

# Reproductive biology and distribution of stone crabs (*Xanthidae*, *Menippe*) in the hybrid zone on the northeastern Gulf of Mexico

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**ABSTRACT:** Reproductive biology and residency patterns of over 800 stone crabs (*Menippe mercenaria*, *M. adina*, and their hybrids) were examined during an 8 mo tagging study in 1986 at artificial, concrete block reefs constructed near intertidal oyster reefs and subtidal seagrass beds in Franklin and Wakulla Counties, Florida, USA. Characteristics of adult crabs occurring intertidally in the summer included a male-biased sex ratio (5M:1F), a prevalence of *M. adina* and hybrids, a high frequency (71%) of molting males, and low sperm content ( $9 \times 10^6$ ) in males. Subtidally in the summer, the adult sex ratio was female-biased (1M:9F), the *Menippe*-complex forms occurred at equivalent frequencies, and male sperm content was higher ( $18 \times 10^6$ ). In the fall, sex ratios became more uniform in both habitats, the intertidal male molting frequency declined (7%), and intertidal male sperm levels increased ( $19 \times 10^6$ ). Spawning frequencies and egg viability did not differ between the species or hybrids and male sperm content did not differ between *Menippe*-complex forms within habitats. Although the *Menippe*-complex forms did not exhibit assortative mating in either habitat, the non-uniform distribution of stone crabs between habitats may result in non-random mating in the hybrid zone as a whole.

## INTRODUCTION

Behavioral information is important in the classification of several decapod crustaceans. In fiddler crabs *Uca* spp., visual and acoustic displays are species-specific characters in 2 sets of species, *U. speciosa* – *U. spinicarpa* (Salmon et al. 1979) and *U. panacea* – *U. pugilator* (Salmon et al. 1978). Likewise, in spider crabs (Lucas 1970) and alpheid shrimps (Knowlton & Keller 1985) behavioral observations of mating-related agonistic encounters are used in the identification of sibling species. The converse phenomenon, morphologically distinct interbreeding forms, appears less common though it has been demonstrated in an ostracod (fairy shrimps; Wiman 1979). Such cases present an interesting question for crustacean taxonomy (Hedgecock et al. 1982) because although taxonomic methods separate forms by morphology, behavioral evidence of interbreeding and hybrid viability violate the biological species concept (sensu Dobzhansky 1935, Mayr 1940). Preliminary evidence suggested stone crabs (*Brachyura*, *Xanthidae*, *Menippe*) fit this description.

The taxon *Menippe mercenaria* was recently separated into 2 species based on morphology and coloration (Williams & Felder 1986). *M. mercenaria* (Say) restricted, which occurs from North Carolina around peninsular and northern Florida and throughout the Caribbean, has a spotted dorsal carapace and distinctly banded legs. *M. adina*, a dark form with no spotting or banding, occurs along the Gulf of Mexico from Tamaulipas State, Mexico eastward to northwest Florida (Apalachee Bay). Along the northeastern coast of the Gulf of Mexico, the 2 species interbreed and produce hybrids with variable and intermediate levels of spotting and banding (Williams & Felder 1986). An electrophoretic study of isozymes also indicated that the 2 species hybridize in these areas (Bert 1986). Bert suggested that a classification of semispecies for the stone crab taxa is appropriate based upon the morphological and biochemical evidence for their interbreeding. The extent of behavioral and ecological divergence in stone crabs has not been examined previously, although there are limited data suggesting habitat segregation by species occurs within the hybrid zone (Williams & Felder 1986). More extensive field observations of

stone crab distributions and mating patterns are needed to understand the ecological relationship between the species.

Assortative mating between hybridizing species limits gene flow, and may lead to reproductive isolation. In addition, gene flow may be restricted if mating is random with respect to species, but the species occupy different microhabitats. *Menippe adina* occurs both subtidally and intertidally throughout its range (Menzel & Nichy 1958, Powell & Gunter 1968, Perry et al. 1983, Wilber 1986). *Menippe mercenaria* occurs subtidally throughout its range (Bert et al. 1978, Sullivan 1979), but occurs intertidally (at low frequencies) only within the hybrid zone (Wilber 1988). Although the ranges of *M. mercenaria* and *M. adina* overlap, the extent to which the species occur sympatrically within habitats is not well documented. Gene flow between populations may be further restricted if the populations exhibit different life history traits (for example, the seasonal timing of molting or egg production). Hence, distribution and demographic data on the stone crab in the hybrid zone may contribute to our understanding of the species' relatedness. This study examines the distribution, growth, mating patterns, and reproductive characteristics of stone crabs in the hybrid zone (northwestern Florida, USA). I specifically address the question whether the *Menippe*-complex forms (which includes the 2 species and their hybrids) exhibit (1) habitat segregation, (2) different growth or reproductive traits, or (3) assortative mating.

## MATERIALS AND METHODS

Stone crabs were sampled from 2 subtidal seagrass and 3 intertidal oyster reef locations in Franklin and Wakulla Counties, Florida. Artificial reefs designed to attract stone crabs were constructed at both subtidal and one intertidal locations. Each reef was composed of 25 concrete blocks (with two 12 × 13 cm holes) placed in 2 parallel rows ca 0.5 m apart, with the holes facing upward. Eight subtidal reefs were placed 150 m apart in 2 to 3 m of water near Lanark Shoal. Four subtidal reefs were placed similarly adjacent to Turkey Point Shoal in 2 m of water. Both subtidal sites were ca 2 km from shore. The mussel *Modiolus squamosa*, a common prey item of stone crabs, was plentiful at both Lanark and Turkey Point Shoal. The subtidal concrete blocks were colonized by a variety of sessile invertebrates including tunicates, bivalves, bryozoans, barnacles, and gorgonians. Gastropods, blennies, and spade fish were also common near the blocks. The intertidal blocks were colonized by barnacles and blue crabs. Stone crabs were sampled from 3 intertidal oyster habitat sites. Six reefs were constructed adjacent to

oyster reefs at Wakulla beach at -0.1 m MLW (Mean Low Water), where many natural burrows were observed. Stone crabs were also sampled from natural burrows at St. Marks and 60 oyster-encrusted intertidal shelters that have been adjacent to the Florida State University Marine Laboratory for more than 15 yr (Wilber 1986, Wilber & Herrnkind 1986).

Crabs at the subtidal reefs were sampled weekly from April through November, 1986. Crabs did not occupy the subtidal (unpubl.) or intertidal (Wilber & Herrnkind 1986) reefs in the winter. Intertidal samples were restricted to periods when the reefs and natural burrows were exposed (i.e. the spring low tide of each lunar cycle). Because the focus of this study and related work concerned stone crab reproductive behavior, sampling was restricted to adult crabs (> 55 mm CW; Wilber 1988). The taxonomic identity of the crabs was assigned according to the criteria described by Williams & Felder (1986). Crabs sampled at the Lanark location were tagged with a numbered piece of plastic tape glued to their dorsal carapace, and released at the surface over the reef where they were captured.

**Distribution.** Species distribution among sites within habitats were analysed with *G*-tests. Because species frequencies did not differ significantly between sites within habitats, sites were combined for an overall between-habitat comparison. This comparison was made with a 4-factor *G*-test using species, sex, season, and habitat as factors. The levels for season were spring (April and May), summer (June, July, and August), and fall (September and October).

**Molting and reproductive states. Males:** Adult males were collected from intertidal and subtidal locations in the summer and fall of 1985 for analyses of their molt and reproductive states. The molt cycle stage of each male was determined by examining setagenesis in the scaphognathites (Aiken 1973).

Decapod sperm are non-flagellated (Brown 1966) and have radial arms that are used to attach the sperm to the egg's surface (Binford 1913, Hinsch 1971). A preliminary study revealed that the anterior portion of the testes contained immature sperm only, i.e. the radial arms were not developed. Therefore, only the white, anterior portions of the vas deferens, which contained mature sperm packaged in spermatophores (Hinsch & Walker 1974), were dissected from males. This tissue was homogenized and then centrifuged for 5 min at 5000 rpm in a graduated centrifuge tube. The sperm volume was then measured, after which sperm were resuspended in seawater and diluted by a factor of 100. Two samples of the diluted mixture were pipetted into a hemacytometer and the number of sperm was counted in 5 hemacytometer fields for each sample. The number of sperm per male was calculated as the mean number of sperm counted in the 10 hemacy-

tometer fields  $\times 10^4$  (hemacytometer factor)  $\times 10^2$  (dilution factor)  $\times$  sperm volume (technique adapted from Paul 1984). The precision of this technique was estimated by comparing the amount of sperm in the right and left vas deferens of 8 individuals. This comparison was based on the assumption that the reproductive tissues develop symmetrically, as is suggested by visual inspection. The sperm contents of subtidal and intertidal males were compared with a 3-factor ANCOVA using habitat, species, and season as factors and male size as the covariate. All sperm data were log-transformed. Male size was analysed by a 3-factor ANOVA with habitat, species, and season as factors.

**Females:** The number of gravid females of each *Menippe*-complex form was compared by season with a 3-factor *G*-test. The color of the eggs carried by females was recorded as either orange (newly deposited), orange-brown (intermediate development) or brown (well developed). Color designations of egg development were based on observations of gravid females held in the laboratory that hatched viable clutches. The relative viability of eggs carried by females of the *Menippe*-complex forms was determined by comparing the number of females carrying brown eggs over time by a 3-factor *G*-test.

**Adult movements.** The residency pattern of stone crabs at the subtidal reefs was examined in 2 ways. First, the number of resighted crabs present on a given day was divided by the number of crabs tagged the previous sampling period, providing information on movement both to and from the reefs. This method provides a conservative estimate of crab fidelity to the reef, because tagged crabs may be missing due to mortality, as well as movement. The second estimate was the percentage of resighted crabs that had moved to another reef since they were last sighted. Crab residency patterns were analysed with a 4-factor *G*-test using the number of originally tagged and resighted crabs, sex, season, and *Menippe*-complex form as factors.

**Mating pattern.** Stone crabs mate exclusively during the female's soft post-molt phase (Binford 1913, Savage 1971) and engage in both pre- and postcopulatory mate guarding (Hartnoll 1969, Wilber 1987). All crabs found in copula, or pre- or postcopulatory mate guarding, were recorded as mating pairs. Mate guarding was defined as a male standing over a pre- or post-molt female. The inclusion of guarding pairs as mating pairs is justified by experiments that showed males copulate with the females they guard and do not guard females they do not mate (Wilber 1987).

The observed frequencies of all possible *Menippe*-form pair combinations were compared to expected frequencies based upon random pair formations. Expected frequencies were weighted by the number of

mating pairs observed in a season and the frequency of each *Menippe*-complex form for each sex within a season. Expected frequencies were too small in 5 subtidal cells and all intertidal cells to calculate an overall Chi square test for non-random mating. Therefore, data were combined to test for overall differences between like (e.g. *M. adina*  $\times$  *M. adina*) and unlike (e.g. *M. adina*  $\times$  hybrid) pairings.

## RESULTS

### Seasonal distribution

A total of 723 crabs were tagged at the 2 subtidal reefs. Adult sex ratios differed markedly with season. In the summer, the intertidal reefs were occupied primarily by males (5M:1F) whereas by fall, the adult sex ratio was more uniform (1.3M:1F;  $\chi^2 = 10.8$ ,  $p < 0.01$ ). At subtidal reefs, adult females were predominant in the summer (1M:9F; Wilber in press); the sex ratio became less female-biased in the fall (1M:3F in October;  $G = 12.92$ ,  $p < 0.005$ ).

The distribution of the *Menippe*-complex forms within the subtidal habitat did not differ between the Lanark and Turkey Point sites ( $\chi^2 = 0.96$ ,  $p > 0.5$ ). The forms were represented equally by *M. mercenaria* (31%), *M. adina* (35%), and their hybrids (34%). The distribution of the *Menippe*-complex forms among the 3 intertidal sites was more heterogeneous ( $\chi^2 = 8.46$ ,  $p > 0.05$ ,  $n = 265$ ). Hybrids (55%) and *M. adina* (31%) comprised the majority of the intertidal population.

The 4-way *G*-test using species, sex, season and habitat as factors showed a significant 3-way interaction between species, sex and habitat (Table 1). This interaction was due to a proportionally higher frequency of *Menippe mercenaria* males in the subtidal habitat (Fig. 1). In addition, subtidally there was a significant interaction between species, sex, and season ( $G = 13.56$ ,  $p < 0.01$ , Table 2), reflecting an increase in *M. mercenaria* males in the fall (Fig. 2).

### Molting and reproductive states

#### Males

In summer 1986, 71% ( $n = 24$ ) of the intertidal males were either pre- or post-molts, compared to only 5% ( $n = 18$ ) of the subtidal males. In fall, few intertidal (7%,  $n = 14$ ) and no subtidal ( $n = 13$ ) males were molting. Male size did not differ among the *Menippe*-complex forms. However, there was a significant habitat by season interaction, ( $F = 4.85$ ,  $p = 0.029$ ; Table 3) reflecting a size difference between intertidal ( $81 \pm$

Table 1 *Menippe* spp. Four-factor G-test using species, sex, time, and habitat as factors. The levels of time were spring (April and May), summer (June, July and August), and fall (September and October)

Source	Df	G	P
Species × Sex	2	17.74	<0.001
Species × Time	4	8.32	0.080
Species × Habitat	2	50.84	<0.001
Sex × Time	2	5.39	0.675
Sex × Habitat	1	177.36	<0.001
Time × Habitat	2	173.08	<0.001
Species × Sex × Time	4	7.44	0.114
Species × Sex × Habitat	2	9.24	0.009
Species × Time × Habitat	4	7.38	0.117
Sex × Time × Habitat	2	2.54	0.282
Species × Sex × Time × Habitat	4	4.81	0.308

Table 2. *Menippe* spp. Four-factor G-test using the number of subtidal crabs tagged and resighted, time, sex, and form as factors

Source	Df	G	P
Resight × Time	2	68.96	<0.001
Resight × Sex	1	25.81	<0.001
Resight × Form	2	1.53	0.464
Time × Sex	2	12.92	0.002
Time × Form	4	5.93	0.205
Sex × Form	2	52.68	<0.001
Resight × Time × Sex	2	4.55	0.103
Resight × Time × Form	4	3.00	0.558
Resight × Sex × Form	2	4.91	0.086
Time × Sex × Form	4	13.56	0.009
Resight × Time × Sex × Form	4	0.92	0.921

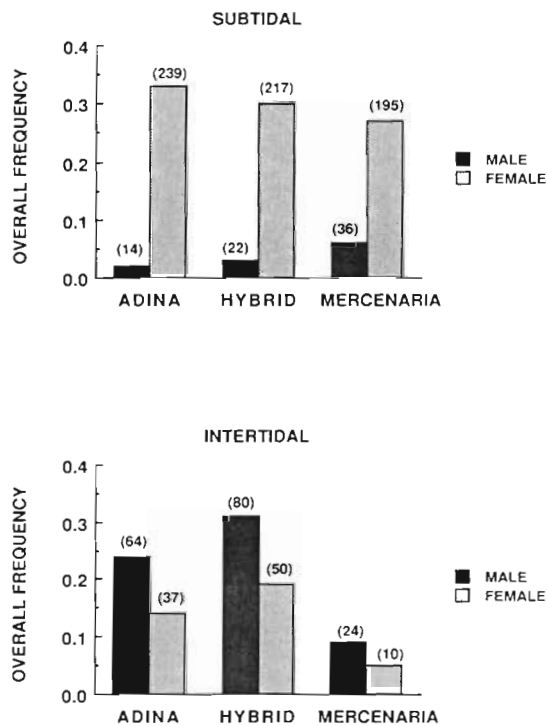


Fig. 1 *Menippe* spp. Overall frequency histograms of the *Menippe*-complex forms within the subtidal and intertidal habitat by sex. Values in parantheses: number of crabs

13 mm) and subtidal ( $92 \pm 12$  mm) males in summer and no size difference in fall (Fig. 3). Intertidal male size increased marginally between summer and fall ( $90 \pm 14$  mm,  $F = 3.77$ ,  $p < 0.10$ ).

The difference in sperm number between the left and right vas deferens of 8 males divided by their mean sperm number was  $12.8 \pm 7.9$  %. This variation may reflect both measurement error and natural differences in sperm content between the 2 sides. The 3-factor

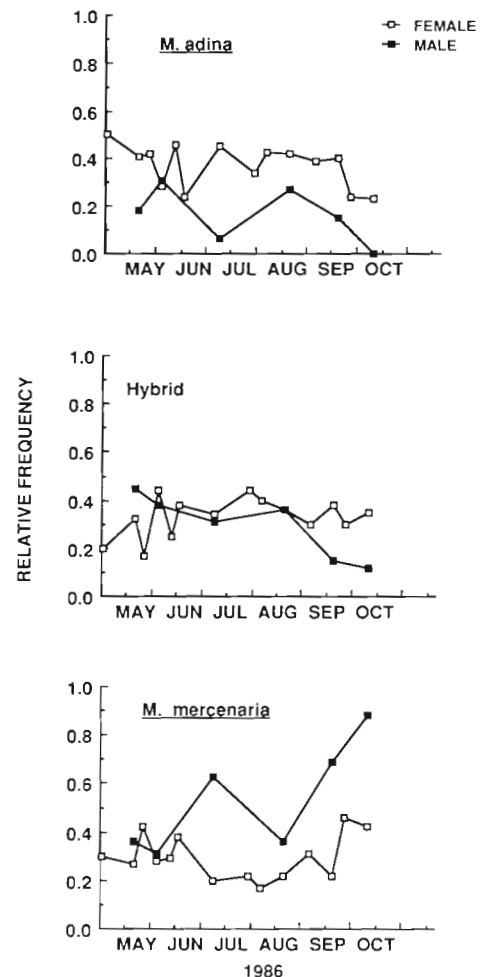


Fig. 2. *Menippe* spp. Relative frequencies of *Menippe*-complex form plotted over time by sex (■: males; □: females) in the subtidal habitat. Data for males were combined from several sampling days to obtain sample sizes of at least 20 individuals



Table 3. *Menippe* spp. Three-factor analysis of variance on male size using habitat, time and species as factors. The levels of habitat were intertidal and subtidal; the levels of time were summer (June, July, and August) and fall (September and October)

Source	Sum of squares	Df	Mean square	F	P
Habitat	1106.4	1	1106.4	7.96	0.005
Time	102.4	1	102.4	0.74	0.392
Species	617.1	2	308.6	2.22	0.112
Habitat × Time	673.6	1	673.6	4.85	0.029
Habitat × Species	165.9	2	82.9	0.60	0.552
Time × Species	83.0	2	41.5	0.30	0.742
Habitat × Time × Species	83.9	2	41.9	0.30	0.740

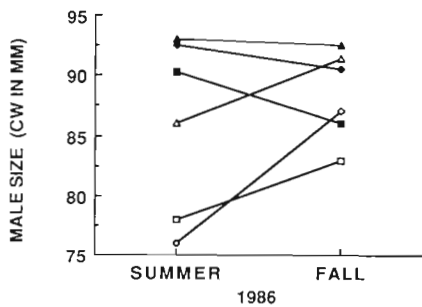


Fig. 3. *Menippe* spp. Mean male size of each *Menippe*-complex form for summer and fall in the subtidal (closed symbols) and intertidal (open symbols) habitats. Squares: *M. adina*; triangles: hybrids; diamonds: *M. mercenaria*

analysis of covariance showed a significant interaction between habitat and time ( $F = 4.64, p = 0.035$ ; Table 4), reflecting a difference in sperm content between intertidal ( $9.01 \times 10^6$ ) and subtidal ( $19.6 \times 10^6$ ) males in summer and no difference in fall 1985 (Fig. 4). Fall intertidal male sperm content ( $18.8 \times 10^6$ ) was higher than the summer level ( $F = 13.4, p < 0.001$ ). Sperm content did not differ among the *Menippe*-complex forms. In addition, the sperm content of summer intertidal pre- and post-molt males did not differ from that of intermolt males ( $F = 0.64, p > 0.5$ ).

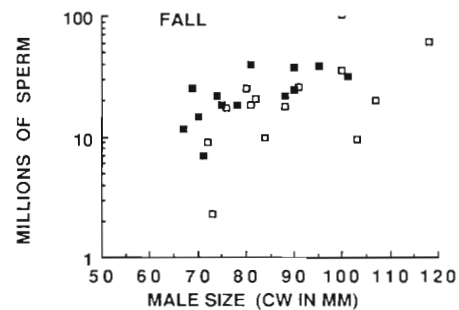
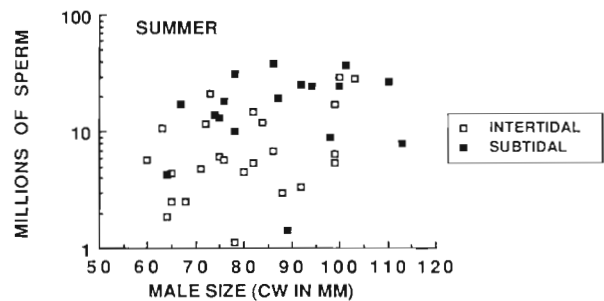


Fig. 4. *Menippe* spp. Number of sperm stored in the anterior vas deferens of subtidal (■) and intertidal (□) males plotted on a log scale for males (all forms) collected in summer and fall

Table 4. *Menippe* spp. Three-factor analysis of covariance on male sperm number (after data were log-transformed) using habitat, species, and time as factors and male carapace width (CW) as the covariate

Source	Sum of squares	Df	Mean square	F	P
Habitat	1.46	1	1.46	15.57	<0.001
Species	0.05	2	0.02	0.27	0.762
Time	0.53	1	0.53	5.63	0.021
Habitat × Species	0.04	2	0.02	0.23	0.800
Habitat × Time	0.44	1	0.44	4.64	0.035
Species × Time	0.18	2	0.09	0.96	0.389
Habitat × Species × Time	0.02	2	0.01	0.14	0.873
CW	1.20	1	1.20	12.79	0.001

### Females

Gravid females were present when sampling started in April at the subtidal reefs. Approximately 80 % of the females were gravid throughout the spring and summer, compared to less than 35 % in late September (Fig. 5). Seasonal counts of gravid females of the

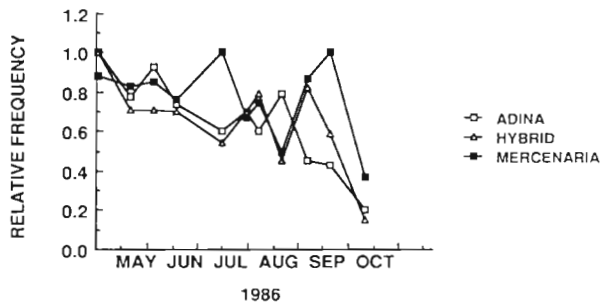


Fig. 5. *Menippe* spp. Proportion of *M. adina* ( $\square$   $n = 235$ ), hybrid ( $\triangle$   $n = 221$ ), and *M. mercenaria* ( $\blacksquare$   $n = 177$ ) females that were gravid over time. Sample sizes include multiple resightings of tagged crabs

*Menippe*-complex forms decreased while fluctuating asynchronously over time (Fig. 5), resulting in a significant species  $\times$  egg-no egg  $\times$  time interaction ( $G = 21.56$ ,  $p < 0.0001$ ). Seasonally, counts of females with brown eggs (compared to all females without brown eggs) did not differ between the *Menippe*-forms ( $G = 1.27$ ,  $p > 0.80$ ; Fig. 6). The observed maximum number of clutches carried by a single female was 5, based on 6 resightings over a 93 d interval.

### Movement

The proportion of individuals at the Lanark reefs that were resighted the next sampling day increased gradually from spring (18 %) through summer (33 %) and into the fall (52 %,  $F = 6.63$ ,  $p < 0.025$ ). About 25 % of the crabs that were resighted had moved to other reefs, regardless of season. The sex ratio of resighted crabs at the subtidal sites (1M:25F) was more female-biased than the sex ratio among originally tagged crabs ( $G = 25.81$ ,  $p < 0.0001$ ; Table 3). The resight frequency did not differ among the *Menippe*-complex forms ( $G = 1.53$ ,  $p > 0.4$ ).

### Mating pattern

Mating pairs were most common in fall in both habitats with 71 % of fall intertidal pairs and 65 % of all subtidal pairs occurring in fall. A secondary peak in mating pair frequency (27 %) occurred in spring in the subtidal habitat. The sizes of neither subtidal males

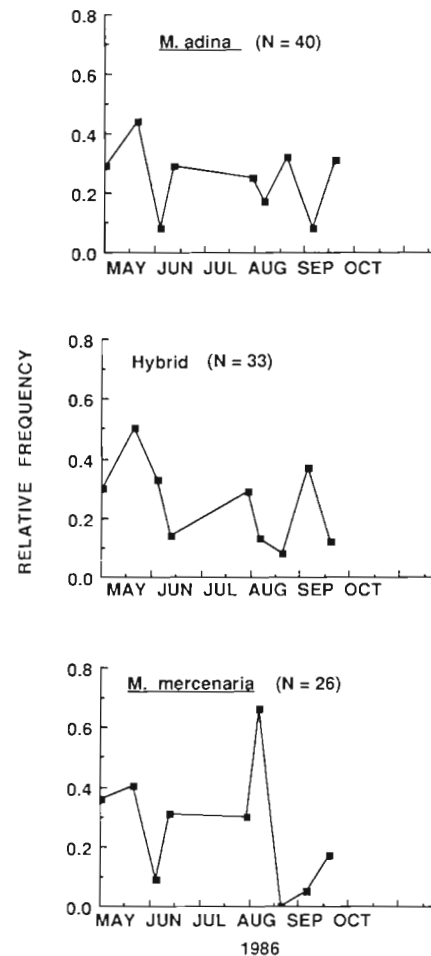


Fig. 6. *Menippe* spp. Frequency of ovigerous *M. adina*, hybrid, and *M. mercenaria* females with brown eggs plotted over time

( $F = 0.18$ ,  $p > 0.75$ ) nor subtidal females ( $F = 0.80$ ,  $p > 0.50$ ) in mating pairs differed between the spring and fall. Subtidal males within mating pairs ( $98 \pm 14$  mm CW) were significantly larger than the average adult subtidal male ( $88 \pm 13$  mm CW,  $F = 13.9$ ,  $p < 0.01$ ). Subtidal crabs paired assortatively by size ( $r = 0.54$ ,  $p < 0.0005$ ) and males tended to be larger than their mates (Fig. 7). Two tagged males that were

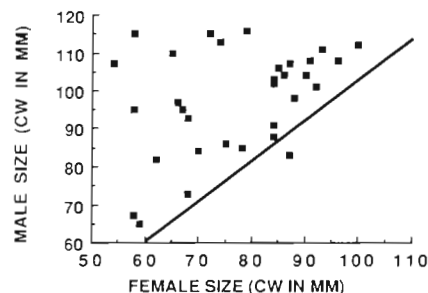


Fig. 7. *Menippe* spp. Carapace widths of crabs in mating pairs. Solid line depicts equal male and female CWs. Male and female size were positively correlated ( $r = 0.54$ ,  $p < 0.0005$ )

sighted in multiple mating pairs had moved between reefs between matings.

There was no evidence of assortative mating among crabs in the *Menippe*-complex paired at the subtidal reefs (Table 5;  $\chi^2 = 0.06$ ,  $p > 0.70$ ; overall test on like vs

Table 5. *Menippe* spp. Frequency of mating pairs of every possible form combination (observed/expected) occurring in either intertidal or subtidal habitats in 1985 and 1986. Expected frequencies were calculated by multiplying the frequencies of the *Menippe*-complex forms for each sex together for each season and year. This product was multiplied by the number of mating pairs observed for the corresponding season and year to yield an expected frequency. The total expected value is the sum of each season's and year's expected frequencies

Intertidal			
	<i>M. adina</i>	Males Hybrid	<i>M. mercenaria</i>
Females			
<i>M. adina</i>	3/1.3	0/2.2	0/0.2
Hybrid	1/1.5	2/2.6	1/2.6
<i>M. mercenaria</i>	1/0.7	2/1.1	0/0.1
Subtidal			
	<i>M. adina</i>	Males Hybrid	<i>M. mercenaria</i>
Females			
<i>M. adina</i>	6/3.6	7/5.7	17/10.7
Hybrid	4/2.3	5/3.8	3/8.8
<i>M. mercenaria</i>	0/2.3	3/3.8	4/8.6

unlike pairings). Likewise, there was no evidence of assortative mating at the intertidal sites, but the sample was too small to test statistically (Table 5).

## DISCUSSION

Geographic speciation is postulated to occur in 2 phases (Ayala 1975): (1) genetic differences accumulate in isolated populations; and (2) secondary contact is established between the genetically distinguishable and, perhaps, incompatible forms. Once sympatry is regained and if there is selection against hybrids, pre-mating barriers (either ethological or functional) may evolve (Templeton 1981), resulting in reproductive isolation. In the absence of selection against hybrids, or if hybrids are selectively favored, secondary contact may result in fusion of the forms. Bert (1986) suggests that the formation (2.9 to 3.2 MYBP [million years before present]) and closure (1.75 MYBP) of the Suwannee Straits represents periods of divergence and secondary contact, respectively, of stone crab populations. If sym-

patry for the 2 present species was reestablished over a million years ago, the current mating patterns may reflect the extent of divergence and the effect of secondary contact. For example, assortative mating may be indicative of reduced hybrid fitness and incipient speciation.

Mating among stone crabs in the hybrid zone, however, was clearly non-assortative in both the intertidal and subtidal habitats and included every possible pairwise combination. *Menippe mercenaria* male  $\times$  *M. adina* female pairs were the most frequent combination ( $n = 17$ ) at the subtidal reefs, exceeding their expected frequency (10.7). The absence of assortative mating between species is consistent with a hypothesis of weak or no selection against hybrids. Data required to estimate overall hybrid fitness were not gathered, although a single indicator, the frequency of eggs that reached maturity, did not differ between gravid females of different *Menippe*-complex forms. A deficiency of particular phenotype-genotype combinations found in a previous study (Bert & Harrison 1988) may have resulted because crabs were only sampled subtidally and does not necessarily suggest reduced hybrid fitness. If a population is subdivided, a significant deficiency of heterozygotes in those loci with different allele frequencies in the subpopulations may result if only one subpopulation is sampled (i.e. the Wahlund effect; Hedgecock et al. 1982).

Although stone crab mating is random with respect to *Menippe*-complex form within habitats, the non-uniform distribution of stone crabs between habitats may result in non-random mating in the hybrid zone as a whole. There is significant habitat segregation between subtidal seagrass beds and intertidal oyster reefs by sex and form. The strongly biased sex ratios probably result from the habitat requirements of ovigerous females (i.e. high, stable temperatures and salinities that are conducive to larval survival; Ong & Costlow 1970). Neither of these conditions are indicative of intertidal habitats and gravid females rarely occur in these areas (Powell & Gunter 1968, Wilber 1988).

Explanations for the prevalence intertidally of *Menippe adina* and hybrids relative to *M. mercenaria* are less obvious. Differential physiological tolerances of intertidal environmental factors (e.g. extreme temperature and salinity fluctuations, or periodic and prolonged aerial exposure) may account for this distribution. The allopatric habitat distributions of both *M. mercenaria* (subtidal) and *M. adina* (subtidal and intertidal) are the same as that in sympatry. Therefore, hypotheses concerning competitive displacement are unwarranted. Both species appear well suited to their habitats. The dark unmottled color pattern of *M. adina* is more cryptic on the muddy substrate around oyster reefs than the disruptive coloration, i.e. spotting and

banding, of *M. mercenaria*, which may be more cryptic in the visually complex seagrass and coral reef communities.

Male growth and reproductive traits also differed between the intertidal and subtidal habitats, but this difference is confounded with the distribution of *Menippe*-complex forms. The summer residency patterns of stone crabs within intertidal oyster habitats (Wilber 1986) indicate that movement by males from the habitat is limited. In the summer, most intertidal males were molting and had relatively low levels of stored sperm, whereas subtidal males were intermolts with higher sperm levels. Because intertidal male molt state and sperm number did not differ between *Menippe*-complex forms within a habitat, these traits appear associated with the habitat occupied rather than the male's form. Seasonal cycles of sperm production occur in a number of decapods, e.g. the Chinese mitten crab *Eriocheir sinensis* (Hoestlandt 1948), *Cyclograpsus punctatus* (Broekhuysen 1941) and the lobster *Jasus lalandii* (Heydorn 1969). Seasonal differences in sperm production in stone crabs, however, occurred only for intertidal males. Although there was no direct association between an individual male's molt state and sperm content, the inverse change in these factors for intertidal males between summer and fall suggests they may be antagonistic processes. Sperm production and molt cycle stage are also not correlated for individual *Portunus sanguinolentus* males (Ryan 1967). Egg production decreased in the late summer and fall for females of all the forms of the *Menippe*-complex, although *M. mercenaria* females were ovigerous later (i.e. in August and September) than hybrid and *M. adina* females. This pattern is consistent with the spawning pattern of allopatric *M. mercenaria* populations in southwest Florida, which exhibit peak egg production in August (Bert 1985) and September (Sullivan 1979). The timing of female molting and mating was the same as that exhibited by *Menippe mercenaria* females in southwest Florida (Bert 1985) with a small peak in the spring and a larger peak in the fall. The sizes of females molting in the spring and fall did not differ, whereas in southwest Florida, the females molting in the spring were smaller than those in the fall.

The resight frequency of subtidal crabs increased gradually through the summer and into the fall indicating that movement decreased in the fall. Movement estimates did not differ between the forms. However, males were less likely to be resighted than females, suggesting that they are more mobile subtidally. In contrast, male and female movement patterns did not differ within intertidal oyster habitats (Marine Lab site; Wilber 1986). Movement data strongly suggest that adult male stone crabs do not defend territories and attract receptive females as do fiddler crabs (Crane

1975) and American lobsters (Atema 1986). The occurrence of males sighted in multiple mating pairs at different reefs is consistent with a transient mate-searching strategy as is exhibited by blue crabs (Ryan 1966, Teytaud 1971).

#### Proposed alternative male mating tactics

Alternative male reproductive tactics are recognized in a variety of taxa including anurans (Emlen 1976, Howard 1980), insects (Thornhill 1981, Waage 1984, Spence & Wilcox 1986), and fishes (Farr 1980, Constantz 1984). However, they are not common within the Crustacea (Salmon 1984). The distribution, growth, and reproductive characteristics of male stone crabs in the hybrid zone are consistent with a mating system that has alternative male tactics. Because large males are more successful at acquiring mates (Wilber 1986, 1987), rapid growth is favored. The mating success of molting males, however, is lowered temporarily while they are in the soft, post-molt state. Males that molt in the summer, when most females are unreceptive, occur in a habitat where female abundance is low and therefore the opportunity for encountering a receptive female is even lower. These males inhabit a relatively food-rich, predator-free environment and become larger males with a higher expected mating success in the fall. Non-molting males occur in subtidal habitats in the summer, where the probability of encountering receptive females is greater. Concomitantly, male density (and therefore inter-male competition) is lower and short-term mating success can be enhanced. Subtidal males appear to be one molt ahead of their intertidal counterparts, a size advantage that is lost in the fall after the intertidal males have molted. Spiny lobsters exhibit a similar pattern of size-dependent growth and reproduction (Lipcius 1986); large adults engage in courtship activities in the winter and spring, whereas small adults molt instead. A causal relationship between male stone crab growth and habitat use is not evident from this study, but is an interesting subject for future experimentation.

Evidence presented in this study suggests that *Menippe mercenaria*, *M. adina*, and hybrids share similar behavioral and ecological features: (1) the forms mate randomly within habitats, (2) life history characteristics that may contribute to reproductive isolation (growth and reproduction) do not differ between the forms, (3) hybrid inviability or sterility is not evident, and (4) the only major difference between the species, i.e. habitat preference, is consistent with their allopatric distributions. It is clear that stone crabs exist as 2 discrete morphological forms with a variety of intermediates (Williams & Felder 1986). Experiments that



examine hybrid fitness, differential physiological tolerances, and crosses between crabs from allopatric populations are needed to define more clearly the extent of divergence in this taxonomic group.

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#### LITERATURE CITED

- Aiken, D. E. (1973). Proecdysis, setal development, and molt prediction in the American lobster (*Homarus americanus*). J. Fish. Res. Bd Can. 30: 1337-1344
- Atema, J. (1986). Review of sexual selection and chemical communication in the lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2283-2290
- Ayala, F. J. (1975). Genetic differentiation during the speciation process. Evol. Biol. 8: 1-78
- 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. Dissertation, Yale University, New Haven, CT
- Bert, T. M. (1986). Speciation in western Atlantic stone crab (genus *Menippe*): the role of geological processes and climatic events in the formation and distribution of species. Mar. Biol. 93: 157-170
- Bert, T. M., Harrison, T. M. (1988). Hybridization in western Atlantic stone crabs (Genus *Menippe*): evolutionary history and ecological context influence species interactions. Evolution 42: 528-544
- Bert, T. M., Warner, R. E., Kessler, L. D. (1978). The biology and Florida fishery of the stone crab, *Menippe mercenaria* (Say), with emphasis on southwest Florida. Florida Sea Grant Tech. Rept. 9: 1-82
- Binford, R. (1913). The germ-cells and the process of fertilization in the crab, *Menippe mercenaria*. J. Morph. 24: 147-210
- Broekhuysen, G. J. (1941). The life history of *Cyclograpsus punctatus*. H. Edw.: breeding and growth. Trans. R. Soc. S. Afr. 28: 331-368
- Brown, G. G. (1966). Ultrastructure studies of sperm morphology and sperm-egg interaction in the decapod *Callinectes sapidus*. J. Ultrastruct. Res. 14: 425-440
- Constantz, G. D. (1984). Sperm competition in Poeciliid fishes. In: Sperm competition and the evolution of animal mating systems. Academic Press, Orlando, p. 465-485
- Crane, J. (1975). Fiddler crabs of the world. Princeton Univ. Press, Princeton, N J
- Dobzhansky, T. (1935). A critique of the species concept in biology. Philos. Sci. 2: 344-355
- Emlen, S. T. (1976). Lek organization and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. 1: 283-313
- Farr, J. A. (1980). Social behavior patterns as determinants of reproductive success in the guppy, *Poecilia reticulata* (Pisces: Poeciliidae) - an experimental study of the effects of intermale competition, female choice, and sexual selection. Behaviour 74: 38-91
- Hartnoll, R. G. (1969). Mating in the Brachyura. Crustaceana 16: 161-181
- Hedgecock, D., Tracey, M. L., Nelson, K. (1982). Genetics. In: Abele, L. G. (ed.) The biology of Crustacea, Vol. 2, Embryology, morphology and genetics. Academic Press, New York, p. 283-403
- Heydorn, A. E. F. (1969). The rock lobster of the south African west coast *Jasus lalandii* (H. Milne-Edwards). 2. Population studies, behaviour, reproduction, molting, growth and migration. Investl Rep. Div. Sea Fish. S. Afr 71: 1-51
- Hinsch, G. W. (1971). Penetration of the oocyte envelope by spermatozoa in the spider crab. J. Ultrastruct. Res. 35: 85-97
- Hinsch, G. W., Walker, M. H. (1974). The vas deferens of the spider crab, *Libinia emarginata*. J. Morph. 143: 1-19
- Hoestlandt, H. (1948). Recherches sur le biologie de l'Eriocheir sinensis en France (Crustace, Brachyoure. Anns Inst. oceanogr., Monaco 24: 1-116
- Howard, R. D. (1980). Mating behaviour and mating success in wood frogs. *Rana sylvatica*. Anim. Behav. 28: 705-716
- Knowlton, N., Keller, B. D. (1985). Two more sibling species of alpheid shrimps associated with the Caribbean sea anemones *Bartholomea annulata* and *Heteractis lucida*. Bull. mar. Sci. 37: 893-904
- Lipcius, R. N. (1986). Size dependent reproduction and molting in spiny lobsters and other long-lived decapods. In: A. Wenner (ed.) Crustacean issues, Vol. I, Crustacean growth. Balkema Press, Rotterdam, p. 129-148
- Lucas, J. S. (1970). Breeding experiments to distinguish two sibling species of *Halicarcinus* (Crustacea, Brachyura). J. Zool. 160: 267-278
- Mayr, E. (1940). Speciation phenomena in birds. Am Nat. 74: 249-278
- Menzel, R. W., Nichy, F. E. (1958). Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, FL. Bull. mar. Sci. 8: 125-145
- Ong, K. S., Costlow, J. D. (1970). The effect of salinity and temperature on the larval development of the stone crab, *Menippe mercenaria* (Say), reared in the laboratory. Chesapeake Sci. 11: 16-29
- Paul, A. J. (1984). Mating frequency and viability of stored sperm in the tanner crab *Chionoecetes bairdi* (Decapoda, Majidae). J. crust. Biol. 4: 375-381
- Perry, H. M., Stuck, K. C., Reissig, D. S. (1983). *Menippe mercenaria*. The potential for development of a fishery. Annual Report to Mississippi Sea Grant. Ocean Springs, MS: Gulf Coast Research Lab.
- Powell, Jr., E. H., Gunter, G. (1968). Observations on the stone crab *Menippe mercenaria* Say, in the vicinity of Port Aransas, Texas. Gulf Res. Repts. 2: 285-299
- Ryan, E. P. (1966). Pheromone: evidence in a decapod crustacean. Science 151: 340-341
- Ryan, E. P. F. (1967). Structure and function of the reproductive system of the crab *Portunus sanguinolentus* (Herbst) (Brachyura: Portunidae). I, The male system. Proc. Symp. on Crustacea, Mar. Biol. Ass. India Ser. 2: 506-521
- Salmon, M. (1984). Courtship, mating systems, and sexual selection in decapods. In: Rebach, S., Dunham, D. (eds.) Studies in adaptation on Crustacea. John Wiley and Sons, New York, p. 143-169
- Salmon, M., Ferris, D., Johnston, D., Hyatt, G., Whitt, G.S. (1979). Behavioral and biochemical evidence for species distinctiveness in the fiddler crabs, *Uca speciosa* and *U. spinicarpa*. Evolution 33: 182-191
- Salmon, M., Hyatt, G., McCarthy, K., Costlow, J. D. (1978). Display specificity and reproductive isolation in fiddler crabs, *Uca panacea* and *U. pugilator*. Z. Tierpsychol. 48: 251-276
- Savage, T. (1971). Mating of the stone crab, *Menippe mer-*

- cenaria* (Say) (Decapoda, Brachyura). *Crustaceana* 20: 315–316
- Spence, J. R., Wilcox, R. S. (1986). The mating system of two hybridizing species of water striders (Gerridae) 2. Alternative tactics of males and females. *Behav. Ecol. Sociobiol.* 19: 87–95
- Sullivan, J. R. (1979). The stone crab, *Menippe mercenaria*, in the southwest Florida fishery. *Fla. Mar. Res. Pub. # 36*, Fl. Dept. of Nat. Res., St. Petersburg, p. 1–37
- Templeton, A. R. (1981). Mechanisms of speciation – a population, genetic approach. *Ann. Rev. Ecol. Syst.* 12: 23–48
- Teytaud, A. R. (1971). The laboratory studies of sex recognition in the blue crab *Callinectes sapidus* (Rathbun). *Univ. Miami Sea Grant Program, Sea Grant Techn. Bull.* 15: 1–63
- Thornhill, R. (1981). *Panorpa* (Mecoptera: Panorpidae) Scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive efforts. *Ann. Rev. Ecol. Syst.* 12: 355–386
- Waage, J. K. (1984). Sperm competition and the evolution of odonate mating systems. In: Smith, R. L. (ed.) *Sperm competition and the evolution of animal mating systems*. Academic Press, Orlando, p. 251–290
- 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. *Mar. Behav. Physiol.* 12: 279–291
- Wilber, D. H. (1987). The role of mate guarding in stone crabs. Dissertation, Florida State University, Tallahassee
- Wilber, D. H. (1988). Observations on the mating patterns and distribution of adult stone crabs (genus *Menippe*) on the northern Gulf of Mexico. In: Bert, T. M. (ed.) *Proceedings of a symposium on stone crab (genus Menippe) biology and fisheries*. Florida Dept of Natural Resources, Bureau of Marine Research, St. Petersburg, p. 75–81
- Wilber, D. H., Herrnkind, W. F. (1986). The fall emigration of stone crabs *Menippe mercenaria* (Say) from an intertidal oyster habitat and temperature's effect on locomotory activity. *J. exp. mar. Biol. Ecol.* 102: 209–221
- Williams, A. B., Felder, D. (1986). Analysis of stone crabs: *Menippe mercenaria* (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae). *Proc. Biol. Soc. Wash.* 99: 517–543
- Wiman, F. H. (1979). Mating patterns and speciation in the fairy shrimps genus *Streptocephalus*. *Evolution* 33: 172–181

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