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# Burrow Distributions and Population Estimates for the Fiddler Crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico Salt Marsh<sup>1</sup>

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**ABSTRACT:** The distribution of fiddler crab (*Uca spinicarpa* and *U. longisignalis*) burrows in coastal marsh habitats is described, and the influence of substratum characteristics on the distributions of each is examined. Burrow densities were higher in vegetated areas than in sparsely vegetated and nonvegetated areas. Elevation and landward distance from shoreline (water's edge) also co-varied with burrow densities along transects. Burrow aperture diameters and burrow numbers m<sup>-2</sup> exhibited seasonal variations for both species of *Uca*. The depth of burrows increased with increased distance from the water's edge (approximate mean sea level) along transects into the marsh. A significant correlation between burrow aperture diameter and carapace width of the inhabitant enabled subsequent estimates of size and biomass in populations. Mean burrow densities for *U. longisignalis* ranged from a high of 182 m<sup>-2</sup> in September 1992 to a low of 26 m<sup>-2</sup> in May–June 1992. Mean burrow densities for *U. spinicarpa* ranged from a high of 46 m<sup>-2</sup> in March–April 1993 to a low of 29 m<sup>-2</sup> in May–June 1992. Estimates of mean biomass ranged from 17.6 g AFDW m<sup>-2</sup> to 13.2 g AFDW m<sup>-2</sup> for a *U. longisignalis*-dominated site and from 6.5 g AFDW m<sup>-2</sup> to 4.9 g AFDW m<sup>-2</sup> for a *U. spinicarpa*-dominated site. Field observations and laboratory soil-choice tests demonstrated that, in mixed populations, *U. spinicarpa* preferred to burrow in substrates of higher percent clay than did *U. longisignalis*.

## Introduction

Fiddler crabs (Decapoda, Ocypodidae, *Uca*), are ubiquitous along coasts of the northern Gulf of Mexico, and include the Gulf endemic species, *Uca longisignalis* Salmon and Atsides and *Uca spinicarpa* Rathbun. *Uca spinicarpa* is found from Tampico, Mexico, to Pensacola, Florida, United States, and usually prefers clayey substrates in brackish water, though in some instances it inhabits fresh or hypersaline environments (Barnwell and Thurman 1984). *Uca longisignalis* ranges from northwestern Florida to Texas and is restricted primarily to sediments of terrigenous origin. It is distributed widely in regions of lower salinity (i.e., upper estuaries and river banks) but also ranges into salt marshes. Where these two species occur in close proximity, preferred habitats appear to differ in elevation, vegetation, and sediment character. However, habitat preference of *U. longisignalis* appears to be interspecifically modulated by the presence or ab-

sence of certain other species (Barnwell and Thurman 1984) and this may also prove true for *Uca spinicarpa*. Both species excavate burrows for shelter, protection, and breeding. Components of the environment important in determining the distribution of fiddler crabs are believed to include substratum, food, salinity, tidal exposure, and presence of other animals (Teal 1958). Specialized as detritivores, different species of the genus *Uca* are known to be morphologically and behaviorally specialized for handling certain size particles of substrate and food (Crane 1975), so distributions are thought to be defined in part on the basis of soil particulate characteristics.

Fiddler crab activities may significantly affect marsh substratum characteristics and the production of emergent vegetation in marshes (Valiela et al. 1978; Montague 1980, 1982; Chalmers 1982). Their activities and by-products can markedly influence transfer of energy and nutrients within the marsh ecosystem (Montague 1980; Daiber 1982). The burrows are often abundant in marsh habitats, where maximum densities are usually estimated at 21–152 m<sup>-2</sup> (Montague 1980). These burrows likely increase soil drainage and soil oxygen levels (Val-

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iel et al. 1978; Montague 1982) while reducing accumulations of metabolic by-products in marsh sediments (Howarth and Hobbie 1982), effects which subsequently impact production of emergent vegetation. Fiddler crab burrowing and deposit-feeding, however, do not occur uniformly across marsh habitats (Crane 1975).

Documentation of temporal and areal variations in fiddler crab populations is essential to relating their activities to salt-marsh productivity in the northern Gulf of Mexico, both in natural and artificially constructed settings. However, the majority of studies to date on distributions within marshes have centered on the Atlantic Coast. Few ecological studies of any kind have involved northern Gulf of Mexico endemic species such as *Uca spinicarpa* and *Uca longisignalis*. The present study compares seasonal burrow abundance and physiography in these two species between marsh and spoil-elevated bank habitats on the Louisiana coast. It also undertakes experimentation to determine the importance of soil composition, independent of vegetation and elevation effects, in habitat selection by these species.

## Materials and Methods

### FIELD MEASUREMENTS

Six transects were established on margins of Joseph's Harbor, a canal in Rockefeller Wildlife Refuge, at a site approximately 100 m from the canal's opening into the Gulf of Mexico. Many years of canal maintenance dredging here have resulted in deposition of clayey spoils on the eastern margin, altering elevation profiles and vegetative cover there. Three transects on the spoil bank (east) side, each of which was 15 m in length, originated at approximately mean sea level (MSL) on the shoreline and extended obliquely across the gently increasing grade of the bank; hereafter, these are termed bank site transects. Three on the marsh (west) side, each of which was 15 m in length, originated at approximate mean sea level on the shoreline and extended into the marsh; hereafter, these are termed marsh site transects. Marsh site transects were vegetated mainly by sea-ox-eye (*Borrhichia frutescens*), cordgrass (*Spartina alterniflora*), glasswort (*Salicornia bigelovii*), saltwort (*Batis maritima*), and salt-marsh grass (*Distichlis spicata*). Soil composition (pool of 20 samples across each site, top 20 cm) for the marsh site was 13.0% sand, 31.4% silt, and 55.6% clay. Bank site transects were higher in elevation and sparsely vegetated compared with the marsh site, with scattered clumps of cordgrass (*Spartina alterniflora*), salt-marsh grass (*Distichlis spicata*), and saltbush (*Baccharis halimifolia*). Soil composition for the bank site was 15.4% sand, 21.0% silt, and 63.7% clay.

From January 1992 through April 1993 (excepting October 1992), relative abundance of each fiddler crab species was noted monthly from a sample of at least 50 animals taken from each habitat. These samples, taken *ad libitum* in repetitive searches of intertransect areas, were subsequently used in another study to monitor reproductive cycles (for further description of sampling, see Mouton and Felder 1995). Also on a monthly basis, crab burrow openings were counted within 1-m<sup>2</sup> quadrats. Counts were obtained for each meter length in the transect without disturbing the soil or the vegetation and were subsequently pooled to obtain means over 3-m intervals. Along with burrow counts, diameters of five burrow openings in each meter of the transect were selected randomly, (repeated throws of a 100-cm<sup>2</sup> quadrat frame) and measured with a small metric ruler. Burrow counts and burrow apertures were analyzed with a one-factor analysis of variance (ANOVA) for repeated measures, and a Student's test, with significance established at  $p < 0.05$ . Burrow morphology was examined in intertransect areas by pouring and excavating casts of polyester resin to determine burrow lengths at different distances from the water's edge. Individuals trapped within burrow casts were removed carefully and carapace widths were measured along with burrow apertures.

Regression analyses were conducted to establish the relationship between burrow aperture and carapace width for each species. Carapace width for each species was correlated to dry weight (DW) and ash-free dry weight (AFDW) in the course of another study (Mouton and Felder 1995); this information provided a basis for using mean burrow counts and aperture sizes to estimate population biomass changes.

### LABORATORY MESOCOSM EXPERIMENTS

Laboratory mesocosms consisted of two modified fiberglass tanks (2.3 m × 1.12 m × 0.3 m). Plywood additions increased the total height of the sides to 79 cm, and lightweight aluminum sheeting over the plywood surface provided a vertical barrier that the fiddler crabs could not scale. A bottom layer of gravel 5 cm thick, separated from the overlying soil by porous, fiber landscaping barrier and nylon window screening, provided drainage. An open area of 0.46 m<sup>2</sup> divided the tank in the middle, was free of soil and gravel, and was a source of standing aerated water. Soil filled both sides of the tank, sloping up from a 10-cm high retaining board at the water's edge to an artificial bank 45 cm high on each side. In each tank, one bank was constructed of soil containing 13.0% sand, 57.7% silt, and 29.3% clay (low clay soil), and the other bank was constructed of soil containing

2.8% sand, 59.2% silt, and 37.9% clay (high clay soil). Both of these well-mixed soils were obtained in a coastal marsh near Cypremort Point, Louisiana. The high clay soil was obtained from a spoil bank and the low clay soil from a lower *Spartina* marsh in an attempt to somewhat duplicate the substrate found at our field study sites. The water between these banks was full strength natural seawater mixed with dechlorinated tap water and maintained at a salinity of 26‰.

Mesocosms were maintained on a 14 h light : 10 h dark cycle using overhead fluorescent lighting. In addition, 1,500-watt halogen lights (controlled to turn on 1 h after and off 1 h before the overhead lights) were installed over each tank to simulate the high light intensity and temperatures characteristic of the natural summer habitat. Soil temperature ranged as high as 30°C during the light period and dropped to 23°C during the dark.

Crabs used for soil-choice experiments in mesocosms were collected in areas adjacent to the field study sites. Within 1 d of return to the laboratory, equal numbers of each sex for each species (at varied total stocking densities) were simultaneously introduced into the center water-filled tray of a mesocosm and allowed to establish burrows on either of the available soil banks during the following 100 d. During this period, equal small amounts of Tetramin® fish flakes were scattered weekly at the water's edge of each bank, both to serve as a direct dietary supplement and to stimulate microbial food growth. Of the five soil selection trials, one was conducted at a stocking density of 10:10 for the two species (5 males and 5 females of each species), and two trials each were conducted with stocking densities of 16:16 (8 males and 8 females of each species), and 32:32 (16 males and 16 females of each species). Following each 100-d trial, all surviving crabs were excavated from the soils on either side of the mesocosm and identified. Significance of results was determined by chi-square testing and by the CATMOD ANOVA on a computer-based SAS package.

## Results

### FIELD MEASUREMENTS

Bank site transects were dominated by *Uca spinicarpa* populations throughout the study. Over the course of monthly sampling the abundance of this species ranged from 94% to 100% of the sampled fiddler crab population, with the remainder *Uca longisignalis*. When present, *Uca longisignalis* was usually restricted to upper intertidal reaches of the bank. By contrast, marsh site transects were dominated by *Uca longisignalis* populations throughout the study. Their relative abundance in monthly

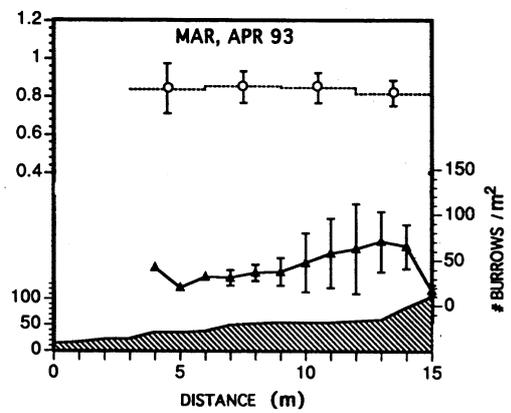
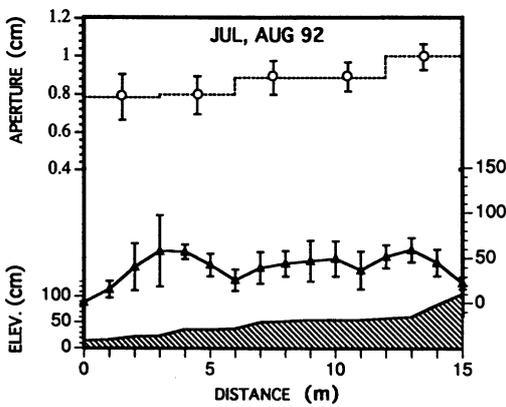
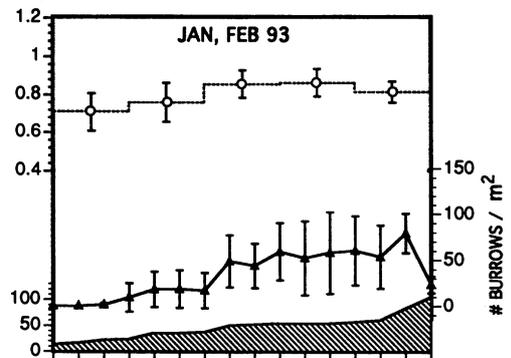
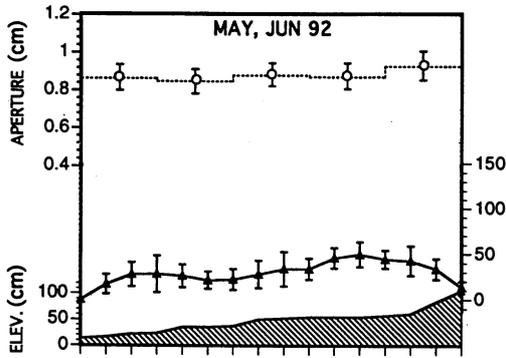
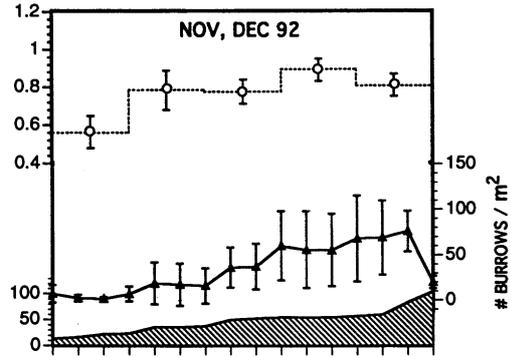
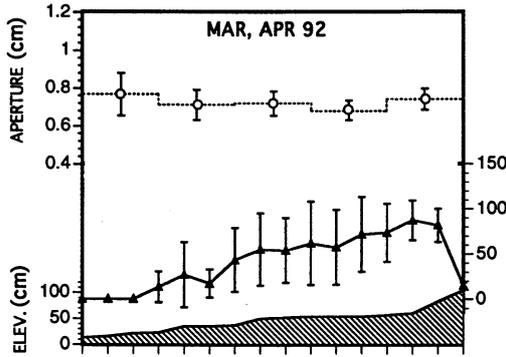
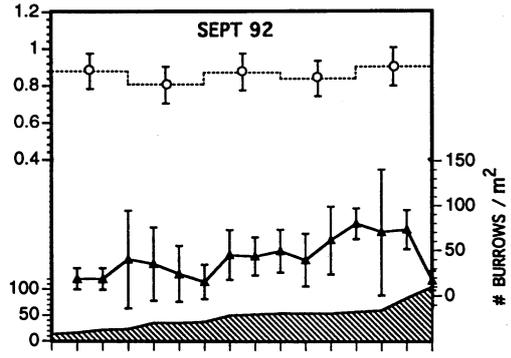
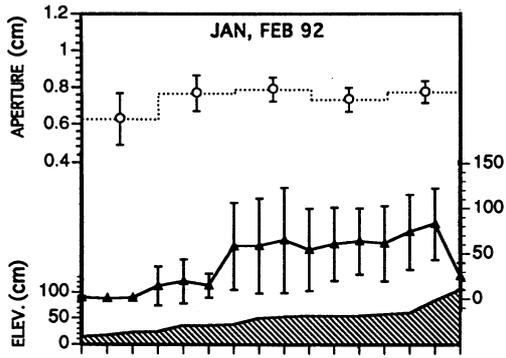
samples at this site ranged from 90% to 100% of the sampled population, with the remainder composed of *Uca spinicarpa* and *Uca rapax*, which were usually restricted to sparsely vegetated areas near the margin of the canal.

In the *U. spinicarpa*-dominated transects of the bank site, burrow densities during most months of the year increased with increasing distance from water's edge, as elevation increased (Fig. 1). However, a marked decrease in density occurred where elevations exceeded 70 cm at the upper end of the transects. The exception to this pattern occurred in the summer months when relatively higher burrow densities were evident in the lower, nearshore reaches of these transects. A remarkable similarity of distribution of both burrow densities and burrow apertures occurred between the two years of monitoring during the winter months (January–February 1992 and 1993). In these winter counts, as well as in those of late fall and (where measurable) early spring, burrow abundance in the nearshore third of the transects was significantly ( $p < 0.05$ ) less than that in upper reaches of the transects. Counts and measurements for the spring of 1993 were prohibited in lower reaches of the transect by unusually high tides.

Mean burrow density across the three transects of the bank site peaked in late winter to spring and was lowest in early summer. The highest observed monthly means occurred in January–February 1993 (46 m<sup>-2</sup>) and March–April 1993 (47 m<sup>-2</sup>). During this January to April period, counts for both 1992 and 1993 were significantly ( $p < 0.02$ ) greater than those observed in May–June 1992. The monthly mean burrow counts in May–June 1992 fell to 29 m<sup>-2</sup>, after which mean monthly densities again increased. This late summer increase in July–August 1992, was initially accounted for by increases in burrow numbers within nearshore areas, and was followed by subsequent increases of burrow densities in upper reaches of the transects during September. The fall and winter pattern of lower densities in nearshore reaches of the transects and higher densities in upper reaches was reestablished by late fall of 1992 and persisted through early spring of 1993. Mean burrow density at the bank site over the entire study was  $39.4 \pm 2.8$  m<sup>-2</sup> (95% CI).

Mean burrow diameters at the bank site, accounted for predominantly by *U. spinicarpa*, did not vary significantly from one another in comparisons between the May–June (0.88 cm), July–August (0.89 cm), and September (0.86 cm) sampling periods (Fig. 1). However, mean diameters of burrows during each of these months were significantly ( $p < 0.05$ ) greater than those of all other months of the year in pairwise comparisons. In

○ MEAN    ▲ MEAN    ▨ ELEV. (cm)



contrast to the May–June and September measures, those taken in the July–August period demonstrated significant ( $p < 0.002$ ) differences in sizes of burrows between the nearshore and upper ends of transects. This was attributable primarily to increased density of small burrows from new recruits to the population within 5 m of the water's edge, but there was also a simultaneous increase in mean burrow diameters in the upper 3 m of these transects. Significant differences ( $p < 0.01$ ) in burrow diameters between nearshore and upper ends of transects were also evident in the November–December sampling period, when the lower 3 m of the transect became dominated almost exclusively by new recruits occupying burrows  $< 0.6$  cm in diameter. During winter months (January–February) of both years, burrow diameters were moderately larger in the more densely populated middle to upper reaches of the bank site transects than in the lower nearshore extremes.

At the marsh site, where *U. longisignalis* dominated habitats, fiddler crab burrow densities along the study transect were usually lowest near the water's edge and highest in the middle to middle-upper reaches of the 15-m transects (Fig. 2). Beyond about 3 m from the water's edge, there was no marked change in marsh elevation with which peak density could have correlated. Counts between the three transects were subject to little variation within most sampling periods, except within the month of September 1992 when mean burrow densities peaked significantly ( $182 \text{ m}^{-2}$ ,  $p < 0.01$ ) compared with any other month. This marked increase was presaged by a smaller but significant increase in burrow density on the nearshore berm of the marsh during July–August 1992, the period of second highest mean burrow density ( $93 \text{ m}^{-2}$ ), and was followed by a rapid decline in burrow numbers during the fall of 1992. While there was no significant difference in mean burrow densities between November–December 1992 ( $71 \text{ m}^{-2}$ ) and the January–February 1992 samples ( $66 \text{ m}^{-2}$ ) over the entire transect, there was a significant decrease ( $p < 0.01$ ) in burrow densities within the shoreward half of the transects in January–February 1993. As at the bank site, the distribution of both burrow densities and burrow apertures at the marsh site was very similar between the two years of winter sampling (January–February 1992 and 1993), and there was no significant difference be-

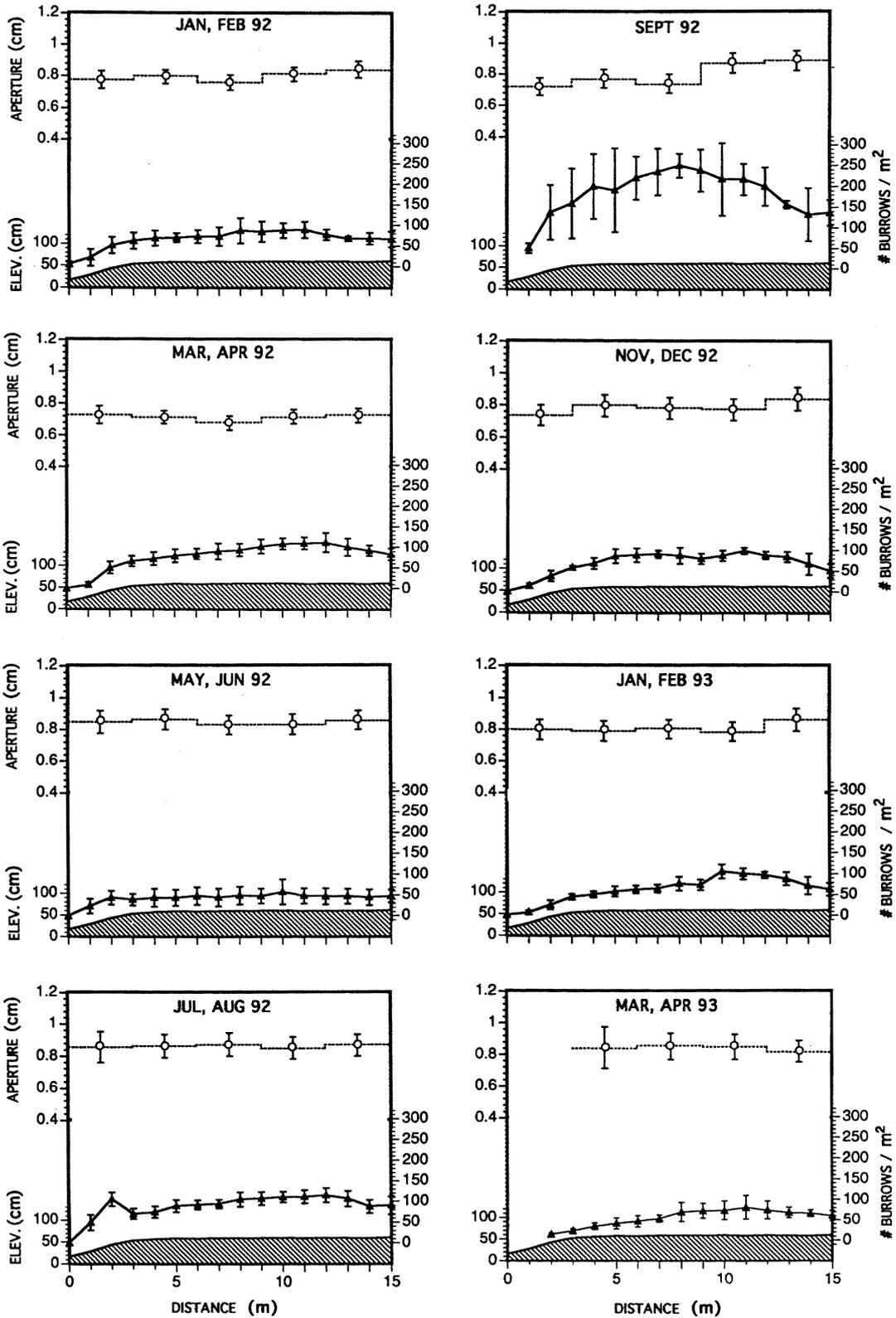
tween the mean of  $65 \text{ m}^{-2}$  in 1992 and the mean of  $61 \text{ m}^{-2}$  in 1993. However, mean burrow densities did vary significantly between years during the March–April period, reaching  $79 \text{ m}^{-2}$  in 1992 and only  $58 \text{ m}^{-2}$  in 1993. This did not appear to be an artifact of limitations to sampling (by high tides) in lower reaches of the transects during 1993, and may be related to temperature differences between years. As at the bank site, lowest mean burrow densities occurred in the May–June sampling period. Mean burrow density at the marsh site over the entire study was  $75.0 \pm 3.4 \text{ m}^{-2}$  (95% CI).

Mean burrow diameters along transects through the *U. longisignalis*-dominated marsh site were largest in the summer samples (0.84–0.86 cm, May–August) (Fig. 2). A slightly, but significantly ( $p < 0.05$ ), smaller mean in September 1992 (0.80 cm) was accounted for by an abundance of small burrows from new recruits in the nearshore half of the transect; these were significantly ( $p < 0.01$ ) smaller in mean diameter than were those of the upper transect and were also significantly ( $p < 0.001$ ) smaller than those in nearshore reaches of the transect in the July–August sampling period. Throughout the fall and winter months (September–February), mean burrow diameters across the entire transect remained significantly ( $p < 0.05$ ) smaller than those of the summer sampling periods. Mean burrow diameters across the marsh site transects also varied markedly between the two years of spring (March–April) sampling. In 1992, the warmer of the two spring periods, burrow diameters were smaller than those of any other sampling period.

Resin casts of fiddler crab burrows were successfully recovered over the full lengths of intertransect areas at the marsh site, while at the bank site success was limited (in part by the difficulty of excavating clayey soils there) to the immediate vicinity of the shoreline (Fig. 3). Given the short distance of the transect sampled, a significant relationship between length of the burrow casting (burrow depth) and distance from shoreline could not be established for the *U. spinicarpa*-dominated bank site. However, such a relationship was clear and significant ( $p < 0.01$ ) along the transects for *U. longisignalis* burrows at the marsh site. At the upper ends of these transects, burrows typically approached or exceeded 0.5 m depths and were often of a branched construction in their deeper

←  
 Fig. 1. Burrow densities ( $\# \text{ m}^{-2}$ ), burrow aperture diameters (cm), and transect elevations (cm above MSL) for the bank site dominated by *Uca spinicarpa*, January 1992–April 1993. Vertical bars indicate 95% CI. Months at top of each figure indicate samples pooled for that analysis. Counts and aperture diameters were pooled across three transects. Counts were made at 1-m intervals, and burrow apertures were pooled over 3-m intervals.

○ MEAN ▲ MEAN ▨ ELEV. (cm)



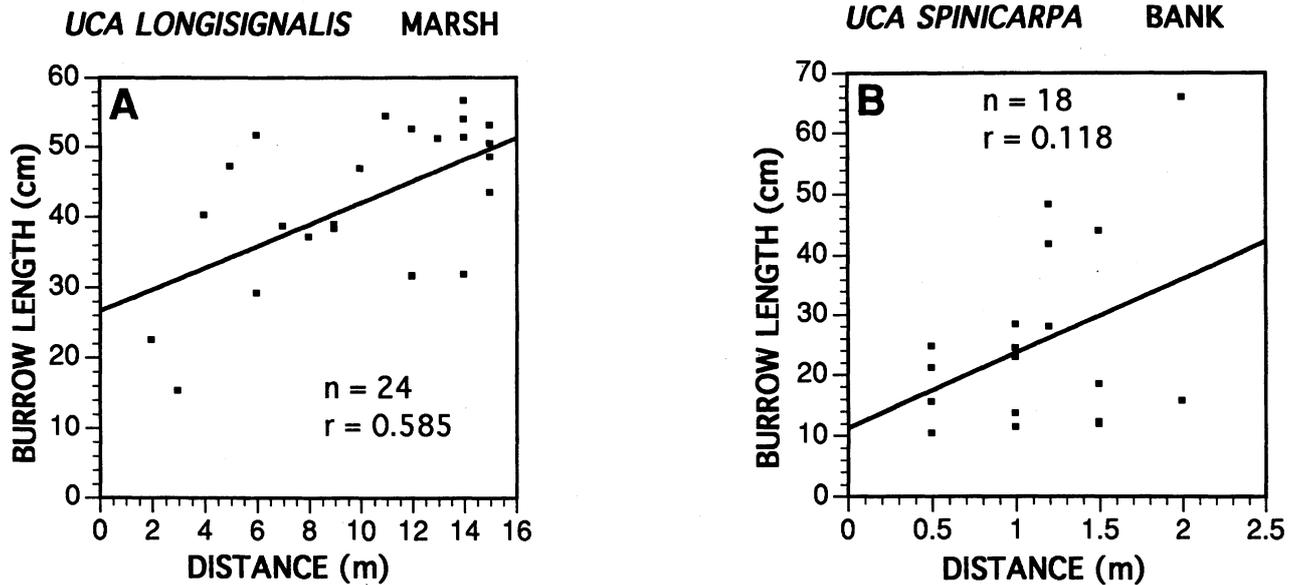


Fig. 3. Relationship between lengths of resin burrow casts (burrow length) and distance from water's edge along transects in (A) marsh site dominated by *Uca longisignalis* and (B) bank site dominated by *Uca spinicarpa*.

reaches. For burrows of both species, the primary tunnel consisted of a J-shaped region below a single aperture, and a slightly enlarged chamber was typically found at the end of the burrow or within the strongest bend of the J-shape. Successful captures of fiddler crabs in resin castings were limited to six specimens of *U. spinicarpa* from the bank site and 14 specimens of *U. longisignalis* from the marsh site (Fig. 4), but these were sufficient to establish a significant ( $p < 0.05$ ) coefficient of relationship between burrow aperture diameter and carapace width for each species. These coefficients, along with empirical determinations of the relationship between carapace width and biomass (as g DW and g AFDW) in a companion study of growth in these two species (Mouton and Felder 1995; Fig. 3) allowed estimation of biomass on the basis of mean burrow aperture diameters and mean burrow numbers within the study transect.

With each burrow assumed to represent a maximum of one animal (see Discussion), it was estimated that the mean biomass of *U. longisignalis* was then maximally  $17.6 \text{ g AFDW m}^{-2}$  at the marsh site over the term of study; this estimate ranged from a high value of  $42.1 \text{ g AFDW m}^{-2}$  in September 1992 to a low of  $13.0 \text{ g AFDW m}^{-2}$  in March–April 1993. Under the same assumption, it was estimated

that the mean biomass over the term of this study for *U. spinicarpa* at the bank site was maximally  $6.5 \text{ g AFDW m}^{-2}$ , or half that of the marsh site; this estimate ranged from a high value of  $7.7 \text{ g AFDW m}^{-2}$  in January–February 1993 to a low value of  $5.5 \text{ g AFDW m}^{-2}$  in May–June 1992.

Median monthly air temperature during the field studies, measured within 10 km of the study site, ranged from  $10.3^\circ\text{C}$  to  $28.2^\circ\text{C}$ . Water temperature, measured along with salinity in shoreline canal waters immediately adjacent to the study sites on each sampling date, ranged from  $10.5^\circ\text{C}$  to  $31.0^\circ\text{C}$ , with cold water temperatures persisting much later into the spring of 1993 than they did in 1992.

#### LABORATORY MESOCOSMS

The low clay and high clay soils used in soil-choice experiments differed in the concentration of clays and sands but were similar in the concentration of silts. Silts constituted a higher fraction in both these soils than they did at either the bank site or marsh site (Fig. 5), but the relative abundance of clays differed between the two mesocosm soils (8.6%) to about the same degree as between the two field sites (8.1%). Sand content in the high

←  
Fig. 2. Burrow densities ( $\# \text{ m}^{-2}$ ), burrow aperture diameters (cm), and transect elevations (cm above MSL) for the marsh site dominated by *Uca longisignalis*, January 1992–April 1993. Vertical bars indicate 95% CI. Months at top of each figure indicate samples pooled for that analysis. Counts and aperture diameters were pooled across three transects. Counts were made at 1-m intervals, and burrow apertures were pooled over 3-m intervals.

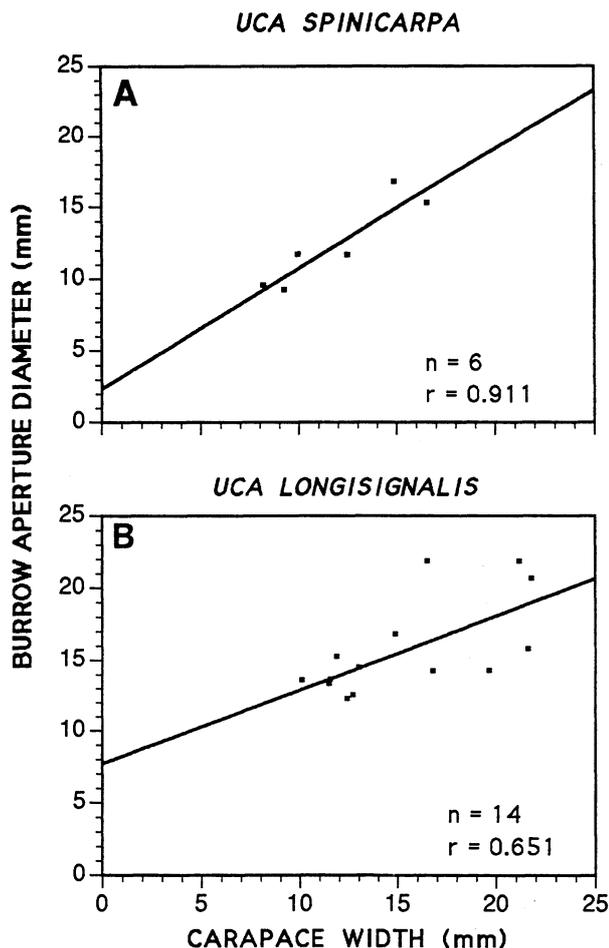


Fig. 4. Relationship of burrow aperture diameters to carapace widths, as determined from measurements of resin burrow casts and measurements of crabs trapped in those castings. A. *Uca spinicarpa* burrows at the bank site; B. *Uca longisignalis* burrows at the marsh site.  $n$  = sample size;  $r$  = regression coefficient.

clay soil was lower than in the low clay soil and than in substrates at either field site.

After 100 d in laboratory mesocosms, distributions of the two fiddler crab species between the two available soils demonstrated a strong selective association of *U. spinicarpa* with the high clay (low sand) soil and a strong selective association of *U. longisignalis* with the low clay (typical sand) soil (Fig. 6). By chi-square analysis and CATMOD ANOVA it was evident that substrate type was highly significant ( $p < 0.001$ ) in accounting for variation in the distribution of the two species between the two soil types and that the three different stocking densities (10:10, 16:16, 32:32) did not have a significant impact on this distribution.

#### Discussion

Despite the dominance of fiddler crabs among macroheterotrophs of intertidal marshes (Mo-

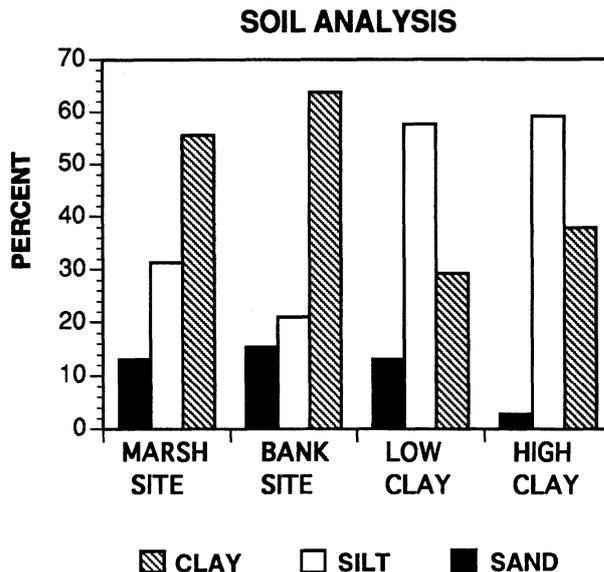


Fig. 5. Relative abundance of clays, silts, and sands in soils from the marsh site and bank site where field studies were conducted and in low clay and high clay soils used in laboratory mesocosm substrate selection experiments with *Uca spinicarpa* and *Uca longisignalis*.

ntague 1980), and the abundance of such biotopes in the Gulf of Mexico, seasonal fluctuations in density and biomass of *Uca* populations in this region are not often estimated. Attempts to do so are limited by the fossorial habits of these animals, but marsh ecologists have found varied methods for censusing *Uca* populations (see Colby and Fonseca 1984: 274). Direct censusing of burrowed individuals, impractical in some heavily rooted peaty or clayey substrates, requires excavation and wet-sieving of sediments to well over 0.5 m depth, while counts of active animals at the surface are confused by periodic inactivity and heterogeneous congregation of these behaviorally complex animals. Quantitative trapping has been attempted in eastern Gulf marshes (Subrahmanyam et al. 1976), but excavation of crabs below ground in traps was limited to 10 cm, and identifications were often limited to the generic level. In other cases (Powers 1973, 1975), counts were apparently limited to observations of active animals, restricted to one season, and not based on populations in typical estuarine marsh biotopes.

Assessment of fiddler crab populations by burrow counts, with acknowledged limitations in some settings, allows for monitoring densities without substantial alterations to study transects. The density of burrows, regardless of possible seasonal variations in the ratio between crab numbers and burrow numbers, can within some error be correlated to population densities. Burrow density also di-

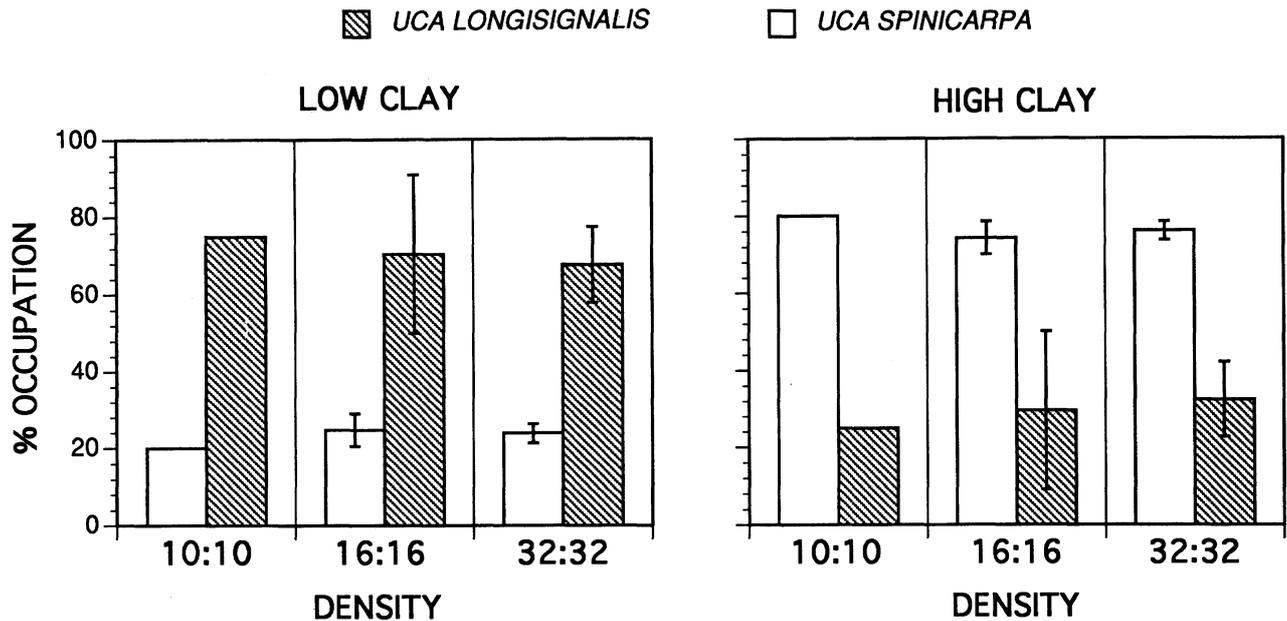


Fig. 6. Relative abundance of *Uca longisignalis* and *Uca spinicarpa* in high clay and low clay soils, following 100-d soil selection experiments in laboratory mesocosms. Stocking densities for the two species were 10:10 for one trial, 16:16 for two trials, and 32:32 for two trials. Vertical lines indicate ranges of replicate trials.

rectly reflects bioturbational activity, which has marked feedbacks to production of marsh vegetation (Montague 1980; Genoni 1991).

The coefficient of relationship between number of burrows and number of crabs per unit area remains questionable and a subject for future study in *U. longisignalis* and *U. spinicarpa* habitats. In *U. rapax* populations on the Atlantic Coast, densities in sandy-mud *Spartina* marshes are about 74% of burrow densities (Genoni 1991). On the Texas coast, mixed populations of three species were estimated to be slightly less than 50% of burrow numbers (Powers 1975), but this estimate was based primarily on *U. panacea* and *U. rapax*, was determined in sandy nontidal settings, and was based upon excavations no deeper than 35 cm. Our experience (D. L. Felder unpublished data, marshes of Vermilion Bay, Louisiana) suggests that numbers of both *U. longisignalis* and *U. spinicarpa* during summer months in intertidal estuarine marshes of coastal Louisiana range typically from 75% to 100% of the burrow numbers (wet-sieve extractions from upper 0.5 m of marsh soil in five 1-m<sup>2</sup> quadrats within each of two habitats). Burrow numbers in excess of animal numbers (supernumerary burrows) were common in only two quadrat counts from exposed shorelines of marshes (areas that also tend to have low burrow densities), with the ratio of burrows to animals more nearly approaching 1:1 in vegetated marshes beyond the immediate shoreline. For this reason, we have stat-

ed our estimates as "maximal biomass" in the present study, and acknowledge that actual biomass could instead be near 75% of those estimates. Assuming that only 75% of the burrows represent animals, our estimates of actual mean biomass would then become 13.2 g AFDW m<sup>-2</sup> for the *U. longisignalis*-dominated site and 4.9 g AFDW m<sup>-2</sup> for the *U. spinicarpa*-dominated site.

Standing stock of *U. pugnax*, an ecological equivalent of *U. longisignalis* on the North American Atlantic Coast, has been estimated at 29 g dry weight m<sup>-2</sup> (Krebs and Valiela 1978), a higher figure than reported from Georgia by Teal (1962) and by Wolf et al. (1975). Relationship between dry weight (DW) and AFDW in our study of *U. longisignalis* yields a regression formula of AFDW = 0.495(DW) + 0.019, or an approximate conversion coefficient of 0.50 over most of the size range. Application of this to reported dry weights of *U. pugnax* suggests a biomass of approximately 15 g AFDW m<sup>-2</sup> in the Krebs and Valiela (1978) study, a measure between those we project for *U. longisignalis* at 75% and 100% of burrow occupancy. Our highest estimate of *U. longisignalis* standing stock occurred when mean burrow densities peaked at 182 m<sup>-2</sup> in September 1992, and biomass ranged from 31.6 g AFDW m<sup>-2</sup> to 42.1 g AFDW m<sup>-2</sup> over the estimated range of 75–100% burrow occupancy. This seasonal high is comparable to that for some populations of a more tropical ecological equivalent, *U. rapax*, which in summer reach mean burrow densities of

212 m<sup>-2</sup> and crab densities of 156 m<sup>-2</sup> (Genoni 1991). Multiplication of those animal densities by the approximate AFDW individual<sup>-1</sup> derived in our studies of *U. longisignalis* (0.25 g individual<sup>-1</sup> without scaling to carapace sizes), suggests an approximate biomass of 39 g AFDW m<sup>-2</sup> for *U. rapax*, a value again within the range we estimated for *U. longisignalis* at its seasonal peak. Biomass of the *U. spinicarpa*-dominated population on the less vegetated bank site was estimated to average about half that of the *U. longisignalis*-dominated marsh site. This reflects lower burrow densities of the *U. spinicarpa* population, from which animal densities were estimated, and smaller mean individual sizes of these animals.

While a moderate disparity in *U. longisignalis* burrow densities between the May–June sampling period and that for July–August might be explained by less burrowing activity during the period of low tidal amplitudes in early summer or by more burrows being plugged in early summer by mating individuals, the more striking September increase almost certainly reflected an increase in populations of both recruits and adults within the transects. In the field, we observed strikingly greater abundance on the surface during September 1992 than during any other period. This may represent relocation of animals from inshore reaches of the marsh to more nearshore areas crossed by our transects, but we cannot readily relate this dynamic to a particular biological activity of the population nor can we conclude that it is an annually recurring event. Several weeks prior to the September 1992 sampling period, both the marsh and bank sites were briefly inundated by storm tides peripheral to Hurricane Andrew, which struck the coast well east of our study area. While this could have effected some redistribution of existing *U. longisignalis* populations at the marsh site, perhaps by enriching wrack or detritus in the nearshore areas of our transects, habitat changes were not obvious in our post-hurricane inspections.

Changes in vegetation and estimated crab population densities coincided along transects at both sites, as appears to occur in other fiddler crab populations (Teal 1958; Kerwin 1971; Powers 1973; Whiting and Moshiri 1974; Ringold 1979; Bertness and Miller 1984). In bank site transects, burrow densities of *U. spinicarpa* below the terminal landward berm generally increased with increasing elevation, often with a density transition around 6 m from shoreline. A secondary berm separated the generally unvegetated lower mudflat from sparse stands of *Distichlis* and *Borrchia* in upper transect reaches. When high densities occurred below this berm, they were restricted to summer months of peak reproductive activity. At the marsh site, a

berm between 1 m and 4 m from the water's edge was densely vegetated by a narrow stand of *Spartina* and *Distichlis*. While this region usually harbored moderate concentrations of *U. longisignalis* burrows, numbers peaked here during July–August. This abundance of nearshore burrows was accounted for in part by readily observable recruits. However, mean burrow diameters were not significantly smaller than those of the previous sampling period, so the peak may also involve seasonal shoreward relocation of reproductively active adults. Landward of the 4-m mark, the marsh site was vegetated primarily by a shorter, open stand of *Borrchia* with scattered *Batis*, and this region usually harbored the densest concentrations of *U. longisignalis* burrows. The centering of maximum abundances of burrows near the 8-m to 12-m marks could not be accounted for by any obvious gradient in vegetative cover or change in elevation. Rather, it suggests some relationship to proximity of the shoreline, perhaps as determined by effects of tidal flooding or deposition of wrack that contributes to food resources. Abundance of such food material is known to influence population structure (Genoni 1985).

While effects of vegetation co-vary with elevation and distance from shoreline, as in most comparable investigations (Fingerman 1957; Teal 1958; Kerwin 1971; Powers 1973; Whiting and Moshiri 1974; Ringold 1979; Bertness and Miller 1984), and are thus difficult to evaluate as independent determinants of abundance, the effect of a substrate difference between the two sites was measurable by experimentation. At least when the species are present together in soil-choice experiments, *U. spinicarpa* selectively occupies the higher clay soil while *U. longisignalis* occupies the lower clay soil, even in absence of vegetation. While anecdotal mention has been made of such substrate affinities in these species (see Crane 1975; Heard 1982; Barnwell and Thurman 1984), experimental evidence was previously lacking. These species may exploit different components of the substrate grain-size continuum, given differences in setation and shape of the maxillipeds used in feeding (Crane 1941, 1975; Altevogt 1955; Ono 1965; von Hagen 1970). It is postulated that species which feed on fine-grained substrates generally possess a higher density of plumose setae, while coarse-grain feeders, such as those preferring sand-dominated substrates, usually have the more abundant and well-developed spoon-tipped setae. Both species here have abundant plumose setae on the second maxilliped, but *U. longisignalis* often lacks spoon-tipped setae (or has up to a maximum of 75; see Felder 1973), while *U. spinicarpa* typically has somewhat more abundant spoon-tipped setae, including

a few with exceptionally long cups. How these setal differences may relate to the observed substrate preferences is not readily obvious. However, shape quantified as (units of third maxilliped area) (units of carapace area)<sup>-1</sup> (10<sup>3</sup>) and expressed as the Ono-von Hagen Index or c-value (see Ono 1965; modification by von Hagen 1970), appears to correlate with substrate preference for members of the genus. Characteristic of species living in muds and clays, *U. spinicarpa* has c-values between 70–80; characteristic of species inhabiting muddy silts, *U. longisignalis* has c-values less than 70.

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