituted part of the diet. Three of five crabs without chela contained partially digested turtle grass, *Thalassia testudinum* (Bender 1971).

The ability of adult *Menippe* to feed upon mollusks has been shown to be dependent upon the generation of enormous crushing forces of up to 19,000 lb/in² (Brown et al. 1979). Claws are also used to cut or tear shell and tissue. Blundon (1988) reported that forces required to crack adult oysters are greater than forces generated anywhere along stone crab dactyls and suggested that the application of sublethal forces may progressively weaken the shell. Brown and Haight (1992) conducted laboratory experiments on prey selection by *M. adina*. Stone crabs selected smaller oysters and oyster drills because of mechanical limitations rather than active choice for smaller prey.

The dactyls of *Menippe* have sensory hairs that have been described as mechanoreceptors (Cohen and Dijkgraaf 1960); consequently, food is probably touched and captured with the walking legs before it is eaten. The mechanisms and behavior that *Menippe* exhibit in opening various types of mollusk shells have been described by Gunter (1955), Vermeij (1978), and Brooks and Mariscal (1985).

Sushchenya and Claro (1973) studied diet and energy balance of *Menippe* in the laboratory. The average daily diet was dependent upon crab weight and was described by a parabolic curve. The average daily diet was approximately 1/3 of the maximum diet.

2.6.4 Predator-Prey Relationships

Menippe larvae are undoubtedly subject to a wide range of primary plankton-feeding carnivores such as adult filter-feeding fishes, larval fishes, and other zooplankton (Costello et al. 1979). In open recirculating tanks used for larval culture, hydrozoans (*Moerisia lyonsi*, *Stylactis arge*, and *Clytia gracilis*) may compete with *Menippe* larvae for food and prey on the larvae as well (Sandifer et al. 1974).

Few predators of juvenile *Menippe* have been identified (Costello et al. 1979); however, juveniles are thought to be subjected to a wider variety of large predators than adults (Bert et al. 1978). Juvenile *Menippe* may be more susceptible to predators because they do not burrow or possess the formidable claw of adults. Juvenile *M. adina* held in the laboratory may be eaten by oyster drills and larger *Menippe* (Powell and Gunter 1968). *Menippe adina* was recorded as a minor food item by red drum, *Sciaenops ocellatus*, in Mississippi by Overstreet and Heard (1982). In northwest Florida, *Menippe* have also been taken from the stomachs of large grouper and black sea bass, *Centropristis striata* (Bender 1971). Gulf toadfish, *Opsanus beta*, also prey upon xanthids in bryozoan colonies (Lindberg and Stanton 1989).

Predation upon adult *Menippe* has also been documented. According to commercial fishermen, *M. mercenaria* in traps are sometimes eaten by octopus, sea turtles, and horse conchs, *Pleuroploca gigantia* (Bert et al. 1978). *Menippe* either disappears or declines in abundance with the appearance of octopus (Lindberg et al. 1990). Fishes such as cobia, *Rachycentron canadum*, and larger groupers may occasionally prey upon adult *M. mercenaria* (Costello et al. 1979).

The impact of *Menippe* predation on oyster reefs was documented by Menzel and Hopkins (1956) and Menzel and Nichy (1958). In Louisiana, oysters were found to be a major food item of *M. adina* (Menzel and Hopkins 1956). Overall, predation was highest on spat and small oysters; however, larger stone crabs consumed oysters of all sizes. Predation was lowest in winter and highest in fall, and the average rate of consumption was 219 oysters per crab per year. Menzel and Hopkins (1956) suggested that *Menippe* may be more destructive to both spat and adult oysters than the oyster drill. Powell and Gunter (1968), however, hypothesized that earlier estimates of *Menippe* predation on oysters were high and that other foods such as acorn barnacles were preferred. In the hybrid zone, Menzel and Nichy (1958) suggested that predators such as the whelk, *Busycon contrarium*, and *Menippe* essentially restrict oysters to the intertidal zone.

In addition to their impact on oyster reefs, *Menippe* in the hybrid zone influences the distribution and abundance of other invertebrates. Kent (1983) noted that the busyconine whelks, *B. contrarium* and *B. spiratum*, were vulnerable to *Menippe* predation and completely disappeared during the summer months when *Menippe* was most abundant.

2.7 Movement and Migration

Understanding movement and migration is a prerequisite in evaluating a species' utilization of habitats and its potential for interaction with other species. The movement of an individual affects encounter rates with food, shelter, predators, and potential mates and may influence growth, survival, and reproduction.

Movement of *Menippe* can be divided into two classes (nondirectional and directional) and may range from a few meters to several kilometers (Bert et al. 1978). Nondirectional movement is inconsistent and related to environmental factors that vary from year to year. Directional movement is probably nonrandom and usually involves seasonal mass movement of primarily one size and/or size class.

Movement of *M. mercenaria* in South Florida has been evaluated by Bert et al. (1978) and Sullivan (1979). Little is known about movement and migration of *M. adina*. The only mark/recapture study of *M. adina* was conducted by Stuck and Perry (1992). They tagged 1,043 individuals in Mississippi Sound, and with the exception of one tagged female that moved 16 kilometers north during a 140 day period, tagged *Menippe* were recaptured within 200 meters of their release point. Stuck and Perry (1992), however, cautioned that tag returns may have reflected sampling effort and not migratory patterns.

WILBER (1980) STUDIED THE DAILY MOVEMENT OF *Menippe* IN THE NORTHWEST FLORIDA HYBRID ZONE IN AN INTERDIGITAL complex of encrusted hardware cloth shelters spaced about 1-2 meters apart. No differences were found in frequency or distance of movement between sexes or size classes. Crabs underwent frequent, short-range movement that resulted in a constant but low level of transiency in and out of the study site.

Seasonal movement of *Menippe* inhabiting an intertidal oyster reef in the hybrid zone was documented by Hembree (1984), Wilber (1986), and Wilber and Herrnkind (1986). Two seasonal patterns were noted: (1) the immigration of adult females into the intertidal oyster reef habitat in early fall and (2) the gradual emigration of nearly all crabs from the intertidal to subtidal regions in late fall and early winter. The late fall migration from the intertidal oyster reefs was associated with recurrent, autumnal cold fronts. Based upon laboratory studies, Wilber and Herrnkind (1986) concluded that temperature fluctuations may influence the onset of fall migrations.

Movement patterns of *Menippe* in the hybrid zone in the vicinity of Cedar Key, Florida, were discussed by Bender (1971) and Lindberg et al. (1990). Although they move from shallow to deep flats as water temperatures increase in the spring (McRae 1950), females are year-round residents of grassflats (Bert et al. 1978). Male crabs normally stay further offshore than do females but apparently move into shallow grassflat areas to mate (McRae 1950, Bender 1971, Bert et al. 1978). Movement patterns of *Menippe* found farther offshore have not been described. Lindberg et al. (1990) evaluated movement of adult *Menippe* from prefabricated concrete modules near Cedar Key, Florida. Stone crabs radiated from dens to prey upon bivalves, gastropods, echinoderms, and annelids. They suggested that home ranging occurred for both sexes with several dens occupied over time when food and refuge is favorable.

2.8 Recruitment

Various species of estuarine crabs have been grouped by degree of larval retention within the estuary (Sandifer 1975, Dittel et al. 1982, Johnson 1985, Epifanio et al. 1984, Brookins and Epifanio 1985). Larvae that are retained within estuaries are prevalent in families that have nonswimming adults such as the Xanthidae. At the other extreme are the portunid crabs with larvae that are normally exported from the estuary.

The collection of ovigerous females, zoeal stages I-V, and megalopae of *M. adina* in Mississippi Sound by Stuck and Perry (1992) suggests that larval development may be completed within the Sound and adjacent offshore waters. Consequently, factors affecting recruitment and abundance are probably more localized than they are for blue crabs. Because complete larval development of *M. adina* can occur within northern Gulf of Mexico estuaries, estuarine retention of larvae may be an important component of their recruitment mechanism. *Menippe adina* (Andryszak 1979, Stuck and Perry 1992) and *M. mercenaria* (Dudley and Judy 1971) zoeae have, however, been collected in offshore waters.

Crab zoeae are incapable of directional swimming at speeds greater than the tidal movement of surface water in many estuaries (Sulkin 1984). Active swimming by zoeae near the surface would thus be ineffective in ensuring retention within the estuary. The direction of net transport of estuarine plankton including zoeae would consequently depend upon their distribution by depth (Cronin and Forward 1982).

Laboratory and field evidence suggest that crab larvae are able to use environmental cues to regulate their vertical swimming or horizontal displacement (Epifanio 1988a and 1988b, McConaugha 1988). *Menippe adina* may exhibit similar behavioral responses; however, the only documented larval response to external stimuli by *M. mercenaria* is their positive phototaxis and shadow response (Forward 1977).

In addition to larval transport mechanisms, a wide variety of environmental conditions (i.e., water temperature, salinity, light, and food) may impact larval survival of *M. adina* and thus influence recruitment. Field (1989) found that larvae survived to megalopae in a wide range of salinities as temperature increased from 25° to 30°C. The ability of *M. adina* larvae to develop in lower salinities at high temperatures may allow larvae to complete development in low salinity estuaries.

Brown (1990) found that *M. mercenaria* larvae demonstrated highest survival at 30°C and 30‰ while juveniles were most successful at 15°C and 35‰ salinity. Effects of salinity on survival, however, decreased during late zoeal stages (Z4 and Z5) suggesting the beginning of osmoregulatory abilities (Brown et al. 1992).

Brown (1990) speculated that spawning during the summer months would increase larval survival due to more optimum temperatures, but juvenile settling may be reduced because of the higher than optimum temperatures. Larvae spawned later in the season should also have near optimal conditions for development, and juveniles settling in the fall should experience lower, more optimum temperatures. Consequently, late season spawning probably produces highest recruitment.

Bert (1985) and Bert et al. (1986) discussed the concept of recruitment areas of *M. mercenaria* along the Florida coast. These areas are characterized by relatively larger numbers of young adults, a high proportion of females in traps, high larval production, successful juvenile settlement, and good survivorship to adulthood. Recruitment of *Menippe* into nonrecruitment areas was hypothesized to be by dispersal of adults from the recruitment ground.

2.9 General Behavior

Behavior of *Menippe* larvae is virtually unknown (Lindberg and Marshall 1984); however, a positive phototaxis and shadow response was documented for *M. mercenaria* by Forward (1977). *Menippe* larvae stopped swimming and sank passively when light levels were suddenly decreased. Forward (1977) suggested that this was an anti-predator tactic.

Juvenile *M. adina* behavior in Texas was observed by Powell and Gunter (1968). Juvenile stone crabs commonly adopted passive defense mechanisms when annoyed. Crabs often feigned death upon capture by folding the ambulatory appendages against the body and extending the open chela as far beneath the body as possible. Rough handling induced this response in small *Menippe* but was rare with larger (>80 mm CW) specimens. Crabs <20 mm CW were also observed attacking a moving object and hugging it with their claws but whether this reaction was a defense mechanism or a means of getting food was not determined (Powell and Gunter 1968). Yang and Krantz (1976) observed aggressive behavior in juvenile *M. mercenaria* in intensive culture situations in the laboratory.

Menippe may stridulate or produce a raspy sound by rubbing the patch of fine, oblique, parallel striae on the inside surface of each cheliped against the thick edge of the second and third anterolateral teeth and outer suborbital tooth. Stridulation was first documented in juvenile and adult *M. adina* by Powell and Gunter (1968). Bender (1971) later observed stridulation in 3-10 cm CW hybrid zone *Menippe* and identified two patterns: (1) downward rasping of the striated ridges of one palm against the interocular manner similar to motions made by fiddler crabs, followed by similar movements of the opposite cheliped and (2) scraping of one cheliped up and down against the carapace for 15-second periods. The function of stridulation in *Menippe* is unknown (Bender 1971, Bert et al. 1978).

Behavior patterns of adult *Menippe* are complex (Lindberg and Marshall 1984). They may exhibit agonistic behavior and defend burrows (Sinclair 1977); stridulate as described previously (Powell and Gunter 1968, Bender 1971); employ diverse modes for feeding on several types of gastropods and bivalves (Vermeij 1978); move offshore and onshore; display complex courtship and mating behavior (Yang 1972, Wilber 1989a and 1989b); guard mates (Wilber 1989a); and utilize autotomy (Powell and Gunter 1968).

Detailed data on the intraspecific, agonistic behavior of *M. mercenaria* was provided by Sinclair (1977). In laboratory encounters, one individual established dominance usually by means of visual or low-intensity, tactile displays. Fights with extensive bilateral aggression were infrequent. Dominance was correlated with larger size, the male sex, and prior possession of a burrow. In visual displays, the degree of aggressiveness appeared dependent upon body elevation, position of the chelae, and movement of the chelae and carapace. Interactions between animals of different sizes or of different sexes were characterized by a lower frequency of fights than encounters between animals of similar size or of the same sex. These data suggest that interactions between stone crabs are ritualized to a high degree (Sinclair 1977). Visual displays are utilized and appear to minimize potential injury between

interacting crabs. Sinclair (1977) implied that agonistic interactions may be an important factor influencing spatial distribution of crabs. The defensive behavior of *M. adina* as observed by Powell and Gunter (1968) is similar to that described by Knudsen (1960) for other xanthids.

Behavior patterns in response to human disturbance were described by Powell and Gunter (1968). *Menippe adina* usually crouched momentarily in an apparent effort to hide from intruders and then retreated slowly out of sight into burrows upon further intrusion. Stone crabs almost invariably attempted to push an intruder away with a quick but powerful lateral motion of the cheliped rather than attack with the chelae. Bert (1985) noted that both juvenile and adult *M. adina* exhibit passive defense behavior that is found only in small juvenile *M. mercenaria*. Stone crabs, however, occasionally raise the chelipeds and bring the chelae together several times with a loud snap. This reflex is common in blue crabs (Teytaud 1971).

Based upon field observations, Powell and Gunter (1968) concluded that *M. adina* are probably crepuscular rather than nocturnal, although they are somewhat active both day and night. Hybrid *Menippe* under laboratory conditions became active doing den maintenance at dusk, but most feeding and walking occurred after dark (Wilber and Herrnkind 1986).

Other incidental observations on *M. adina* behavior were documented by Powell and Gunter (1968). After a severe freeze, some *M. adina* plugged the entrance to their burrows with bits of debris and mud. They suggested that this phenomenon was a defense against cold weather rather than attack. Stone crabs also exhibited the "Aufbaum" reflex (the crab fully extends both open chelae and raises the body to a position almost perpendicular to the ambulatory appendage and the plane of support) when disturbed.

3.1 Geographic Distribution

Crabs of the genus *Menippe* are broadly distributed in the Caribbean and tropical and subtropical Americas. Of the probable eight species of *Menippe* (Martin et al. 1988), three species have been documented in the Gulf of Mexico. *Menippe adina* occurs from northwest Florida westward and then southward around the Gulf of Mexico to the state Tamaulipas, Mexico. *Menippe mercenaria* ranges from Cape Lookout, North Carolina, around peninsular Florida to northwest Florida, through the Bahamas and Greater Antilles to St. Thomas, Virgin Islands, Yucatan Peninsula to southwestern state of Campeche, Mexico, and to Belize (Williams and Felder 1986). The *M. adina* - *M. mercenaria* hybrid in the Gulf of Mexico ranges from Panama City to Steinhatchee, Florida (Williams and Felder 1986). Powers (1977) indicated that the only valid Gulf of Mexico record of *M. nodifrons* is probably from Havana, Cuba, as reported by Rathbun (1930). The latter's record of *M. nodifrons* from Louisiana was questioned by Felder (1973), disregarded by Bert (1986), and synonymized by Williams and Felder (1986) under *M. adina*.

3.2 General Habitat Conditions

3.2.1 Larvae

Menippe larvae are planktonic. Zoeae of *M. adina* occur in nearshore coastal waters (Andryszak 1979) and within estuaries (Stuck and Perry 1992). Stuck and Perry (1992) collected all larval stages of *M. adina* within Mississippi coastal waters.

3.2.2 Juveniles

General habitats of juvenile *M. adina* were characterized in Texas (Powell and Gunter 1968) and Mississippi (Perry et al. 1984, Stuck and Perry 1992). Juveniles <30 mm CW utilize readily available hiding places such as crevices in and beneath rock or shell. Stuck and Perry (1992) collected juvenile *M. adina* from a variety of habitats in Mississippi Sound including mud, sand, oyster reefs, and "shell hash" bottoms. Highest densities, however, were obtained from inshore oyster reefs and on mud bottoms along channels in intermediate salinities.

Habitat preferences of juvenile *Menippe* in the hybrid zone were documented by Wass (1955) and Bender (1971). Small juveniles (<1.3 cm CW) occur over muddy bottoms in deep channels or in deep seagrass beds (Wass 1955, Bender 1971). Larger juveniles occur on oyster reefs and among submerged and intertidal rock (Bender 1971). Bender (1971) noted that juveniles were abundant on shell bottoms, sponges, and *Sargassum* mats; and Lindberg and Stanton (1988, 1989) found them associated with colonies of the bryozoan, *Schizoporella pungens*.

3.2.3 Adults

The preferred habitats of adult *M. adina* have been identified as intertidal mud flats, oyster reefs, rock jetties, and other debris-cluttered substrates in shallow estuarine waters within salinity regimes of 35‰ to less than 10‰ (Powell and Gunter 1968, Williams and Felder 1986). *Menippe adina* occurs both subtidally and intertidally throughout its range (Powell and Gunter 1968, Wilber 1989b, Stuck and Perry 1992, Wilber 1992). In offshore waters, *M. adina* is occasionally taken in trawls (Hildebrand 1954, Springer and Bullis 1956, Bullis and Thompson 1965, Defenbaugh 1976) but is probably more characteristically associated with oil production platforms (Gallaway et al. 1981) and ship wrecks (Powell and Gunter 1968). Bullis and Thompson (1965) collected *Menippe* in the Gulf of Mexico to depths of 22 fathoms.

Adult *M. adina* characteristically inhabit solitary burrows in mud flats just below the low-tide mark, among rocks in jetties, on reefs, and among dead shell or grass clumps (Whitten et al. 1950, Menzel and Hopkins 1956, Powell and Gunter 1968). Colonial burrows may occur, but most are solitary (Powell and Gunter 1968). Each burrow is characterized by a conical depression at the entrance and a mound of mud and debris. Some burrow mouths are closed in cold weather. Burrows of larger *M. adina* (>75 mm CW) are dug obliquely while smaller

M. adina (44-73 mm CW) excavate short burrows extending straight downward (Powell and Gunter 1968). In addition to providing cover and protection, burrows are used by *Menippe* for molting, mating, stockpiling food, and cold weather refuge (Bender 1971, Powell and Gunter 1968).

The distribution of *Menippe* complex forms in the hybrid zone was discussed by Wilber (1987). *Menippe adina* comprised 34% of the subtidal and 30% of the intertidal *Menippe* populations. Hybrids were more common intertidally (56%) than subtidally (33%), and *M. mercenaria* was more common subtidally (33%) than intertidally (14%).

Both *Menippe* species appear to be well suited to their habitats (Wilber 1989b). The dark unmottled color pattern of *M. adina* is more cryptic on the mud substrates common to northern Gulf estuaries than the disruptive coloration (i.e., spotting and banding) of *M. mercenaria* which blends with the seagrass and coral communities of peninsular Florida.

Highly variable trap catch per unit of effort (CPUE) values for *M. adina* reported by Horst and Bankston (1986); Boslet (1989); Stuck (1987, 1989); Landry (1992); and Stuck and Perry (1992) may be attributed to season, area fished, trap type, depth, and differences in substrate. In Galveston Bay, Texas, highest catch rates were found in deep ship channels with a fine mud/clay substrate and lowest catch rates over shallow oyster reef/mud bottom habitats (Landry 1992). Stable water temperatures and salinities; adequate amounts of darkness; firm substrate suitable for burrow construction; possible migration routes to the Gulf; lack of competition from other fisheries (e.g., shrimp); and water exchange due to tidal flushing and boat traffic may have accounted for higher catch rates along channels. Lower densities of *M. adina* on oyster reefs were attributed to trap placement and to intensive oyster dredging with associated stone crab mortality. Low catches over mud-bottomed bayous were ascribed to shallow depths and absence of suitable substrates for either constructing or maintaining burrows. In Barataria Bay, Louisiana, CPUE values were highest over oyster reefs and mixed clay/shell substrates and increased with water depth (Horst and Bankston 1986). The most productive areas in Mississippi Sound were those with firm mud bottoms near the barrier islands and along deep channels leading to the passes (Stuck 1987, 1989; Stuck and Perry 1992).

3.2.4 Community Interrelationships

In inshore waters, *M. adina* has been classified as a member of the high salinity oyster reef community (Gunter 1950, Hedgpeth 1953, Parker 1960). Other prominent members of the oyster reef community include mud crabs and blue crabs. A variety of invertebrates including tunicates, bivalves, barnacles, snapping shrimp, and blue crabs were associated with *Menippe* in oyster encrusted hardware cloth shelters (Wilber 1986). Gallaway et al. (1981) classified biotic communities associated with petroleum platforms in the Gulf of Mexico and placed *M. adina* along with a polychaete, *Neanthes succinea*, in a cluster group characteristic of nearshore platforms.

In the hybrid zone, *Menippe* and other decapod crustaceans were associated with bryozoan, *Schizoporella pungens*, colonies (Lindberg and Stanton 1988, 1989). As suggested by laboratory observations, juvenile *Menippe* compete directly with the xanthid crab, *Pilumnus sayi* (Lindberg and Stanton 1989).

Stone crab burrows provide habitats for a wide variety of invertebrates and fish that use the burrows for protection, food, and survival (Powell and Gunter 1968, Bender 1971). Powell and Gunter (1968) listed numerous species associated with burrows in Texas Bays. *Menippe adina* burrows strongly influence the biotic community especially in areas of extensive flats that are frequently and periodically exposed by low tides (Powell and Gunter 1968).

3.3 Environmental Tolerances

3.3.1 Temperature and Salinity

Information exists from both field and laboratory studies to describe temperature and salinity tolerance capabilities of various life history stages of *M. adina* (Boslet 1989, Field 1989, Stuck 1989, Brown et al. 1992, Stuck and Perry 1992, Perry et al. unpublished data). Environmental conditions of temperature and salinity and

corresponding abundance of larvae, juveniles, and adults of *M. adina* in Mississippi Sound are summarized in Table 3.1. All size classes are generally found in waters of medium to high salinity at temperatures above 10°C.

Table 3.1. Summary of environmental salinity and temperature from *M. adina* distribution study in Mississippi Sound (Stuck and Perry 1992).

Size Class	Ambient Salinity (‰ & % of crabs)	Ambient Temperature (° & % of crabs)
Zoeae	15 to 30 (95%)	above 23 (95%)
Megalopae	15 to 30 (90%)	above 26 (87%)
Juveniles	15 to 34 (88%)	above 24 (75%)
Small adults	15 to 19 (72%)	10 to 14*
Large adults	13 to 34 (100%)	13 to 29 (100%)

*greatest proportion

3.3.1.1 Larvae

Temperatures and salinities influence mortality rates and ultimately the distribution and abundance of larvae in nearshore habitats. Stuck and Perry (1992) provided the most comprehensive data set on *M. adina* zoeal and megalopal abundance. Zoeae were present in samples from Mississippi Sound, Mississippi, from April through September with greatest numbers occurring in May of 1984. Monthly catches ranged from approximately 1 to 14/100 m³ in 1983 and from 2 to 49/100 m³ in 1984. Zoeae were collected in water temperatures ranging from 22.0° to 32.0°C; however, 90% of the total catch occurred in water temperatures between 27.0° and 31.0°C.

Most zoeae were found in salinities ranging from 17.0‰ to 30.0‰, although some were taken from salinities as low as 9‰. Ninety-five percent of the zoeae were collected in waters with salinities from 15‰ to 30‰. Stuck and Perry (1992) suggested that the distribution and abundance of zoeae may vary greatly between years primarily because of salinity fluctuations.

Stuck and Perry (1992) recorded peak abundance of megalopae in Mississippi Sound from July through September. Most megalopae were present in water temperatures from 27° to 34.0°C and salinities from 15.0‰ to 30.0‰ although they were taken in temperatures and salinities as low as 18.0°C and 9.0‰, respectively. Stuck and Perry (1992) concluded that megalopae were widely distributed in Mississippi Sound but were most common in higher salinity areas.

A laboratory study on the effect of salinity and temperature on survival and development of larvae of *M. mercenaria* and *M. adina* was reported by Field (1989). Highest survival to first crab occurred at 30‰ and 30°C for both species; however, *M. adina* larvae were more tolerant of low salinities (≤ 20 ‰) than *M. mercenaria*.

Plankton tows within the northwest Florida hybrid zone at Cedar Key, Florida, contained stone crab larvae at temperatures of 25°-31°C and salinities from 17‰ to 32‰ (W.J. Lindberg unpublished data as cited by Brown 1990). Settling plates at the same location contained megalopae at temperatures from 20° to 31°C and salinities from 19‰ to 32‰. The lowest temperatures and salinities where larvae were found in the hybrid zone were slightly higher than those recorded for *M. adina* (Stuck and Perry 1992) but were lower than the lower limits for survival found for *M. mercenaria*.

3.3.1.2 Juveniles

Stuck and Perry (1992) quantitatively sampled juveniles in Mississippi Sound with "habitat bags" of clam shells, *Rangia cuneata*. Juveniles were found throughout the year with peak abundance in August or September. Juvenile densities were positively correlated with temperature, and 75% of the total number of juveniles were collected in temperatures $\geq 25^{\circ}\text{C}$.

Juveniles were taken over a wide range of salinity but were most abundant (88%) in salinities 15.0‰ to 34.0‰ (Stuck and Perry 1992). Juveniles were found to tolerate salinities below 5‰ for periods of three to four weeks. Stuck and Perry (1992) noted that *M. adina* juveniles were more tolerant of lower salinities than hybrid-zone *Menippe* or *M. mercenaria*.

Perry et al. (unpublished data) conducted a series of temperature/salinity tolerance studies on juvenile *M. adina* (10-40 mm CW). Mean survivorship was 88% over all tested combinations of temperature and salinity (Figure 3.1). At 15°C , survival was 100% over all salinities (5‰, 15‰, 25‰, and 35‰). Yates et al. (1991) reported on survival rates of juvenile *M. adina* subjected to catastrophic dilutions in salinity. Juvenile crabs in their study survived a 20‰ drop in salinity (from 35‰ to 15‰) with no mortality and a 30‰ drop with 50% mortality. No crabs survived when transferred to 0‰. These data suggest that *M. adina* juveniles are highly tolerant of environmental fluctuations in salinity.

3.3.1.3 Adults

Stuck and Perry (1992) collected adult *M. adina* from waters ranging from 13° to 29°C and salinities from 13‰ to 34‰. The mean size of male and female crabs was larger in higher salinity regions of the Mississippi Sound. In the salinity range from 15‰ to 19‰, 72% of the crabs were below 90 mm CW.

The lowest salinity where *M. adina* has been recorded was 0.1‰ at Marsh Island, Louisiana (Juneau and Barrett 1975). In coastwide estuarine inventory surveys in Louisiana (Perret et al. 1971) and Mississippi (Christmas and Langley 1973), *M. adina* was not collected in salinities below 10‰ and 15‰, respectively. In Texas, Gunter (1950) collected *M. adina* at salinities as low as 11.6‰.

The local abundance of adult *M. adina* may also vary depending upon hydrological conditions. Hoese (1960) described biotic changes in Mesquite Bay, Texas, that occurred in conjunction with fluctuating salinity regimes due to drought and flooding conditions. During drought conditions, *M. adina* were collected in salinities from 14‰ to 39‰, but during high Guadalupe River discharges and associated low salinities, the species was displaced. *Menippe* and other marine species reinvaded the bay in association with high tides caused by Hurricane Audrey.

Perry et al. (unpublished data) also conducted a series of temperature/salinity tolerance studies on adult (≥ 60 mm CW) *M. adina*. Adult survival rates varied from 10% to 100% over the range of test salinities and temperatures with an overall mean survival rate of 74% (Figure 3.2). Survival was generally favored at the mid-temperatures (15° and 25°C) and the higher salinities (15‰ to 35‰). Survival was lowest in 5‰ salinity at extreme temperatures, 5°C (10%) and 35°C (40%).

Concurrent with the temperature/salinity studies, R. Henry (personal communication) measured ionic and osmotic concentrations of the hemolymph of surviving adult *M. adina* and compared these with seawater. At high salinity (35‰), they were osmotic conformers; their hemolymph osmolality was in equilibrium with the seawater. At 25‰ and below, survivors were classified as osmotic regulators; their hemolymph osmotic concentration was greater than the ambient seawater. Based on these findings, *M. adina* can be classified as a moderately strong osmoregulator.

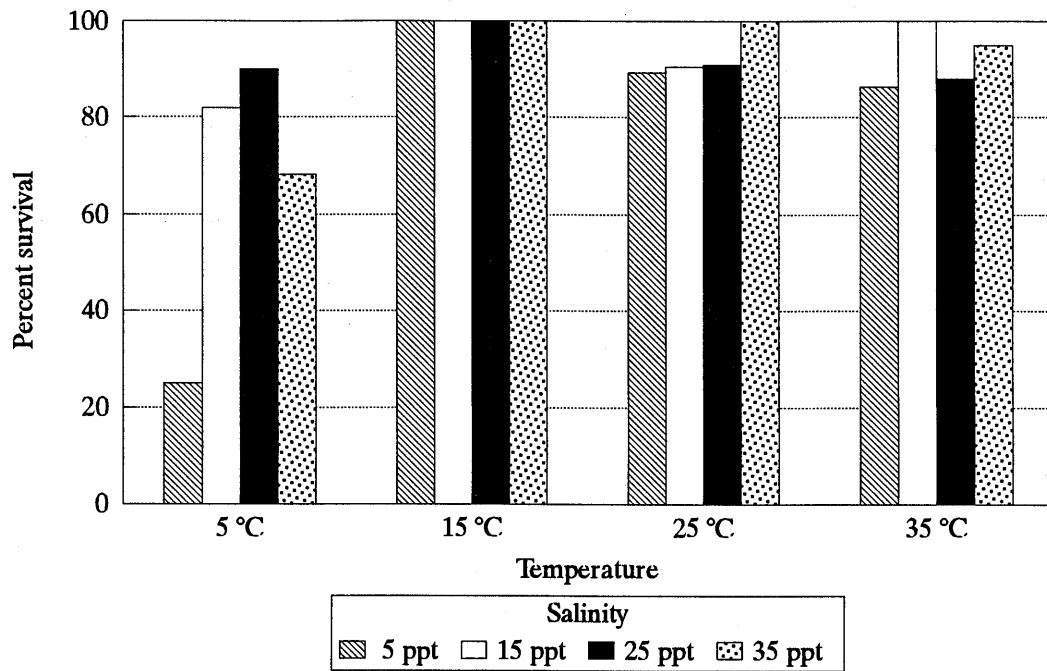


Figure 3.1. Percent survival, juvenile *Menippe adina*.

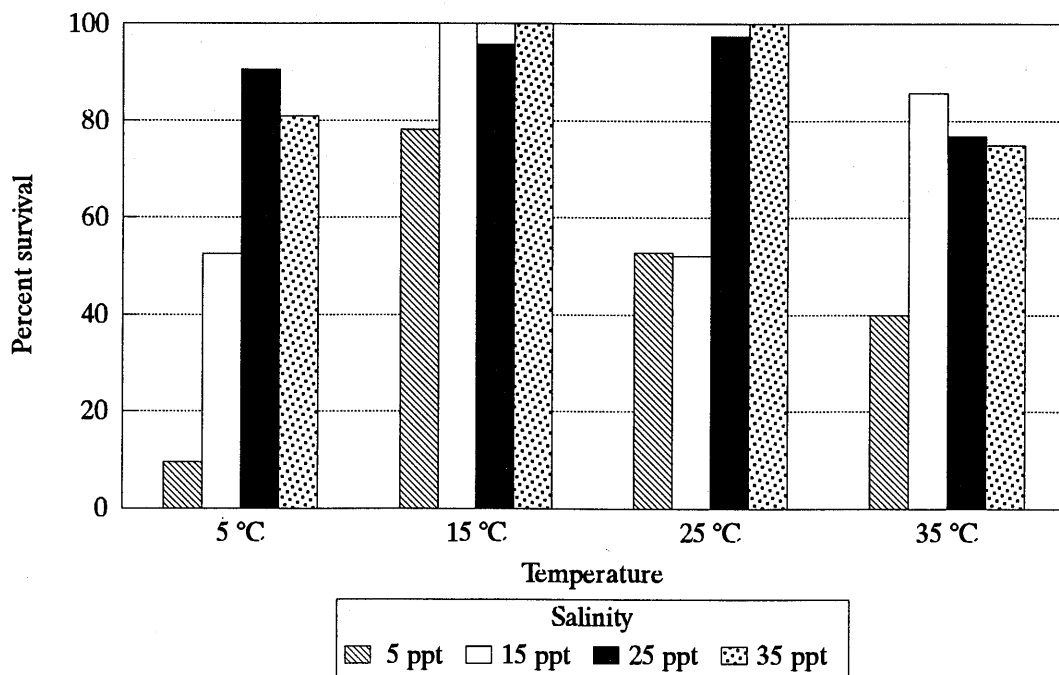


Figure 3.2. Percent survival, adult *Menippe adina*.

3.3.2 Dissolved Oxygen

Adult stone crabs apparently tolerate reduced dissolved oxygen; however, the prolonged effects on viability and reproduction are unknown (Lindberg and Marshall 1984). During exposure at low tides, *Menippe* typically move into burrows to settle in shallow depressions in the hydrogen-rich, reducing sediments. Karandeyeva and Silva (1973) reported that *Menippe* can survive from 17 to 21 hours in anoxic seawater. Albert and Ellington (1985) noted that *Menippe* survives severe hypoxia by a reliance on fermentation of glycogen to lactate, and the species is capable of tolerating high levels of accumulated lactate.

In vitro studies of *M. mercenaria* indicated relatively constant metabolic rates in oxygen concentrations ranging from 0.8 to 5.6 ml O₂/liter of water (Leffler 1973). Ayers (1938) and Vernberg (1956) showed that the oxygen consumption of *M. mercenaria* was relatively low compared to that of other species. The effects of acclimation temperature on hemocyanin-oxygen transport were examined in hybrid-zone *Menippe* by Mauro and Mangum (1982). The performance of the transport system was maximized at 15°C.

3.3.3 Pollutants/Toxicants

Estuarine crabs occupy an ecological niche in the coastal environment that is especially susceptible to manmade and natural pollutants. Williams and Duke (1979) indicated that pollutants entering the coastal zone are accumulated and often concentrated by estuarine brachyurans. Crabs may be acutely or chronically affected, or they may serve as indicators of pollution from exposure to sublethal doses (Williams and Duke 1979). Few studies, however, have been conducted on the specific effects of pollutants on *Menippe*.

Bookhout et al. (1972) found that with increasing Mirex® concentration, *M. mercenaria* showed no increase in developmental times of individual zoeal stages, but the frequency of the extra sixth zoeal stage increased. Sublethal concentrations of other pollutants also increased the frequency of the sixth zoeal stage (Bookhout and Costlow 1974).

Costlow (1979) evaluated the effects of Dimilin® (TH-6040), an insect growth regulator used to control salt marsh mosquitoes, on larval *M. mercenaria*. No larvae survived beyond the first zoeal stage at Dimilin® levels ranging from 0.5 to 0.6 parts per billion (ppb). Effects are usually expressed in mortality or morphological abnormalities that are not apparent until molting. Costlow (1979) concluded that use of Dimilin® in salt marshes adjacent to estuaries where *Menippe* is found could only be described as potentially disastrous.

The effect of red tide, *Gymnodinium breve*, on *M. mercenaria* was examined in the laboratory by Roberts et al. (1979). No evidence of toxicity was present.

4.0 DESCRIPTION OF THE FISHERY

The current status of *M. adina* stocks is unknown. The majority of the fishery is nondirected, and there is limited potential for development of directed fisheries. Estimates of abundance have been reported in several studies; however, the overall population in the northern and western Gulf is unknown. Supplemental fisheries exist in Texas, Louisiana, and Mississippi.

4.1 Commercial Fishery

Only Texas and Louisiana have reported landings for *M. adina*. Directed fishing activities for stone crabs are limited; a few fishermen target stone crabs by locating blue crab traps near hardbottom substrates such as oyster reefs and jetties. In Texas and Louisiana, most of the production results from nondirected fishing activities.

4.1.1 Texas

Landings data for stone crabs were collected by Texas Parks and Wildlife Department (TPWD). Seafood dealers who purchase edible marine products are required to submit a monthly aquatic products report (MAPR) listing species, pounds, price per pound, and location of catch. Coastwide landings and ex-vessel value for stone crab claws landed in Texas are shown in Table 4.1 and Figure 4.1. Landings increased from 3,800 pounds in 1984 when commercial landings were first reported to 38,400 pounds in 1986. Following a decline in 1987 to 15,200 pounds, landings peaked in 1991 at a high of 84,800 pounds. Observed fluctuations in reported landings may not necessarily reflect stock abundance but may have resulted from changes in harvesting regulations that limited catch to a single claw and improved dealer reporting. Yearly production within and among bay systems varied greatly (Figures 4.2 and 4.3). The San Antonio, Matagorda, and Corpus Christi bay systems produced the majority of catch from 1984 through 1986. From 1987 through 1990, Aransas Bay consistently outproduced the other bay systems and accounted for the majority of reported landings. In 1991, San Antonio Bay accounted for 83% of reported landings; however, in 1992, landings were more evenly distributed among bay systems.

Table 4.1. Landings and ex-vessel value for Texas stone crab claws.

Year	Pounds x1000	Value (\$) x1000
1984	3.8	9.6
1985	34.0	110.2
1986	38.4	77.7
1987	15.2	31.2
1988	67.0	136.1
1989	43.2	122.2
1990	52.2	134.1
1991	84.8	195.7
1992	21.0	52.2

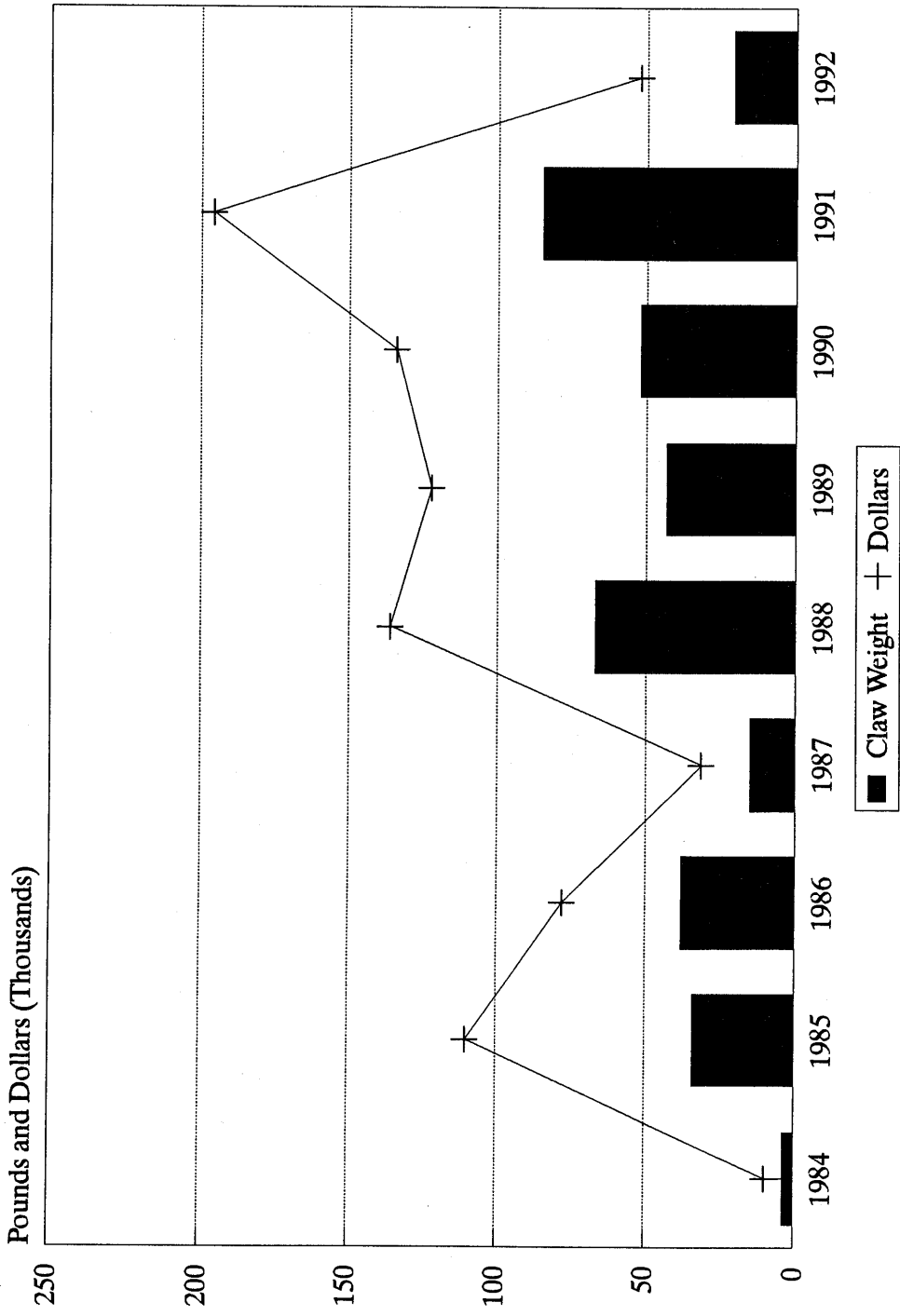


Figure 4.1. Landings and value for stone crab claws, Texas, 1984-1992.

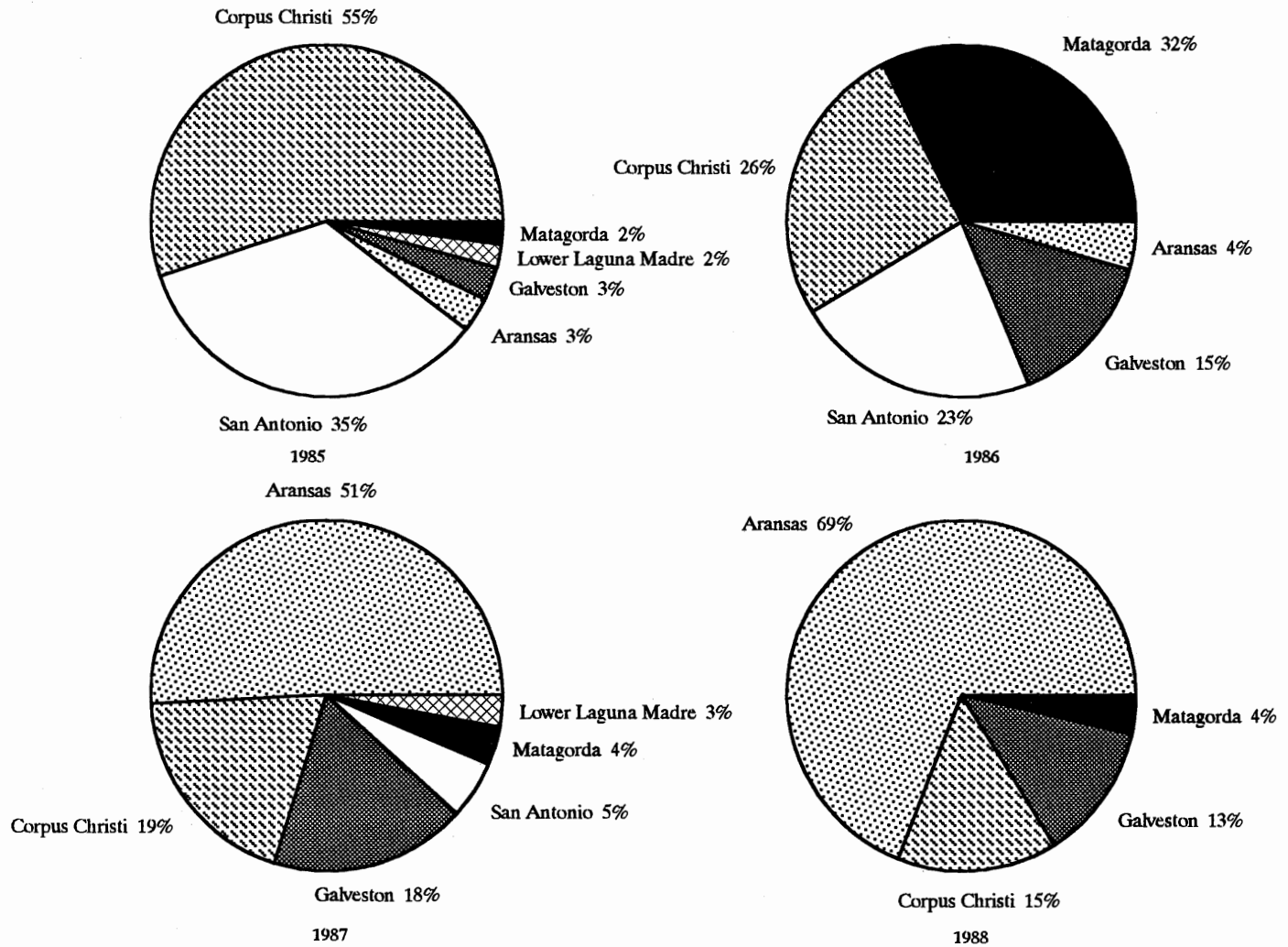


Figure 4.2. Percent of landings by bay system, Texas, 1985-1988.

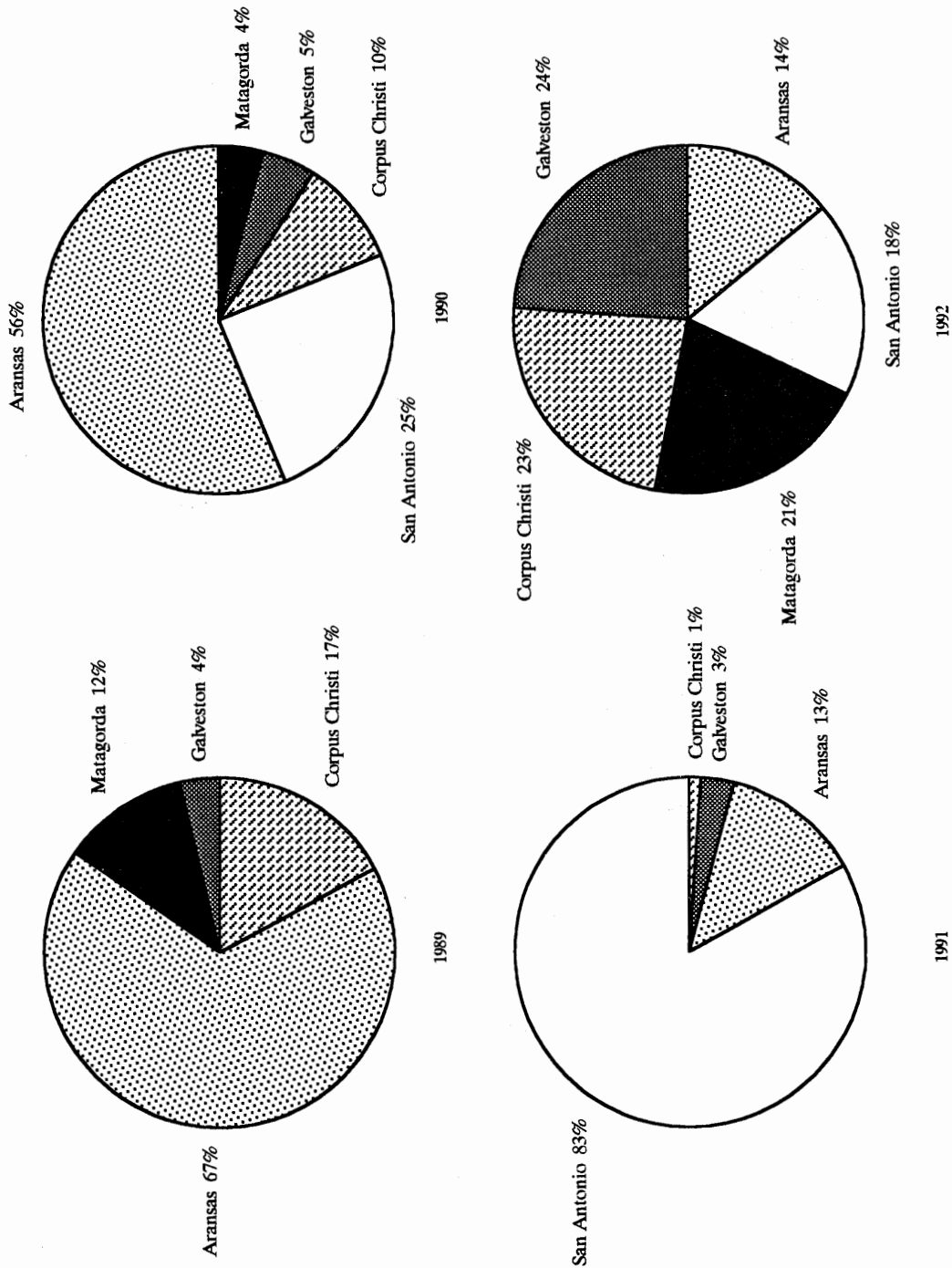


Figure 4.3. Percent of landings by bay system, Texas, 1989-1992.

4.1.2 Louisiana

Landings data for the Louisiana stone crab fishery were collected by the National Marine Fisheries Service (NMFS) from 1985 through 1989. An individual reporting system was instituted in 1990 with seafood dealers reporting landings statistics directly to the Louisiana Department of Wildlife and Fisheries (LDWF).

Reported landings (claw weight) and value for stone crabs are shown in Table 4.2 and Figure 4.4. Peak production occurred from 1987 to 1989 with landings decreasing dramatically from 1990 to 1992. The decrease in landings could have been caused by changes to the reporting system, the cyclic abundance of crabs, reduced fishing effort, or a combination of these factors.

Table 4.2. Landings and ex-vessel value for Louisiana stone crab claws.

Year	Pounds x1000	Value (\$) x1000
1985	<0.1	<0.1
1986	1.0	2.2
1987	9.8	21.0
1988	5.0	10.1
1989	8.5	18.7
1990	0.3	0.6
1991	--	--
1992	--	--

4.2 Recreational Fishery

No data are available on the recreational fishery. Some limited, directed, recreational fishing occurs in high salinity waters near the barrier islands of Louisiana. Camp owners in these areas may occasionally fish for stone crabs with blue crab traps near bulkheads or jetties.

4.3 Fishery-Related Population Characteristics

Population characteristics of *M. adina* from various Gulf of Mexico estuaries are summarized in Table 4.3. Mean size, male to female ratio, handedness, percent availability of legal claws, CPUE, and spawning season are described from studies conducted in Texas, Louisiana, and Mississippi.

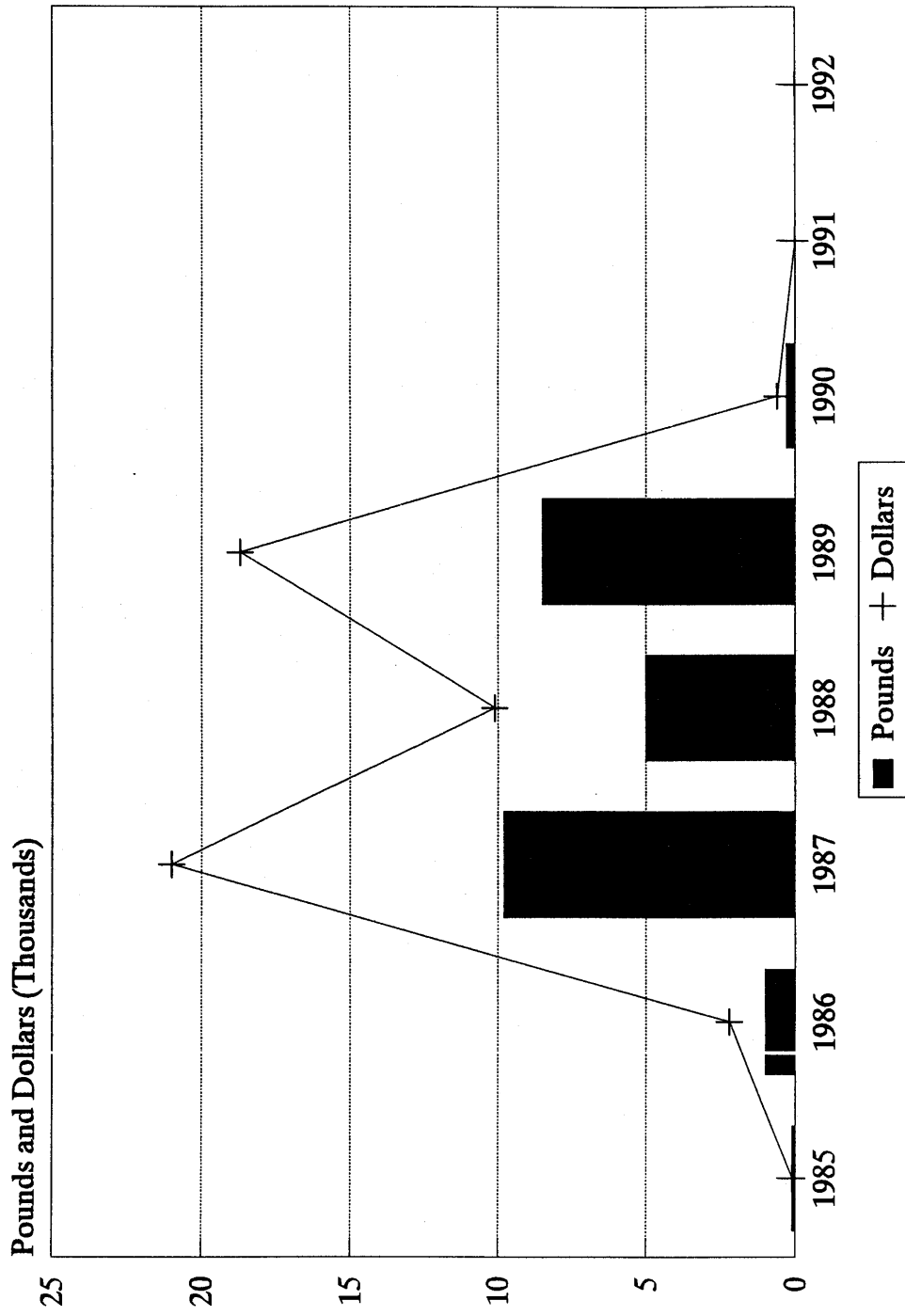


Figure 4.4. Reported landings and value for stone crab claws, Louisiana, 1985-1992.

Table 4.3. Population characteristics of *M. adina* from various Gulf of Mexico studies.

Study/State	Gear Type Adult Studies	M:F Ratio	Mean Size (CW) M	Mean Size (CW) F	Mean Size (CW) Overall	Mean Size (CW) Ovigerous F	Occurrence Ovigerous F
Hammerschmidt 1988 Texas	Gill Net	1.2:1.0	75% > 89 mm				
Boslet 1989 Texas	Plastic coated wire BC	1.0:4.0				80-100 range	Jun-Sep
Landry 1992 Texas	Plastic SC Wooden SC Plastic coated wire BC	1.0:2.5	87.0	91.0	91.0		
Dugas Louisiana	Wire BC	1.5:1.0	72.6	74.2			
Baltz & Horst 1992 Louisiana	Wooden SC	1.0:1.8					Mar-May
Stuck 1987 Mississippi	2.5 cm plastic coated bait box wire	1.0:2.3 spring 1.0:1.1 fall			90.4 94.4		spring
Stuck & Perry Mississippi	Plastic SC	1.0:1.7	87.7	91.9	90.3	92.4	Apr-Sep peak May-Jun

Table 4.3. Population characteristics of *M. adina* from various Gulf of Mexico studies (continued).

Study/State	Gear Type Adult Studies	Mean CPUE Crabs/Traps/ Day	Percent Right Handed	Percent Legal Major	Percent Legal Minor	Percent Legal All
Hammerschmidt 1988 Texas	Gill Net		75			43.9
Boslet 1989 Texas	Plastic coated wire BC	0.43/24 hr				35.3
Landry 1992 Texas	Plastic SC Wooden SC Plastic coated wire BC	0.3/24 hrs	73			43
Dugas Louisiana	Wire BC					16
Baltz & Horst 1992 Louisiana	Wooden SC					39.4
Perry et al. 1984 Mississippi	Plastic coated wire BC		75.1	50	12.3	30.9
Stuck 1987 Mississippi	2.5 cm plastic coated bait box wire	0.35/24 hrs 0.42/24 hrs				36 55
Stuck and Perry Mississippi	Plastic SC	0.35/24 hrs				50

4.3.1 Texas

Landry (1992) provided data on seasonal abundance, spatial and temporal distribution, and fishery-related morphometric parameters for stone crabs in Galveston Bay. Plastic and wooden "Florida style" stone crab traps were used to sample crabs in the lower bay from January through December 1985. With few exceptions, mean number of stone crabs/trap-day did not exceed 0.3. Legally harvestable claws (≥ 70.0 mm PL) were attained at 80.0 mm and 90.0 mm CW for males and females, respectively. Fifty-three percent of the stone crabs trapped had at least one legal claw. Right propodi were crushers 73% of the time and were of legal size 59% of the time. Female crabs were more abundant than male crabs with an overall female to male ratio of 2.5:1. Average carapace width for males (87.0 mm) was slightly smaller than for females (91.0 mm).

Additional data from Texas came from gill net samples taken in the spring and fall of 1983 and 1984 (Hammerschmidt 1988) and from gill net data supplied by TPWD personnel for subsequent years. Crabs taken in gill nets were measured to the nearest mm CW, and propodus length was estimated (Hammerschmidt 1988) using the regression equations of Perry et al. (1984). Combining both sexes and all claw types, 43.9% of the stone crabs had propodus lengths ≥ 70 mm. Carapace widths ranged from 63 to 179 mm with 75% of the crabs ≥ 89 mm CW. Mean size of claws by year and bay system was computed with data from 1987-1989 and is shown in Figures 4.5 and 4.6, respectively (TPWD unpublished data).

Boslet (1989) provided data on the distribution and abundance of *M. adina* in Galveston Bay from June through November 1987. Female crabs outnumbered male crabs 4.0:1.0 in her samples. Highest catches for both sexes occurred in the 80-90 mm CW size class. Ovigerous females were noted in samples from June through September but were a small portion of the total catch. Combining all data, 41% of the crabs had legal propodi, and 35.3% of all claws were harvestable (≥ 70 mm PL).

4.3.2 Louisiana

Trapping studies conducted in Louisiana waters include those of Horst and Bankston (1986) and C. Dugas (unpublished data). Both studies were conducted in lower Barataria Bay.

Horst and Bankston (1986) used "Florida style" wooden stone crab traps from March through May 1985. These data were used to assess fishery potential (Horst and Bankston 1986) and to define biological aspects of the population (Baltz and Horst 1992). Horst and Bankston (1986) reported catching 959 stone crabs from 2,193 trap pulls or about 0.44 crabs/trap. Data presented by Baltz and Horst (1992) were used to characterize the trapped population.

During the three month study, females outnumbered males 1.8:1.0. Propodus lengths were recorded for all crabs; however, carapace width data were not taken. Right handed individuals predominated in both sexes with 79.9% of males and 73.7% of females with a right major claw. Average size of major claws was 77.4 mm PL for males and 71.9 mm PL for females. Right crushers tended to be larger than left crushers in both sexes. Over 60% of the claws were < 70 mm PL, the legal size for harvest in Florida.

Stone crab populations near Grand Terre, Louisiana, were sampled by C. Dugas (unpublished data). Blue crab traps were set adjacent to a rock jetty. Sixty-six percent of the crabs captured were between 60.0 and 84.9 mm CW. Average size of male and female crabs was 72.6 and 74.2 mm CW, respectively. Average size of right and left major claws was 55.9 and 53.6 mm PL, respectively. Over 84% of all claws sampled were < 70 mm PL. In contrast to the findings of Baltz and Horst (1992), males were predominant in samples. Carapace width/weight regression data for this population are shown in Table 4.4 and Figure 4.7.

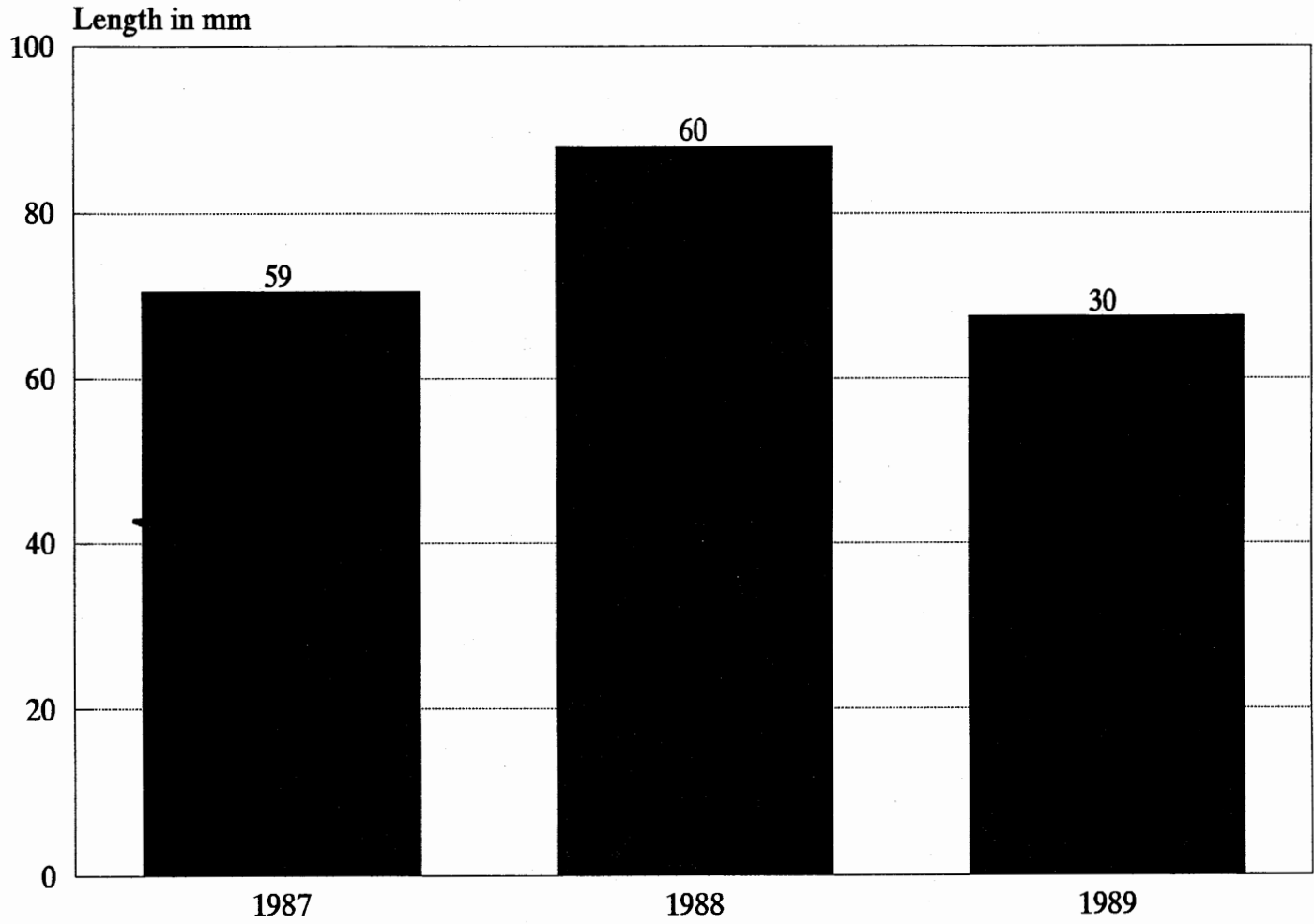


Figure 4.5. Mean propodus length, all bays combined, Texas.

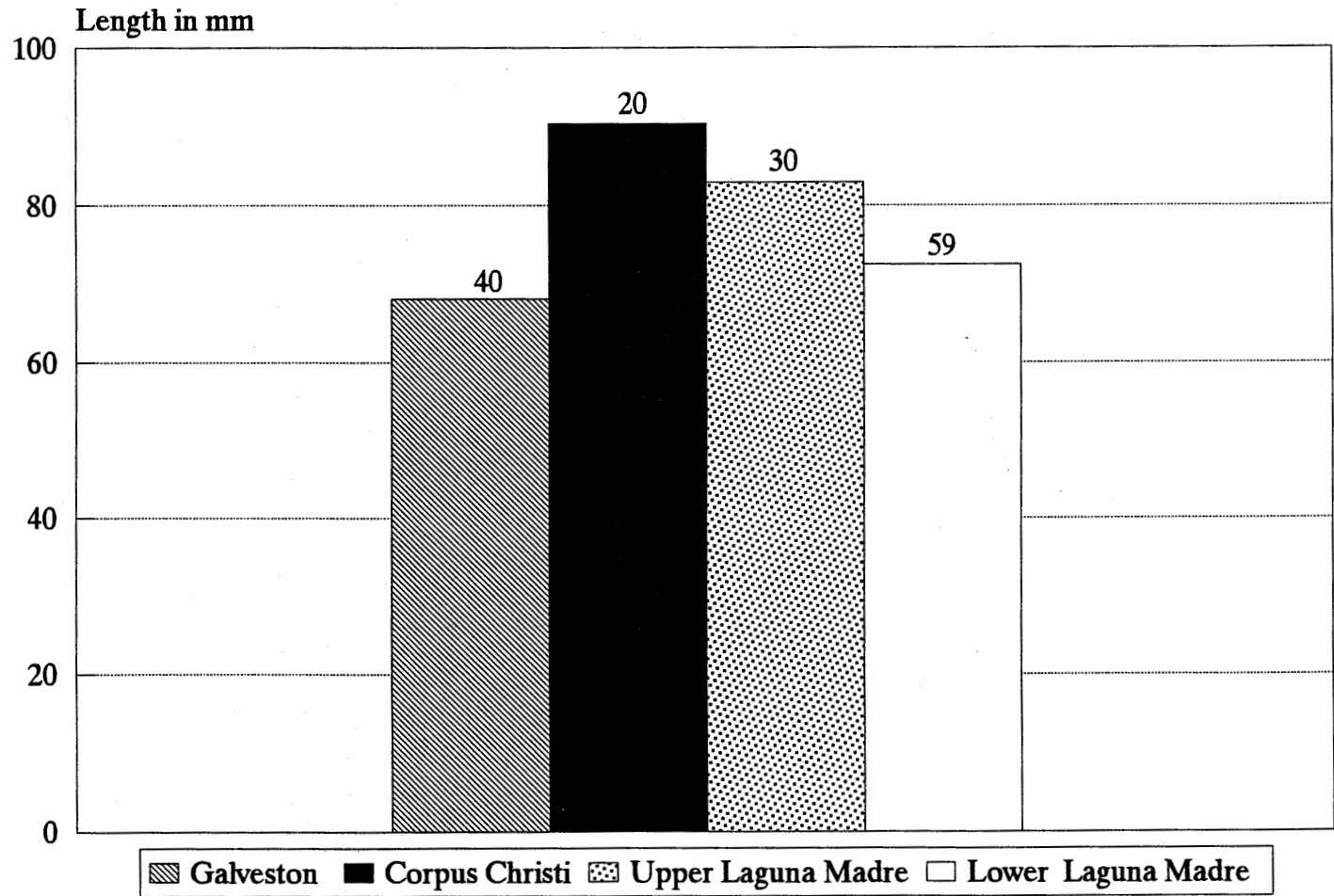


Figure 4.6. Mean propodus lengths by Texas bay system.

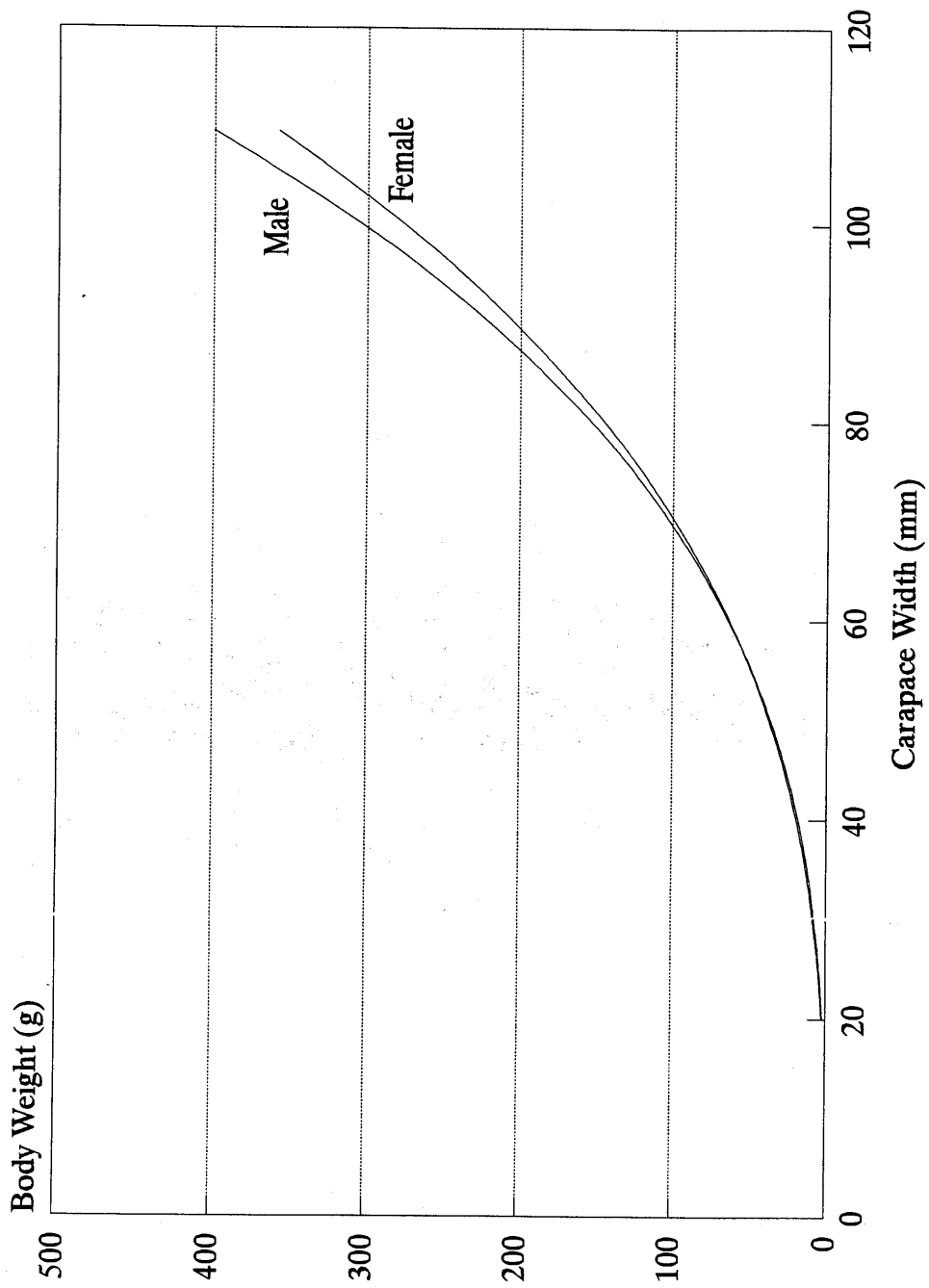


Figure 4.7. Untransformed representation of log transformed carapace width/body weight regressions for *M. adina* (C. Dugas unpublished data).

Table 4.4. Least square regression for *M. adina*, log transformed body weight versus log transformed carapace width.

Sex	Intercept	Slope	R ²
Male	-8.439	3.073	.917421
Female	-7.733	2.899	.952516

4.3.3 Mississippi

Trapping studies in Mississippi include those of Perry et al. (1984); Stuck (1987, 1989); and Stuck and Perry (1992). Both fishery-dependent and fishery-independent data were collected during the course of these studies.

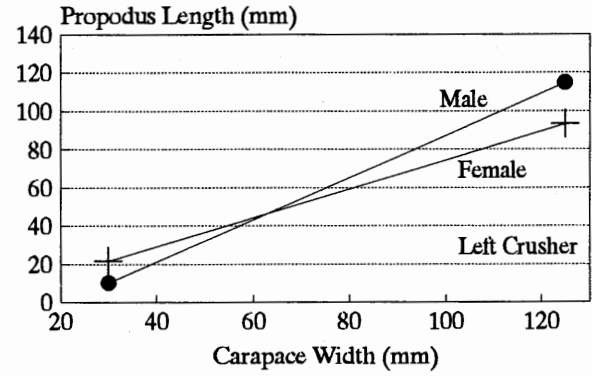
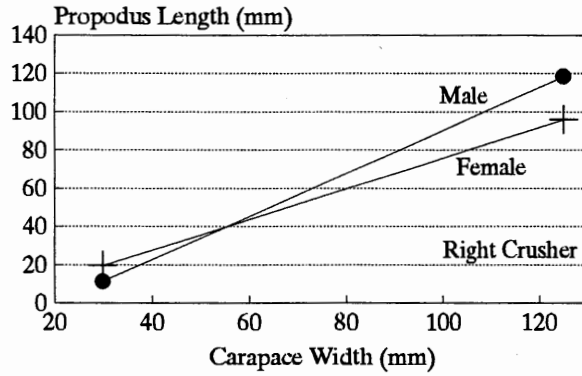
Perry et al. (1984) collected morphometric data on 533 stone crabs entering the commercial, blue crab fishery in 1983. Because stone crabs were not the target species in this study, seasonal and areal distribution and abundance data necessarily reflect blue crab fishing effort and patterns. Over one-half of all crabs collected were taken in July and August. Catches of female crabs exceeded catches of male crabs in eight of the twelve months. Female stone crabs comprised 69.2% of the total catch with 44.7% collected in July. Ovigerous females occurred in samples from April through September but were most abundant in July. Over 63% of the catch was taken in the vicinity of the barrier islands of Cat, Horn, and Petit Bois.

Over 71% of the stone crabs entering blue crab traps were between 80.0 and 104.9 mm CW. Considering all claw types, 69.1% were <70 mm PL. Fifty percent of the crushers and 12.3% of the pincers were ≥70.0 mm PL. Relationships between carapace width and propodus length of major and minor claws were determined for male and female stone crabs (Figure 4.8). In all comparisons there was a significant relationship between carapace width and propodus length. Male claws were always larger than female claws at carapace widths >62.0 mm. Right major claws and left minor claws for both sexes were slightly larger than left major claws and right minor claws. Using the legally harvestable size limit in Florida (≥70 mm PL) for comparative purposes, male claws of all types reached harvestable size at smaller carapace widths than did female claws. Perry et al. (1984) compared their data to the data presented for *M. mercenaria* by Sullivan (1979). For both *M. adina* and *M. mercenaria*, the slope of the line was always greater for males than for females.

Both claws were intact on 479 of the 533 crabs measured. Using those individuals with both claws intact and those crabs for which claw types were surmised based on a single intact claw, 75.1% of the adult stone crabs were right handed (Perry et al. 1984).

Stuck (1987) used traps constructed of plastic-coated, bait-box wire to intensively sample stone crabs in the vicinity of Dog Keys Pass in the spring and autumn of 1986. Morphometric data were taken on all crabs >50 mm CW, and crabs >70 mm CW were tagged with a sphyron spaghetti tag. Concurrent with this effort, catch efficiency was compared among "Florida style" wood and plastic stone crab traps, bait-box wire traps, and blue crab traps in Ship Island Pass.

In Dog Keys Pass, there were significant differences in the size of crabs trapped during the spring and fall sampling periods. Crabs captured in the fall were larger than crabs taken in the spring. Mean size (CW) of males was slightly larger than females during both seasons.



Stone Crabs Taken in Blue Crab Traps/Mississippi

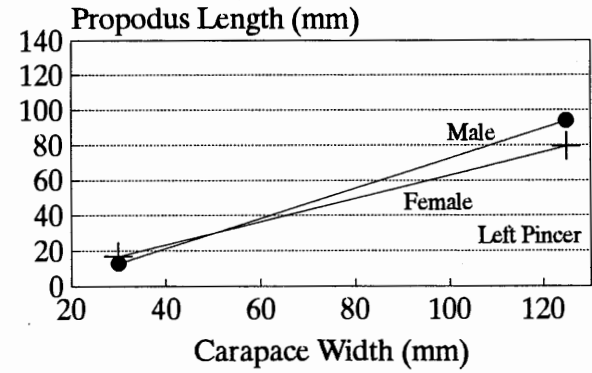
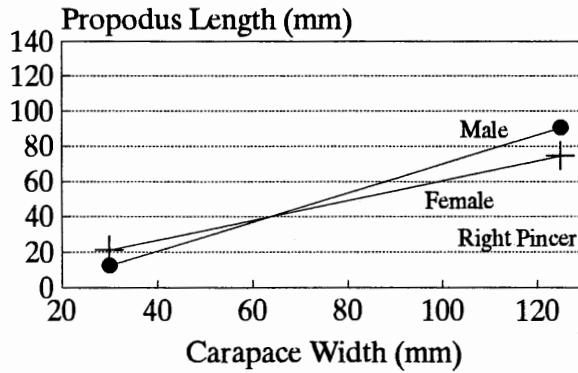


Figure 4.8. Least squares regressions, carapace width/propodus length, for all claw types, Mississippi.

Sex ratios differed significantly for the study periods. In the spring, females outnumbered males. Overall male to female ratio in the fall was near 1:1. Ovigerous females comprised 80.3% of female crabs collected in the spring. Percentage of claws ≥ 70 mm was greater in the fall (55%) than in the spring (36%).

In the trap comparison study conducted in Ship Island Pass, wood traps caught more crabs overall and had a higher catch/trap/night than did the other trap types. In contrast to the Dog Keys Pass study, male crabs constituted a greater proportion of the catch in the spring and autumn. Ovigerous females were collected in large numbers throughout the spring. No ovigerous females occurred in samples after the second week in September.

Overall catch per unit of effort (CPUE) of *M. adina* was highest in Dog Keys Pass. Grams of legal size (≥ 70.0 mm PL) claws/trap/night fished averaged 22.1 in the spring and 38.5 in the fall. Based on estimates of population size and the percentage of crabs with legal size claws, Stuck (1987) estimated that the number of commercially harvestable stone crabs in Dog Keys Pass varied from 600 to 6,125/km² in the spring and from 10,780 to 27,650/km² in autumn. Because tag returns during this study were low (8 out of 417 crabs tagged were recovered), these estimates should be viewed with caution.

To further evaluate the population of *M. adina* in lower Mississippi Sound and to determine the distribution and abundance of stone crabs in offshore waters, Stuck (1989) conducted a trapping study in May and June 1988 using wooden "Florida style" stone crab traps. Soak times were variable and ranged from 8 to 22 days. As in Stuck (1987), highest catches were recorded in the immediate vicinity of the barrier island passes. Stations located in offshore waters one to two km south of the passes were not productive. Overall catch was dominated by females. Male crabs were collected in equal or greater numbers at four of seven stations. Thirty-five percent of the claws measured had propodus lengths of ≥ 70.0 mm. Because substantial trap loss occurred during the May/June sampling effort, a series of 24 hour samples was taken at selected stations with the traps attended to prevent tampering and/or loss. As in the May/June effort, stations located nearest barrier island passes recorded the highest catches. Catch from Dog Keys Pass was significantly greater than the catch from other stations. Second highest catch occurred at Horn Island Pass. Catch per unit of effort estimates using weight of claws ranged from a low of 56.7 grams/trap/night (south of Ship Island Pass) to 311.6 grams/trap/night (Dog Keys Pass). Overall mean catch from all stations was 114.8 grams/trap/night. Twenty-six percent of the claws were ≥ 70.0 mm PL. Variations in CPUE between the two studies were attributed to differences in soak times; rate of escapement increased with soak times over 24 hours (Stuck 1989).

Stuck and Perry (1992) collected adult *M. adina* throughout Mississippi waters during all seasons. Catch per unit of effort was lowest in the winter and highest in the fall. Relative abundance and size of crabs in traps increased with increasing salinity. Highest catches were associated with high-salinity waters in eastern Mississippi Sound and waters south of the Intracoastal Waterway. Crabs captured north of the Intracoastal Waterway were smaller (78.4 mm CW males, 86.2 mm CW females) than crabs taken in higher-salinity waters to the south (88.7 mm CW males, 92.4 mm CW females). Catch per unit of effort was lowest in the winter and highest in the fall. Highest CPUE occurred in the vicinity of Dog Keys Pass with claws ≥ 70.0 mm PL comprising 50% of all claws measured. During the period of peak abundance (spring through fall), an average yield of 45 grams of claws/trap/day were recorded (Stuck and Perry 1992).

Females predominated in traps except during the fall. Overall male to female ratio was 1:1.7. Ovigerous females were present from mid-April through September. The proportion of females carrying eggs apparently decreased with the increasing size at carapace widths above 100 mm.

4.4 Fishery-Related Population Characteristics of *M. adina*

4.4.1 Morphometric Relationships

Perry et al. (1995) used combined morphometric data for *M. adina* from a variety of sources to examine the relationships between male and female carapace width and major and minor propodus length. Both fishery-dependent and fishery-independent data were used in calculations. Meristic data for *M. adina* were compared to similar data for *M. mercenaria*. Carapace width/propodus length size relationships were similar for *M. adina* and

M. mercenaria, thus for a given claw type (crusher or pincer) a 70 mm PL claw can come from the same size crab regardless of the species. In *M. adina*, harvestable claws (70 mm) occur at carapace widths of 82 and 92 mm for males and females, respectively. These values agree with the data of Landry (1992) who noted that 70 mm PL claws corresponded to body sizes of 80 mm CW in males and 90 mm CW in females. According to Sullivan (1979), claws of *M. mercenaria* reach harvestable sizes at approximately 80.0 and 87 mm CW for males and females, respectively. Savage and Sullivan (1978) reported that females produced legal claws at 89.0 mm CW.

Menippe exhibits allometric growth between sexes (Sullivan 1979, Perry et al. 1995) and between juveniles and adults (Manning 1961). In *Menippe*, differential growth appears to begin with the onset of sexual maturity in females. Sullivan (1979) derived relationships for carapace width and propodus length for all combinations of claw types and handedness for *M. mercenaria*. With the exception of left minor claws, the points of divergence occurred between 55.0 and 65.0 mm CW. In *M. adina*, transition points for right major claws occur at carapace widths of 60.0 mm and 64.0 mm for males and females, respectively (Perry et al. 1995). According to Bender (1971), Savage and Sullivan (1978), and Bert et al. (1986), female *Menippe* begin to reach sexual maturity at Age I; and this occurs at carapace widths between 40.0 and 60.0 mm. Sullivan (1979) noted that based on the presence of egg masses, *M. mercenaria* females were sexually mature at 60.0 mm CW. Working with crabs from the hybrid zone in Florida, Wilber (1992) concluded that sexual maturation begins at about 60.0 mm CW based on the presence of sperm in the seminal receptacles of female crabs. These data provide strong evidence that sexual maturity in the female contributes to differential growth in stone crabs.

Carapace widths based on propodus lengths of 64 mm and 70 mm (current minimum standards for harvest in Texas and Florida, respectively) were determined for all claw types for male and female *M. adina* using reduced major axis regression (Perry et al. 1995). Right major claws with a propodus length of 70 mm occurred at carapace widths of 82 mm and 92 mm for males and females, respectively. At 64 mm PL, carapace widths were 77 mm for males and 85 mm for females (Table 4.5).

Perry et al. (1995) determined that 50% sexual maturity for *M. adina* males was 71.0 mm CW, an estimate identical to the 71 mm CW given by Bert et al. (1986) for maturity in male *M. mercenaria*. Fifty percent sexual maturity was calculated at 73 mm CW for female *M. adina*, a size somewhat larger than the 63 mm CW estimated for female *M. mercenaria* by Restrepo (1989b). Carapace widths for claws 70 mm PL for *M. adina* are above the calculated size for 50% maturity regardless of the sex or claw type (Table 4.5).

The carapace width to weight relationship of *M. adina* is comparable to what Sullivan (1979) found for *M. mercenaria*. Males above a certain carapace width were always heavier than females for a given carapace width, and the difference increased at larger sizes (Figure 4.7).

4.4.2 Biological Population Characteristics

Legal minimum harvestable size of 70.0 mm PL was set to provide for an acceptable market product and to allow for sufficient spawning prior to harvest (Costello et al. 1979). Size at spawning is variable in both species. Ovigerous *M. adina* have been found ranging from 33.8 mm (Powell and Gunter 1968) to above 110 mm CW (Stuck and Perry 1992). Savage and Sullivan (1978) found ovigerous female *M. mercenaria* as small as 36.9 mm CW; however, Sullivan (1979) noted that large scale participation in egg production did not occur until approximately 60.0 mm CW. He observed that ovigerous *M. mercenaria* females occurred more frequently in size classes above 95.5 mm CW. Maximum reproductive output in both species occurs as carapace widths exceed 80.0 mm. Stuck and Perry (1992) found the highest incidence of ovigerous female *M. adina* in the 80.0 to 89.9 mm CW size class, and the proportion of egg-bearing females decreased above and below this interval. Percent abundance of ovigerous females in Galveston Bay, Texas, was also generally highest in the 80.0 to 90.0 mm CW size group (Boslet 1989). Applying the Florida minimum size of 70.0 mm PL to *M. adina* would allow for at least one reproductive season before entry into the fishery.

Table 4.5. *Menippe adina* predicted carapace widths for 64 mm and 70 mm propodus lengths for all claw types and handedness using the upper line of reduced major axis regressions.

Sex	Hand	Claw Type	Propodus Length	
			64 mm	70 mm
Carapace Width (mm)				
M	Right	Major	77	82
F	Right	Major	85	92
M	Left	Minor	88	94
F	Left	Minor	99	108
M	Left	Major	77	82
F	Left	Major	86	93
M	Right	Minor	86	96
F	Right	Minor	99	107

4.4.3 Implications for Management

Comparison of morphometric data for *M. mercenaria* and *M. adina* shows similarities in morphometric characteristics. Propodus lengths for given carapace widths in adults of both species differ between the sexes with males having proportionally longer propodi than females. As a result, males reach harvestable size at smaller carapace widths than do females. Size at 50% sexual maturity is similar for males of both species. Calculated size at 50% sexual maturity for female *M. adina* occurs at a larger size than for *M. mercenaria*. In both species maximum reproductive output in females occurs at carapace widths above 79.9 mm with spawning activity beginning at approximately 60.0 mm CW.

Similarities in morphometric characteristics would suggest that a uniform minimum claw size could be applied for the two species throughout the Gulf; however, data from northern Gulf studies of *M. adina* indicate that crabs available to the fishery show a moderately low percentage of legal-size claws. In Louisiana, 60.6% of the claws from crabs in Barataria Bay were below minimum legal size (Baltz and Horst 1992). Landry (1992) reported that 47% of the claws from crabs in Galveston Bay, Texas, did not meet minimum standards. In Mississippi, the percentage of legal-size claws appeared to be related to the area fished. Perry et al. (1984) found that 69.1% of the claws taken in nearshore waters by blue crab fishermen did not meet harvestable standards. In waters near the offshore barrier islands of Mississippi, the percentage of claws ≥ 70 mm increased to over 50% (Stuck and Perry 1992).

Bert (1985) compared mean size (mm CW) of trap-caught *M. adina* (from Perry et al. 1984) and *M. mercenaria* (composite data from several studies) and noted that the average size of crabs trapped by Perry et al. (1984) was notably smaller (88.6 mm CW) than *M. mercenaria* males trapped in her studies (96.4 mm CW). Female *M. adina*, however, were slightly larger (90.0 mm CW) than female *M. mercenaria* (86.0 mm CW). Stuck and Perry (1992) reported a mean size of 90.3 mm CW for crabs taken near the barrier islands in Mississippi suggesting that larger crabs with proportionally larger claws may be found in waters further offshore. With the exception of Stuck and Perry (1992), studies in the northern Gulf of Mexico were conducted in nearshore waters where later (= larger)

age classes may not be present. Additionally, a variety of trap types were used in these studies. These factors may account for the smaller size of trapped *M. adina*.

Size of crabs available to fishermen in Texas prompted a review of the 70.0 mm PL minimum size limit in that state. Hammerschmidt (1988) noted that lowering the minimum size to 64.0 mm PL would make at least 16.3% more crabs available for harvest. Reduction of the minimum claw size would still allow for some measure of protection to the spawning stock (female crabs would become available for harvest at approximately 86 mm CW); however, the economic impact and biological changes associated with a lower limit must be carefully weighed.

Restrepo (1989b) examined the relationship between claw size of *M. mercenaria* and fishing mortality. He generated a simulation model of cohort exploitation using available biological data and exploitation rates of stone crabs and derived yield and egg production on a per-recruit basis. Yield-per-recruit isopleths for male and female *M. mercenaria* depicted that a gain in yield (grams-per-recruit) would result from either an increase in fishing effort or a decrease in claw size from the current minimum of 70 mm PL. The same simulation models were used to obtain egg-per-recruit isopleths that suggested that egg production was at 96% of its maximum level when female claws were harvested at 70 mm PL even at high levels of fishing effort. Restrepo (1989b) noted that depending upon the accuracy of the parameters used in the simulations, reduction of claw size in females could significantly lower the reproductive capacity of the stock. He cautioned that the detrimental impact on equilibrium egg production caused by lowering the minimum claw size could include recruitment failure.

Although meristic similarities suggest a uniform management policy might be applied to both species, management of the fishery for *M. adina* must take into consideration the smaller size of the fishable populations, limited fishing areas, the preponderance of females in the catch, and the potential for gear conflicts in the heavily-shrimped waters of the northern Gulf of Mexico.

4.5 Potential for Directed Fishery Development

Studies to characterize adult populations and to determine the potential for fishery development were conducted in Texas (Boslet 1989, Landry 1992); Louisiana (Horst and Bankston 1986, Baltz and Horst 1992); and Mississippi (Perry et al. 1984; Stuck 1987, 1989; Stuck and Perry 1992, Perry et al. 1995). The species is apparently too uncommon in Alabama to support a commercial fishery (Swingle 1971, 1977). While these studies suggested the possibility of limited, directed fishery development in selected areas of the northern Gulf, abundance of stocks does not appear to be sufficient to support large-scale, commercial fishing activities. Areal distribution of available stocks, absence of in-state markets, and insufficient support from industry and government were also identified as barriers to development.

4.5.1 Texas

Boslet (1989) reported that Galveston Bay could support a supplemental fishery for stone crabs during August in areas of highest production and that a fisherman working 300 traps could expect \$270 to \$540 in additional income/week during this period. Based on a fishery-independent trapping study in lower Galveston Bay, Landry (1992) suggested that there were insufficient stone crab densities to support a directed commercial fishing effort. Fishery-dependent data from Galveston Bay, however, suggested that small-scale, directed fishing activities may be profitable. Weekly catches from five fishermen ranged from 24 to 400 kg of claws with nearly 22,350 kg of claws landed by these fishermen during the 1985-1986 season. Impediments to development in Texas include lack of information on stocks, absence of in-state markets, and insufficient support from industry and government (Landry 1992).

4.5.2 Louisiana

Based on catch rates (1-1.5 crabs/trap/sampling event) from Barataria Bay and anecdotal evidence of large catches of stone crabs in areas east of the Mississippi River (Black Bay, Breton Sound, Chandeleur Sound, lower Lake Borgne), Baltz and Horst (1992) suggested that inshore Louisiana waters could support a marginally profitable commercial fishery. Estimates of income based on fishery-independent catch data from Barataria Bay (113 grams

of salable claws/animal) and the spring 1985 claw price of \$4.50/pound ranged from \$336 to \$504 per 300 traps or \$1.12 to \$1.68/trap (Horst and Bankston 1986).

4.5.3 Mississippi

Stuck (1989) estimated a yield/trap of commercial-size claws of \$2.56. This estimate was based on an average catch of 114.8 grams/trap/night and assumed an average dock-side price of \$4.50/pound. The estimate of yield from the area of maximum abundance (Dog Keys Pass) was \$6.08/trap/night. These estimates were based on 24 hour soak times. Using data from Dog Keys Pass, Stuck and Perry (1992) estimated that each trap would yield \$3.25 for a seven-day fishing period assuming an average price of \$4.50/pound and catch estimates of 45 grams/trap/night.

Stuck and Perry (1992) suggested that the potential for development of a limited, directed, commercial fishery existed in Mississippi; however, several factors would impede development. First, the areas of maximum abundance in Mississippi are limited in size and may be easily depleted with sustained fishing effort. Second, since females form the principal component of the trapped population, heavy fishing activity during the summer reproductive season may adversely affect recruitment to subsequent adult populations resulting in further population depletion. Finally, the most serious impediment to development may be areal distribution of stocks and the potential for conflict with the shrimp fishery. Areas of maximum abundance coincide with areas of high shrimp abundance, and loss of traps could pose a significant problem. Because of the potential for conflict, directed fishing activities near the barrier islands would be economically feasible from mid-April until the opening of the shrimp season in June and again in October and November when catch rates of male crabs are high and trawling activity is low.

4.6 Mariculture

Commercial mariculture of stone crabs has been considered since the late 1960s. Highly variable commercial landings coupled with high market demand and premium prices initially stimulated interest in stone crab mariculture.

Ong and Costlow (1970) concluded that compared to other commercially important crab species, *M. mercenaria* might be a more suitable species for large scale mariculture because of their high survival rates (60%-72%), their moderate range of salinity tolerance, and a larval-development period of approximately 21 days under optimum conditions. Several adaptive characteristics of the stone crab listed by Bert et al. (1978) were considered by McConnaughey and Krantz (1992) to render the species suitable for mariculture: high fecundity, opportunistic feeding habits, an extended spawning season, and good resistance to oxygen impoverishment. These factors are consistent with high survival and low maintenance. McConnaughey and Krantz (1992) also noted the efficient assimilation of energy into growth and reproduction and acceleration of larval development times in mass culture operations. Most early efforts to culture stone crab larvae were small-scale, laboratory-based studies for taxonomic identification of physiological studies (McConnaughey and Krantz 1992, Hyman 1925, Porter 1960, Ong and Costlow 1970).

In the laboratory, stone crabs reared from eggs have reproduced successfully (Yang 1972, Roberts 1975) and winter mating has been induced (McConaughy et al. 1980). Steward (1972) utilized thermal discharges from Tampa Electric Company's Big Bend Power Plant on Tampa Bay to culture a limited number of *Menippe*. McConaughy et al. (1980) conducted a study to determine if nonseasonal breeding could be induced in *Menippe* by elevated temperature control. They concluded that a year-round breeding population may be maintained in the laboratory and, in conjunction with mass culture techniques, could provide seedling stocks for extensive mariculture.

Other researchers have portrayed a more pessimistic outlook for large-scale *Menippe* mariculture. Bardach et al. (1972) concluded that the relatively slow growth rates of *Menippe* precluded this species from major mariculture efforts; however, they suggested that if the period of claw regeneration is brief or if growth can be increased by artificial means then perhaps the species has mariculture potential.

Yang and Krantz (1976) conducted an intensive, large-scale mariculture experiment from eggs to marketable adults in outdoor tanks and ponds and developed a comprehensive manual detailing techniques, procedures, and facilities. Larval survival under mass culture to the first crab stage ranged from 4.1% to 15.0%, much lower than the 60% to 70% survival rate reported by Ong and Costlow (1970) under more controlled, small culture conditions. Yang and Krantz (1976) attributed their lower survival rates to poor water quality during the late zoeal and megalopal stages. In addition to water quality, hydrozoans may impact survival of *Menippe* in closed-system, larval culture (Sandifer et al. 1974). Yang and Krantz (1976) concluded that larval culture procedures were inadequate for commercial mariculture because of the logistics of feeding large numbers of larvae and the difficulty in maintaining water quality in large-volume, culture tanks. Yang and Krantz (1976) also found extreme variation in growth rates and poor survival of juvenile crabs due to cannibalism and aggressive behavior. These factors make the species a poor candidate for intensive mariculture in tank and pond systems. Yang and Krantz (1976) suggested that the species may be better utilized in extensive culture systems possibly using natural habitat and natural food.

McConnaughey and Krantz (1992) later described an intensive, hatchery-production system for larval *M. mercenaria* that largely resolved the larval culture problems of the past. They utilized kreisels with spiral, upwelling circulation; stocked zoeae at a rate of 42.5/l; fed larvae a quality strain of freshly hatched *Artemia* nauplii; and routinely used husbandry practices such as half-weekly draining of kreisels. McConnaughey and Krantz (1992) indicated that their postlarvae production rates compare favorably with commercial hatcheries for *Macrobrachium* and penaeid shrimp but conceded that major hurdles, particularly those associated with growout operations, must be overcome prior to commercial production of *Menippe*.

5.0 RULES AND REGULATIONS

5.1 Florida (State Waters)

1. It is unlawful to catch or have in possession, regardless of where taken, for his own use or sell or to offer for sale any stone crab, or parts thereof, between May 15 and October 15 of each year.
2. Traps may be placed in the water and baited 10 days prior to the opening of the stone crab season and shall be removed within five days after the close of the stone crab season.
3. Nonwooden crab traps must have a biodegradable section.
4. The permit number issued to each fishermen must be attached permanently to each trap.
5. It is unlawful to willfully molest any stone crab trap, line, or buoy without the permission of that license holder.
6. Ownership of stone crab traps may be transferred if the following conditions are met:
 - a) The owner must notify the Division of Law Enforcement of the Department of Environmental Protection within five days of acquiring ownership and request issuance of a stone crab permit if they are not a current permit holder.
 - b) Buoys must be numbered and recolored at the first pulling of traps after purchase.
 - c) The new permit must be permanently attached to the traps prior to setting such traps in the following open season.
 - d) The new owner must retain a valid bill of sale.
7. Stone crab claws must have a forearm (propodus) length of $2\frac{3}{4}$ inches, measured by a straight line from the elbow to the tip of the lower immovable finger.
8. A tolerance level of 1% by count of claws in any individual box, bag, or container shall be allowed for possession of undersize claws onboard a fishing vessel, or on the premises of a licensed wholesale seafood dealer prior to cooking and grading, but sale or further transport or possession of undersize claws is unlawful. Undersize claws shall not be sold and shall be destroyed immediately after cooking and grading.
9. Except as provided in Number 10, it is unlawful to possess or transport by boat, land vehicle, airplane, or other conveyance any intact stone crab or stone crab body whether dead or alive.
10. Live stone crabs may be held onboard a vessel while it is at sea until such time as the claws are removed, provided the crabs are held in shaded containers and wet with seawater every 30 minutes, or more often, if necessary, to keep the crabs in a damp condition. Containers shall not be stacked in such a manner as to crush the crabs.
11. It is unlawful to remove claws from egg-bearing female stone crabs or to have any egg-bearing female stone crabs onboard a vessel.

5.2 Alabama, Mississippi, and Louisiana

No rules and regulations specific to stone crabs have been promulgated.

5.3 Texas

1. Crabs may be taken in any number and at any time by crab line, crab trap, and umbrella net (not exceeding 16 square feet). Crabs caught in the devices legally used for taking fish or shrimp and operated in legal places and at legal times may be retained.
2. Crab traps may be used only in the coastal waters of the state, although there are areas where traps are not allowed or are restricted.
3. No more than 300 crab traps may be used by any person.
4. Crab traps may not exceed 16 cubic feet in volume and must be equipped with at least 2 escape vents (minimum $2 \frac{2}{3}$ inches inside diameter) in each crab-retaining chamber and located on the lower edge of the outside trap walls.
5. Each crab trap must have a crab trap tag firmly attached.
6. Crab trap buoys must be marked with a gear tag valid for only 30 days after date set out. Buoys must be white, floating, visible, and not less than 6 inches in width, and 6 inches in height, or with white plastic bottles of not less than 1 gallon size.
7. Only the right claw may be removed from a stone crab and the crab must be returned immediately to the waters where taken.
8. The minimum claw size is $2\frac{1}{2}$ inches as measured from the tip of the immovable claw finger to the first joint behind the claw.
9. It is unlawful to possess egg-bearing female crabs (sponge crabs) or stone crabs. No person may buy or sell a female crab that has its abdominal apron detached and was taken from coastal waters.

5.4 Federal

The harvest of stone crabs in the Gulf of Mexico is managed by *The Fishery Management Plan for the Stone Crab Fishery of the Gulf of Mexico*. The fishery management plan (FMP) was published in the Federal Register on April 3, 1979, and implemented by the Secretary of Commerce on September 14, 1979.

Although the FMP considered the resource throughout its range from Florida to Texas, the area regulated under this FMP is confined to the waters of the west coast of Florida including the Florida Keys and in the EEZ.

The original regulations contained in the FMP are listed below by topic:

5.4.1 Size Restrictions

- Minimum claw size of $2\frac{3}{4}$ inches PL

5.4.2 Harvest Practices

- Declawed crab bodies must be returned to the water and not landed.
- Live crab holding box must be shaded
- Illegal to pull another person's traps

- Traps may be pulled only in daylight hours
- Both claws may be harvested

5.4.3 Seasons

- Season closed between May 15 and October 15
- Grace period for trap placement and recovery (10 days before and 5 days after open season)

5.4.4 Closed Areas

- An area of the EEZ to be closed to trawling from January 1 to May 20, inshore of a "line of separation" as defined on pages 21-22 of the Gulf of Mexico Fishery Management Council's *Amendment Number 1 to the Fishery Management Plan for the Stone Crab Fishery of the Gulf of Mexico*

5.4.5 Gear Restrictions

- Degradable panel required in nondeteriorating traps

5.4.6 Vessel Enumeration

- Enumeration for informational purposes of all stone crab vessels fishing in the EEZ
- Fisherman classified as full or part time

5.4.7 Statistical Reporting

- Monthly reporting of pounds and value of catch and pounds and value of processed products by wholesale dealers and processors
- Monthly submission of trip tickets or log books by commercial fishermen of catch, number of traps, and area of capture

5.4.8 Amendments

Since the implementation of the FMP, four amendments have been adopted by the Gulf of Mexico Fishery Management Council. Regulations adopted under each amendment are listed below.

5.4.8.1 Amendment 1

- Prohibited trawling inside of a line of separation in southwest Florida from January 1 to May 20 except for limited, supervised, exploratory trawling and bait shrimping
- Identification marking required on live bait vessels

5.4.8.2 Amendment 2

- Extended the line of separation off west central Florida
- Established a procedure for terminating or resolving conflicts between shrimp and stone crab fishermen off west central Florida

5.4.8.3 Amendment 3

- Required that stone crabs held aboard prior to declawing be kept damp and held in a manner to avoid compression mortality
- Prohibited declawing or possession of ovigerous females
- Extended the grace period for removal of traps after the season upon individual request due to hardship
- Adopted a uniform vessel identification system utilized by the state of Florida
- Deleted the mandatory reporting requirements because of the new Florida trip monitoring system

5.4.8.4 Amendment 4

- Defined overfishing as existing when the realized egg production per recruit is reduced below 70 percent of potential production. Overfishing will be avoided when there is a minimum claw length that assures survival of the crabs to achieve the 70 percent egg production per recruit potential.
- Should overfishing occur, the Council and state of Florida will adjust the minimum claw length or fishing mortality rate (F) by regulatory amendment as authorized under this measure to increase the egg production potential to at least 70%

6.0 LITERATURE CITED

- Albert, J.L. and W.R. Ellington. 1985. Patterns of energy metabolism in the stone crab, *Menippe mercenaria*, during severe hypoxia and subsequent recovery. *Journal of Experimental Zoology* 234(2):175-183.
- Andryszak, B.L. 1979. Abundance, distribution, and partial descriptions of reptant decapod crustacean larvae collected from neritic Louisiana waters in July 1976. Master's Thesis. Louisiana State University, Baton Rouge, Louisiana. 102 pp.
- Anger, K., R.R. Dawirs, V. Anger, and J.D. Costlow. 1981a. Effects of early starvation periods on zoal development of brachyuran crabs. *Biological Bulletin* 161(2):199-212.
- Anger, K., R.R. Dawirs, V. Anger, J.W. Goy, and J.D. Costlow. 1981b. Starvation resistance in first stage zoeae of brachyuran crabs in relation to temperature. *Journal of Crustacean Biology* 1(4):518-525.
- Ayers, J.C. 1938. Relationship of habitat to oxygen consumption by certain estuarine crabs. *Ecology* 19(4):523-527.
- Baltz, D.M. and J.W. Horst. 1992. Depth and substrate selection, sex ratio, and size distribution in an unexploited stone crab (*Menippe adina*) population in Barataria Bay, Louisiana. Pages 74-81. In: Theresa M. Bert (editor), Proceedings of a Symposium on Stone Crab (genus *Menippe*) Biology and Fisheries. Florida Department of Natural Resources, Marine Research Publication Number 50.
- Bardach, J.E., J.H. Ryther, and W.O. McLarney. 1972. Aquaculture: the farming and husbandry of freshwater and marine organisms. Wiley-Interscience, New York, New York. 868 pp.
- Bender, E.S. 1971. Studies of the life history of the stone crab, *Menippe mercenaria* (Say), in the Cedar Key area. Master's Thesis. University of Florida, Gainesville, Florida. 110 pp.
- Bert, T.M. 1992. Summary of workshop on current issues related to stone crab (genus *Menippe*) biology and fisheries. Pages 108-115. In: Theresa M. Bert (editor), Proceedings of a Symposium on stone crab (genus *Menippe*) Biology and Fisheries. Florida Department of Natural Resources, Marine Research Publication Number 50.
- Bert, T.M. 1986. Speciation in western Atlantic stone crabs (genus *Menippe*): the role of geological processes and climatic events in the formation and distribution of species. *Marine Biology* 93(2):157-170.
- 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. Doctoral Dissertation. Yale University, New Haven, Connecticut. 306 pp.
- Bert, T.M. and R.G. Harrison. 1988. Hybridization in western Atlantic stone crabs (genus *Menippe*): evolutionary history context influence species interactions. *Evolution* 42(3):528-544.
- Bert, T.M., J. Tilmant, J. Dodrill, and G.E. Davis. 1986. Aspects of the population dynamics and biology of the stone crab (*Menippe mercenaria*) in Everglades and Biscayne National Parks as determined by trapping. National Park Service, Report SFRC-86/04. 77 pp.
- Bert, T.M., R.E. Warner, and L.D. Kessler. 1978. The biology and Florida fishery of the stone crab, *Menippe mercenaria* (Say), with emphasis on southwest Florida. University of Florida, Sea Grant Technical Paper Number 9. 82 pp.
- Binford, R. 1913. The germ-cells and the process of fertilization in the crab *Menippe mercenaria*. *Journal of Morphology* 24(2):147-201.

- Blundon, J.A. 1988. Morphology and muscle stress of chelae of temperate and tropical stone crabs *Menippe mercenaria*. *Journal of Zoology* 215(4):663-674.
- Bookhout, C.G. and J.D. Costlow, Jr. 1974. Crab development and effects of pollutants. *Thalassia Jugoslavica* 10(1/2):1-11.
- Bookhout, C.G., A.J. Wilson, Jr., T.W. Duke, and J.I. Lowe. 1972. Effects of Mirex® on the larval development of two crabs. *Water, Air, and Soil Pollution* 1(2):165-180.
- Boslet, J.M. 1989. Abundance and distribution of the western Gulf stone crab (*Menippe adina*) in Galveston Bay, Texas. Master's Thesis. Texas A&M University, College Station, Texas. 73 pp.
- Bowman, T.E. and L.G. Abele. 1982. Classification of the recent Crustacea. Pages 1-27. In: L.G. Abele (editor), Systematics, the fossil record, and biogeography. *The Biology of Crustacea, Volume 1*. Academic Press, New York, New York.
- Brookins, K.G. and C.E. Epifanio. 1985. Abundance of brachyuran larvae in a small coastal inlet over six consecutive tidal cycles. *Estuaries* 8:60-67.
- Brooks, W.R. and R.N. Mariscal. 1985. Protection of the hermit crab, *Pagurus pollicaris* (Say), from predators by hydroid-colonized shells. *Journal of Experimental Marine Biology and Ecology* 87(2):111-118.
- Brown, K.M. and E.S. Haight. 1992. The foraging ecology of the Gulf of Mexico stone crab, *Menippe adina* (Williams and Felder). *Journal of Experimental Marine Biology and Ecology* 160(1):67-80.
- Brown, S.C., S.R. Cassuot, and R.W. Loss. 1979. Biomechanics of chelipeds in some decapod crustaceans. *Journal of Zoology* 188(2):143-159.
- Brown, S.D. 1990. Temperature and salinity effects on survival and development of early stage stone crabs, *Menippe mercenaria* (Say 1818). Master's Thesis. University of South Florida, St. Petersburg, Florida. 107 pp.
- Brown, S.D. T.M. Bert, W.A. Tweedle, J.J. Torres, and W.J. Lindberg. 1992. The effects of temperature and salinity on survival and growth of early life stages Florida stone crabs (*Menippe mercenaria* Say). *Journal of Experimental Marine Biology and Ecology* 157(1):115-136.
- Bullis, H.R., Jr. and J.R. Thompson. 1965. Collections by the exploratory fishing vessels OREGON, SILVER BAY, COMBAT, and PELICAN made during 1956-1960 in the southwestern north Atlantic. U.S. Fish and Wildlife Service, Special Scientific Report - Fisheries Number 510. 130 pp.
- Caldwell, M.A. 1986. Autecology of the stone crab, *Menippe mercenaria* (Say), near the northern extent of its range. Master's Thesis. College of Charleston, Charleston, South Carolina. 72 pp.
- Chen, F., B. Reid, G. Ramos, and C.R. Arnold. 1990. Growth and development of the Gulf stone crab, *Menippe adina*, from zoeae to juveniles in the laboratory. Unpublished report. University of Texas, Marine Science Institute, Port Aransas, Texas. 17 pp.
- Cheung, T.S. 1976. A biostatistical study of the functional consistency in the reversed claws of adult male stone crabs, *Menippe mercenaria* (Say). *Crustaceana* 31(2):137-144.
- 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. *Bulletin of the Institute of Zoology, Academia Sinica (Taipei)* 12(1):1-11.

- Cheung, T.S. 1969. The environmental and hormonal control of growth and reproduction in the adult female stone crab, *Menippe mercenaria* (Say). *Biological Bulletin* 136:327-346.
- Cheung, T.S. 1968. Trans-molt retention of sperm in female stone crab, *Menippe mercenaria* (Say). *Crustaceana* 15(2):117-120.
- Christmas, J.Y. and W. Langley. 1973. Estuarine invertebrates, Mississippi. Pages 255-319. *In*: J.Y. Christmas (editor), Cooperative Gulf of Mexico Estuarine Inventory and Study, Mississippi. Gulf Coast Research Laboratory, Ocean Springs, Mississippi.
- Cline, G.B., C.W. Hardwick, Jr., and R.A. Angus. 1992. Genetic differentiation between stone crab populations from Mississippi Sound, Apalachicola Bay, and South Florida as determined by isoelectric focusing. Pages 4-9. *In*: T.M. Bert (editor), Proceedings of a Symposium on Stone Crab (genus *Menippe*), Biology and Fisheries. Florida Department of Natural Resources, Marine Research Publication Number 50.
- Cobb, J.S. and J.F. Caddy. 1989. The population biology of decapods. Pages 327-374. *In*: J.Caddy (editor), Marine Invertebrate Fisheries: Their Assessment and Management. John Wiley and Sons, New York, New York.
- Cohen, M.J. and S. Dijkgraaf. 1960. Mechanoreception. Pages 65-108. *In*: T. Waterman (editor), The Physiology of the Crustacea, Volume I. Academic Press, New York, New York.
- Costello, T., T.M. Bert, D.G. Cartano, G. Davis, G. Lyon, C. Rockwood, J. Stevely, J. Tashiro, W.L. Trent, D. Turgeon, and J. Zuboy. 1979. Fishery management plan for the stone crab fishery of the Gulf of Mexico. *Federal Register* 44(65), Book 1:19,444-19,496.
- Costlow, J.D., Jr. 1979. Effect of Dimlin® on development of larvae of the stone crab *Menippe mercenaria*, and the blue crab, *Callinectes sapidus*. Pages 355-363. *In*: W.B. Vernberg, A. Calabrese, F.P. Thurberg, and F.J. Vernberg (editors), Marine Pollution: Functional Responses. Academic Press, New York, New York.
- Cronin, T.W. and R.B. Forward, Jr. 1982. Tidally timed behavior. Pages 505-520. *In*: V. Kennedy (editor), Estuarine Comparisons. Academic Press, New York, New York.
- Davis, T.A. 1987. Laterality in Crustacea. *Proceedings of the Indian National Science Academy* 53(1):47-60.
- Defenbaugh, R.E. 1976. A study of the benthic macroinvertebrates of the continental shelf of the northern Gulf of Mexico. Doctoral Dissertation. Texas A&M University, College Station, Texas. 476 pp.
- Dittel, R., A.I. Epifanio, and C.E. Epifanio. 1982. Seasonal abundance and vertical distribution of crab larvae in Delaware Bay. *Estuaries* 5(3):197-202.
- Dudley, D.L. and M.H. Judy. 1971. Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. National Marine Fisheries Service, NMFS Special Scientific Report- Fisheries Number 637:1-10.
- Dugas, C. Unpublished data. Louisiana Department of Wildlife and Fisheries, P.O. Box 98000, Baton Rouge, Louisiana 70898-9000.
- Dumortier, B. 1963. Morphology of sound emission apparatus in Arthropoda. Pages 277-345. *In*: R.G. Busnel (editor), Acoustic Behavior of Animals. Elsevier Publishing Company, Amsterdam, Netherlands/New York, New York.
- Epifanio, C.E. 1988a. Transport of crab larvae between estuaries and the continental shelf. *Lecture Notes on Coastal and Estuarine Studies* 22:291-305.

- Epifanio, C.E. 1988b. Transport of invertebrate larvae between estuaries and the continental shelf. Pages 104-114. In: M.P. Weinstein (editor), Larval Fish and Shellfish Transport Through Inlets. American Fisheries Society Symposium 3.
- Epifanio, C.E., C.C. Valenti, and A.E. Pembroke. 1984. Dispersal and recruitment of blue crab larvae in the Delaware Bay, USA. Estuarine, Coastal and Shelf Science 18(1):1-12.
- Factor, J.R. 1982. Development and metamorphosis of the feeding apparatus of the stone crab, *Menippe mercenaria* (Brachyura, Xanthidae). Journal of Morphology 172(3):299-312.
- Felder, D.L. 1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. Louisiana State University, Sea Grant Publication, LSU-SG-73-02. 103 pp.
- Field, C.J. 1989. Effects of salinity and temperature on survival and development time of the larvae of stone crabs, *Menippe mercenaria* (Say 1818) and *Menippe adina* (Williams and Felder 1986) (Decapoda: Brachyura: Xanthidae). Master's Thesis. Louisiana State University, Baton Rouge, Louisiana. 157 pp.
- Forward, R.B., Jr. 1977. Occurrence of a shadow response among brachyuran larvae. Marine Biology 39(4):331-341.
- Gallaway, B.J., M.F. Johnson, F.J. Margraff, R.L. Howard, L.F. Martin, G.L. Lewbel, and G.S. Balard. 1981. Ecological investigations of petroleum production platforms in the central Gulf of Mexico. Volume II. The Artificial Reefs. Southwest Research Institute, Final Report for SWRI Project 01-5245 (Contract AA551-CT8-17, Bureau of Land Management, Department of the Interior, USA). 199 pp.
- Gunter, G. 1950. Seasonal population changes and distributions as related to salinity in certain invertebrates of the Texas coast, including the commercial shrimp. Publications of the Institute of Marine Science, University of Texas 1(2):7-51.
- Gunter, G. 1955. Mortality of oysters and abundance of certain associates as related to salinity. Ecology 36(4):601-605.
- Hammerschmidt, P.C. 1988. Evaluation of minimum stone crab claw length regulations in Texas. Texas Parks and Wildlife Department, Management Data Series Number 135:1-13.
- Hartnoll, R.G. 1969. Mating in the Brachyura. Crustaceana 16(2):161-181.
- Hedgpeth, J.W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. Publications of the Institute of Marine Science, University of Texas 3(1):107-224.
- Hembree, D.E. 1984. The offshore migration of stone crabs and temperatures effect on locomotor activity. Master's Thesis. Florida State University, Tallahassee, Florida. 64 pp.
- Henry, R. Personal communication. Department of Zoology, Auburn University, Alabama.
- Hildebrand, H.H. 1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publications of the Institute of Marine Science, University of Texas 3(2):233-366.
- Hoese, H.D. 1960. Biotic changes in a bay associated with end of a drought. Limnology and Oceanography 5(3):326-336.
- Horst, J. and D. Bankston. 1986. The potential for a stone crab (*Menippe mercenaria*) commercial fishery in Barataria Bay, Louisiana. Louisiana State University, Center for Wetland Resources, Technical Report Number TS-85-06. 21 pp.

- Humes, A.G. 1941. Notes on *Octolasmis mulleri* (Coker), a barnacle commensal on crabs. Transactions of the American Microscopical Society 60(1):101-103.
- Hyman, O.W. 1925. Studies on the larvae of crabs of the family Xanthidae. Proceedings of the United States National Museum 67(8):1-22.
- Iversen, E.S. 1986. A bibliography of parasites, symbionts, diseases, and biotic communities of North American marine shellfish. University of Miami, Sea Grant Report 86:138-139.
- Iversen, E.S. and G.L. Beardsley. 1976. Shell disease in crustaceans indigenous to south Florida. Progressive Fish Culturist 38(4):195-196.
- Johnson, D.F. 1985. The distribution of brachyuran crustacean megalopae in the waters of the York River, lower Chesapeake Bay and adjacent shelf. Estuarine, Coastal, and Shelf Science 20:693-705.
- Juneau, C.L., Jr. and B. Barrett. 1975. An inventory and study of the Vermilion Bay-Atchafalaya Bay complex. Louisiana Wildlife and Fisheries Commission, Technical Bulletin Number 13. 153 pp.
- Kakati, V.S. 1977. Larval development of the crab, *Menippe rumphii* (Fabricius) as observed in the laboratory. Pages 634-641. In: Proceedings of a Symposium on Warm Water Zooplankton. Special Publication UNESCO/NIA.
- Karandeyeva, O.G. and A. Silva. 1973. Intensity of respiration and osmoregulation of the commercial crab, *Menippe mercenaria* (Say), from Cuban coastal waters. Pages 292-310. In: Investigations of the Central American Seas (translated from Russian). Published for the Smithsonian Institution and National Science Foundation by the Indian National Scientific Document Center, New Delhi, India.
- Kent, B.W. 1983. Patterns of coexistence in busyconine whelks. Journal of Experimental Marine Biology and Ecology 66(3):257-283.
- Knudsen, J.W. 1960. Aspects of the ecology of the California pebble crabs. Ecological Monographs 30(2):165-185.
- Kurata, H. 1970. Studies of the life histories of decapod Crustacea of Georgia. University of Georgia, Marine Institute, Sapelo Island, Georgia. Unpublished Report.
- Landry, A.M., Jr. 1992. Characterization and fishery development of Galveston Bay, Texas, stone crab stocks. Pages 67-73. In: T.M. Bert (editor), Proceedings of a Symposium on Stone Crab (genus *Menippe*), Biology and Fisheries. Florida Department of Natural Resources, Marine Research Publication No. 50.
- Leffler, C.W. 1973. Metabolic rate in relation to body size and environmental oxygen concentration in two species of xanthid crabs. Comparative Biochemistry and Physiology 44(4A):1,047-1,052.
- Lindberg, W.J. and G.R. Stanton. 1989. Resource quality, dispersion, and mating prospects for crabs occupying bryzoan colonies. Journal of Experimental Marine Biology and Ecology 128:257-282.
- Lindberg, W.J. and G.R. Stanton. 1988. Bryzoan-associated decapod crustaceans: community patterns and a case of cleaning symbiosis between a shrimp and crab. Bulletin of Marine Science 42(3):411-423.
- Lindberg, W.J. and M.J. Marshall. 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida)--stone crab. U.S. Fish and Wildlife Service, FWS/OBS-82/11.21. 17 pp.
- Lindberg, W.J., T.K. Frazer, and G.R. Stanton. 1990. Population effects of refuge dispersion for adult stone crabs (*Menippe*). Marine Ecology Progress Series 66(3):239-249.

- Manning, R.B. 1961. Some growth changes in the stone crab, *Menippe mercenaria* (Say). Quarterly Journal of the Florida Academy of Sciences 23(4):273-277.
- Martin, J.W., F.M. Truesdale, and D.L. Felder. 1988. The megalopa state of the Gulf stone crab, *Menippe adina*, with a comparison of megalopae in the genus *Menippe*. Fishery Bulletin 86(2):289-297.
- Mauro, N.A. and C.P. Mangum. 1982. The role of the blood in the temperature dependence of oxidative metabolism in decapod crustacean. II. Interspecific adaptations to latitudinal changes. Journal of Experimental Zoology 219(2):189-195.
- McConaughy, J.R. 1988. Export and reinvasion of larvae as regulators of estuarine decapod populations. Pages 90-103. In: P. Weinstein (editor), Larval Fish and Shellfish Transport Through Inlets. American Fisheries Society Symposium 3.
- McConaughy, J.R., K. McNally, J.W. Goy, and J.D. Costlow. 1980. Winter inducing mating in the stone crab, *Menippe mercenaria*. Proceedings of the World Mariculture Society 11:544-547.
- McConaughy, R.A. and G.E. Krantz. 1992. Hatchery production of stone crab, *Menippe mercenaria* (Say), megalopae. Pages 60-66. In: T.M. Bert (Editor), Proceedings of a Symposium on Stone Crab (genus *Menippe*), Biology and Fisheries. Florida Department of Natural Resources, Marine Research Publication Number 50.
- McRae, E.J., Jr. 1950. An ecological study of the xanthid crabs in the Cedar Key area. Master's Thesis. University of Florida, Gainesville, Florida. 72 pp.
- Menzel, R.W. and F.E. Nichy. 1958. Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. Bulletin of Marine Science, Gulf and Caribbean 8(2):125-145.
- Menzel, R.W. and S.H. Hopkins. 1956. Crabs as predators of oysters in Louisiana. Proceedings of the National Shellfisheries Association 46:177-184.
- Mootz, C.A. and C.E. Epifanio. 1974. An energy budget for *Menippe mercenaria* larvae fed *Artemia* nauplii. Biological Bulletin 146(1):44-55.
- Noe, C. 1967. Contribution to the life history of the stone crab *Menippe mercenaria* (Say), with emphasis on the reproductive cycle. Master's Thesis. University of Miami, Coral Gables, Florida. 55 pp.
- Ong, K.S. and J.D. Costlow, Jr. 1970. The effect of salinity and temperature on the larval development of the stone crab, *Menippe mercenaria* (Say), reared in the laboratory. Chesapeake Science 11(1):16-29.
- Overstreet, R.M. and R.W. Heard. 1982. Food contents of six commercial fishes from Mississippi Sound. Gulf Research Reports 7(2):137-149.
- Parker, R.H. 1960. Ecology and distributional patterns of marine macroinvertebrates, northern Gulf of Mexico. Pages 302-337. In: F. Shepard, F.B. Phleger, and T.H. Van Andel (editors), A Symposium Summarizing the Results of Work Carried on in Project 51 of the American Petroleum Institute. American Association of Petroleum Geologists, Tulsa, Oklahoma.
- Passano, L.M. 1960. Molting and its control. Pages 473-536. In: T. Waterman (editor), Physiology of Crustacea, Volume 1. Academic Press, New York, New York.
- Perret, W.S., W.R. Latapie, J.F. Pollard, W.R. Mock, G.B. Adkins, W.J. Gaidry, and C.J. White. 1971. Section I. Fishes and invertebrates collected in trawl samples in Louisiana estuaries. Pages 40-105. In: W.S. Perret

- Perry, H.M. Unpublished data. Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, Mississippi 39566-7000.
- Perry, H.M., K.C. Stuck, and D.S. Reissig. 1984. *Menippe mercenaria*: the potential for development of a fishery. 1983 Annual Report. Mississippi-Alabama Sea Grant Consortium, Publication MASGP-83-010. 42 pp.
- Perry, H.M., W.T. Brehm, C.B. Trigg, and K.C. Stuck. 1995. Fishery-related morphometric characteristics of *Menippe adina*. Manuscript in Press, North American Journal of Fisheries Management.
- Porter, H.J. 1960. Zoéal stages of the stone crab, *Menippe mercenaria* (Say). Chesapeake Science 1(3-4):168-177.
- Powell, E.H., Jr. and G. Gunter. 1968. Observations on the stone crab *Menippe mercenaria* (Say), in the vicinity of Port Aransas, Texas. Gulf Research Reports 2(3):285-299.
- Powers, L.W. 1977. A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico. Contributions in Marine Science, Supplement 20. 190 pp.
- Rathbun, M.J. 1930. The canceroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. United States National Museum, Bulletin 152. 607 pp.
- Rathbun, R. 1887. The crab, lobster crayfish, rock lobster, shrimp, and prawn fisheries. Pages 650-669. In: G.B. Goode (editor), The Fisheries and Fishery Industries of the United States, Section 5, Volume 5, Volume 2, Part 21. U.S. Commission of Fish and Fisheries, Washington, DC.
- Rathbun, R. 1884. The stone crab *Menippe mercenaria*, Gibbes. Pages 772-774. In: G.B. Goode (editor), The Fisheries and Fishery Industries of the United States, Section 1, Part 5. U.S. Commission of Fish and Fisheries, Washington, DC.
- Restrepo, V.R. 1989a. Growth estimates for male stone crabs along the southwest coast of Florida: a synthesis of available data and methods. Transactions of the American Fisheries Society 118:20-29.
- Restrepo, V.R. 1989b. Population dynamics and yield-per-recruit assessment of southwest Florida stone crabs, *Menippe mercenaria*. Doctoral Dissertation. University of Miami, Coral Gables, Florida. 224 pp.
- Roberts, B.S., G.E. Henderson, and R.A. Medlyn. 1979. The effect of *Gymnodinium breve* toxin(s) on selected mollusks and crustaceans. Pages 419-430. In: D.L. Taylor and H.H. Seliger (editors), Toxic Dinoflagellate Blooms. Developments in Marine Biology, Volume 1. Elsevier/North Holland, New York, New York.
- Roberts, M.H., Jr. 1975. Culture techniques for decapod crustacean larvae. Pages 209-220. In: W.L. Smith and M.H. Chenley (editors), Culture of Marine Invertebrate Animals. Plenum Press, New York, New York.
- Rodriguez, G.A. and W.T. Yang. 1977. Regeneration of chelae and growth in the first crab stage [*Menippe mercenaria* (Say)] under laboratory conditions. Pages 565-579. In: National Oceanographic Congress, Volume 5. Instituto Tecnológico y los Estudios Superiores de Monterrey, Guaymas, Mexico.
- Ros, R.M., D. Perez, and R. Menocal. 1981. Fecundidad en el cangrejo moro, *Menippe mercenaria* (Say, 1818). Revista de Investigaciones Marinas 2(1):73-91.
- Sandifer, P.A. 1975. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. Estuarine and Coastal Marine Science 3(3):269-279.

- Saunders, F.A., I.J.J. Simin, and D.K. Calder. 1974. Hydrozoans as pests in closed-system culture of larval decapod crustaceans. *Aquaculture* 4(1):55-59.
- Savage, T. 1971a. Effect of maintenance parameters on growth of the stone crab, *Menippe mercenaria* (Say). Florida Department of Natural Resources, Marine Research Laboratory, Special Scientific Report 28. 5 pp.
- Savage, T. 1971b. Mating of the stone crab, *Menippe mercenaria* (Say) (Decapoda, Brachyura). *Crustaceana* 20(3):315-317.
- Savage, T. and M.R. McMahan. 1968. Growth of early juvenile stone crabs, *Menippe mercenaria* (Say 1819). Florida State Board of Conservation, Marine Research Laboratory Special Scientific Report 21. 17 pp.
- Savage, T. and J.R. Sullivan. 1978. Growth and claw regeneration in the stone crab *Menippe mercenaria*. Florida Department of Natural Resources, Florida Marine Research Publication 32. 23 pp.
- Schram, F.R. 1986. Crustacea. Oxford University Press, New York, New York. 606 pp.
- 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. *Fishery Bulletin* 77(2):359-386.
- Simonson, J.L. 1985. Reversal of handedness, growth, and claw stridulatory patterns in the stone crab *Menippe mercenaria* (Say) (Crustacea: Xanthidae). *Journal of Crustacean Biology* 5(2):281-293.
- Simonson, J.L. and P. Steele. 1981. Cheliped asymmetry in the stone crab, *Menippe mercenaria* (Say), with notes on claw reversal and regeneration. *Northeast Gulf Science* 5(1):21-30.
- Sinclair, M.E. 1977. Agonistic behavior in the stone crab, *Menippe mercenaria* (Say). *Animal Behavior* 25:193-207.
- Somerton, D.A. 1980. A computer technique for estimating the size of sexual maturity in crabs. *Canadian Journal of Fisheries and Aquatic Sciences* 37(10):1,488-1,494.
- Sprague, V. 1949. Species of *Nematopsis* in *Ostrea virginica*. *Journal of Parasitology* 35 (Supplement):42.
- Sprague, V. and J. Couch. 1971. An annotated list of protozoan parasites, hyperparasites, and commensals of decapod crustaceans. *Journal of Protozoology* 18(3):526-537.
- Sprague, V. and P.E. Orr, Jr. 1955. *Nematopsis ostrearum* and *N. prytherchi* (Eugregarinina: Porosporidae) with special reference to the host-parasite relations. *Journal of Parasitology* 41:89-104.
- Springer, S. and H.R. Bullis, Jr. 1956. Collections by the OREGON in the Gulf of Mexico. List of crustaceans, mollusks, and fishes identified from collections made by the exploratory fishing vessel OREGON in the Gulf of Mexico and adjacent seas 1950 through 1955. U.S. Fish and Wildlife Service, Special Scientific Report - Fisheries Number 196. 134 pp.
- Steward, V.N. 1972. Observations on the potential use of thermal effluent in mariculture. *Proceedings of the World Mariculture Society* 3:173-178.
- Stuck, K.C. 1987. Abundance and population characteristics of the stone crab, *Menippe mercenaria* (Say), and gear efficiency in Mississippi coastal waters. Mississippi-Alabama Sea Grant Consortium, Publication MASGP-87-045. 20 pp.

- Stuck, K.C. 1989. Distribution and abundance of the adult stone crab, *Menippe adina*, in Mississippi coastal and offshore waters and the potential for development of a fishery. Mississippi-Alabama Sea Grant Consortium, Final Report Project Number L/LR-20-PD. 20 pp.
- Stuck, K.C. and H.M. Perry. 1992. Life history of *Menippe adina* in Mississippi coastal waters. Pages 295-360. In: T.M. Bert (editor), Proceedings of a Symposium on Stone Crab (genus *Menippe*), Biology and Fisheries. Florida Department of Natural Resources, Marine Research Publication Number 50.
- Sulkin, S.D. 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. *Marine Ecology Progress Series* 15:181-205.
- Sulkin, S.D. and W.F. van Heukelem. 1980. Ecological and evolutionary significance of nutritional flexibility in planktotrophic larvae of the deep sea red crab, *Geryon quinquedens*, and the stone crab, *Menippe mercenaria*. *Marine Ecology Progress Series* 2(2):91-95.
- Sullivan, J.R. 1979. The stone crab, *Menippe mercenaria* (Say), in the southwest Florida fishery. Florida Department of Natural Resources, Florida Marine Research Publication 36. 37 pp.
- Sushchenya, L.M. and R. Claro. 1973. Quantitative regularities of feeding and their connection with the balance of energy of the commercial crab *Menippe mercenaria* (Say). Pages 311-335. In: Investigations of the Central American Seas. Published for the Smithsonian Institution and the National Science Foundation, Washington, DC, by the Indian National Documentation Centre, New Delhi. Translated from Russian by Fisheries Research Board of Canada, "Naukova Dumka," Kiev, USSR, 1966.
- Swartz, R.C. 1978. Reproductive and molt cycles in the xanthid crab, *Neopanope sayi* (Smith, 1889). *Crustaceana* 34(1):15-32.
- Swingle, H.A. 1977. Coastal fishery resources of Alabama. *Alabama Marine Resources Bulletin* 12:31-58.
- Swingle, H.A. 1971. Biology of Alabama estuarine areas - cooperative Gulf of Mexico estuarine inventory. *Alabama Marine Resources Bulletin* 5:123 pp.
- Teissier, G. 1960. Relative growth. Pages 537-560. In: T. Waterman (editor), *The Physiology of the Crustacea*, Volume 1. Academic Press, New York, New York.
- Texas Parks and Wildlife Department. Unpublished data. 4200 Smith School Road, Austin, Texas 78744.
- Teytaud, A.R. 1971. The laboratory studies of sex recognition in the blue crab *Callinectes sapidus* Rathbun. University of Miami, Sea Grant Technical Bulletin 15. 62 pp.
- Tweeddale, W.A., T.M. Bert, and S.D. Brown. 1993. Growth of postsettlement juveniles of the Florida stone crab, *Menippe mercenaria* (Say) (Decapoda:Xanthidae) in the laboratory. *Bulletin of Marine Science* 52(3):873-885.
- Vermeij, G.J. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge, Massachusetts. 323 pp.
- Vernberg, F.J. 1956. Study of the oxygen consumption of excised tissues of certain marine decapod Crustacea in relation to habitat. *Physiological Zoology* 29(3):227-234.
- Wass, M.L. 1955. The decapod crustaceans of Alligator Harbor and adjacent inshore areas of northwestern Florida. *Quarterly Journal of the Florida Academy of Sciences* 18(3):129-176.
- Wear, R.G. 1970. Notes and bibliography on the larvae of xanthid crabs. *Pacific Science* 24(1):84-89.

- Weiss, H.W. 1966. Barnacles of the northwestern Gulf of Mexico. *Quarterly Journal of the Florida Academy of Sciences* 29(2):81-95.
- Whitten, H.L., H.F. Rosene, and J.W. Hedgpeth. 1950. The invertebrate fauna of Texas coast jetties: a preliminary survey. *Publications of the Institute of Marine Science, University of Texas* 1(2):53-87.
- Wilber, D.H. 1992. Observations on the distribution and mating patterns of adult stone crabs (genus *Menippe*) on the northern Gulf coast of Florida. Pages 10-16. In: T.M. Bert (editor), *Proceedings of a Symposium on Stone Crab (genus Menippe), Biology and Fisheries*. Florida Department of Natural Resources, Marine Research Publication Number 50.
- Wilber, D.H. 1989a. The influence of sexual selection and predation on the mating and postcopulatory guarding behavior of stone crabs (Xanthidae, *Menippe*). *Behavioral and Ecological Sociobiology* 24:445-451.
- Wilber, D.H. 1989b. Reproductive biology and distribution of stone crabs (Xanthidae, *Menippe*) in the hybrid zone on the northeastern Gulf of Mexico. *Marine Ecology Progress Series* 52:235-244.
- Wilber, D.H. 1987. The role of mate guarding in stone crabs. Doctoral Dissertation. Florida State University, Tallahassee, Florida. 137 pp.
- Wilber, D.H. 1986. The distribution and daily movement of stone crabs (*Menippe mercenaria*) in an intertidal oyster habitat on the northwest coast of Florida. *Marine Behavior and Physiology* 12:279-291.
- Wilber, D.H. and W.F. Herrnkind. 1986. The fall emigration of stone crabs *Menippe mercenaria* (Say) from an intertidal oyster habitat and temperature's effect on locomotory activity. *Journal of Experimental Marine Biology and Ecology* 102:209-221.
- Williams, A.B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC. 550 pp.
- Williams, A.B. 1965. Marine decapod crustaceans of the Carolinas. *Fishery Bulletin* 65(1). 298 pp.
- Williams, A.B. and T.W. Duke. 1979. Crabs (Arthropoda: Crustacea: Decapoda: Brachyura). Pages 171-233. In: C.W. Hart and S.M. Fuller (editors), *Pollution Ecology of Estuarine Invertebrates*. Chapter 6. Academic Press, New York, New York.
- Williams, A.B. and D.L. Felder. 1986. Analysis of stone crabs: *Menippe mercenaria* (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae). *Proceedings of the Biological Society of Washington* 99(3):517-543.
- Yang, W.T. 1972. Notes on the successful reproduction of stone crabs, *Menippe mercenaria* (Say) reared from eggs. *Proceedings of the World Mariculture Society* 3:183-184.
- Yang, W.T. 1971. Preliminary report of the culture of the stone crab, *Menippe mercenaria*. *Proceedings of the World Mariculture Society* 2:53-54.
- Yang, W.T. and G.E. Krantz. 1976. "Intensive" culture of the stone crab, *Menippe mercenaria*. University of Miami, Sea Grant Technical Bulletin 35. 15 pp.
- Yates, C., N. Maggard, H. Perry, and C. Trigg. 1991. Mortality of juvenile stone crabs, *Menippe mercenaria* and *Menippe adina*, exposed to catastrophic dilutions in salinity. *Journal of the Mississippi Academy of Science* 36(1). 55 pp.