Do Indian River Lagoon Wetland Impoundments (Eastern Florida) Negatively Impact Fiddler Crab (Genus *Uca*) Populations?

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ABSTRACT. Quantitative sampling of fiddler crabs was performed in June–July between 1992 and 1994 along transects at three St. Lucie County mosquito impoundments, Florida, running from the Indian River Lagoon (IRL) shore and across the impoundment perimeter dikes, and in one impoundment across the perimeter ditch. A total of 929 specimens representing four species were found: *Uca pugilator*, *Uca rapax*, *Uca speciosa*, and *Uca thayeri*. The quantitative sampling showed that there was no correlation between the number of *Uca* burrow openings on the sediment surface and the actual number of crabs in the sediment. Differences were recorded in abundance and distributional patterns between impoundments, but no correlation was recorded between substrate organic content and species distributional patterns. The male/female ratio was close to 1 for all species, except for *U. thayeri*; the males dominated for this species (ratio, 1.8:1). High water temperatures potentially lethal to fiddler crabs occurred in the impounded marsh in the summer. *U. pugilator* and *U. rapax* were unlikely to be impacted by the impoundment flooding as they are highly motile and not very site specific. *U. speciosa* and *U. thayeri* were more restricted to the very soft, dark, and wet substrate along perimeter ditch banks and may therefore be impacted during periods of flooding because they are dependent on nonflooded areas for feeding and reproduction.

INTRODUCTION

Burrowing crustaceans, such as fiddler crabs, impact the ecology of associated infaunal communities and, consequently, the ecosystem as a whole (Crane, 1975; Montague, 1982; Dittman, 1996). According to Montague (1980), fiddler crabs are the most abundant macrobenthic crustacean inhabitants of North American estuaries. Their impacts on bioturbation activity and oxygenation of the substrate are considerable (Bertness, 1985). Fiddler crabs may also play an important role in recycling nutrients (Macintosh, 1982; Bertness, 1985). They feed by scraping up and ingesting surface sediment (Crane, 1975; Kraeuter, 1976; Heard, 1982; Macintosh, 1982; Weis and Weis, 2004) and are in that respect very important in overturn of substrates. Fiddler crabs are also an important food source for birds, fish, and mammals (Peterson and Peterson, 1979; Montague, 1980; Grimes et al., 1989; Gilmore et al., 1990). There is a relatively diverse *Uca* species assemblage within the Indian River Lagoon (IRL) region, with seven species reported in the IRL (Salmon, 1967; Kerr, 1976; M. Salmon, Florida

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Atlantic University, personal communication, 1992), four tropical species, *Uca rapax* (Smith), *Uca thayeri* Rathbun, *Uca speciosa* (Ives), and *Uca mordax* (Smith), and three temperate species, *Uca pugnax* (Smith), *Uca pugilator* (Bosc), and *Uca minax* (Le Conte). Only four species were found during these studies: *Uca pugilator*, *U. rapax*, *U. speciosa*, and *U. thayeri*.

That the impoundment of 90% of the marginal wetlands (primarily for mosquito control) of the IRL has a potential negative impact on regional *Uca* populations has been a controversial issue for many years. Each impoundment and the management procedures are described in detail in Rey and Kain (1991). Preliminary studies by Gilmore et al. (1991) revealed that no *Uca* spp. were observed from marsh-mangrove habitats in flooded (short-term and long-term) impoundments, while they were present in large numbers at unimpounded sites adjacent to impoundments. This difference could be associated with a number of factors, because many aspects of the reproduction of *Uca* (including courtship, female receptivity, egg maturation, and hatching) are closely synchronized with the semidiurnal and semilunar tidal cycles (Fingerman, 1957; Barnwell, 1968; Wheeler, 1978; Zucker, 1978; Montague, 1980; DeCorsey, 1983; Salmon et al., 1986). However, according to Fingerman (1957), the tidal rhythm differs between species (*U. pugilator* and *U. speciosa*). The exclusion of natural tidal cycles within several impoundments may therefore have serious impacts on populations of *Uca* spp. In addition, prolonged periods of inundation that usually occur from May to September (management for mosquito control) may displace *Uca* spp., which need periods of exposure of the burrow entrances for survival. Periods of heavy precipitation, mainly during the summer, may also drastically reduce the salinity within these impoundments.

The main objectives of this study were (a) to evaluate survival and adaptation of *Uca* populations to manipulated ecological conditions along the impoundment perimeter ditches (compared with the natural IRL conditions), (b) to determine if these potential adaptations differed among species, and (c) to elucidate zonation patterns of each species (from the IRL shore, across the dike road, down to the impoundment ditch).

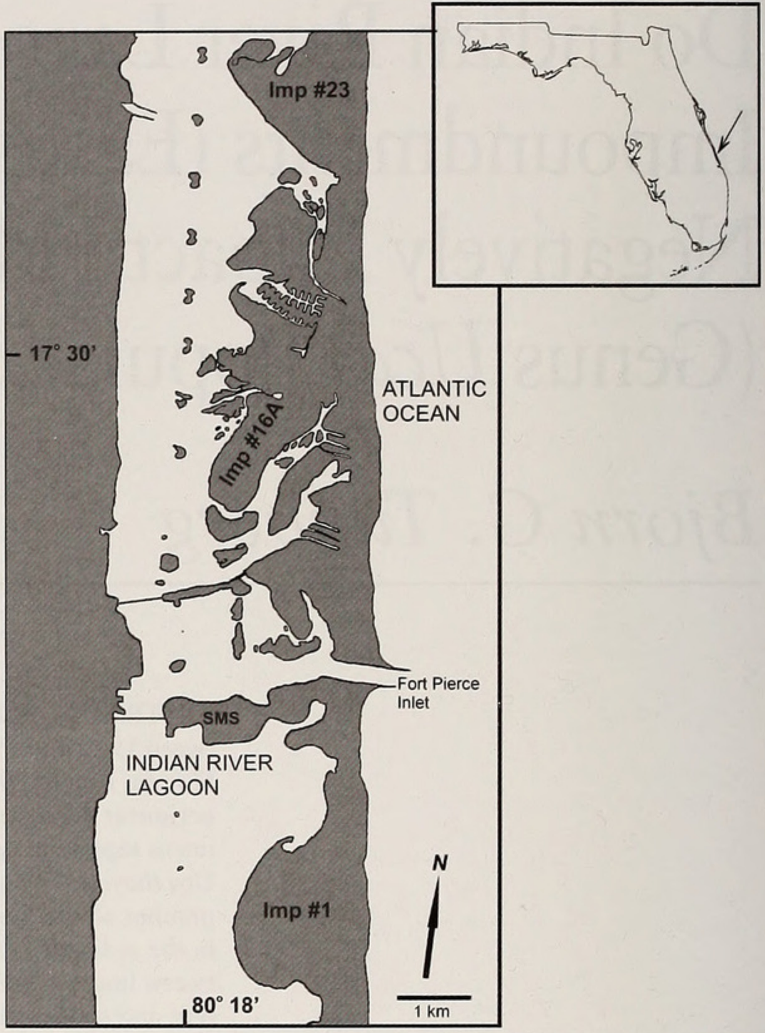

FIGURE 1. The three sampling impoundments (Imp) within St. Lucie County, Florida; SMS = Smithsonian Marine Station.

METHODS

Figure 1 shows the location of the three studied impoundments, which are described in detail in Rey and Kain (1991). Blue Hole Point (impoundment [Imp.] #23) is a 122 ha breached impoundment. The 20 m breach in the western dike allowed natural tidal access between the impoundment and the IRL. This breach was a result of a severe 1981 winter storm and was left open to the natural tidal cycles of the IRL. The main reason for not repairing the breach was that this impoundment could be used as a reference/control site for numerous impoundment studies (James R. David, St. Lucie County Mosquito Control District, personal communication, 1992). Jack Island State Preserve (Imp. #16A) is a 161 ha impoundment divided into four cells. This impoundment was open via culverts to the IRL during the winter months but was artificially flooded during the summer months (early May through August). Bear Point (Imp. #1) is a 255 ha impoundment. Since August 1993, the culverts here were left open to tidal exchange.

Quantitative sampling was performed in these impoundments, Imp. #23 and Imp. #16A in June-July 1992, 1993, and 1994 and Imp. #1 in July 1994 along a portion of transect lines previously established for burrow counts (Gilmore et al., 1991). One transect line had been established in each impoundment. These transects ranged from the edge of the IRL (0 m), continued across the artificial dike, and ended at the impoundment perimeter ditch (Figure 2). Four permanent metal stakes indicated the sampling sites (see below). Because of the very hard substrate on top of the actual dike (the road), it was impossible to sample these sites (10 m and 15 m) quantitatively (see below). The 0 m stake was placed at the waterline (low tide) on the IRL side, and the other three stakes (markers) were placed at 5 m intervals across the dike, with the 0 m stake as the starting point. The 15+ m site was between the 15 m stake and the upper bank of the perimeter ditch (Gilmore et al., 1991; see Figure 2). Additional sites were also established for the studies: site A was at the edge of the water (low tide) on the dike side of the perimeter ditch and site B in the corresponding area of the impoundment marsh side of the ditch (Figure 2). It was not possible to establish a site B in Imp. #16A, because of the summer artificial flooding, or in Imp. #1, because it was flooded naturally. The width of the perimeter ditches was about 5 to 6 m. The ditch shores in all impoundments had a very dense (but only about 1.5 to 2 m wide) mangrove vegetation (primarily *Rhizophora mangle*). Two additional sites were established in Imp. #23: site C, about 2 m into the impoundment marsh from site B, immediately behind the dense mangrove vegetation along the ditch shore (see Figure 2), and site D on the sand flat within the marsh (25 m from the ditch). The distance from site 0 m to site C was about 25 m and to site D about 47 m. The sampling sites were 2 × 2 m permanent squares situated at each marker (sites 0 m, 15+ m, C, and D), within which four replicate samples were randomly collected on each sampling date. Sites A and B were sampled the same way (on the exposed substrate at low tide) close to the dense mangrove vegetation at each side of the perimeter ditch. The Imp. #23 impoundment marsh was never flooded during my studies. The random sampling was performed by means of a stainless steel cylinder (0.1 m^2, 40 cm high) with a sharpened bottom edge. Sampling was always performed at low tide and when no, or very few, specimens were observed on the sediment surface. Sampling was never performed when many crabs were observed out of their burrows. Sampling at such times would have resulted in erroneous quantitative results because *Uca* spp., when disturbed on the sediment surface, seek shelter in the closest burrow or even migrate out into the water. The cylinder was forced down to a sediment depth of at least 25 cm. The number of *Uca* burrows within the cylinder area was recorded, and then the sediment was removed with a shovel (with a straight edge). The uppermost fraction (0–10 cm) was sieved (in the field) in seawater through a 2 mm stainless steel mesh sieve. In the remaining fraction (10–25 cm) the crabs were removed by hand in the field. This procedure was deemed acceptable as small crabs only occurred in the uppermost layer of the sediment. The specimens were transferred to plastic bags and kept in a cooler in the field. In the laboratory, the samples were either processed immediately or stored in a freezer for later processing. The crabs were sorted by hand in a tray filled with seawater. They were then placed in labeled glass jars in a solution of 5% borax-neutralized formalin, diluted in seawater. After 4 to 5 days the formalin was replaced with 70% ethanol. All specimens larger than 5 mm carapace width (CW) were later identified and weighed (wet weight) and have been archived for possible future studies. All individuals smaller than 5 mm were regarded as "juveniles." It was not possible to identify these to species level with certainty. The literature sources used for species determination were Tashian and Vernberg (1958), Salmon (1967), and Crane (1975). A total of 140 quantitative samples were collected during the entire study period: 84 in Imp. #23, 40 in Imp. #16A, and 16 in Imp. #1.

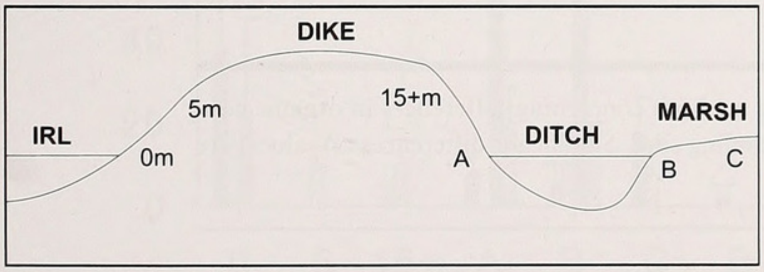

FIGURE 2. Cross section of a typical mosquito impoundment in the Indian River Lagoon (IRL), showing locations of the fiddler crab sampling sites. The dike road was approximately 1.5 m above low tide level in the IRL at three investigated sites (site D is not shown).

Water temperature was measured midafternoon on 26 July 1993 and 1 August 1994 within the marsh of Imp. #16A (which was artificially flooded), in the middle of the adjacent perimeter ditch, and in the IRL (about 5 m from the shore). The measurements were taken at 5 cm water depth.

Because many impoundments are closed for natural tidal exchange to the estuarine waters of the IRL during the artificial flooding periods (impoundment pumps), salinity may drop rapidly during periods of heavy rainfall.

An experiment was therefore performed to investigate tolerance to rapid salinity changes among the four *Uca* species. The laboratory setup consisted of twenty 2 L round plastic containers equipped with a lid. A separate air supply was provided to each container. Four treatments and one control (four replicates per treatment) were established: 100%, 75%, 50%, 25%, and 0% seawater. Laboratory-supplied seawater was diluted with distilled water. The salinities of the different treatments were 100% = 36–37 ppt (parts per thousand), 75% = 27–29 ppt, 50% = 19 ppt, 25% = 9–10 ppt, and 0% = 0 ppt, measured with an ocular refractometer. The water temperature was very stable during the experimental period, 24.0°–26.0°C. Each experiment lasted for seven days. The crabs were collected 48 hours before each experiment and acclimated in 100% aerated seawater during this period. Seven randomly selected female crabs of each species were placed in each experimental container. It was not possible to find enough specimens of *U. thayeri* during the period for these studies. Therefore only 25% and 0% seawater were used as treatments, and each replicate contained five crabs. The experiments were monitored twice a day, and any dead crabs were removed. Water was changed only in the containers where dead crabs were found. These experiments were performed between 4 July and 27 July 1994.

Sediment samples for analysis of organic content (loss on ignition) were collected in 1994 along the three transects. Three sediment cores (inner diameter, 30 mm) were collected to a depth of 5 cm at randomly chosen points at each site. As stated above it was not possible to establish a site B in Imp. #16A or in Imp. #1. The sediment was treated in the laboratory according to the procedures described in Holme and McIntyre (1971).

A one-way analysis of variance (ANOVA) (Holm–Sidak method) was performed to compare the respective monitored sites in the three impoundments regarding organic content (LOI) in the sediment (Table 1).

RESULTS

ABUNDANCE

Abundance data from the three transects sampled in 1992, 1993, and 1994 at Imp. #23 and Imp. #16A are presented in Figures 3 and 4, and the one transect sampled in 1994 at Imp. #1 in Figure 5. High water levels prevented sampling 0 m (IRL) at Imp. #16A in 1992 and site A (ditch shore) in 1994.

The results from Imp. #23 were similar the three sampling years (Figure 3). *U. pugilator* and *U. rapax* were relatively evenly distributed across the transect, and a few specimens of *U. rapax* were sometimes observed on the dike road (DIKE; see Figure 2). *U. speciosa*, the dominant species, was found only at site 0 m, and in very high densities in the wet, soft, and dark mud on both sides of the perimeter ditch (sites A and B). *U. thayeri* was also found on both sides of the perimeter ditch (sites A and B), in addition to a few specimens at site 0 m in 1992.

In contrast, at Imp. #16A (Figure 4), *U. pugilator* dominated in abundance at site 5 m whereas *U. rapax* was most abundant at site A (perimeter ditch shore). *U. speciosa* was almost exclusively found at site A and *U. thayeri* at site 0 m.

At Imp. #1 the distributional patterns were similar to the other impoundments. However, *U. pugilator* was found in comparatively low densities, whereas *U. rapax* was abundant at both sites 0 m and 5 m. *U. speciosa* was found in high densities in the wet muddy areas at site 0 m and at site A. *U. thayeri* was found at the 0 m site and to even a greater extent at site A (dike side of the ditch).

No statistical tests were performed to elucidate any potential difference between years at each site, but it was of higher interest to statistically compare abundance patterns between impoundments. Therefore, correlation analyses (Pearson product moment correlation) were performed on the mean abundance data (1992, 1993, 1994) for sites 0 m

TABLE 1. One-way analyses of variance (Holm–Sidak method) concerning differences in organic content (LOI) between the different impoundment and sampling sites. Significant differences (*P* values) are in ***bold italic***.

	Site					
Impoundment no.	0 m	5 m	15+	A	C	D
23 vs. 16A	***0.025***	0.068	0.158	***0.0002***	***0.0001***	***0.001***
23 vs. 1	0.148	***0.044***	0.123	0.124		
16A vs. 1	***0.004***	***0.003***	***0.014***	***0.00006***		

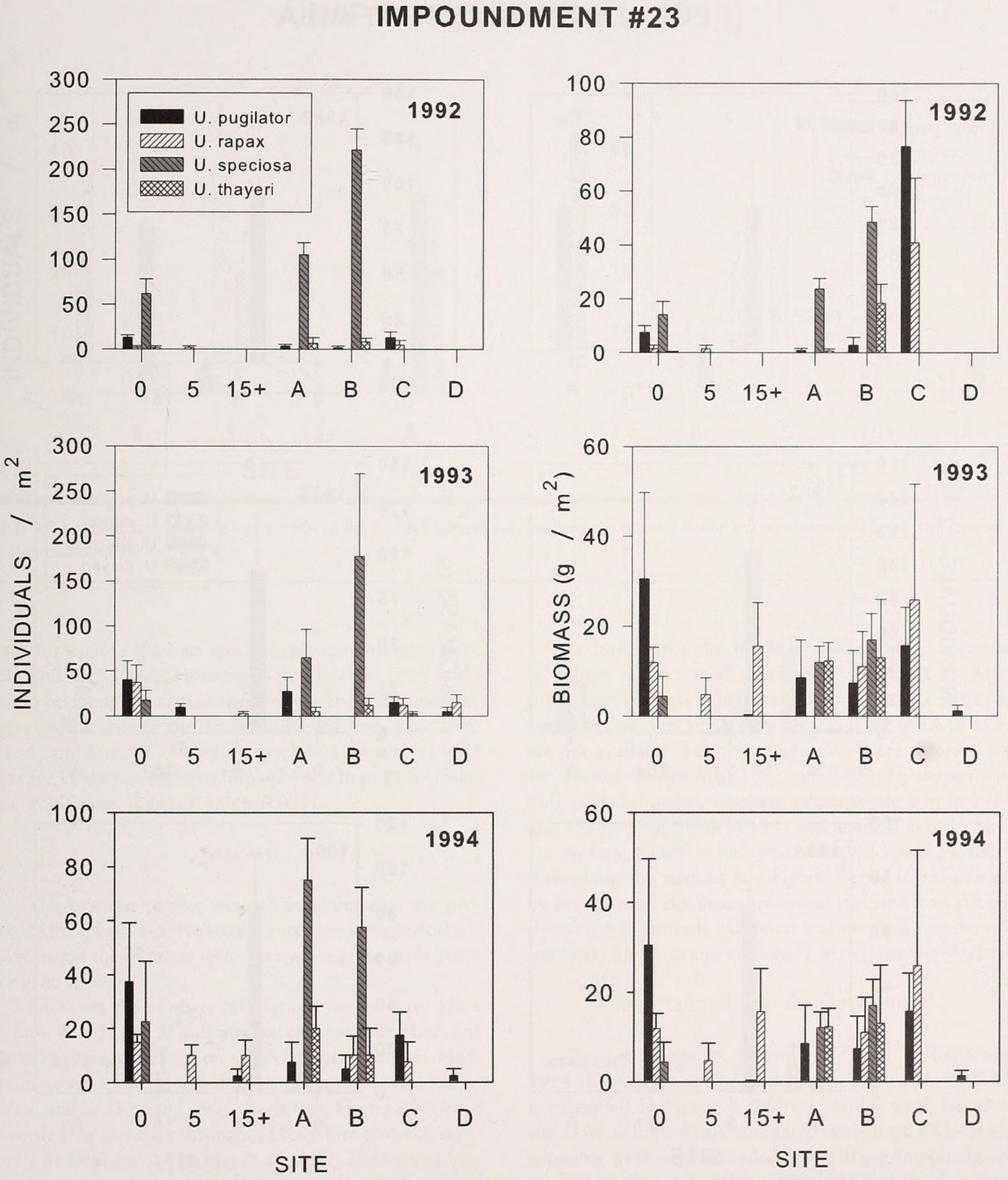

FIGURE 3. Abundance and biomass (wet weight) between 1992 and 1994 of the four fiddler crab species along the impoundment #23 transect. Error bars represent + standard error values ($N = 4$). Note the different scaling on the *y*-axes.

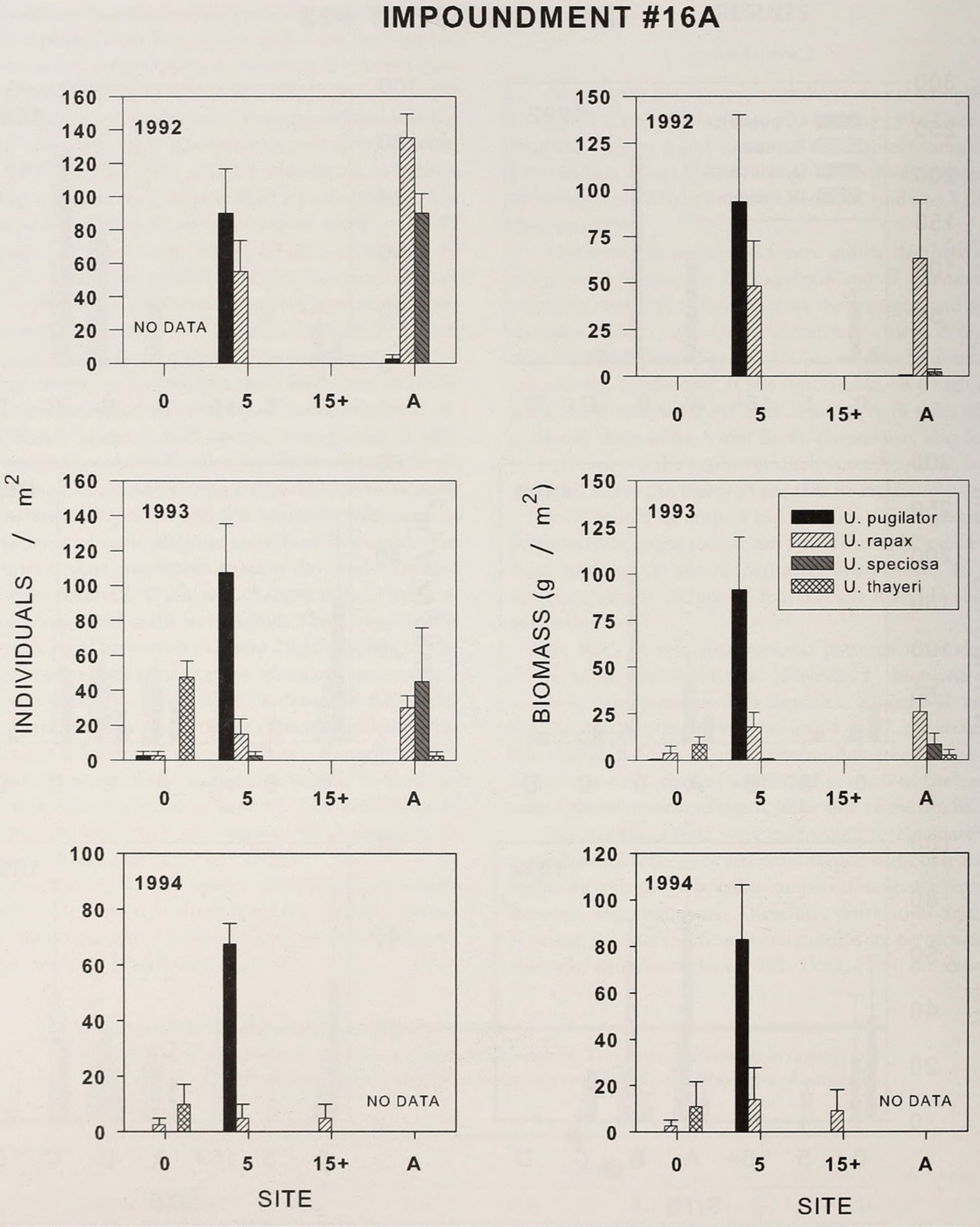

FIGURE 4. Abundance and biomass (wet weight) between 1992 and 1994 of the four fiddler crab species along the transect within impoundment #16A. Error bars represent + standard error values ($N = 4$). Note different scaling on y-axes.

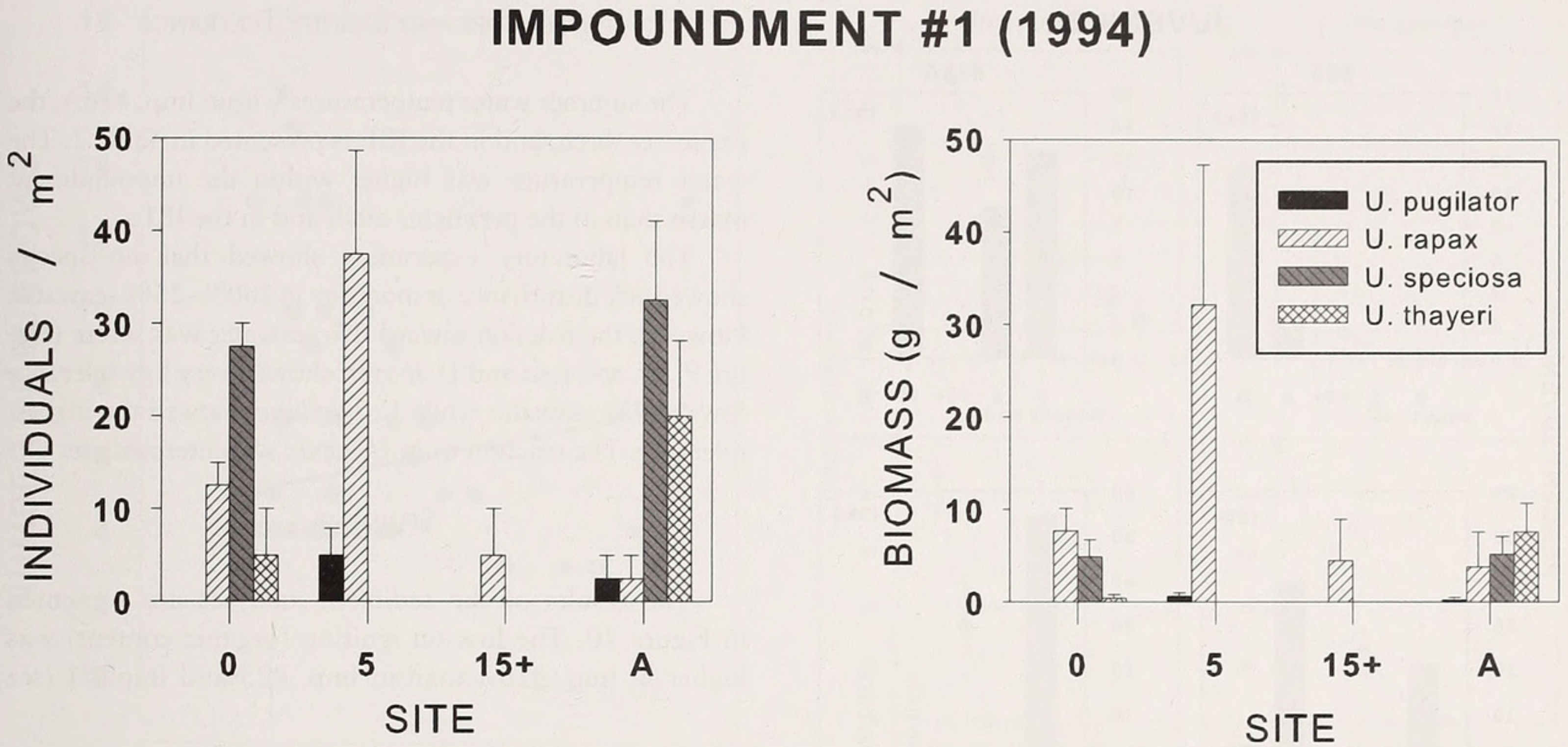

FIGURE 5. Abundance and biomass in 1994 of the four fiddler crab species along the transect within impoundment #1. Error bars represent + standard error values ($N = 4$).

to A for each of the four species separately between Imp. #23 and Imp. #16A. However, no correlation ($P > 0.05$) could be found for any of the species. The same analyses were performed for the 1994 data from Imp. #23, Imp. #16A, and Imp. #1. The only correlation (positive) found was for *U. thayeri* between Imp. #23 and Imp. #1 (correlation coefficient, 0.968; *P* value, 0.031).

BIOMASS

The biomass (g wet weight) measurements are presented in Figures 3–5. No significance tests were performed concerning the biomass difference among the three years for each species.

However, the biomass calculations for the three years in Imp. #23 (Figure 3) indicate that changes took place, but these changes are based on subjective observations. High biomass values were recorded for *U. pugilator* in 1992 at site C and in 1993 and 1994 at site 0 m. High values were recorded for *U. rapax* throughout the entire transect, especially in 1993 and 1994, except at site D. The highest biomass values for *U. speciosa* were recorded on both sides of the perimeter ditch (sites A and B), especially on the marsh side of the ditch (site B). High *U. thayeri* biomass values were recorded along the perimeter ditch (sites A and B).

At Imp. #16A the biomass values for *U. pugilator* were high at site 5 m all three years (see Figure 4). Relatively high biomass values were recorded for *U. rapax* at sites 5 m and A in 1992. However, data for site A in 1994 are not available. Low biomass values were recorded for *U. speciosa* at site A in 1992 and 1993. *U. thayeri* was only recorded at low biomass values at site 0 m in 1993 and 1994 and at site A in 1993 and at site 0 m in 1994.

At Imp. #1 low values were observed for *U. pugilator* throughout the transect (see Figure 5), but *U. rapax* was, by far, the most dominant (biomass) species across the entire transect. The only exception was site A, where the values for *U. speciosa* and *U. thayeri* were somewhat higher.

REPRODUCTION AND SEX DISTRIBUTION

The percentage of "juveniles" found in 1993 and 1994 at the different sites within Imp. #23 and Imp. #16A is presented in Figure 6. More juveniles were found at site 0 m at Imp. #16A compared with Imp. #23. Many juveniles were also recorded along these impoundment ditch shores (sites A and B in Imp. #23 and site A in Imp. #16A). The sex distribution among adults of the four species from the 1992, 1993, and 1994 (combined) collections (June–July) is presented in Figure 7 with the number

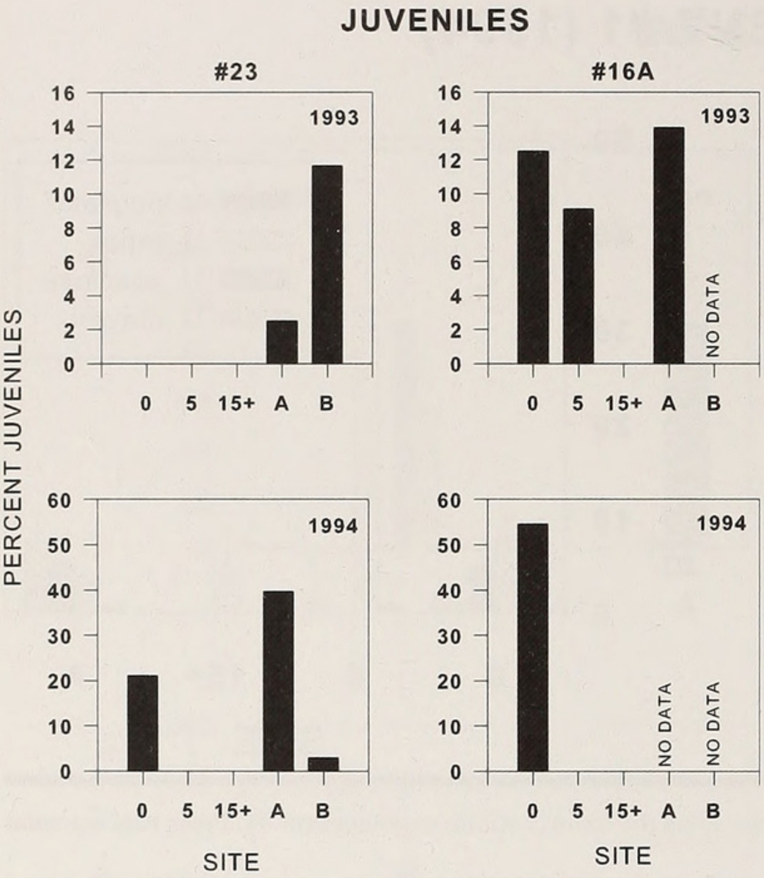

FIGURE 6. Percentage specimens having a carapace width (CW) less than 5 mm (juveniles) of all collected individuals of *Uca* spp. from each site in 1993 and 1994. Note different scaling on *y*-axes.

of ovigerous females. As shown, the sex ratio was near to 1.0 among all four species except for *U. thayeri* where the male/female ratio was approximately 1.8:1. The highest ovigerous rate was found among *U. pugilator* (22.0%) and the lowest among *U. rapax* (3.4%). The corresponding figures for *U. speciosa* and *U. thayeri* were 6.9% and 10.0%, respectively.

BURROWS

The correlation between the number of burrows and the actual number of crabs found within each sample in 1992 and 1993 is presented in Figure 8. A Wilcoxon signed-rank test showed that there was no correlation between these two parameters: $P = 0.097$ (linear regression: $R^2 = 0.02$, P [analysis of variance] $= 0.23$). This finding has also been reported by Colby and Fonseca (1984). The same lack of correlation was also found by the author in a larger and more detailed multiyear study at Merritt Island impoundments (close to Cape Canaveral, eastern Florida.).

TEMPERATURE AND SALINITY TOLERANCE

The summer water temperatures within Imp. #16A, the perimeter ditch, and in the IRL is presented in Table 2. The water temperature was higher within the impoundment marsh than in the perimeter ditch and in the IRL.

The laboratory experiment showed that no species showed any disturbance or mortality in 100%–25% seawater. However, the reaction toward 0% seawater was severe (Figure 9). *U. speciosa* and *U. thayeri* showed very low tolerance toward 0% seawater while *U. pugilator* showed the highest tolerance. The reaction from *U. rapax* was intermediate.

SEDIMENT

The results of the sediment analyses are presented in Figure 10. The loss on ignition (organic content) was higher in Imp. #16A than in Imp. #23 and Imp. #1 (see

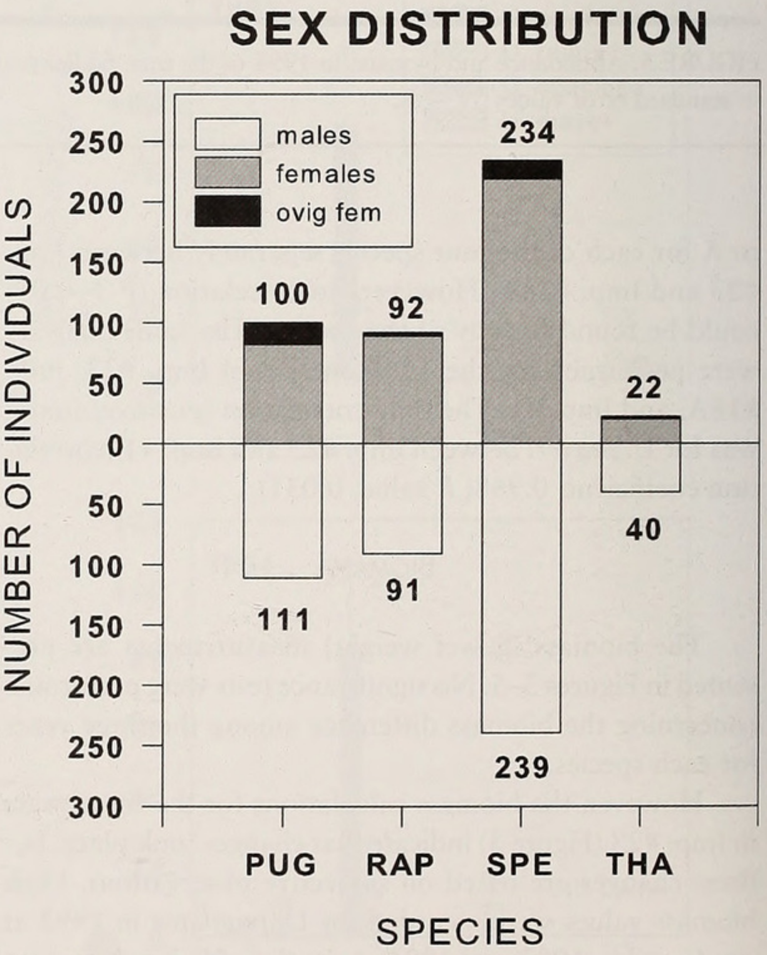

FIGURE 7. Sex distribution of all fiddler crab individuals larger than 5 mm collected during 1992–1994 combined within impoundments #23, #16A, and #1. The bars show sex distribution for each species found throughout the study period; PUG = *Uca pugilator*; RAP = *U. rapax*; SPE = *U. speciosa*; THA = *U. thayeri*.

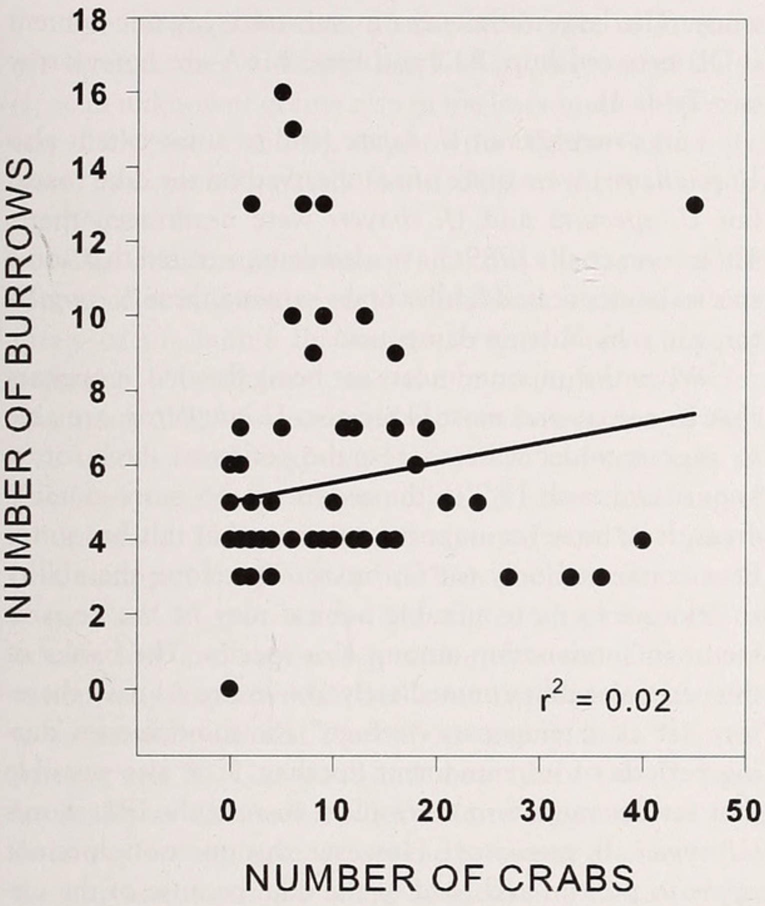

FIGURE 8. Relationship between number of burrows and number of fiddler crabs found in each quantitative sample.

Table 1). The lowest values on the IRL side (site 0 m) were recorded from Imp. #1 and the highest from Imp. #16A. At the ditch (site A) the highest organic value was recorded at Imp. #16A and the lowest at Imp. #1. Within the marsh (site C) (Imp. #23 and Imp. #16A only), the loss on ignition was very high within Imp. #16A and very low within Imp. #23. As indicated in Table 1, Imp. #16A deviated significantly the most from the other two impoundments, with generally the highest organic content (LOI).

TABLE 2. Water temperatures (°C, 5 cm water depth) at impoundment site #16A, measured in midafternoon during July 1993 and July 1994.

Location[a]	1993	1994	Mean
Marsh	44.3	42.4	43.4
Ditch	37.1	36.1	36.6
IRL	37.5	35.2	36.4

[a] Marsh = impoundment marsh; ditch = impoundment perimeter ditch; IRL = Indian River Lagoon.

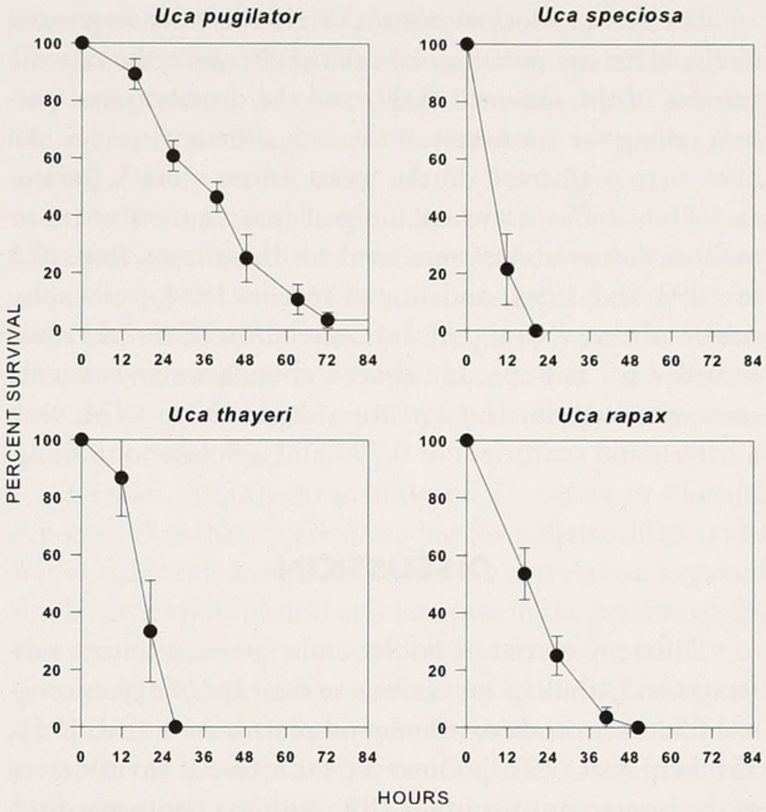

FIGURE 9. Percent survival in fresh (distilled) water of the four fiddler crab species. Error bars represent standard error values ($N = 4$).

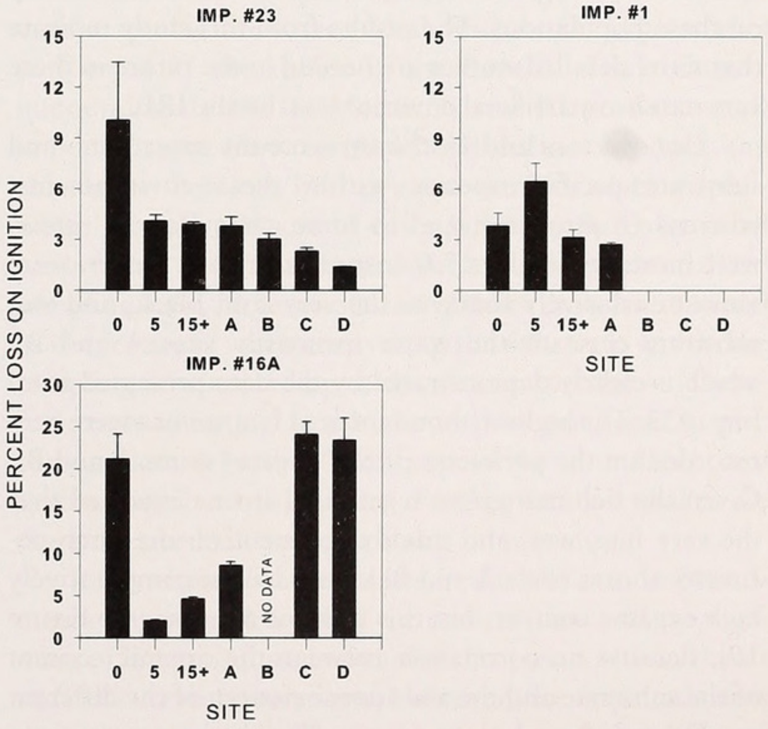

FIGURE 10. Sediment organic content (percent weight loss on ignition) at the sampling sites within the three impoundments in 1994. The error bars represent standard error values ($N = 3$). Note different scaling on y-axes.

Pearson product moment correlation tests were used to elucidate any potential correlation between the organic content of the sediment (LOI) and the distributional pattern (along the transects) of the four different species. All tests were performed on the mean values of each parameter. Only transects where a significant amount of information was available were used for these tests: Imp. #23 in 1993 and 1994, and Imp. #16A in 1994 (see explanation above). No significant correlation ($P > 0.05$) was recorded for any species between abundance and organic content, except for *U. pugilator* at Imp. #23 in 1994, with a correlation coefficient of 0.797 and a P value of 0.032.

DISCUSSION

Different species of fiddler crabs prefer different substrates and salinities for reasons of their specific physiological tolerances and environmental preferences (Teal, 1958; Vernberg et al., 1973). However, the artificial environment of the impoundments in the IRL, with the perimeter ditch and dike, poses a completely new, different type of environment for the *Uca* populations. The occurrence and distributional patterns of the different species of fiddler crabs in these impoundment dikes and perimeter ditches have not been investigated earlier, so this is a first basic study on these populations. The results from this study indicate that more detailed studies are needed in the future in these very extensive artificial environments in the IRL.

Uca speciosa and *U. thayeri* were the most "site- and substrate-specific" species within these environments, whereas *U. pugilator*, and in some cases also *U. rapax*, were more "generalists." *Uca speciosa* and *U. thayeri* were almost exclusively found in the very soft, black, and wet substrate close to the water (primarily sites A and B), which is clearly demonstrated by the data presented from Imp. #23. The highest abundances of *U. speciosa* were here recorded on the perimeter ditch "shores" (sites A and B). Given the rich mangrove vegetation, it was expected that the very fine, wet, and muddy sediment on the ditch perimeter shores (sites A and B) would have a comparatively high organic content, but this was not the case (see Figure 10). Because no correlation between the organic content of the substrate and the abundance pattern of the different species were found, the grain-size distribution, water content, the chemical content of the sediment, root mat density, physiological tolerances, and interspecific interactions may be more important factors in fiddler crab distributional patterns (Teal, 1958; Ringold, 1979; Bertness and Miller, 1984). No root mat areas were investigated in this study. The large differences in substrate organic content (LOI) between Imp. #23 and Imp. #16A are noteworthy (see Table 1).

Large numbers of *U. rapax* (and to some extent also *U. pugilator*) were quite often observed on the dike roads, but *U. speciosa* and *U. thayeri* were never seen there. Thompson et al. (1989) have also demonstrated that some species of desiccated fiddler crabs, among these *U. pugilator*, can rehydrate on damp sand.

When the impoundments are being flooded, it appears that *U. rapax*, and most likely also *U. pugilator*, are able to migrate under water, across the perimeter ditch (often anoxic and with H_2S in the sediment), to more suitable areas. It is, however, important to note that this has so far been confirmed only for *U. rapax*. Therefore, the ability to relocate to more suitable habitat may be the decisive factor in survivorship among *Uca* species. The banks of the perimeter dike (immediately above site A) may therefore act as a temporary "refuge" for some species during periods of impoundment flooding. It is also possible that further migration takes place toward the IRL shores (*U. rapax, U. pugilator*). However, this question does not apply to the rim and road of the dike because of the unsuitable substrate. Furthermore, the distance to the water table is also too great (at least 1 m).

The two species *U. rapax* and *U. pugilator* are probably not adversely affected by impoundment management. Visual observations, and also in situ experiments, have revealed that these species are highly motile within the impoundment areas. According to Thurman (2003) *U. rapax* is typically collected in brackish water. Yoder et al. (2005) have also found that the "herding behavior" in *U. pugilator* is a water-conserving group effect, and this behavior makes them less vulnerable to desiccation. Many specimens of *U. pugilator* and *U. rapax* have been observed (by the author) to migrate over long distances within and outside the impoundments (marked individuals, not reported here). However, further studies need to be performed to clarify these patterns.

Although *U. pugilator* and *U. rapax* thrive in these areas, the fate of the other two species is more uncertain. According to the quantitative sampling results and intensive visual in situ studies, *U. speciosa* and *U. thayeri* are confined to substrate-specific areas of the impoundments, and this may have a negative effect on the populations of these species when the impoundments are being managed (flooded). However, the results from Imp. #16A, which was flooded frequently for mosquito control, seem to contradict this assumption. In spite of this management, a rich community of *U. speciosa* was recorded on the ditch shore (site A), but with low densities of *U. thayeri*.

Even though the data on the occurrence of juveniles are limited, they indicate that fiddler crab reproduction (species unknown) occurs also in the impoundment perimeter ditch (site A and B). As shown in Figure 6, juveniles were, as expected, mainly found close to the water (sites 0 m, A, and B).

The dilution experiments indicate that none of the four species is sensitive to low salinities, a situation that rarely occurs within the impoundments. During this experiment *U. pugilator* was the most tolerant species. Thurman, (2003) investigated the osmoregulation of eight *Uca* species and found that *U. speciosa* and especially *U. pugilator* are able to withstand high "osmotic challenge." Additionally, Thurman (2005) reported that *U. rapax* is best equipped for living in brackish habitats and that *U. thayeri* and *U. speciosa* are best suited physiologically to inhabit low and moderately saline habitats. This observation may explain why the latter two species are able to successfully inhabit the impoundment ditch "shores" (sites A and B). *U. rapax,* and most likely also *U. pugilator* are, as discussed earlier, able to migrate over long distances, for example, across the perimeter ditches (when the impoundments are being flooded) and dikes (studies by the author on ~1,200 of marked *U. rapax* individuals). However, this is most likely not the case with *U. speciosa* and *U. thayeri.* As *U. speciosa* is a comparatively small species, it may therefore be more vulnerable to desiccation than the other three species (Pellegrino, 1984).

High summer temperatures in the shallow impoundment water (see Table 2) pose a threat to the fiddler crab populations. Even though the temperature measurements only were performed twice within Imp. #16A (Table 2), they show that the temperature in the shallow (flooded) areas in the impoundment marsh may reach at least 44°C, which is significantly higher than in the nearby IRL. Large numbers of dead individuals were observed in very shallow water during these high temperature periods (within the marsh of Imp. #16A), but never at lower temperatures, and it was assumed that death was the result of short-term hyperthermia. Replicated laboratory experiments on *U. pugilator* and *U. rapax* collected inside Imp. #23 showed that lethal water temperatures (LD_{50}) on individuals from this area are 41°–42°C. Teal (1958) reported a lethal temperature (LD_{50}) between 39.5° and 40.0°C for *U. pugilator*, *U. minax*, and *U. pugnax*, and Vernberg and Tashian (1959) found that *U. rapax* was more resistant to temperatures of 42°–44°C than was *U. pugnax*. Wilkens and Fingerman (1965) performed a thorough study on lethal temperatures for *U. pugilator* in both saturated and dry air. LD_{50} in saturated air was reached at 40.7°C, which corresponds well to the results from my observations. Powers and Cole (1976) have also demonstrated that burrow temperature decreased rapidly with depth, proving the major heat refuge for *U. panacea* on open sand flats during a study on Mustang Island, Texas. Edney (1961), in a study on a number of fiddler crabs at Inhaca Island, Mozambique, found that the temperature within the burrows during the warmer months was considerably cooler than the sand on the surface. Preliminary results within this study (not presented) also indicate that the temperature drops significantly with sediment depth in the mosquito impoundments.

Genoni (1985), on a study on *U. rapax* in Florida, reported that there were more burrows than fiddler crabs in the sediment. Even if there was no correlation between fiddler crabs (all species) and burrows in the present study, the results were often the opposite from the results by Genoni (1985). Mouton and Felder (1996) investigated the quantitative distribution of *U. spinocarpa* and *U. longisinalis* by quantitatively counting the number of *Uca* burrows along transects in a Gulf of Mexico salt marsh. However, no studies were performed regarding the number of individuals (and species) living in these burrows. Excavating the substrate is a very labor-intensive procedure but obviously necessary to be able to evaluate the actual fiddler crab species distribution and abundance within specific areas (see Methods, above). The studies performed by the author in the three St. Lucie County impoundments and at Merritt Island (Cape Canaveral) impoundments (not reported here) did not produce any correlation between burrows and number of *Uca* specimens. Actually, in several cases when no burrows at all were found on the sediment surface within the 0.1 m^2 sampling area, large amounts of fiddler crabs were found in deeper areas when excavating the substrate within the sampling area according to the description above. Therefore, only counting *Uca* burrows does not seem to give correct data regarding *Uca* population abundance and species distributional pattern. Further detailed studies are therefore needed to elucidate this relationship.

In conclusion, these studies in the St. Lucie impoundments do not indicate that the construction and management of IRL mosquito impoundments pose a serious threat to fiddler crab populations. However, the impoundments may change the distributional patterns of the different species. It is important to note that new, highly suitable habitats were created when the impoundments were constructed, such as the perimeter ditch margins (sites A and B), especially preferred by *U. speciosa* and *U. thayeri* in impoundments with tidal access to the IRL. However, the fate of these two species at the marsh side of the perimeter ditch (site B) during the prolonged artificial summer flooding is still unknown.

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