

## HABITAT AND HOST SPECIFICITY OF TREMATODE METACERCARIAE IN FIDDLER CRABS FROM MANGROVE HABITATS IN FLORIDA

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**ABSTRACT:** Fiddler crabs (*Uca* spp.) are common inhabitants of temperate and tropical coastal communities throughout the world, often occupying specific microenvironments within mangrove and salt marsh habitats. As second intermediate hosts for trematodes, we investigated patterns of host distribution and parasitism for 3 species of sympatric fiddler crabs in mangrove habitats adjacent to the Indian River Lagoon, Florida. Fiddler crab distribution varied among species, with *Uca speciosa* dominating the low and mid intertidal regions of mangrove banks. This species also exhibited higher prevalence and abundance of *Probolocoryphe lanceolata* metacercariae compared with *Uca rapax*, which is relatively more abundant in the high intertidal zone. We conducted a field experiment to test whether *U. speciosa* was more heavily parasitized by *P. lanceolata* as a result of its habitat distribution by raising *U. speciosa* and *U. rapax* under identical environmental conditions. After exposure to shedding cercariae under the same field conditions, all individuals of *U. speciosa* became parasitized by *P. lanceolata*, whereas no *U. rapax* were parasitized, suggesting that differences in parasitism were driven by host selection.

Trematodes target a diverse suite of second intermediate hosts both taxonomically (e.g., arthropods, molluscs, annelids) and ethologically (benthic, pelagic, sessile) (Combes et al., 1994). Although trematodes often use many different species as second intermediate hosts, some host species are infected more frequently, or at higher intensities than other host species, or both (Bush et al., 1993). This pattern may occur because some hosts are more frequently in contact with the infective stages than other hosts, they behave in ways that can increase or decrease their risk of parasitic infection, they vary in their ability to provide metabolic resources necessary for parasite development, or they vary in their immunological ability to eliminate their parasitic infection (Adamson and Cairn, 1994; Combes, 2001; Kirchner and Roy, 2001).

The role of habitat and habitat structure on the distribution of parasites among and within intermediate host populations can play an important role in influencing the probability of contact between the parasite and potential host (Sousa and Grosholz, 1991). For example, Lafferty et al. (2005) showed that prevalence of trematodes in snail intermediate hosts was higher in habitats with vegetative cover, compared with mudflats, suggesting that parasite transmission is higher in habitats that support more final hosts (Hoff, 1941; Robson and Williams, 1970; Sousa and Grosholz, 1991; Esch et al., 1997; Smith, 2001; Hechinger and Lafferty, 2005). Similarly, Skirnisson et al. (2004) found that trematode infections in mud snails were attributed to the habitat use of salt marsh ponds by bird final hosts. Physical factors such as turbulence and storm events can also influence the temporal and spatial distribution of infective stages in the water column, thereby affecting patterns of infection in subsequent intermediate hosts (Fingerut et al., 2003).

In subtropical coastal communities, the zonation of mangroves, which is linked to changes in elevation, tidal influence, and environmental factors (Macnae, 1968; Lugo and Snedaker, 1974), has the potential to affect parasite transmission by affecting the spatial distribution of potential hosts. For example, certain species of fiddler crabs (*Uca* spp.) dominate particular

elevations or soils within mangrove and salt marsh habitats (Teal, 1958; Macnae, 1968). Such habitat selection is influenced by their sediment preferences and their ability to osmoregulate (Teal, 1958; Hartnoll, 1987; Thurman, 2003; Ribeiro, 2005). Furthermore, parasitism by trematodes varies among fiddler crabs, with some *Uca* spp. more readily parasitized than others (Heard, 1976). In mangrove habitats of Florida, differences in parasitism also exist among *Uca* spp. (N. Smith, pers. obs.). Such differences may reflect their ecological or physiological preferences to occupy certain microenvironments within mangrove habitats, thereby affecting their risk of infection. Differences may also arise from the specificity of parasites to infect certain species of *Uca* more readily than others.

To address the issue of ecological or host specificity, we examined populations of 3 species of fiddler crabs (*U. speciosa*, *U. rapax*, *U. thayeri*) for trematode metacercariae across a habitat gradient. These populations overlap in their distribution on the banks of mangrove-dominated swamps, a habitat that varies in elevation, tidal influence, and soil composition. Here, we present data on the distribution of the sympatric fiddler crabs within this habitat gradient, and the prevalence and abundance of their trematode metacercariae. We found that *U. speciosa* was more frequently and heavily parasitized by *Probolocoryphe lanceolata* compared with other fiddler crab species (*U. rapax*, *U. thayeri*). To better understand these differences in parasitism, we conducted a field experiment to test whether *U. speciosa*, which inhabits the lower intertidal zone, has a higher risk of trematode infection than *U. rapax*, which lives relatively higher in the intertidal zone. For this, *U. speciosa* and *U. rapax* were exposed to shedding cercariae while raised under identical environmental conditions.

## MATERIALS AND METHODS

### Study system

Our study was conducted at 2 mosquito impoundments, Impoundment 12 (21-ha marsh), Indian River Co. (27°33'45"N, 80°20'W), and Impoundment 23 (122-ha marsh), St. Lucie Co. (27°32'30"N, 80°20'W), Florida, both located on North Hutchinson Island, a barrier island located between the Indian River Lagoon (IRL) and Atlantic Ocean. Both impoundments were constructed in the 1960s to control populations of the marsh mosquito (*Aedes taeniorhynchus*, *Ae. sollicitans*) and sandfly (*Culicoides furens*) (Rey and Kain, 1989). Impoundments were created by excavating and depositing sediment around the perimeter of the marsh and then enclosing the marsh with a channel (1–3 m depth) and earthen dike (3–5 m wide). Culverts placed at various locations under

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the dike allow free exchange of water between the IRL and impounded marshes. The banks along the excavated channel are dominated by a thick stand mixture of red mangrove (*Rhizophora mangle*) and black mangrove (*Avicennia germinans*). The substratum near the shoreline is loose and muddy, and it becomes more compact and sandy toward the upper intertidal. Fiddler crabs are abundantly distributed in the sediment among the mangrove prop roots and pneumatophores.

Three species of fiddler crabs were examined for trematode metacercariae, including the longfinger fiddler, *U. speciosa*; the Caribbean fiddler, *U. rapax*; and the mangrove fiddler, *U. thayeri*. In Florida, *U. speciosa* occurs from Vero Beach to the Florida Keys, *U. rapax* occurs from Daytona Beach to the Florida Keys, and *U. thayeri* occurs from St. Augustine to Sarasota (Tashian and Vernberg, 1958; Salmon, 1967). Many species of fiddler crabs of the Caribbean and North America have been shown to be parasitized by larval trematodes (Heard, 1976; Dunn et al., 1990). Of 8 species of fiddler crabs examined by Heard (1976) in salt marshes along the northern Gulf of Mexico, 6 were naturally infected with 1 to 5 species of trematodes. In addition to trematodes, fiddler crabs (*U. rapax*) from the east coast of Florida have also been shown to be infected by 2 species of larval acanthocephalans (Nickol et al., 2002).

The ladder horn snail, *Cerithidea scalariformis* (Say, 1925), co-occurs with fiddler crab populations, where they inhabit the mangrove fringe of creeks and mudflats, grazing on detritus and algae. *Cerithidea scalariformis* serves as the first intermediate host to several species of larval trematodes (Holliman, 1961; McNeff, 1978; Smith, 2001), 1 of which (*P. lanceolata*) infects *Uca* spp. (Heard, 1976). Snails become infected after ingesting a *P. lanceolata* egg containing a miracidium. The miracidium metamorphoses into a sporocyst and then undergoes asexual reproduction, producing a large population of sporocysts in the gonad. Free-swimming cercariae are released from sporocysts and the snail host, and then they enter the branchial cavity of fiddler crabs. Metacercariae encyst in the hepatopancreas, and trematode development is completed when infected crabs are ingested by a crab-eating mammal or bird (Heard and Sikora, 1969; Heard, 1976; McNeff, 1978). Other potential first intermediate hosts were not examined in this study.

#### Fiddler crab distribution in the mangrove intertidal zone

To examine the spatial distribution of fiddler crabs along a mangrove-lined bank, 5 parallel transects (20 m apart, 2 m long) were established perpendicular to the shoreline along a channel in Impoundment 23. At each transect, 0.25-m<sup>2</sup> quadrats were taken at 3 elevations (low intertidal, mid intertidal, high intertidal), spread approximately 0.25 m apart, during a neap tide on 29 August 1994. Collections were made by placing a metal frame over the marsh surface and excavating all burrows within the quadrat. Fiddler crabs were identified and kept separated by quadrat until examined for trematodes (see trematode survey below). Fiddler crab abundance (measured as number of crabs per 0.25 m<sup>2</sup>) was compared among the 3 intertidal zones by a Kruskal–Wallis test (estimated by a chi-square), because data did not meet assumptions for parametric tests.

#### Trematode survey

Three species of fiddler crabs collected from the mangrove habitats were assayed for trematode metacercariae, including crabs collected from Impoundment 23 (as described above) and Impoundment 12. At Impoundment 12, fiddler crabs were collected by pitfall traps over 4 consecutive days in August 1994 by placing approximately 25.5-cm plastic containers in the ground so that the open end of the container was flush with the marsh surface. Here, collections were conducted in a mudflat with scattered mangroves, near the impoundment channel with all pitfall traps positioned at the same elevation. For both sites, the carapace width (millimeters) of each fiddler crab was measured to examine the relationship between host size and parasitism, because size may influence infection risk. Fiddler crabs were kept alive until dissected for metacercariae. All soft tissues were thoroughly examined, and metacercariae from infected crabs were counted and identified. We assumed that metacercariae occurring in large masses in the same tissue, seeming morphologically identical, represented the same species. For identification purposes, metacercariae were excysted by incubating cysts in a saline water bath at 40 C for several hours.

#### Field experiment: Host specificity of metacercariae

Differences in prevalence and intensity of metacercariae among fiddler crab species from our surveys prompted us to test whether host specificity was largely responsible for the differences observed. Specifically, *U. speciosa*, which is more abundant in the low and mid intertidal zone, experienced higher prevalence and intensity of *P. lanceolata* metacercariae than the other fiddler crabs species (see Results). We conducted a transplant experiment to determine whether *U. speciosa* has a higher risk of trematode infection to *P. lanceolata* than *U. rapax* as a result of its habitat preference for the lower half of the intertidal zone. To control for habitat heterogeneity (elevation, tidal gradient, soil composition) and exposure to shedding cercariae, fiddler crabs were transplanted to another site within Impoundments 12 and 23, where the first intermediate host, *C. scalariformis*, is known to occur.

Enclosures were constructed to confine and expose *U. speciosa* and *U. rapax* to shedding cercariae from the surrounding infected snail populations and to standardize their habitat environment so that tidal elevation and sediment composition were identical among enclosures. Parallel studies on parasitism in *C. scalariformis* showed that prevalence of *P. lanceolata* was 26 and 1% at Impoundments 23 and 12, respectively. Enclosures were constructed of 4-mm Vexar nylon mesh walls, supported by wooden stakes. All enclosures were constructed with bottoms and covers (attached via cable ties) to prevent fiddler crabs from escaping and entering enclosures. The enclosures were buried to a depth of 15 cm and rose to a height of 62 cm above the sediment surface, providing a surface area of 0.25 m<sup>2</sup> for burrowing and feeding.

Five enclosures, placed 25 m apart, were placed at each site. On 8 August 1994, 50 (25 males and 25 females) *U. speciosa* and *U. rapax* were collected along the mangrove intertidal in Impoundment 23 and transplanted to each site. Each enclosure was stocked with 5 individual crabs of each species, randomly distributed with respect to size and sex, for a total of 10 crabs per enclosure. This density is within the range typically observed for fiddler crabs that inhabit these sites. Two weeks before the experiment was initiated, preliminary samples of fiddler crabs from Impoundment 23 were collected to determine what size range should be used for the experiment. Fiddler crabs with a carapace width under 13.0 mm had low prevalence and mean intensity ( $\pm$  SD) of *P. lanceolata* (*U. speciosa*: prevalence 38%, mean intensity 2.30  $\pm$  3.7; *U. rapax*: prevalence 0%). Because future infections and host susceptibility may be influenced by the presence of existing parasites, using crabs that are likely to have a low abundance of metacercariae can reduce these confounding effects. Thus, we used fiddler crabs with a carapace width of 8.0–12.9 mm for our experiment. After 2 mo, some of the fiddler crabs transplanted to the 2 sites had died from drowning, due to the unexpected high tides that occurred that summer, forcing us to terminate the experiment. After 72 days of being raised under identical field conditions, fiddler crabs were collected from the enclosures and assayed for *P. lanceolata*. Because the number of live crabs varied among enclosures, we randomly selected 12 crabs of each species from each site. We calculated prevalence (percentage of infected crabs in each sample) and mean intensity (mean number of metacercariae per infected crab host in each sample) for each trematode species and field site (Margolis et al., 1982). Parasitism data did not meet the assumptions of parametric tests, e.g., normality or homogeneity of variance; thus, the Wilcoxon signed rank test was used to test for differences in prevalence and intensity of *P. lanceolata* infection between *U. speciosa* and *U. rapax*. Sample sizes were too low to allow us to compare differences in parasitism by sex. All statistical analyses were conducted using Statistical Analytical Software, version 8.0 (SAS Institute, Cary, North Carolina).

## RESULTS

#### Fiddler crab distribution in the mangrove intertidal zone

*Uca speciosa* significantly varied in abundance among the 3 zones ( $\chi^2 = 7.62$ ,  $P < 0.05$ ), with more crabs in the low and mid intertidal zones compared with the high intertidal (Fig. 1A). Additionally, *U. speciosa* represented a greater proportion of quadrat samples in the low and mid intertidal zones relative to the other species (Fig. 1B). However, there were no differences

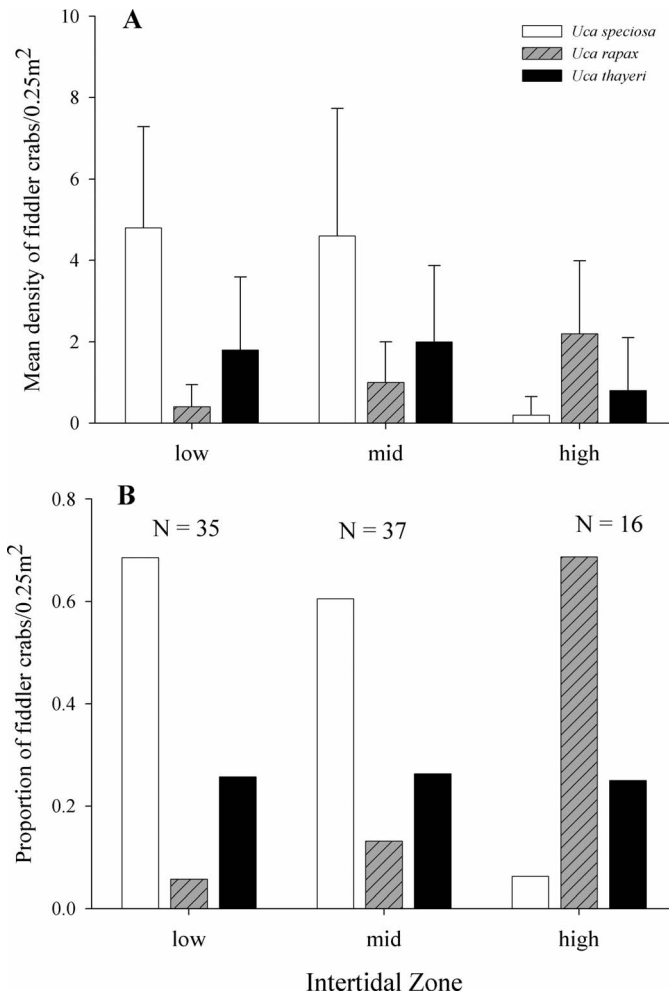


FIGURE 1. Abundance and distribution of 3 species of fiddler crabs along an elevation gradient in a mangrove intertidal zone in the Indian River Lagoon, Florida. (A) Mean density ( $\pm$  SD) of fiddler crabs per 0.25 m<sup>2</sup>. (B) Proportion of each fiddler crab species that occupied the intertidal zone. N represents the total number of fiddler crabs collected from each zone.

in the density of *U. rapax* or *U. thayeri* among zones (*U. rapax*:  $\chi^2 = 4.52$ ,  $P > 0.05$ ; *U. thayeri*:  $\chi^2 = 1.49$ ,  $P > 0.05$ ; Fig. 1A), although *U. rapax* was the most abundant species in the high intertidal relative to *U. speciosa* and *U. thayeri* (Fig. 1B). When all 3 species were pooled for each zone, there was no significant difference in fiddler crab density among the three zones ( $\chi^2 = 3.29$ ,  $P > 0.05$ ).

### Trematode surveys

Three species of metacercariae were observed among the 3 species of fiddler crabs that were collected from the 2 localities and field experiment: *P. lanceolata* occurred in the hepatopancreas and it was observed in all 3 fiddler crab species; *Maritrema prosthometra* metacercariae were found in the thoracic musculature of *U. speciosa* and *U. rapax*, but they were not observed in *U. thayeri*; and metacercariae of *Gynaecotyla adunca* were found encysted in the antennal gland of all 3 fiddler crab species, but they usually occurred in low abundance (Table I).

Prevalence and intensity of *P. lanceolata* was higher in *U. speciosa* than in the other fiddler crab species (Table I), with infected crabs harboring between 1 and 103 cysts. *Uca rapax* experienced relatively higher levels of parasitism by *M. prosthometra* compared to the other 2 species at both sites (Table I), with infected individuals harboring 1 to 61 cysts. Of the 3 fiddler crab species, *U. thayeri* experienced low prevalence and intensity of metacercariae (Table I).

For *U. speciosa*, there was a significant positive association between host size and intensity of *P. lanceolata* ( $R^2 = 0.46$ ,  $P < 0.01$ ) and *M. prosthometra* ( $R^2 = 0.17$ ,  $P < 0.01$ ) (Fig. 2), but not for *U. rapax* (*P. lanceolata*:  $R^2 = 0.01$ ,  $P > 0.05$ ; *M. prosthometra*:  $R^2 = 0.06$ ,  $P > 0.05$ ) (Fig. 2), nor for *U. thayeri* (*P. lanceolata*:  $R^2 = 0.07$ ,  $P > 0.05$ ) (data pooled across the intertidal).

### Field experiment: Host specificity of metacercariae

Fiddler crabs transplanted to the 2 localities (Impoundments 12 and 23) exhibited different patterns of parasitism (Fig. 3). Specifically, all individuals of *U. speciosa* became parasitized with *P. lanceolata*, but no *U. rapax* became infected with *P. lanceolata* from either site. Intensity of *P. lanceolata* was significantly higher in *U. speciosa* than *U. rapax* at Impoundment 12 (Wilcoxon signed rank test,  $P < 0.001$ ) and at Impoundment

TABLE I. Prevalence and mean intensity of parasitism in 3 species of fiddler crabs (*Uca speciosa*, *U. rapax*, *U. thayeri*) collected from Impoundments 23 and 12.

	N	Prevalence (%)			Mean intensity ( $\pm$ SD)		
		<i>Probolocoryphe lanceolata</i>	<i>Maritrema prosthometra</i>	<i>Gynaecotyla adunca</i>	<i>P. lanceolata</i>	<i>M. prosthometra</i>	<i>G. adunca</i>
<b>Impoundment 23</b>							
<i>U. speciosa</i>	48	45.8	4.2	0	4.2 $\pm$ 10.7	0.1 $\pm$ 0.5	0
<i>U. rapax</i>	18	5.6	77.8	16.7	0.1 $\pm$ 0.2	11.2 $\pm$ 10.7	4.3 $\pm$ 7.1
<i>U. thayeri</i>	22	22.7	0	4.5	0.5 $\pm$ 1.3	0	4.2 $\pm$ 4.5
<b>Impoundment 12</b>							
<i>U. speciosa</i>	21	85.7	52.4	0	36.0 $\pm$ 33.3	5.1 $\pm$ 7.9	0
<i>U. rapax</i>	21	14.3	66.7	0	3.0 $\pm$ 10.2	10.7 $\pm$ 16.1	0

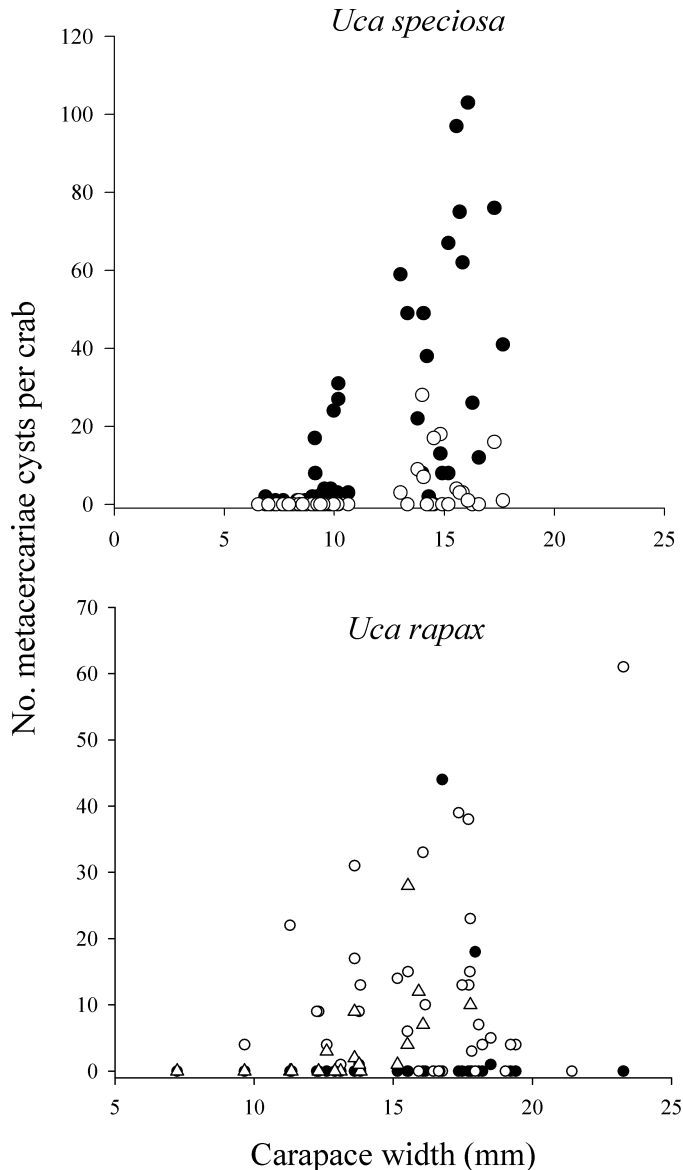


FIGURE 2. Number of metacercariae of *Probolocoryphe lanceolata* (closed circles), *Maritrema prosthometra* (open circles), and *Gynaecotyla adunca* (open triangles) in *Uca speciosa* and *U. rapax* collected from Impoundments 23 and 12, illustrating relationships between trematode abundance and host size. Note that *G. adunca* was not found in *U. speciosa*.

23 ( $P < 0.001$ ). Both *U. speciosa* and *U. rapax* became infected with *M. prosthometra*, with *U. rapax* exhibiting higher parasitism than *U. speciosa* at both Impoundment 12 (Wilcoxon signed rank test,  $P < 0.001$ ) and Impoundment 23 ( $P < 0.001$ ). Furthermore, both fiddler crab species become infected with *G. adunca*, but there was no significant difference in intensity between both species at each site (Wilcoxon signed rank test,  $P > 0.05$ ).

## DISCUSSION

Of the 6 species of fiddler crabs that occur along the Atlantic coast of Florida (Salmon, 1967; Barnwell and Thurman, 1984), 3 species were collected from the banks of mangrove swamps

along the Indian River Estuary, including *U. speciosa*, *U. rapax*, and *U. thayeri*. A fourth species, *U. pugilator*, the sand fiddler crab, was frequently observed in adjacent sand and mudflats, but it was not found in our surveys, because we did not sample beyond the mangrove intertidal. We found that fiddler crab distribution along a mangrove bank, which varied in elevation and tidal influence, was not uniform; rather, certain zones were dominated by certain species of *Uca*, which is consistent with other findings (Teal, 1958; Macnae, 1968; Montague, 1980; O'Conner, 1993). Specifically, *U. speciosa* dominated the lower and mid-intertidal zones, and *U. rapax* was more abundant in the high intertidal relative to the lower zones. Such microhabitat preferences may reflect their ecological and physiological adaptations to inhabit environments with certain biotic and physical conditions, e.g., sediment composition, salinity, vegetative cover. For example, Thurman (2005) experimentally showed that *U. rapax* had higher survivorship than *U. speciosa* and *U. thayeri* at high saltwater concentrations ( $>2,500$  mOsm), potentially allowing *U. rapax* to inhabit and survive in the high intertidal zone.

Fiddler crabs have been documented to host trematode metacercariae and larval acanthocephalans (Ahmed and Khan, 1976; Heard, 1976; Overstreet, 1983; Nickol et al., 2002), providing a rich and instantaneous helminth community to a variety of vertebrates that feed on *Uca* (Hutton, 1964; Heard, 1970; Bush and Forrester, 1976; Kinsella, 1988). The present study represents the first report of *Probolocoryphe lanceolata* (syn. *Cercaria caribbea* XXV, Cable, 1956; *Cercaria lanceolata*, Holli-man, 1961; *Cercaria* XXIII, Wardle, 1974; and *P. glandulosa*, Heard and Sikora, 1969; Heard, 1970; Bush and Forrester, 1976; Kinsella, 1988) in *U. speciosa*. Eight species of fiddler crabs, including *U. rapax*, are known to naturally or experimentally serve as second intermediate hosts of *P. lanceolata* (Heard, 1976). Interestingly, Heard (1976) exposed *U. speciosa* to more than 200 *P. lanceolata* cercariae, but no infections resulted. Furthermore, no parasites were found in more than 30 specimens of *U. speciosa* collected from the Gulf coast of Florida, although *P. lanceolata* was present in first intermediate hosts (Bush et al., 1993). These findings suggest that along its geographic range, populations of *U. speciosa* may be genetically different, adapted to local conditions, or both, thereby influencing its compatibility as a suitable host for parasite development (Combes, 2001). Although we observed *P. lanceolata* in all 3 fiddler crab species during our surveys, only *U. speciosa* became infected with this parasite when raised under the same environmental conditions as *U. rapax*. Furthermore, our experiment showed that at even at a low prevalence (1%) of *P. lanceolata* in the first intermediate host (*C. scalariformis*), all individuals of *U. speciosa* became infected, and at much higher intensities relative to the parasite surveys.

Results of the transplant experiment indicate that microhabitat preferences in the mangrove intertidal do not account for differences in parasitism between *U. speciosa* and *U. rapax*. Because *U. speciosa* and *U. rapax* were presumably equally exposed to shedding cercariae, and they were confined to the same tidal height, factors other than host distribution may play an important role in influencing the nature or outcome of their interactions with larval trematodes. For example, differences in parasitism between *U. speciosa* and *U. rapax* may be attributed to the degree of openness of the encounter and compatibility

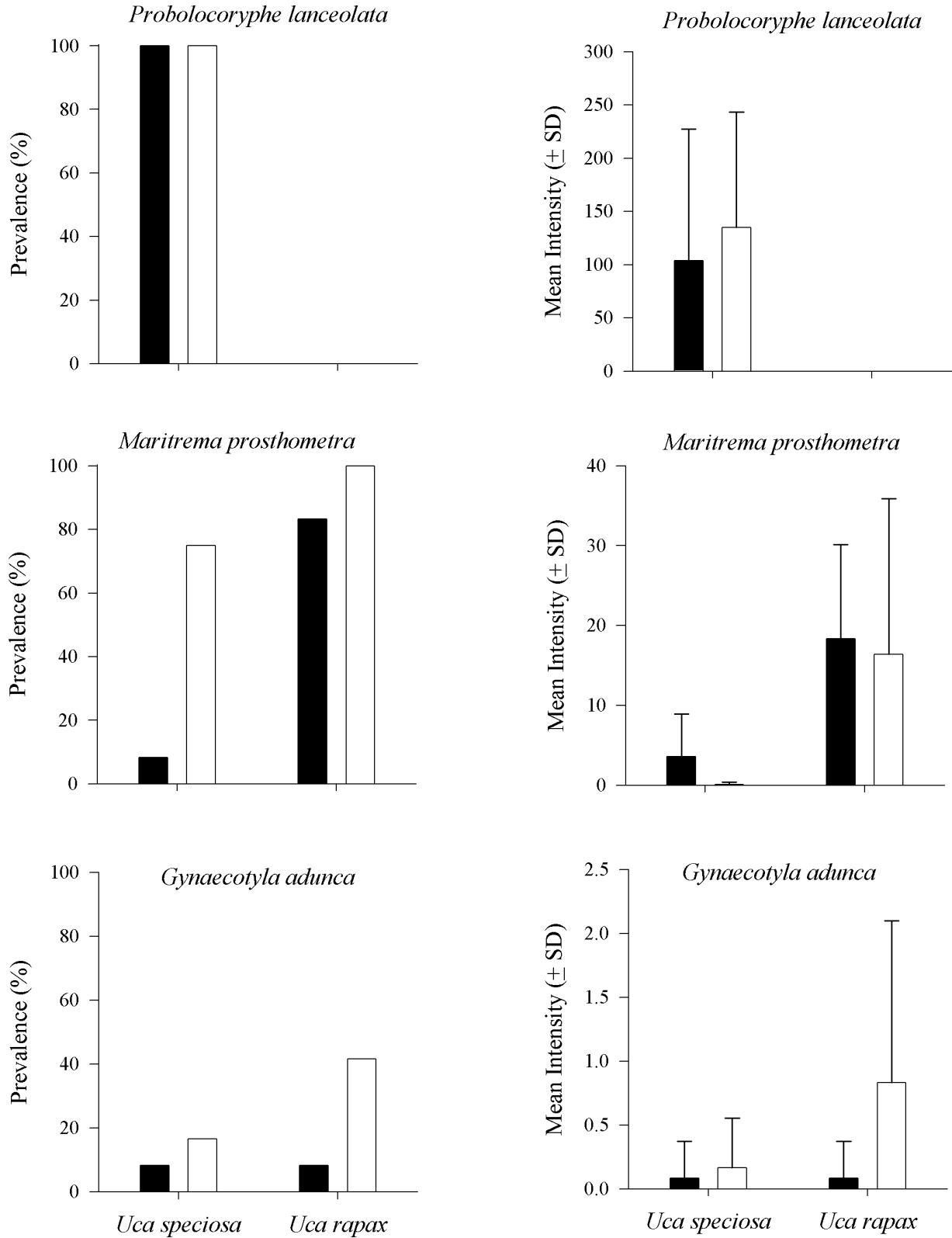


FIGURE 3. Prevalence (%) and mean intensity ( $\pm$  SD) of *Probolocoryphe lanceolata*, *Maritrema prosthometra*, and *Gynaecotyla adunca* metacercariae in *Uca speciosa* and *U. rapax* transplanted to Impoundments 12 (black bars) and 23 (white bars). Fiddler crabs experienced identical environmental conditions at each site over 72 days. Note differences in the mean intensity on the y-axis scale.

filter (sensu Combes, 2001) for each species. For a parasite to successfully infect a host, it must both encounter the host and be compatible, operating as 2 consecutive stages, or stepwise filters, that determine infection (Combes, 2001; Kuris et al., 2007). Specifically, the parasite must be able to locate and infect the potential host (encounter filter) and be able to develop successfully within the host after the encounter (compatibility filter). Because *P. lanceolata* has been found to naturally infect multiple species of *Uca*, including *U. speciosa* and *U. rapax*, this trematode is compatible with several hosts, but it may prefer certain species over others. When *U. speciosa* and *U. rapax* were raised together under the same field conditions, cercariae were given a choice between potential hosts, and they chose to infect *U. speciosa* over *U. rapax*, showing that *U. speciosa* is a relatively more preferable host. Over time, *P. lanceolata* cercariae may have evolved a mechanism to find and identify the most compatible host (*U. speciosa*), thereby avoiding less suitable hosts (Combes, 2001). Furthermore, the presence of *U. speciosa* may close or reduce the encounter filter of *U. rapax*, causing *U. speciosa* to act as a population sink for cercariae. To determine whether the presence of *U. speciosa* influences the probability of contact between cercariae and *U. rapax*, the encounter filter can be artificially widened in the laboratory by exposing *U. rapax* to cercariae in the absence of *U. speciosa*. If *U. rapax* was found compatible after experimental exposure, then one can assume that the encounter filter is closed in nature when in the presence of *U. speciosa*.

Additionally, gill morphology and behaviors associated with respiration may play an important role during the encounter process, because *P. lanceolata* infects fiddler crabs by entering the branchial chamber with the respiratory currents. Specifically, the setae of the third maxilliped, which prevents sand and mud from entering the branchial chamber, varies in morphology among *Uca* spp. (Macnae, 1968), which may allow or prevent cercariae from entering the host. The setae of the scaphognathite (gill bailer) and other setal lobes of the maxillae could also prevent cercariae from entering the branchial chamber. Furthermore, as water is pumped across the gills in the branchial chamber by the gill bailer, crabs may respond or behave differently to cercariae within the water column. Transmission can also be influenced by water levels, tides, and currents, by affecting the concentration of cercariae in the water column and in crab burrows. During an outgoing or low tide, fiddler crabs carry a supply of water in their branchial chambers that is circulated over the gills (Montague, 1980). Thus, the need to replenish their branchial water supply may influence their encounter rate with cercariae. The enclosures used in our study offer many advantages over other field techniques, e.g., mark-recapture; however, we cannot discount the possibility that the enclosures, which restricted fiddler crab movement and potentially altered their interaction with the water levels and cercariae may have influenced infection patterns between *U. speciosa* and *U. rapax*.

Differences in parasitism among sympatric species may also result from differences in the hosts' immunological ability to destroy a parasite after encounter. Crustaceans can elicit a cell-mediated response (hematocyte aggregation, often followed by melanization) after exposure to some foreign bodies and parasites (Gotz, 1986; Kuris et al., 2007). After *P. lanceolata* penetrates the branchial chamber of the crab host, the larvae migrate to the hepatopancreas, the final site of encystment, during

which they must respond and survive the host defense system. Signs of encapsulation by host cells have been observed as early as 7 days after infection (Heard, 1976). Metacercariae begin to encyst 19 days after penetration, becoming fully developed and infective after 50 days (Heard, 1976). Indeed, encystment, or sequestration, may be an adaptive strategy to reduce or minimize its interactions with the host that would otherwise compromise its survival (Adamson and Cairn, 1994). Because the host defense system may respond differently to parasitic infection as a result of genetic or physiological heterogeneity within a species (Karp, 1990), variation in compatibility among host strains or species is likely to occur.

In sum, our study supports previous findings that fiddler crabs often occupy specific microenvironments within coastal marsh habitats. In mangrove marshes of Florida, their distribution varied across the mangrove intertidal, with various zones dominated by different species of *Uca*. *Uca speciosa* occurred most abundantly in the low intertidal; therefore, it may be exposed to relatively high levels of *P. lanceolata* cercariae. However, the higher prevalence and intensity of this trematode in *U. speciosa* compared with *U. rapax*, which occupied higher regions of the intertidal, was shown to be driven by host selection. Differences in their encounter and compatibility filters, gill morphology, behavioral activities, and defense systems may contribute to the significant differences in parasitism among host species.

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#### LITERATURE CITED

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