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# Reproduction of the Fiddler Crabs *Uca longisignalis* and *Uca spinicarpa* in a Gulf of Mexico Salt Marsh<sup>1</sup>

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**ABSTRACT:** Monthly field sampling of active animals in a Louisiana coastal salt marsh monitored changes in size class frequency distributions, ovarian development of females, and rates of egg extrusion for two species of *Uca* endemic to the Gulf of Mexico. Oviparous females occurred no earlier than February for *Uca spinicarpa* and April for *Uca longisignalis*. Peak percentages of oviparous females were observed in June 1992 for *Uca longisignalis* (67%) and in March 1993 for *Uca spinicarpa* (85%). Peaks in ash-free dry weight (AFDW, in g) of females coincide with peak periods of ovarian development and subsequent ovigery. Mean biomass as AFDW of males and females combined for *Uca longisignalis* was 0.26 g individual<sup>-1</sup> and for *Uca spinicarpa* was 0.17 g individual<sup>-1</sup>. A significant correlation existed between AFDW and carapace width in both species, males and females. *U. longisignalis* appears to be of warm-temperate lineage, and its reproductive activity is the more seasonally restricted, with later ovarian development, earliest egg laying delayed to late spring, and peak ovigery in summer. In keeping with putative tropical affinities of *Uca spinicarpa*, ovarian development is episodic over a longer period from late winter to summer, and eggs are produced earlier in the year. The more striking seasonality in reproductive activity and biomass peaks for *Uca longisignalis* may also reflect some nutritional dependency on temperate, annual marsh plants that characterize its preferred habitats.

## Introduction

Fiddler crabs (Ocypodidae: *Uca*) are common intertidal inhabitants of marshes, salt flats, and mangrove swamps along tropical, neotropical, and temperate coastlines. Often dominant forms in intertidal settings, these animals have adapted to a wide range of temperature, salinity, and relative humidity (Edney 1961; Miller and Vernberg 1968; Miller and Maurer 1973; Rabalais and Cameron 1985). Various species of this semiterrestrial group selectively burrow into intertidal substrata, from coarse beach sand to fine clay-rich marsh muds (Teal 1958), and changes in elevation, vegetation, and sediment composition appear in part to determine which species dominates in a given setting. Tidal frequencies and magnitudes, along with temperature, appear to provide important environmental regulators for feeding, burrowing, courtship, chromatophore dispersal, and locomotor activities (Bennett et al. 1957; Fingerman 1957; Crane 1958; Barnwell 1966; Powers and Cole 1976;

Montague 1980). Zucker (1978) reported cyclicity of reproductive activity in *Uca* and found a monthly (rather than semi-monthly) cycle tied to a specific lunar phase in three tropical *Uca* species. Surface activity (which includes courtship, feeding, and combat) for these intertidal crabs is restricted to low-tide periods. Since temperate species hibernate in the winter (Crane 1943), males court (wave their major cheliped) throughout all low-tide periods in the warmer months (Salmon 1965). Subtropical species, exposed to longer periods of warm weather, court only during diurnal and early evening low-tide hours (Salmon and Atsides 1968). In the Gulf of Mexico, where tidal magnitudes are relatively small and climatic conditions vary from warm temperate to tropical, reproductive cycles of even the dominant forms of *Uca* are poorly known.

In the northern Gulf of Mexico, expansive intertidal brackish, intermediate, and salt marshes are often dominated by the endemic species *Uca longisignalis* and *Uca spinicarpa*. While distributions of these species are sympatric over most of their ranges (Felder 1973; Heard 1982), and the species frequently co-exist within a given area of marsh or mudflat, burrows of one or the other usually dom-

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inate at different elevations or different soil compositions. Our observations of seasonal changes in varied habitats of these species also indicate significant changes in burrow abundances and sizes of these species, which are in turn presumed to be dependent upon cycles of reproduction, recruitment, and growth in these species. However, prior to the present study, reproductive ecology of neither species has been investigated.

As the burrowing activities of *Uca* are known to profoundly affect marsh substrata and the production of vascular plants rooted in them (Montague 1980; Bertness 1985), understanding of population dynamics in fiddler crabs becomes an essential underpinning to studies of wetland productivity. Measures of rates and periodicities in reproduction and recruitment may ultimately serve to explain observable areal and temporal variations in burrow densities, bioturbation rates, and fecal or feeding-pellet production rates that subsequently affect the growth of marsh vegetation (Katz 1980; Montague 1980; Bertness 1985). Likewise, the understanding of such measures in established coastal marsh settings will serve to provide benchmarks against which to judge the functional success of restored or constructed wetlands in the northern Gulf of Mexico, an area in which numerous such restoration projects (Neill and Turner 1987; Turner et al. 1989) are underway in hopes of checking massive wetland loss (see Turner 1990).

The present study is focused on reproductive ecology of *U. longisignalis* and *U. spinicarpa* in coastal Louisiana. The two populations that we monitored occur on opposite banks of the same small tidal inlet, with *U. longisignalis* dominating the lower *Spartina* marsh habitat on one side and *U. spinicarpa* dominating a more elevated spoil bank on the other side. Information is presented on annual cycles in ovarian activity and egg-laying, variations in egg weights and numbers, changes in size-class frequencies in each population, and relationships between size classes and biomass. Burrow distributions and population estimates are addressed in a companion study (Mouton and Felder in press).

## Materials and Methods

### FIELD SAMPLES

Both species of fiddler crabs (*Uca longisignalis* and *Uca spinicarpa*) were randomly sampled (50 of each species) on a monthly basis from January 1992 to April 1993 (excepting October 1992). Specimens were collected from coastal Louisiana habitats in Rockefeller Wildlife Refuge (approximately 29°38'N, 92°46'W) at the mouth of a tidal channel, Joseph's Harbor, approximately 100 m from the Gulf of Mexico. The specimens of *Uca*

*longisignalis* were collected from one side of the channel in a low marsh dominated by sea-oxeye (*Borrhchia frutescens*), saltwort (*Batis maritima*), glasswort (*Salicornia bigelovii*), salt marsh grass (*Distichlis spicata*), and cordgrass (*Spartina alterniflora*). Specimens of *Uca spinicarpa* were collected from a spoil bank on the opposite side of the canal, which was higher in elevation and had sparse vegetative cover. Cordgrass (*Spartina alterniflora*) and salt marsh grass (*Distichlis spicata*) were the dominant vegetative cover when present. Crabs were extracted from upper reaches of burrows into which they had retreated or were caught as they ran for burrow openings and other cover objects. The sample was thus based upon animals active at the time of sampling and available without excessive excavation and habitat alteration. Sampling within the first 3 m of the water's edge was avoided in order to prevent bias of the sample to recent recruits, though ancillary collections and notes were made when juveniles were abundant in these areas. To prevent injuries and autotomy of appendages, all collected animals were placed in individual perforated vials without water and transported to the laboratory on ice. While uninjured specimens were found to survive for several weeks in such containers if they are partially submerged in clean seawater, animals taken for our analyses were processed promptly upon return to the laboratory to avoid attrition in tissue mass.

### LABORATORY ANALYSIS

Within 24 h of return to the laboratory, crabs were weighed, sexed, measured, and if female, dissected for analysis of ovaries. Wet weight was determined on a top loading balance to  $\pm 0.01$  g after crabs were blotted dry with tissue paper. Crabs were then sexed and carapace width (CW) was determined to  $\pm 0.01$  mm with dial calipers. Ova of the females were removed, blotted, weighed on an analytical balance to  $\pm 0.001$  g. Color was noted of both the ovaries and, if present, the egg mass on the abdominal pleopods. Specimens were placed in numbered aluminum weigh pans for weight and observations, and thereafter folded into the pans for storage in a freezer prior to drying and ashing.

Specimens were dried in a lyophilizer for 24 h and weighed immediately after to obtain dry weight (DW). They were then placed in a muffle furnace at 550°C for 6 h, allowed to cool in desiccant in a sealed container and weighed soon after to obtain ash weight. Ash weight was subtracted from the dry weight to obtain the ash-free dry weight (AFDW). Reported weights for females always included both the ovary weight and, if ovigerous, the weight of the egg mass.

Analysis of 18 egg masses from *Uca longisignalis*

and 43 egg masses from *Uca spinicarpa* were used to estimate the number of eggs per gram wet weight of egg mass and the total number of eggs per egg mass. This was determined by weighing and counting a subset of eggs from each of the different egg masses, dividing total mass weight by the subsample weight and multiplying this value by the number of eggs in the subsample. Color for each of these egg masses was also noted.

### Results

Size-class structure of samples taken for this study (Figs. 1 and 2) does not serve to portray recruitment and growth fully for the overall population of each species. The monthly samples are instead based on readily collectable individuals, active at the time of sampling. No effort was made to include proportional representation of early recruits from the lower intertidal, and all smaller size classes were likely underrepresented because they were less conspicuous. While presence of small recruits on nearshore extremes of the sampling site was noted when it occurred, and supplementary samples were sometimes taken to ascertain size ranges, these samples were not part of the size-class analysis. The samples also do not represent strictly contained adult populations, and migrations in and out of the populations probably occurred over the course of the study. While the samples do not precisely represent the times and rates at which small sizes of new recruits entered the population, they do show eventual entry of these cohorts into the reproductively active size classes in the primary habitats for each of these species.

For both species, the samples included a more substantial representation of smaller size classes, presumably recruits from the previous reproductive season, in winter and early spring (January through April) than in summer and fall. In winter-spring samples of 1992, entry of these size classes into the sample was somewhat episodic, suggesting that juveniles evident in the January 1992 sample were supplemented by a later cohort of small individuals that did not become evident until April. In addition, for both species, seasonal transition in size structure was far more pronounced in the spring samples from 1992 than in those from spring of 1993. For *Uca longisignalis* (Fig. 1), mean carapace width of the overall monthly sample was smallest in January 1992 (13.9 mm) and had a second, but less pronounced, minimum in January 1993 (14.7 mm). The largest mean carapace width occurred in June 1992 (18.1 mm), though a few males of the largest size classes were also represented in the spring samples (March and April) of both years. The June 1992 sample was also dominated by an unusually high percentage of males

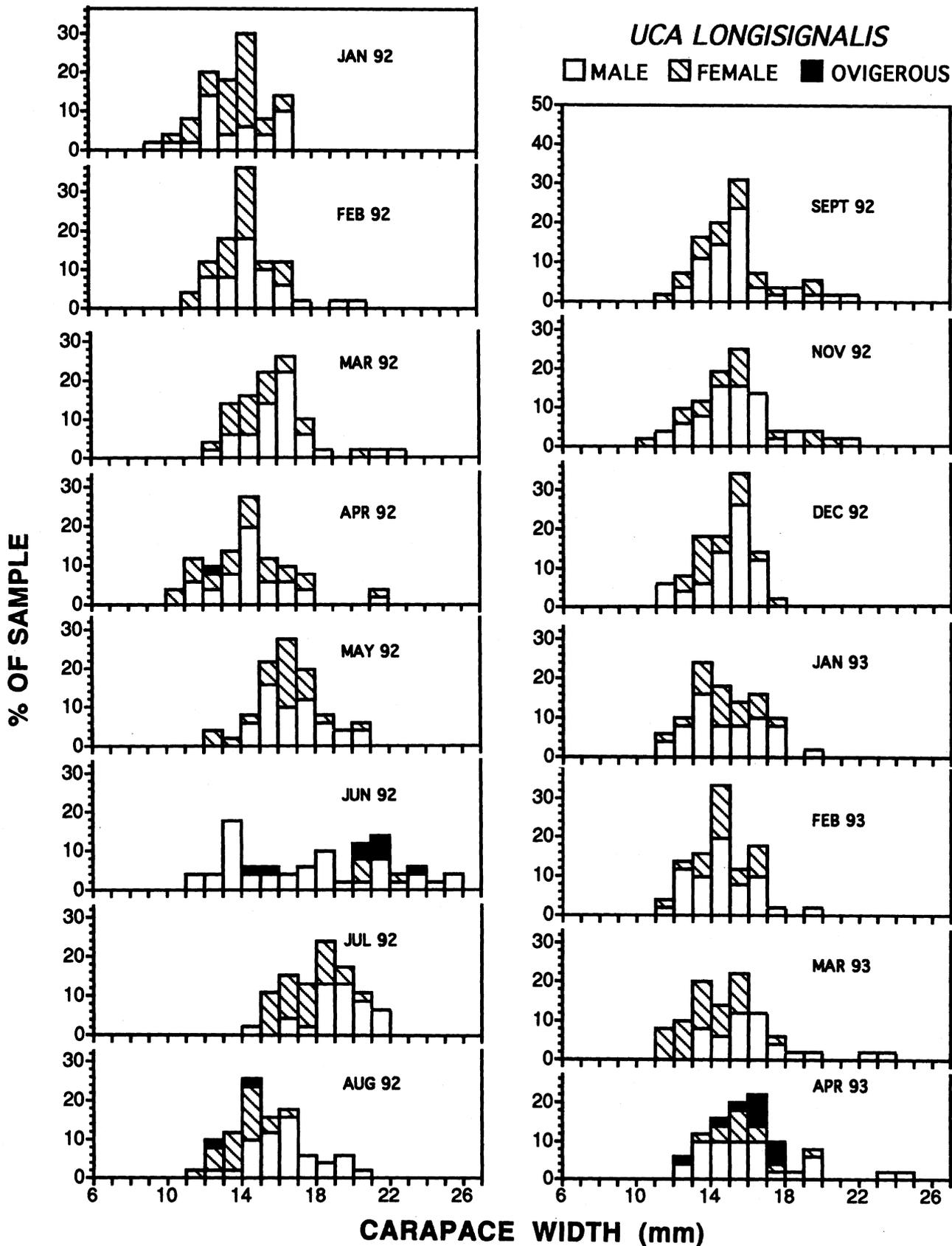
(77%), perhaps owing to their conspicuous surface activity at this time during a peak period of sexual display. For *Uca spinicarpa* (Fig. 2), mean carapace width of the overall monthly sample was smallest in January 1992 (12.1 mm), and did not approach a similar low until April 1993 (12.1 mm). The largest mean carapace width (13.9 mm) was only modestly larger than those of other summer and fall months and occurred in June 1992, the only month in which some males exceeded carapace widths of 18 mm. Overall, measurements from these samples reflected a maximum carapace width in *Uca longisignalis* about 4–6 mm greater than in *U. spinicarpa*.

Segregated by sex, mean carapace widths showed the same pattern as they did for the overall sample. In *U. longisignalis* (Fig. 1), females ranged from mean carapace widths of 13.9 mm in January 1992, to 14.2 mm in April 1992, to a maximum of 20.3 mm in June 1992, and to 13.8 mm in March 1993. Those of males ranged from minima of 13.8 mm in January 1992 and 14.5 mm in February 1993 to maxima of 17.4 mm in June 1992 and 19.0 mm in July 1992. In *Uca spinicarpa* (Fig. 2), the episodic entry of recruits to the population was suggested by the periodic occurrence of small females, which accounted for mean female carapace widths of 11.8 mm in January 1992, 11.9 mm in April 1992, and 11.4 mm in August 1992. These ranged to maxima of 13.7 mm in February 1992 and 14.2 mm in January 1993. Those of males ranged from widths of 12.3 mm in January 1992, 12.4 mm in April 1992, and 12.2 in April 1993, to maxima of 14.1 mm in March 1992 and 14.2 mm in June 1992.

The presence of ovigerous females in monthly samples provided one index of reproductive periodicity. The smallest ovigerous female of *U. longisignalis* had a carapace width of 12.3 mm, while the overall average carapace width for all ovigerous females was 17.1 mm. Ovigerous females of *U. longisignalis* first occurred in April of both 1992 and 1993 (Fig. 1). The limited occurrence in April 1992 (4.4%) consisted of females that averaged 12.8 mm in carapace width, these possibly representing recently matured recruits from the previous reproductive season. While ovigerous females of April 1993 also appeared to include this small cohort, the average carapace width of females was much larger (16.0 mm) since a much larger percentage of females (48%) was ovigerous and dominated by females from 16–18 mm in carapace width. However, the largest percentage (67%) of females was ovigerous in June 1992, when egg-bearing females appeared to be distributed between two size cohorts, one of carapace widths of 14–16 mm and the other of widths >20 mm. A less

*UCA LONGISIGNALIS*

□ MALE   ▨ FEMALE   ■ OVIGEROUS



marked occurrence of ovigerous females in August 1992 was confined to 10% of the female population and was vested solely in smaller mature females averaging 13.2 mm in carapace width.

The smallest ovigerous female of *U. spinicarpa* taken during the study had a carapace width of 9.5 mm, while the overall average carapace width for all ovigerous females of this species was 12.8 mm. Ovigerous females first occurred in February 1992 and March 1993 (Fig. 2). The limited occurrence in February 1992 (2.0%) did not appear to include a small, recently matured cohort; carapace widths of these ovigerous females ranged from 12 mm to 17 mm and averaged 14.5 mm. Much higher percentages were ovigerous in March 1992 (70%) and March 1993 (85%), when egg-bearing females peaked in abundance. In both March samples, the small ovigerous females 9–10 mm in carapace width appeared to be recently matured recruits from the previous reproductive season. Mean carapace widths of ovigerous females in March samples (12.6 mm in 1992, 12.8 mm in 1993) reflected the inclusion of smaller size classes in this reproductively active group. Lower percentages of ovigerous females occurred in samples from April 1992 (23%) and April 1993 (42%), both of which included small ovigerous females (9–11 mm CW). Mean carapace widths of ovigerous females in these samples were 12.7 mm in 1992 and 12.9 mm in 1993. Egg-bearing females of *U. spinicarpa* were absent after April in 1992. Their diminished occurrence in April 1993, the final month of sampling, suggested a pattern similar to that in 1992.

Because ash-free dry weights (AFDW) of tissues vary in large part as a function of size (Fig. 3), the annual cycle in AFDW (Fig. 4) reflects maxima that coincide with occurrence of the largest mean carapace widths. However, as may be expected for animals with a large inorganic component in the exoskeleton, the relationship of body mass to body size is exponential (Fig. 3). Thus, presence of larger animals in a monthly sample contributes substantially to higher mean AFDW for that month, and this accounts in part for high AFDW values for both species in the early summer. To explain other seasonal variations in this measure, interpretation must be made in the context of two allometric dynamics: growth of the male major chela and development of the female ovaries. While these features of sexual development are to some degree synchronized seasonally in the sexes, with a slightly

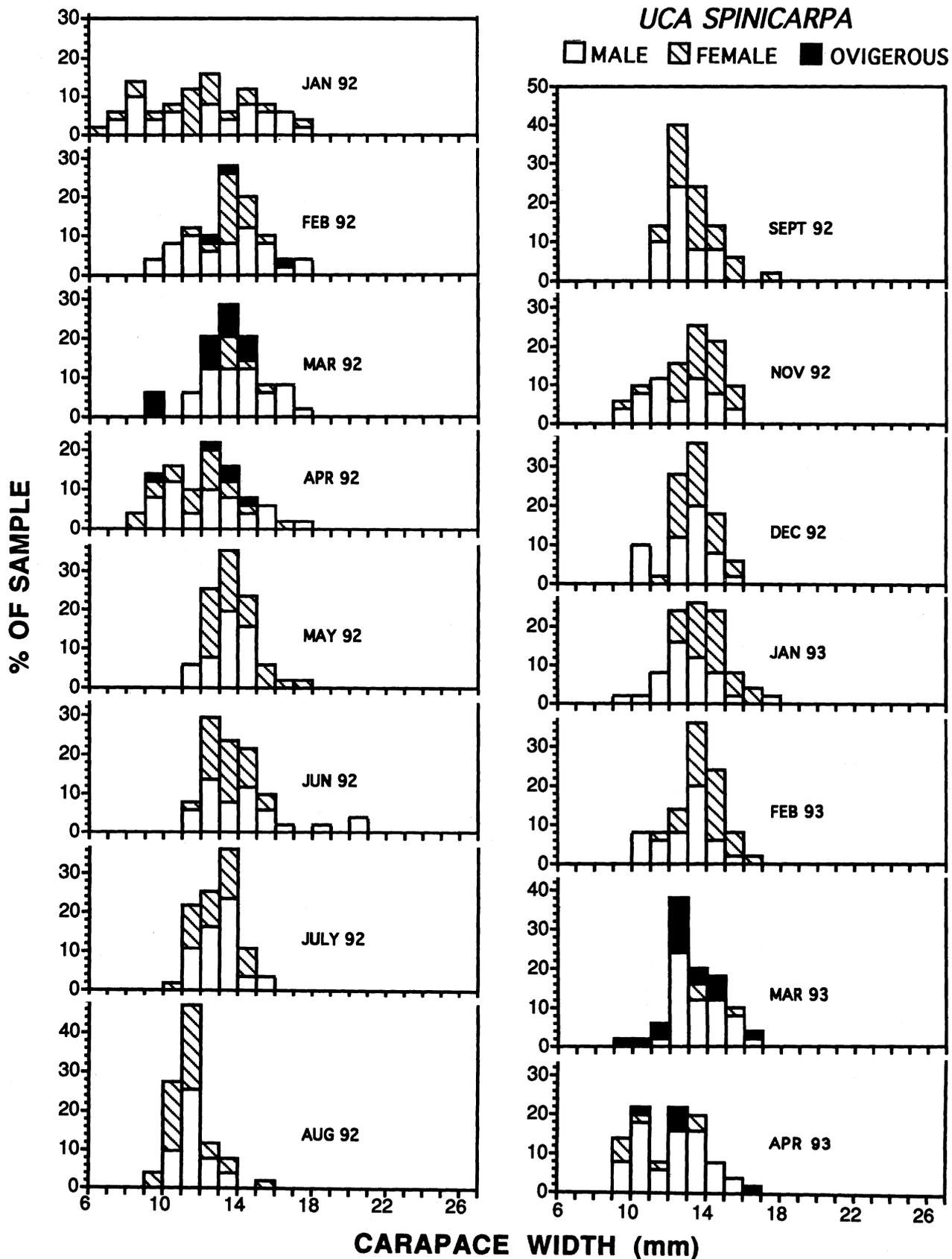
higher AFDW of males accounted for by development of the major chela (Fig. 4), the accrual of ovarian tissue is abruptly punctuated by periods of egg-laying and egg release that should be reflected as reductions in AFDW. This was evident for *U. spinicarpa* as significant decreases in AFDW of females (Fig. 4A) during March and April, followed by a distinct peak in body mass of the females during the winter months. This phenomenon closely tracked the occurrence of most ovigerous females of this species in March and April (Fig. 2). A second, less pronounced peak occurred in May (Fig. 4A), as would be expected given the small but sexually developed females that appeared to enter the population in late spring (Fig. 2). These may have ultimately resorbed ova or could have become ovigerous and not been detected in summer samples. Similarly, the summer breeding peak of *U. longisignalis* was marked by increased AFDW of females, followed by an abrupt decrease (Fig. 4B), while a nearly coincident peak in male AFDW most likely resulted from a high abundance of large males with well-developed major chelae.

Cycles in relative ovarian weights (Figs. 5, 6A, and 7A) more directly reflect the annual pattern of gonadal development. They also show a difference in the pattern of the two successive years in which winter–spring development was monitored. In the spring of both years, *U. spinicarpa* females reached maximal ovarian development earlier than *U. longisignalis*. As expected with entry of small maturing females to the sampled population (Fig. 2), spring–summer ovarian development appeared to be less smoothly incremental in *U. spinicarpa* than in *U. longisignalis*, the latter of which (Fig. 5) appeared to show a slower, winter–spring, incremental development of ovaries presaging the major egg-laying event in June 1992 (Figs. 1 and 7B).

The more pronounced peaks in ovarian development evident in winter–spring of 1993 (Fig. 5), especially those for *U. spinicarpa*, may indicate little more than some delay in initiation of egg-laying, resulting in more females with well-developed ovaries because fewer had laid early egg masses. However, the relative weights of these gonadal tissues (Figs. 6A and 7A) are significantly greater in the 1993 peaks, so it cannot be ruled out that some nutritional or other physiological factor also enhanced gonadal growth in the second season. In both species (Figs. 6B and 7B), egg-laying appeared to be initiated gradually in 1992 but more

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Fig. 1. Size-class (carapace width) frequency distributions among monthly samples of 50 active animals including males (open bars), nonovigerous females (hatched bars), and ovigerous females (solid bars) of *Uca longisignalis* from Joseph's Harbor, Louisiana.



abruptly in 1993. For both species in 1993, and for *U. spinicarpa* in 1992, the ovaries of a high percentage of females were heavily mature (dark red) immediately prior to the first evidence of egg-laying. Egg-laying thereafter commenced with the occurrence of high percentages of ovigerous females. By contrast, the more protracted period of ovigery for *U. longisignalis* in 1992 was also evident in the relatively lower percentages of ovaries that were mature prior to this period (Fig. 7B).

In addition to other differences in periodicity and pattern of reproduction, *U. longisignalis* and *U. spinicarpa* apparently differ in fecundity (Fig. 8; Table 1). Numbers of eggs in egg masses from ovigerous females of both species were proportional to carapace widths, but total egg numbers differed markedly between the species. *U. longisignalis* averaged near 20,000 per female and occasionally exceeded 45,000 per female, while in *U. spinicarpa*, they averaged less than 10,000 and did not exceed 25,000. Maximum numbers typically occurred in females over 20 mm in carapace width in *U. longisignalis*, and in females 12–15 mm in carapace width in *U. spinicarpa*, reflecting the difference in mature sizes of these animals. In addition to eggs being more numerous in egg masses, the freshly deposited eggs of *U. longisignalis* were individually smaller than those of *U. spinicarpa* (Table 1) and, over the course of development to a stage just before hatching (gray in color), they increased more markedly in size than did those of *U. spinicarpa*.

### Discussion

Ranges of the Gulf of Mexico endemic species *U. longisignalis* and *U. spinicarpa* both encompass warm-temperate environments. *U. longisignalis* is relatively restricted to these habitats in the northern Gulf of Mexico where temperatures are similar to those of the Carolinian biogeographic province on the Atlantic Coast. While *U. spinicarpa* is sympatric with *U. longisignalis* over most of this range (from about 31°N to 26°N), its western Gulf limits appear to extend much further south (to about 18°N) into fully tropical coastal habitats of Tabasco, Mexico, in the southwestern Gulf of Mexico (Barnwell and Thurman 1984; D. L. Felder unpublished data). Systematic affinities of these two Gulf of Mexico species also differ (Crane 1975). *U. longisignalis* is apparently derived from a similar lineage as *U. minax* and *U. pugnax*, members of the subgenus *Minuca* that tend to be temperate to warm-

temperate in distribution. *U. spinicarpa* is most closely related to a sibling species of the subgenus *Celuca*, *Uca speciosa*, which is distinctly tropical in distribution (Barnwell and Thurman 1984). Thus, both by virtue of current range and probable lineage, the two Gulf endemics may be contrasted as the more temperate form, *U. longisignalis*, and the tropical form, *U. spinicarpa*.

The significance of this difference, as manifest in the timing of the reproductive cycle, may relate to many aspects of ovarian development, egg laying, and recruitment. While many nearshore decapods adapted to temperate regions appear to restrict ovarian development and egg production to relatively narrow temperature optima of spring and summer, tropical and subtropical forms often have more extended periods of reproduction, without peaks that are obviously defined primarily by temperature optima (Sastry 1983; Steele 1988; Bauer 1992). When such species occur sympatrically in warm-temperate habitats, the relatively less conserved reproductive timing of the tropical species may be evident in earlier, prolonged, or repeated cycles of egg production, production of eggs by marginally mature females, and production of early eggs that are not viable (Felder 1982).

In keeping with putative affinities of the species, the reproductive cycle of *U. spinicarpa* appears to show at least some evidence of a less-temperate adaptation. Ovarian development commenced much earlier, females first carried eggs at much smaller sizes, eggs were produced earlier in the year, and ovarian development was somewhat episodic over a long period of the late winter to summer months. Extended breeding periods with multiple peaks are found in two tropical *Uca* species in southwestern India (Pillay and Nair 1968, 1971) and seasonality is not evident in three tropical species from Panama (Zucker 1978).

By contrast, the reproductive cycle of *U. longisignalis* shows more evidence of seasonal restriction, with later ovarian development, earliest egg-laying delayed to late spring, and peak occurrence of ovigerous females in summer. Even AFDW, used as a measure of variation in tissue resources of this species over the course of the year, appeared to vary precisely in phase with the seasonally delimited reproductive peak, and the pattern was evident in both males and females. The control of such peaks, regardless of whether they occur in AFDW, sexual displays or some index of

Fig. 2. Size-class (carapace width) frequency distributions among monthly samples of 50 active animals including males (open bars), nonovigerous females (hatched bars), and ovigerous females (solid bars) of *Uca spinicarpa* from Joseph's Harbor, Louisiana.

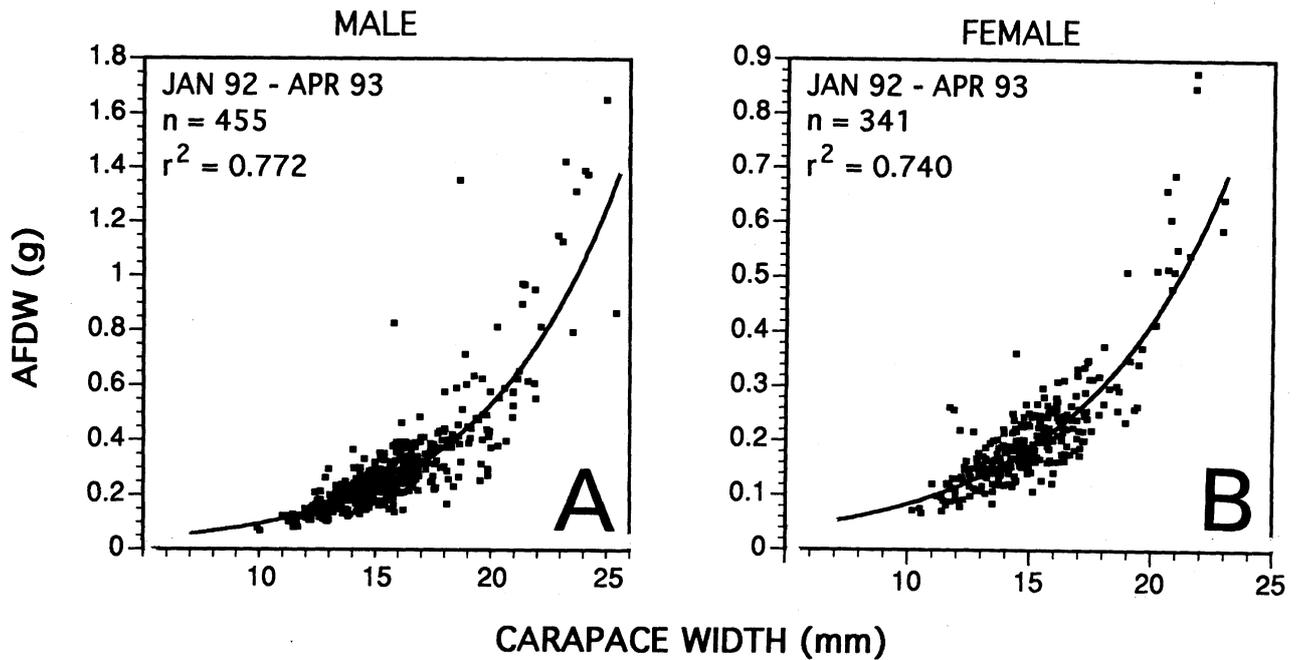
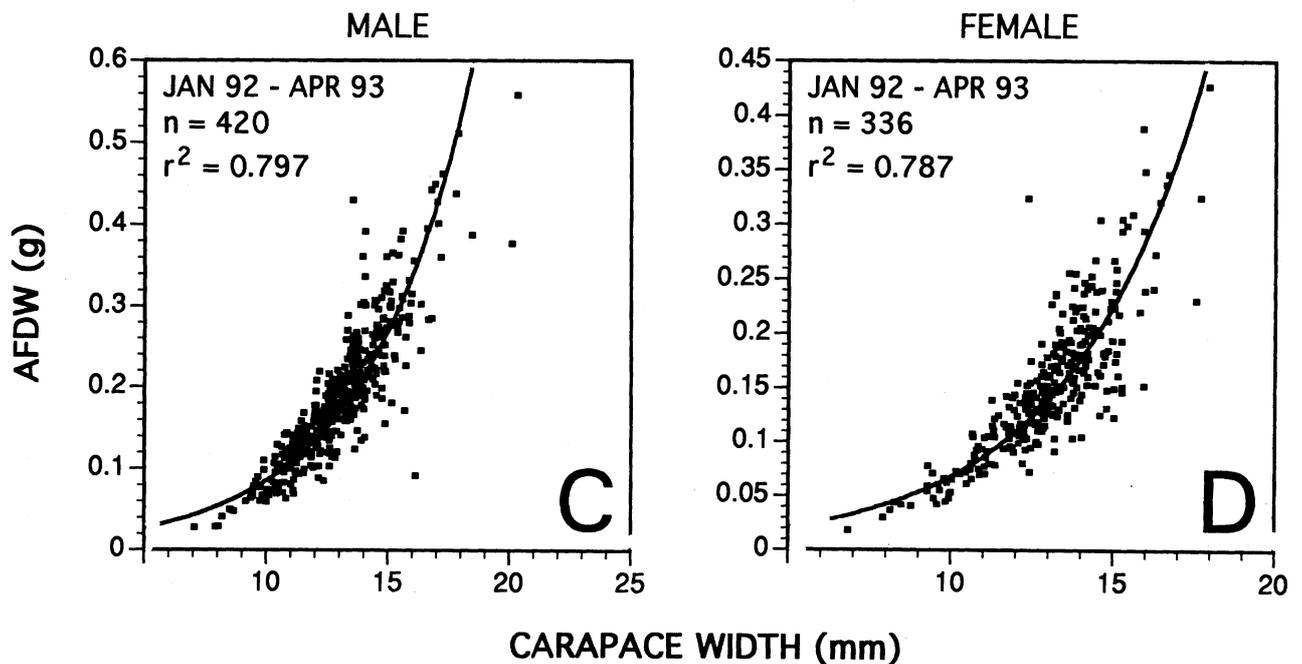
*UCA LONGISIGNALIS**UCA SPINICARPA*

Fig. 3. Curvilinear relationship (exponential fit) of ash-free dry weight (g) to carapace width for A) males of *Uca longisignalis*, B) females of *Uca longisignalis*, C) males of *Uca spinicarpa*, D) females of *Uca spinicarpa*. For females, weights include ovaries, and for ovigerous females, weights include egg masses.

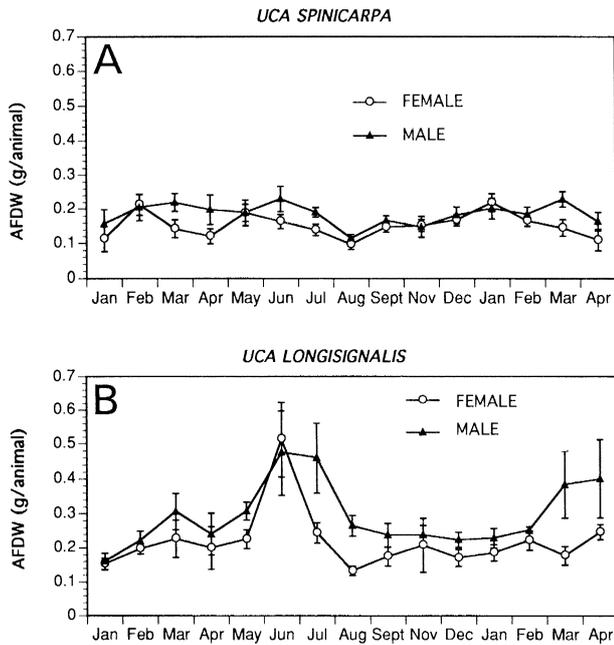


Fig. 4. A) Mean ash-free dry weight (AFDW, in g) for males and females of *Uca spinicarpa*, January 1992–April 1993. B) Mean AFDW for *Uca longisignalis* males and females, January 1992–April 1993. For females, weights include ovaries and for ovigerous females, weights include egg masses. Sex ratio for sample of 50 animals each month is as shown in Figs. 1 and 2; vertical lines define 95% CI.

ovarian development, is almost certainly linked to temperature. However, there is little direct evidence of the specific temperature-modulated control mechanisms or their synergy with mechanisms controlling circatidal (or semilunar) and circadian rhythms in these and other intertidal species (Brown et al. 1953; Barnwell 1966; von Hagen 1970; Zucker 1976; Christy 1978; Zimmerman and Felder 1991). What is evident is that for any given species ranging from temperate to warm-temperate habitats, activity and reproductive periods are, within some range, shorter at colder latitudes and longer in the warmer (Pearse 1912; Hyman 1922; Crane 1943, 1975; Williams 1965, 1984; Herrnkind 1968; Salmon and Astaides 1968). For the same species, spawning periods constrained to July and August in Massachusetts and New York (above 40°N), may extend from May to September at slightly lower latitudes. Molting in marsh fiddler crabs, which is temperature-dependent and may be inhibited at temperatures below 20°C (Passano 1960; Miller and Vernberg 1968; Weis 1976), may serve as a primary modulator of the reproductive period.

All aspects of activity, rather than just spawning, are under latitudinally varied seasonal influence in the intertidal temperate to warm-temperate spe-

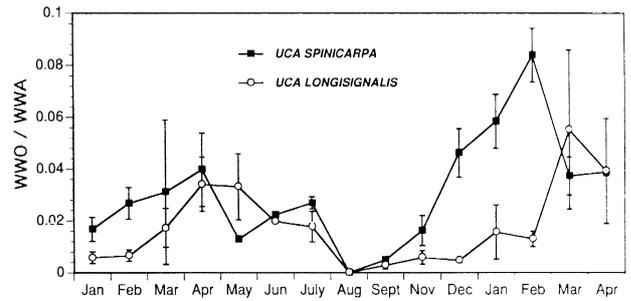


Fig. 5. Relative ovarian development in all females of *Uca longisignalis* and *Uca spinicarpa* collected from January 1992 through April 1993, including those with undeveloped or trace weights of ovaries. WVO = wet weight ova; WWA = wet weight animal. Sample for each month consists of combined nonovigerous and ovigerous females shown in Figs. 1 and 2; vertical lines define 95% CI.

cies. For example, at sites in Maryland (just above 37°N latitude), *U. minax* has been reported to overwinter in a state of continuous torpor in burrows below the frost depth from October to late April (Gray 1942), a behavior unknown in southern extremes of the population. In the warm-temperate to tropical species *Uca panacea*, a wide-ranging en-

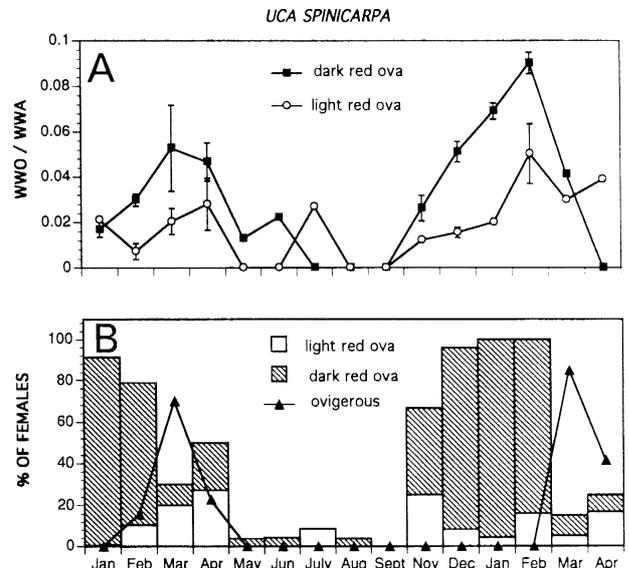


Fig. 6. A) Relative ovarian development expressed as unit ovary wet weight (WVO) per unit animal wet weight (WWA), in females of *Uca spinicarpa* collected from January 1992 through April 1993; developing females include only those with  $WVO / WWA \geq 0.01$ ; sample is divided between females with light red (less mature) ova and those with dark red (more mature) ova; vertical lines define 95% CI. B) Percentages among developing females defined as those with  $WVO / WWA \geq 0.01$ , of *Uca spinicarpa* with light red developing ovaries and dark red developing ovaries (bars) as compared to percent ovigerous in samples of females from January 1992 through April 1993; total height of each bar indicates total percentage of developing females.

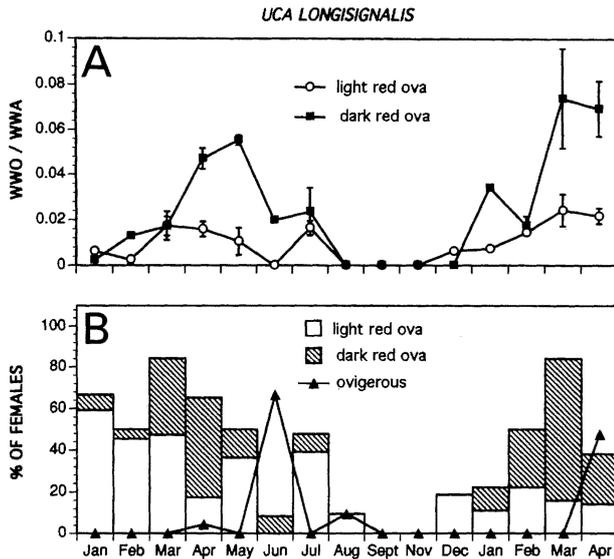


Fig. 7. A) Relative ovarian development expressed as unit ovary weight (WWO) per unit animal wet weight (WWA), in developing females of *Uca longisignalis* collected from January 1992 through April 1993; developing females include only those with  $WWO / WWA \geq 0.01$ ; sample is divided between females with light red (less mature) ova and those with dark red (more mature) ova; vertical lines define 95% CI. B) Percentages among developing females of *Uca longisignalis* with light red developing ovaries and dark red developing ovaries (bars) as compared to percent ovigerous in samples of females from January 1992 through April 1993; total height of each bar indicates total percentage of developing females, defined as those with  $WWO / WWA \geq 0.01$ .

demoid of the Gulf of Mexico, northern Gulf populations (near 28°N) emerge from burrows and feed only sporadically at the surface during winter months, usually only after temperatures have warmed for a 2-d to 3-d period to 22–24°C (Powers and Cole 1976). Even on these occasions it is estimated that no more than 10–40% of populations there emerge to feed actively, at least until warmer conditions prevail in the spring. However, this species is observed to be an active feeder almost year-round where it has been studied in the southwestern Gulf of Mexico (near 19°N; D. L. Felder unpublished data). Thus both temperature-modulated feeding activity and seasonal variation of food resources (abundance and quality, themselves temperature modulated) may serve as a secondary control of maturation rates and timing of ovarian development and egg-laying.

Methodological differences between Genoni (1985) and the present study may account for much of the substantial disparity between reported organic content of AFDW in *U. rapax* (near 65% of DW) and those we have measured for *U. longisignalis* and *U. spinicarpa* (both of which had AFDW nearer 50% of DW). However, as consistent methodology was applied across all treatments during the former study, it nonetheless provides evidence that marsh-dwelling fiddler crabs are food-limited. Where the quantity of decomposing *Spartina* was augmented in the subtropical to warm-temperate marsh habitats of *U. rapax*, there followed not only increases in recruitment and population density,

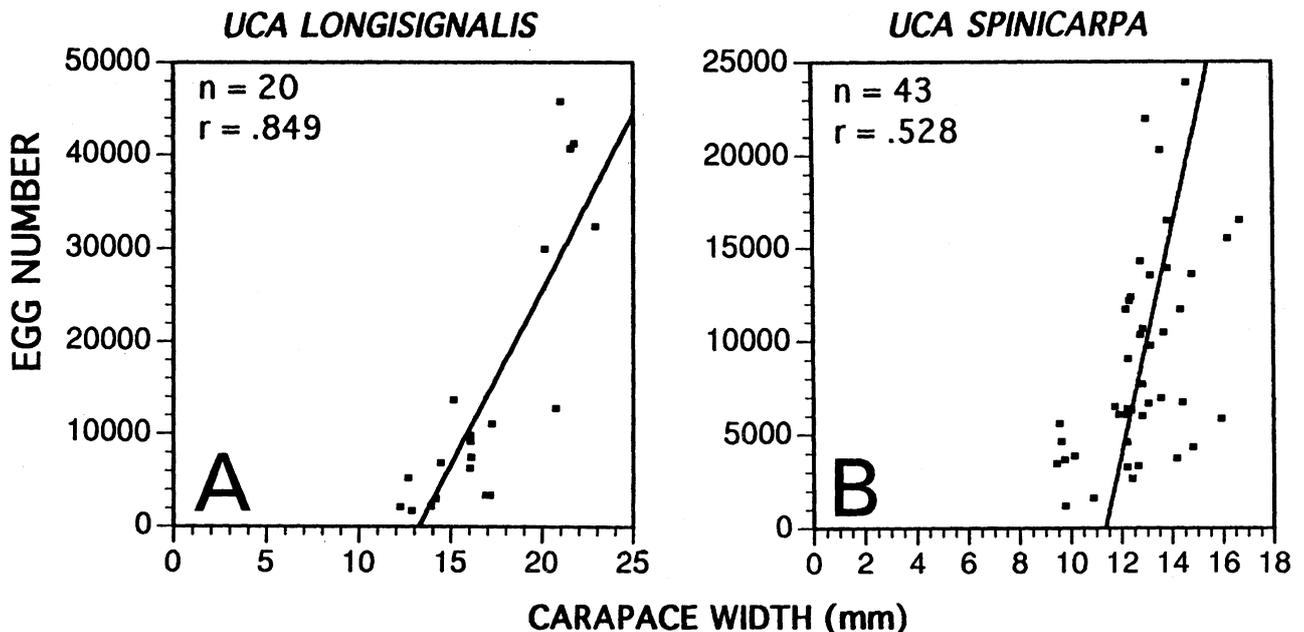


Fig. 8. Regression of egg number on carapace width for ovigerous females of *Uca longisignalis* (A) and *Uca spinicarpa* (B).

TABLE 1. Egg characteristics for sampled ovigerous females of *Uca longisignalis* and *Uca spinicarpa* indicating sample size (n), egg color, mean number of eggs per mg wet weight of egg mass, mean number of eggs per ovigerous female, and mean mg wet weight of individual egg. Means are shown  $\pm$  95% CI. For *Uca longisignalis*, differences are significant between individual weights of dark red and gray eggs (\* =  $p < 0.05$ ). For *Uca spinicarpa*, differences were not significant between individual weights of dark red and gray eggs.

Species	n	Egg Color	Eggs/mg (Wet Weight)	Eggs/Female	mg/Egg (Wet Weight)
<i>Uca longisignalis</i>	13	dark red	456 $\pm$ 200	20,237 $\pm$ 9,357	0.0264 $\pm$ 0.0050*
<i>Uca longisignalis</i>	5	gray	229 $\pm$ 119	4,226 $\pm$ 1,659	0.0769 $\pm$ 0.0342*
<i>Uca spinicarpa</i>	39	dark red	254 $\pm$ 37	8,937 $\pm$ 1,829	0.0365 $\pm$ 0.0063
<i>Uca spinicarpa</i>	4	gray	375 $\pm$ 203	9,387 $\pm$ 4,318	0.0393 $\pm$ 0.0047

but also increases in organic content (AFDW) of the animals (Genoni 1985). Such nutritional feedbacks to the population, particularly where there is direct trophic dependency upon marsh vegetation or detritus that vary seasonally in quantity, could more substantially serve to define timing and rates of maturation, development, and reproduction in marsh-dwelling species like *U. longisignalis* than in clayey bank-dwelling forms like *U. spinicarpa*. The annual cycles of population change in organic weight, growth, and maturation do appear to reflect a pattern for *U. longisignalis* that could be dependent upon seasonal variation in food resources, perhaps with spring vegetational resources being essential to rapid growth and development for reproduction. Annual variations in the quality and quantity of these resources may then also, at least in part, account for the variations we have observed in biomass and reproductive development over 2 yr of study. As fiddler crab burrows enhance the growth of *Spartina* and other marsh vegetation, we suggest that a complex system of feedbacks may exist between burrowing behavior during one season and development for reproductive success in the next.

Differences in egg numbers between *U. longisignalis* and *U. spinicarpa* may or may not be related to fundamental differences in reproductive strategies of these species. From other studies in progress (M. F. Flynn and D. L. Felder unpublished data), it is evident that neither species shows abbreviation of development, as both have five zoeal larval stages. Thus, the more numerous eggs in the egg masses and the smaller size of the initially deposited eggs in *U. longisignalis* do not imply a longer life history, as may be the case in some other species of this genus (see Rabalais 1991). Rather, the developing eggs of the *U. longisignalis* egg mass tend to increase in size more markedly than do those of *U. spinicarpa*, resulting in eggs which are larger at hatch than those of *U. spinicarpa*. This agrees with comparisons of sizes of the first zoeal larvae stages in these two species; *U. longisignalis* consistently has larger zoeal stages

(M. F. Flynn and D. L. Felder unpublished data). While our findings suggest that egg numbers per egg mass also decrease dramatically for *U. longisignalis* over the course of development to the immediate pre-hatch gray-colored stage, we would caution that size differences of the females examined (for which we did not correct) could also account for some or most of this apparent change, as fecundity directly varies with female size in crustaceans (Hines 1982; Somers 1991). Ranges in egg numbers per female for the genus have previously been reported to vary from 1,500 to 94,000 (DeCoursey 1979). Specifically in the Atlantic Coast marsh fiddler, *U. pugnax*, they have been reported to range from 4,500 to 23,700 (Shanholtzer 1973), values very near those we have reported here for *U. longisignalis*.

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