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Field and Laboratory Evaluation of Habitat Use by Rainwater Killifish (*Lucania parva*) in the St. Johns River Estuary, Florida

Frank Jordan*

Department of Biological Sciences, Loyola University New Orleans, 6363 St. Charles Avenue, New Orleans, Louisiana 70118

ABSTRACT: I examined the relative importance of beds of tapegrass (*Vallisneria americana*) and adjacent unvegetated habitats to juvenile and adult (6–35 mm standard length) rainwater killifish (*Lucania parva*) over a large spatial scale within the St. Johns River estuary, Florida. Abundance of rainwater killifish did not differ between oligohaline and tidal freshwater portions of the estuary and this species was relatively rare at opposite ends of the St. Johns River estuary. The presence of rainwater killifish at a given site was determined in part by large-scale variation in environmental factors such as habitat complexity and salinity. When present at a site, rainwater killifish were found almost exclusively in structurally complex beds of tapegrass. Behavioral observations in the laboratory indicated that rainwater killifish preferred vegetated over unvegetated habitats in the absence of both potential prey and predators and that use of vegetated habitats increased further upon addition of predatory largemouth bass (*Micropterus salmoides*). A laboratory predation experiment indicated that survival of rainwater killifish exposed to largemouth bass was significantly higher in vegetation than over open sand. Strong preferences for structurally complex vegetation likely reflect an evolved or learned behavioral response to risk of predation and help explain habitat use of rainwater killifish in the St. Johns River estuary.

Introduction

Beds of submerged aquatic vegetation (SAV) provide important habitat for estuarine fishes and often support significantly higher numbers of fishes than adjacent unvegetated habitats (Orth et al. 1984; Heck et al. 1989; Heck and Crowder 1991). Increased abundance of fishes within SAV beds is due to a myriad of factors, including enhanced foraging opportunities and lowered risk of predation (Rozas and Odum 1988). Predators play a predominant role in mediating habitat use by estuarine fishes, either directly by consuming vulnerable prey (Heck and Orth 1980; Stoner 1983) or indirectly by influencing habitat-use decisions (Bell and Westoby 1986a,b; Sogard and Olla 1993; Jordan et al. 1996).

Risk of predation for small fishes is considerably lower in vegetated habitats than in adjacent unvegetated habitats (e.g., Savino and Stein 1982; Rozas and Odum 1988; Hayse and Wissing 1996). Structurally complex beds of SAV provide small fishes with a refuge from larger predatory fishes, which are locally abundant within estuarine systems (Ryan 1981; Sogard et al. 1989; Bartolini 1998). Considering the behavioral flexibility of fishes (Lima and Dill 1990), it is likely that increased numbers of small fishes in beds of SAV reflect predator-mediated habitat selection rather than different rates of predation on randomly distributed individuals (Bell and Westoby 1986a,b). Additional research, combining field surveys of habitat use and habitat choice experiments, is needed to evaluate the role that habitat selection plays in the spatial ecology of estuarine fishes (Gotceitas and Brown 1993; Jordan et al. 1996).

The diminutive rainwater killifish, *Lucania parva,* is an excellent model species for studying habitat selection because it appears to be strongly associated with beds of SAV and other vegetated habitats in estuaries along the Gulf and Atlantic coasts (e.g., Sogard et al. 1987; Provancha and Hall 1991; Sogard and Able 1991; Rogers et al. 1992; Tremain and Adams 1995; Duffy and Baltz 1998). The generality of habitat preferences can also be evaluated over a large spatial scale because rainwater killifish are tolerant of a wide range of salinity and other environmental conditions (Dunson et al. 1993). In this paper, I describe the results of field and laboratory studies designed to evaluate the role that habitat selection plays in determining the distribution of rainwater killifish in estuarine portions of the St. Johns River, Florida. I compared use of SAV beds and adjacent sand flats by rainwater killifish across nine widely separated locations in the field. I performed a habitat selection experiment in the laboratory to determine preferences of rainwater killifish for vegetated and unvegetated habitats in the absence and presence of predatory largemouth bass (*Micropterus salmoides*). I also exposed rainwater killifish to predatory largemouth bass to determine whether relative risks of preda-

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* Tele: 504/865-3829; fax: 504/865-3829; email: jordan@loyno.edu.

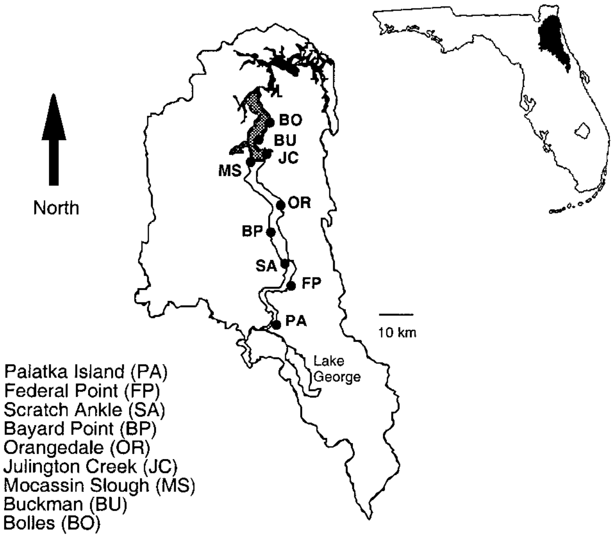

Fig. 1. Location of study sites within oligohaline (gray) and tidal freshwater (white) portions of the St. Johns River estuary, Florida. Submergent vegetation is absent from the mesohaline (black) portion of the estuary. Outer line around map and black portion of inset correspond to the boundary of the lower St. Johns River basin. FP is located at 29°45′N, 81°31′W.

tion in vegetated and unvegetated habitats could contribute to patterns of habitat use observed in both the field study and behavioral experiment. I hypothesized that risk of predation played an important role in mediating habitat selection because rainwater killifish are preyed upon heavily by piscivorous fishes in the St. Johns River (Bartolini 1998).

Materials and Methods

Study Area

The St. Johns River is the longest river in Florida and flows northward 480 km from its headwater marshes in Indian River, St. Lucie, and Brevard Counties to its mouth in northeastern Duval County. The St. Johns River is an extremely shallow and low gradient system that typically experiences daily tidal reversals to Lake George, which is 160 km upstream of its mouth. The fauna is considered estuarine up to about Lake George, although marine derived fishes and invertebrates (e.g., *Mugil cephalus, Callinectes sapidus*) are commonly encountered even further upstream (DeMort 1991).

The St. Johns River estuary can be divided into mesohaline, oligohaline, and tidal freshwater portions (Fig. 1) that support no, sporadic, and abundant beds of SAV, respectively. Salinity, low light penetration, lack of suitable substrata, and dredging all appear to limit the distribution and size of SAV beds in the mesohaline portion of the estuary (DeMort 1991; Kraemer et al. 1999). Low light levels also appear to be the primary reason that beds of SAV are restricted to the shallow margins (generally less than 1.5 m) within much of the estuarine portion of the river. Tapegrass (*Vallisneria americana*) is the dominant SAV with respect to areal coverage and biomass with pondweed (*Potamogeton* spp.) and water nymph (*Najas guadalupensis*) being locally and seasonally abundant. Tapegrass is present year round in the St. Johns River. Beds of SAV are interspersed with mud and sand flats within the shallow margins of oligohaline and tidal freshwater portions of the St. Johns River estuary, forming a complex habitat mosaic. Nine widely separated sites (Fig. 1) were selected for sampling based upon the presence of tapegrass beds, location within the estuary (oligohaline versus tidal freshwater), and proximity to long-term SAV study plots of the St. Johns River Water Management District (SJRWMD). The Bolles, Buckman Bridge, Julington Creek, and Moccasin Slough sites were within the oligohaline portion of the estuary, whereas the Orangedale, Bayard Point, Scratch Ankle, Federal Point, and Palatka sites were within the tidal freshwater portion of the estuary (Fig. 1).

Quantification of Habitat Use

An aluminum throw trap (100 × 100 × 75 cm) was used to collect rainwater killifish from tapegrass beds and adjacent unvegetated habitats at the 9 sites described above. Throw traps and other enclosure sampling devices provide quantitative density estimates for small nektonic organisms such as rainwater killifish (Kushlan 1981; Freeman et al. 1984; Chick et al. 1992; Jordan et al. 1997; Rozas and Minello 1997). The throw trap was deployed haphazardly into the desired habitat and then pressed firmly into the substrate. Plants were removed, placed into a mesh bag, twirled until excess water was removed, and then weighed to the nearest g wet weight. A bar seine with 3.0-mm mesh was then passed through the trap until three consecutive sweeps produced no fishes. Six throw trap samples were collected from within each habitat at each site, and the order in which tapegrass beds and sand flats were sampled was alternated. Rainwater killifish were preserved in 10% buffered formalin in the field and later enumerated in the laboratory. Sampling was performed during daylight hours (0800–1800) on a quarterly basis between May 1996 and August 1997.

Rainwater killifish abundance data were averaged for each set of six throw traps and then $\log_{10}$-transformed prior to parametric analyses to reduce observed heterogeneity of variances. Analysis of variance (ANOVA) determined the effects of estuarine location, habitat, month, and the interaction between habitat and month on the abundance of rainwater killifish. For this analysis, location within the estuary was considered a block effect and habitat was considered a fixed effect. It appears that problems with temporal autocorrelation may be minimal for intervals of about 60 d or more (Osenberg et al. 1996). Since collections were about 3 mo apart, sampling period was treated as an independent factor rather than a repeated factor in the analysis of variance. Bonferonni-Dunn corrected multiple comparisons were used to test if mean densities of rainwater killifish varied among sampling locations and among sampling periods.

Two methods were used to determine if variation in the abundance of rainwater killifish in tapegrass beds was related to differences in selected physical features among estuarine locations. Water depth and plant wet biomass data were included in the ANOVA described above as covariates to test for responses of rainwater killifish to small-scale variation in habitat structure. In light of extensive spatial and temporal variability within estuaries, it is unlikely that the limited measurements from throw trap samples adequately describe physical features of different estuarine locations. I also used long-term salinity and maximum plant stem length data collected by the SJRWMD during 1995–2000 (Sagan 2001) to test for responses of rainwater killifish to large-scale variation in habitat structure. Partial correlation analysis was used to examine relationships between the abundance of rainwater killifish, salinity, and maximum plant stem length averaged for each estuarine location ($n = 9$). Statistical procedures followed Winer et al. (1991) and Sokal and Rohlf (1995).

HABITAT SELECTION EXPERIMENT

A habitat selection experiment was performed in the laboratory to determine whether predatory largemouth bass affected the use of grass or sand habitats by rainwater killifish. Largemouth bass are abundant in the St. Johns River and feed heavily upon rainwater killifish (Bartolini 1998). Rainwater killifish (SL ± SD: 22 ± 1 mm) and largemouth bass (87 ± 15 mm) were seined from beds of tapegrass, transported to the laboratory, and transferred to separate aquaria containing aerated tap water. Prey fish were allowed to acclimate to laboratory conditions for 48 h and fed flake food ad libitum, whereas predators were acclimated for 7 d and fed a mixture of small prey fishes including rainwater killifish ad libitum.

Habitat selection trials were performed in 90 × 30 × 40-cm glass aquaria containing a 3–4 cm layer of clean beach sand and filled with 110 liters of dechlorinated tap water. One half of each aquarium was left barren to mimic a sand flat, whereas a 45 × 30-cm plot of artificial grass was placed within the other half of the aquarium to mimic a bed of tapegrass. Artificial grass is often used in behavioral experiments because it is easily quantified and free of epiphytic organisms that might influence habitat use decisions (Savino and Stein 1982; Sogard and Olla 1993; Hayse and Wissing 1996). Artificial grass was assigned randomly to either half of the aquarium in order to avoid confounding habitat type with location. Artificial grass was created by tying 108 bipartite strips (15 × 400 mm) of dark green plastic to a plastic mesh, which was then buried beneath the sand. A density of 1,600 blades m^{-2} was used in this experiment, which is within the range of densities (338 to 3,505 m^{-2}) observed for tapegrass within the lower St. Johns River (SJRWMD unpublished data).

Eight rainwater killifish were introduced into each aquarium and allowed to acclimate for 30 min. The number of rainwater killifish swimming in grass and over open sand was then recorded after 20, 40, and 60 min. A well-fed predator was then added to each aquarium and allowed to acclimate for 30 min. Once again, the number of rainwater killifish swimming in grass and over open sand was then recorded after 20, 40, and 60 min. Numbers of rainwater killifish swimming in each habitat were totaled and converted into percentage habitat use for the periods before and after a predator was added. The experiment was replicated six times over a 2-d period with different fish being used in each trial. Largemouth bass did not consume any rainwater killifish during this experiment. Day of trial did not affect habitat use ($t_4 = 08$, $p = 0.4772$) and data were pooled for further analyses. One-tailed, paired *t*-tests were used to test the hypotheses that rainwater killifish prefer vegetated habitat versus unvegetated habitat in the absence of a predator and that rainwater killifish increase their use of vegetated habitats after the addition of a predator.

PREDATION EXPERIMENT

A second laboratory experiment was performed to test the hypothesis that survival of rainwater killifish is greater in vegetated habitats than in unvegetated habitats. By assessing predation rates in the laboratory, I was able to control experimental conditions (e.g., plant density, predator species and size, predator hunger levels) and avoid potential design problems associated with tethering prey fishes in the field (Peterson and Black 1994). Rainwater killifish (27 ± 4 mm) were collected and maintained as above. Ten largemouth bass (130 ± 5 mm) were collected and maintained for more than 30 d prior to use to ensure that they would

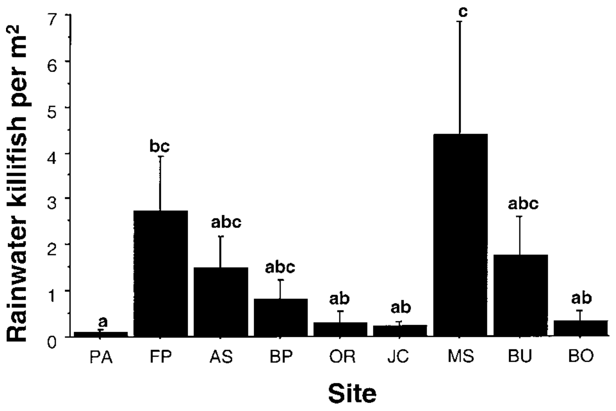

Fig. 2. Mean (+ 1 SE) density of rainwater killifish in tapegrass beds at nine widely separated locations within the St. Johns River estuary. Means with different letters are significantly different based on Bonferonni-Dunn multiple comparisons.

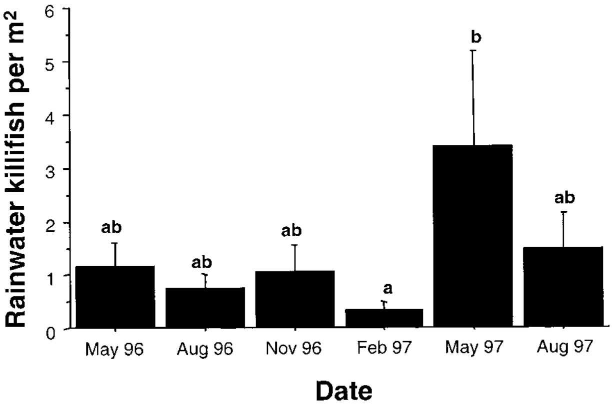

Fig. 3. Seasonal variation in the mean (+ 1 SE) density of rainwater killifish in the St. Johns River estuary. Means with different letters are significantly different based on Bonferonni-Dunn multiple comparisons.

feed aggressively under laboratory conditions. Largemouth bass were fed small-sized fishes and grass shrimp ad libitum up to 48 h prior to use in this experiment.

Predation trials were carried out in 90 × 30 × 40-cm glass aquaria filled with 110 liters of dechlorinated tap water. Five aquaria contained only 3–4 cm of clean beach sand for substrate, whereas another five aquaria contained sand and a 90 × 30-cm mat of artificial grass that simulated a patch of tapegrass. Artificial grass was created as described above for the habitat selection experiment at a density of 1,600 blades m^{-2}.

Ten rainwater killifish were added to each tank at 0930 and a single largemouth bass was added to each tank 30 min later, allowed to feed for 24 h, and then removed. Grass was then removed and surviving rainwater killifish were counted in all tanks. A one-tailed, unpaired *t*-test was used to test the hypothesis that survival of rainwater killifish is higher in vegetated habitats than in unvegetated habitats.

Results

A total of 871 rainwater killifish were collected (n = 648 throw trap samples), yielding an overall density of 1.3 rainwater killifish m^{-2}. Rainwater killifish were not distributed evenly between tapegrass beds and adjacent sand flats ($F_{1,88} = 68.1$, $p = 0.0001$). Structurally complex beds of tapegrass (2.6 m^{-2}) supported 43 times as many rainwater killifish as sand flats (0.06 m^{-2}). Habitat accounted for 31% of the variation in abundance of rainwater killifish. The abundance of rainwater killifish also varied among sites within the St. Johns River estuary ($F_{8,88} = 5.2$, $p = 0.0001$; Fig. 2). Sampling site accounted for about 19% of the variation in rainwater killifish abundance. A planned comparison indicated that rainwater killifish abundance did not differ between oligohaline and tidal freshwater portions of the estuary ($F_{1,8} = 1.1$, $p = 0.2944$). Rainwater killifish were rarely collected from sites furthest upstream (Palatka) and downstream (Bolles). Moccasin Slough supported significantly higher numbers of rainwater killifish than other sites. Although statistically significant ($F_{5,88} = 2.7$, $p = 0.0277$; Fig. 3), sampling period accounted for only 6% of the variation observed in the abundance of rainwater killifish, and there was no interaction between habitat type and sampling period ($F_{5,88} = 1.5$, $p = 0.1974$). Standard length ranged from 6 to 35 mm and averaged 20.2 ± 5.6 mm.

Abundance of rainwater killifish was not related to variation in plant wet biomass ($F_{1,86} = 1.1$, $p = 0.2857$) or water depth ($F_{1,86} = 0.1$, $p = 0.8479$) within habitats. Analysis of long-term data collected by the SJRWMD (Sagan 2001) indicated that the abundance of rainwater killifish was positively correlated with both plant stem length (partial $r_6 = 0.843$, $p < 0.05$) and salinity (partial $r_6 = 0.6461$, $p < 0.05$) over a large spatial scale.

Laboratory experiments indicated that observed patterns of habitat use by rainwater killifish in the St. Johns River estuary could be explained in part by habitat choice. In the absence of predators and food, rainwater killifish were three times more likely to occupy vegetation than open sand ($t_5 = 2.2$, $p = 0.0408$; Fig. 4). After addition of a predator, rainwater killifish were 16 times more likely to occupy vegetation than open sand ($t_5 = 11.3$, $p = 0.0001$; Fig. 5). Survival of rainwater killifish exposed to predatory largemouth bass was almost twice as great in tanks containing vegetation than in tanks containing only bare sand ($t_8 = 2.5$, $p = 0.020$; Fig. 5), further indicating that habitat-use

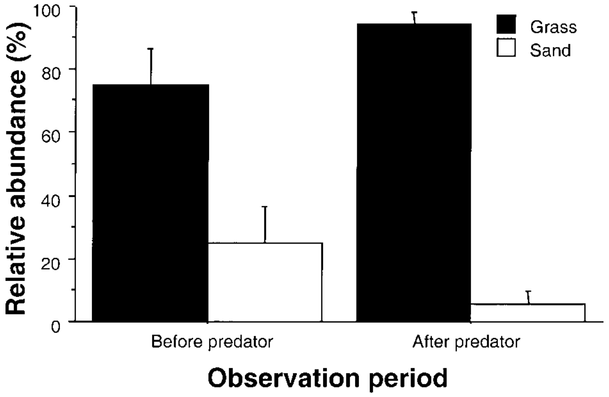

Fig. 4. Mean (+ 1 SE) relative abundance (%) of rainwater killifish observed in vegetated (grass) and unvegetated (sand) sides of experimental tanks before and after the addition of predatory largemouth bass.

decisions by rainwater killifish were motivated in part by risk of predation.

Discussion

HABITAT USE

Estuaries are comprised of mosaics of habitats that differ with respect to plant species composition, structural complexity, and environmental conditions (Day et al. 1989). Beds of SAV and unvegetated sand and mud flats are interspersed throughout much of the littoral zone of the St. Johns River estuary (DeMort 1991) and provide fishes with a wide spectrum of opportunities (e.g., prey resources, mates) and risks (e.g., competitors, predators) that ultimately affect individual fitness, population demographics, and community organization (Wiens 1976; Pulliam 1988). Behavioral flexibility allows mobile fishes to respond to these opportunities and risks (Lima and Dill 1990), which in turn contributes to non-random patterns of habitat use within estuaries (Heck and Crowder 1991). Greatly elevated abundance of fishes in structurally complex beds of SAV (see reviews in Orth et al. 1984; Heck et al. 1989) may in part reflect active habitat selection (and avoidance) behavior (Bell and Westoby 1986a,b; Jordan et al. 1996). A primary reason for studying habitat use by rainwater killifish was to test the general importance of behavior in determining fish distribution within estuarine habitat mosaics.

Duggins (1980 p. 535) observed that rainwater killifish were "invariably taken in the presence of aquatic vegetation." Sogard and Able (1991) found that rainwater killifish were abundant in beds of *Zostera marina* within estuaries of southern New Jersey, but practically absent from adjacent sand flats. Several other researchers have noted high densities of rainwater killifish in densely vegetated estuarine habitats (e.g., Harrington and Harrington 1961; Sogard et al. 1987; Provancha and Hall 1991; Rogers et al. 1992; Tremain and Adams 1995; Duffy and Baltz 1998). Consistent with these earlier studies, I found rainwater killifish to be abundant within structurally complex beds of tapegrass and virtually absent from adjacent sand flats within the St. Johns River estuary. Unlike many other estuarine fishes associated with SAV (e.g., Stoner 1983), rainwater killifish were not affected by variation in plant biomass within beds of tapegrass. Sogard et al. (1987) also noted a lack of association between rainwater killifish abundance and seagrass structural complexity in Florida Bay.

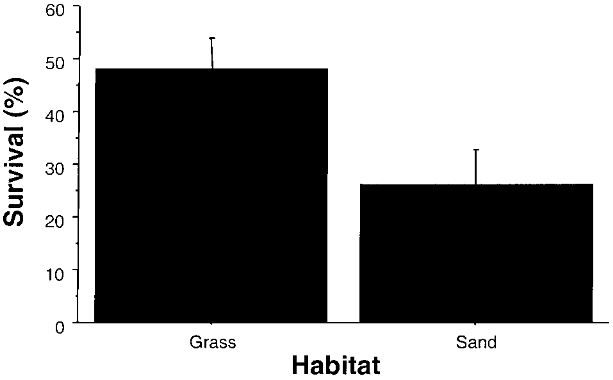

Fig. 5. Mean (+ 1 SE) survival of rainwater killifish exposed to predatory largemouth bass for 24 h in experimental tanks containing either grass or sand.

Which demographic mechanisms (i.e., birth, immigration, death, emigration; sensu Pulliam 1988) are responsible for patterns of habitat use by rainwater killifish? Rainwater killifish eggs are deposited on vegetation, and larvae tend to remain in the vegetated habitat in which they are spawned (Foster 1967). Habitat-specific differences in birth rate and low post-recruitment emigration away from beds of SAV may contribute considerably to patterns of habitat use by rainwater killifish. My predation experiment indicates that survival may be considerably higher in beds of SAV due to decreased predation in these structurally complex habitats (see Heck and Crowder 1991). My habitat selection experiment also showed that rainwater killifish preferred vegetation over open sand in the absence of both predators and prey, and that preference for vegetation increased after the addition of a predator. Considering the results of these two experiments, it appears that rainwater killifish use beds of SAV (and avoid unvegetated habitats) in part to reduce their risk of predation. Piscivores such as largemouth bass are abundant in the estuarine portion of the St. Johns River and dietary studies indicate that rainwater killifish are a common prey item (Bartolini 1998).

Preference for structurally complex beds of SAV appears to be either an innate or learned antipredator response since this behavior was observed in the absence of predator stimuli. Bell and Westoby (1986a) found that six species of estuarine fishes quickly emigrated away from cropped patches of seagrass in both the presence and absence of potential predators. Jordan et al. (1996) found that vulnerable pinfish (*Lagodon rhomboides*) are behaviorally more flexible, using unvegetated habitats freely until exposed to predator stimuli (also see Gotceitas and Brown 1993; Sogard and Olla 1993). Whether facultative or obligatory, it appears that risk of predation can motivate habitat selection and affect the distribution of fishes within estuarine habitat mosaics (Orth et al. 1984). Other factors (e.g., prey availability) may also contribute to habitat-use decisions (Rozas and Odum 1988; Connolly 1994). Multifactorial experiments manipulating predation intensity, prey availability, density of conspecifics, and other relevant factors are needed to enhance our understanding of habitat selection by estuarine fishes.

DISTRIBUTION WITHIN THE ESTUARY

Large spatial variation in predator abundance, larval transport, habitat complexity, prey availability, environmental conditions, and other factors within estuaries may affect the relative importance of SAV beds to estuarine fishes (e.g., Stoner 1983; Livingston 1984; Bell and Westoby 1986c; Bell et al. 1987; Sogard et al. 1987). Studies of habitat use by estuarine fishes should be performed over a large enough spatial scale to ensure generality of results (Ferrell and Bell 1991). The most upstream and downstream sites in this study were separated by approximately 100 km and estuarine location accounted for 19% of the variation observed in rainwater killifish abundance. Processes operating across extensive environmental gradients appear to regulate population sizes of rainwater killifish in the St. Johns River estuary.

Sites that supported few rainwater killifish (i.e., Bolles, Julington Creek, and Palatka) tended to have poorly developed beds of tapegrass. Distribution of tapegrass and other species of SAV are regulated by factors such as salinity, light penetration, nutrient enrichment, dredging, and geomorphology of the river channel (Kraemer et al. 1999). Elevated salinity levels, low light penetration, dredging, and lack of suitable substrata preclude the colonization and growth of tapegrass and more salinity tolerant species of SAV such as *Ruppia maritima* in the lower reaches of the St. Johns River (DeMort 1991). The Bolles site supported only patchy beds of tapegrass, perhaps due to elevated salinity levels (Sagan 2001). Patchy or limited distribution of tapegrass probably reflected elevated urban runoff at the Julington Creek site and relatively narrow littoral zones at the Orangedale and Palatka sites (Sagan 2001). From a conservation perspective, changes in the distribution of tapegrass within the St. Johns River will likely affect rainwater killifish, largemouth bass (Bartolini 1998), and other fishes that depend upon SAV for food and shelter.

Availability of well-developed beds of SAV alone cannot account for the distribution of rainwater killifish in the St. Johns River because this species is rarely encountered in the extensive beds of tapegrass upstream of the Palatka site. Salinity is another primary physical feature that varies predictably across the St. Johns River estuary (Fig. 1) and that appears to affect the distribution of rainwater killifish. Significant positive partial correlations indicate that the abundance of rainwater killifish increases with increasing salinity as long as vegetated habitat is available. Dunson and Travis (1991) demonstrated that salinity does not directly affect survival of rainwater killifish within the range of salinities observed between Palatka (0.3 ± 0.1‰) and Bolles (1.6 ± 1.9‰). Salinity probably plays an important role in mediating the outcome of competitive interactions between rainwater killifish and ecologically similar species that are more tolerant of freshwater. Dunson and Travis (1991) found that the relative competitive ability of rainwater killifish and the typically freshwater bluefin killifish (*Lucania goodei*) reversed along a salinity gradient. The same is likely true for the eastern mosquitofish (*Gambusia holbrooki*) and golden topminnow (*Fundulus chrysotus*), which are morphologically and ecologically similar to rainwater killifish. Rainwater killifish are replaced entirely by eastern mosquitofish, golden topminnows, and bluefin killifish upstream of Lake George, despite the presence of extensive beds of submergent and emergent vegetation (Jordan et al. 1998). More salinity tolerant species that prefer open sand and emergent salt marsh habitats (e.g., the topminnows *Fundulus confluentus, F. heteroclitus,* and *F. majalis*) replace rainwater killifish in the lower reaches of the St. Johns River estuary (Weaver and Sulak 1998; Jordan unpublished data) where SAV is absent.

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ST. JOHNS RIVER WATER MANAGEMENT DISTRICT. Office of Communications and Governmental Affairs, P.O. Box 1429, Palatka, Florida 32178–1429.

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