Influence of climate-mediated shifts in wetland vegetation on prey fish habitat use and schooling dynamics

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ABSTRACT: Intertidal wetlands provide vital habitat for numerous species by serving as a basal resource and refuge for shelter-seeking fauna. These environments are particularly important for transient nekton that trophically link marine and terrestrial food webs via migration into the intertidal during the flooding tide. Changes in coastal vegetation due to a warming climate, such as the replacement of temperate saltmarshes with tropical mangroves, may alter habitat use by transient species due to differences in food provisioning and the structural attributes of mangrove and saltmarsh vegetation. In northeast Florida (USA), *Fundulus heteroclitus* (mummichog) and *F. majalis* (striped killifish) are abundant, trophically important, transient fishes that may exhibit behavioral changes with coastal habitat shifts. We experimentally manipulated predator presence in a large-scale mesocosm containing an array of 4 habitats found at the mangrove–saltmarsh ecotone: marsh vegetation (smooth cordgrass *Spartina alterniflora*), 2 species of mangroves (red mangrove *Rhizophora mangle* and black mangrove *Avicennia germinans*), and sand, and measured prey fish habitat use and schooling dynamics. Mummichogs utilized black mangrove habitat to the same degree as cordgrass regardless of the presence of a predator, indicating that mummichogs perceive both habitats as providing equivalent protection. Killifish exhibited little affinity for any particular habitat and exhibited schooling behavior over seeking refugia for predator avoidance, suggesting that vegetation changes may have little effect on killifish behavior. Further research on how such patterns of habitat use combined with habitat-specific dietary constituents of fundulids will help to predict how saltmarsh loss at the ecotone will influence nutrient and energy flows in coastal food webs.

KEY WORDS: Predator–prey interactions · Habitat complexity · Ecotone · *Fundulus heteroclitus* · Mummichog · *Fundulus majalis* · Striped killifish · Marsh grass · Mangroves

1. INTRODUCTION

Coastal wetlands occupying the intertidal zone are vital as both nursery and refugia habitat for many juvenile and prey species during periods of tidal inundation (Beck et al. 2001, 2003). The structural complexity created by coastal vegetation can decrease the threat of predation by hindering the movements of larger nekton, limiting the ability of visual predators to detect and pursue their prey, and suppressing the rates at which predators encounter prey (Diehl 1988, Willis et al. 2005). Additionally,

these habitats serve as an essential food source for many organisms that rely on coastal vegetation, detritus, and associated benthic or epiphytic algae as a substantial part of their diet (Darnell 1958, 1961, Boesch & Turner 1984). Derived in part by the protection and sustenance functions they provide, coastal wetlands are highly productive ecosystems that support ecosystem services. For example, within the Gulf of Mexico, saltmarsh wetlands support 66 % of the shrimp and 25 % of the blue crab production in the region (Zimmerman et al. 2002, Barbier et al. 2011). Similarly, in many Central American countries, the productivity of mangrove-dependent fisheries represents a significant percentage of national incomes (FAO 2007, Walker et al. 2022).

However, coastal wetlands are particularly threatened by the growing influence of climate change, including warming temperatures, rising sea levels, and increasing frequency and severity of storm events (Gilman et al. 2008, Kirwan & Megonigal 2013). The poleward expansion of tropical mangroves into temperate regions formerly dominated by saltmarshes as a result of increasing winter temperatures is a highly visible example of climate-related changes in coastal wetlands. Such dynamics have resulted in the transformation of the mangrove–saltmarsh ecotone toward mangrove dominance in several regions across the globe, including Australia, Asia, New Zealand, Southern Africa, and both North and South America (Kelleway et al. 2017, Perillo et al. 2018). Although the value of mangroves and saltmarshes as habitat provisioners is well documented (Minello et al. 2003, Mumby et al. 2004, Barbier et al. 2011, Whitfield 2017), it remains poorly understood how this globally prevalent change in coastal vegetation will affect ecosystem functions, particularly for native saltmarsh fauna with behavioral or life history adaptions that are dependent upon herbaceous vegetation.

Two such native species whose abundance, behavior, and ecological functioning makes them representative of transient prey species that may be influenced by mangrove encroachment are *Fundulus heteroclitus* (mummichog) and *F. majalis* (striped killifish). Both species inhabit estuaries across the eastern USA, with the southern extent of their range occurring in northeastern Florida (Abraham 1985, Duggins et al. 1995, Gonzalez et al. 2009). Coincidently, northern Florida also marks the northern extent of mangrove range expansion. Locations such as St. Augustine, in northeastern Florida, have experienced a twofold increase in mangrove cover since the 1980s, primarily *Avicennia germinans* (black mangrove) and to a lesser extent the less freeze-tolerant *Rhizophora mangle* (red mangrove), replacing the dominant saltmarsh vegetation *Spartina alterniflora* (smooth cordgrass) (Cavanaugh et al. 2014). It is unclear whether the southern range extent of mummichogs and striped killifish is confined by the change in vegetated habitat or other associated environmental variables. However, evidence for the former is apparent, as both species are replaced by congener species south of the ecotone, with striped killifish replaced by *F. similis* (longnose killifish) and mummichogs with *F. grandis* (gulf killifish) (Duggins et al. 1995, Gonzalez et al. 2009). The range distributions of these congeners may be influenced by decreased fitness of mummichogs and striped killifish in mangrove habitats and/or the relaxed competition with mummichogs and killifishes that allow longnose killifish and gulf killifish to occur in higher-latitude saltmarshes in the Gulf of Mexico than on the Atlantic coast (Galleher et al. 2010).

Fundulus is a highly abundant fish genus, with mummichog productivity estimates reaching the highest levels reported for all saltmarsh fish (Meredith & Lotrich 1979, Abraham 1985, Kneib 1986). Because of their abundance, fundulids serve both as an important consumer and prey in saltmarshes. Mummichog and striped killifish (hereafter referred to as killifish) are opportunist omnivores, with slight differences in their preferred foraging habitats and diets. Mummichogs frequently forage on algae and small crustaceans from marsh surfaces (Allen et al. 1994), whereas the killifish diet is largely composed of small bivalves and crustaceans found in sandy substrates (Steele et al. 1995, Harvey 1998). As a result of their broad diet and large populations, fundulids may exert top-down control on benthic intertidal communities (Clymer 1979). Fundulids are also a major food source for a variety of saltmarsh predators: wading birds, including herons, egrets, terns, and gulls; predatory fish, such as striped bass, bluefish, summer flounder, white perch, and red drum; and a variety of benthic and free-swimming crabs (Valiela et al. 1977, Abraham 1985, Kneib 1986). As a highly abundant consumer and prey organism, fundulids facilitate the movement of organic matter into and out of saltmarsh systems (Kneib et al. 1980, Abraham 1985). Due to the integral role of fundulids in saltmarsh trophic interactions, determining the potential effects of mangrove expansion on these fish is fundamental to our understanding of the ecological consequences of this climate-mediated range shift in coastal wetland foundation species.

Of the differences in habitat attributes between mangrove and saltmarsh vegetation that may affect

fundulid behavior and habitat use, perhaps the most apparent is structure. Specifically, herbaceous salt-marsh grasses and mangrove trees vary markedly in stem or shoot density and shape, which are known to affect habitat utilization (Diehl 1988, Cocheret de la Morinière et al. 2004, Willis et al. 2005, Walker et al. 2019). Habitat structure has been heavily studied in the context of its effect on predator–prey interactions, with increased structural complexity correlated with decreased predation (Diehl 1988, Willis et al. 2005, Scheffel et al. 2017). Thus, structural changes in vegetation associated with the expansion of mangroves into saltmarshes have the potential to alter predator–prey relationships involving fundulids. Many prey species rely on the visual complexity of their habitats to elude predation, causing them to move into complex habitats when predators are present (Kjernsmo & Merilaita 2012). Along the US east coast, changes in complexity with the introduction of mangroves have the potential to alter mummichog and killifish susceptibility to predation and reliance on additional antipredator behaviors such as schooling.

Because the life histories of killifish and mummichogs are unique, the 2 species are likely to exhibit distinct responses to the introduction of mangroves as well as to the threat of predation in different habitat types. Both species demonstrate tidally driven migrations, utilizing the marsh surface at high tide; however, killifish are primarily found in marshes containing small creeks or rivulets that are only accessible at high tide, whereas mummichogs also inhabit marshes connected to larger channels (Hettler 1989). Killifish have also been shown to inhabit other areas such as sand runnels (i.e. small channels that form on the beach during low tide), which provide predator protection and access to preferred prey items such as surf clams (Harvey 1998). Mummichogs, however, are dependent on food from the marsh surface to maintain a normal growth rate and conduct the majority of their feeding during high tide when marsh habitats are accessible (Weisberg & Lotrich 1980, Werme 1981, Abraham 1985).

Given the different sub-habitats within coastal wetlands occupied by these fundulids, it is likely that these fishes are exposed to diverse predator assemblages and predator strategies. For example, major predators in the vegetated intertidal include fish and crab species that rely on ambush predation, a tactic that is reliant on sitting and waiting for their prey and benefits from the concealment of the more complex environment (Thiriet et al. 2014). In contrast, unvegetated sandy bottom habitats tend to support more active searching predators such as birds and some

fish species, which rely on the longer sightlines of more open habitats that allow them to use chase and stalk–attack tactics (Kushlan 1976, Thiriet et al. 2014). As a result, there is potential that these 2 fundulids could have different responses to a predator and use habitats differently (Martin et al. 2010).

Prey species that are typically exposed to visual predators within open environments often move in groups such as schools. Schooling is effective in reducing predation by diluting the likelihood of any given individual being eaten and increasing the ability to detect threats from predators (Duke et al. 1998). Godin & Morgan (1985) found that larger schools of *F. diaphanus* (banded killifish) detected an approaching predator sooner than individual fish but delayed their flight response, allowing the group more time to assess the threat and avoid energetically costly false alarms. This implies that increased schooling is a beneficial strategy for fish that feed in more open environments such as sand, within sight of a predator, allowing for protection from predation as well as allowing the group to spend more time on essential activities such as feeding without wasting energetic resources on false alarms. Schooling, however, increases potential detection by a predator. Therefore, its value as an antipredator strategy lies in the group's behavior after recognition by the predator (Godin & Morgan 1985, Switzer 1993). Thus, schooling may be less advantageous for defense against ambush predators whose encounter rate depends on prey density (Thiriet et al. 2014).

To determine how the climate-driven migration of mangroves affects the habitat use, schooling behaviors, and predator–prey interactions of mummichogs and killifish, we implemented an experiment using a large-scale, outdoor mesocosm including an array of the following habitat types: historically dominant saltmarsh vegetation (smooth cordgrass *S. alterniflora*); 2 species of mangroves expanding into the region (red mangrove *R. mangle* and black mangrove *A. germinans*); and unvegetated sand bottom. Through replicated trials in which either killifish or mummichogs were placed in the mesocosm, we examined how each species made use of each habitat type and adapted their schooling behavior in the presence and absence of a predator. We chose *Sciaenops ocellatus* (red drum) as a representative predator in our trials, as this species feeds on both mummichog and killifish in the area (Abraham 1985, Robins & Ray 2016). Because of their demonstrated dependence on cordgrass, we hypothesized that mummichogs would utilize cordgrass over the other habitats (Abraham 1985, Allen et al. 1994, Currin et

al. 2003). We also hypothesized that predator presence would further increase mummichog use of more structurally complex cordgrass as a predator-avoidance strategy over increasing schooling behaviors, as this is likely a more effective strategy against ambush predators typically found in complex habitats. In contrast, we hypothesized that killifish would utilize the cordgrass and sand habitats to a higher extent than the novel mangrove habitats. During the predator-present stage, we hypothesized that killifish would increase schooling as an antipredator response because of their known use of unstructured habitats and effectiveness against stalking and chasing predators found in these environments.

2. MATERIALS AND METHODS

This study was performed in the experimental mesocosm facility at the Whitney Laboratory for Marine Biosciences, located in St. Augustine on the Atlantic coast of Florida in the marsh–mangrove ecotone region. An outdoor 6 m diameter cylindrical holding mesocosm was filled with seawater to a depth of 60 cm, supplied by a flow-through system connected to the adjacent Matanzas River estuary. Flow was suspended during trials and the tank was completely drained (for a minimum of 24 h) between trials. Salinity and water temperature were based on ambient conditions of the estuary during the trial period (September–November 2018: water temperature mean: 25°C, range: 19–30°C; salinity mean: 12 psu, range: 5–18 psu). The mesocosm was sub-divided into 4 equal sections (~4.5 m²) separated by 0.3 m wide strips left bare between sections (Fig. 1). Each quarter was randomly assigned to one of 4 habitat types: cordgrass (tillers), black mangrove (pneumatophores and 2 standing dead trees), red mangrove (prop roots, 2 standing dead trees), and sand. We collected the vegetation from respective habitats near the Whitney Laboratory, removed epibionts, mounted mangrove trees and roots in concrete, and placed the cordgrass in shallow pots. The entire bottom was then covered in sand 15 cm deep, and the standing dead trees were covered with window screening to create shading that matched the average canopy shade of 20 trees of each species as measured by a photosynthetically active radiation meter in local mangrove stands (average shade effect of 93% in red mangrove and 80% black mangrove stands). All vegetation was collected and installed in natural densities that we recorded in St. Augustine: cordgrass tillers, ~60 m⁻²; black mangrove pneumatophores, ~90 m⁻²; red mangrove prop roots,
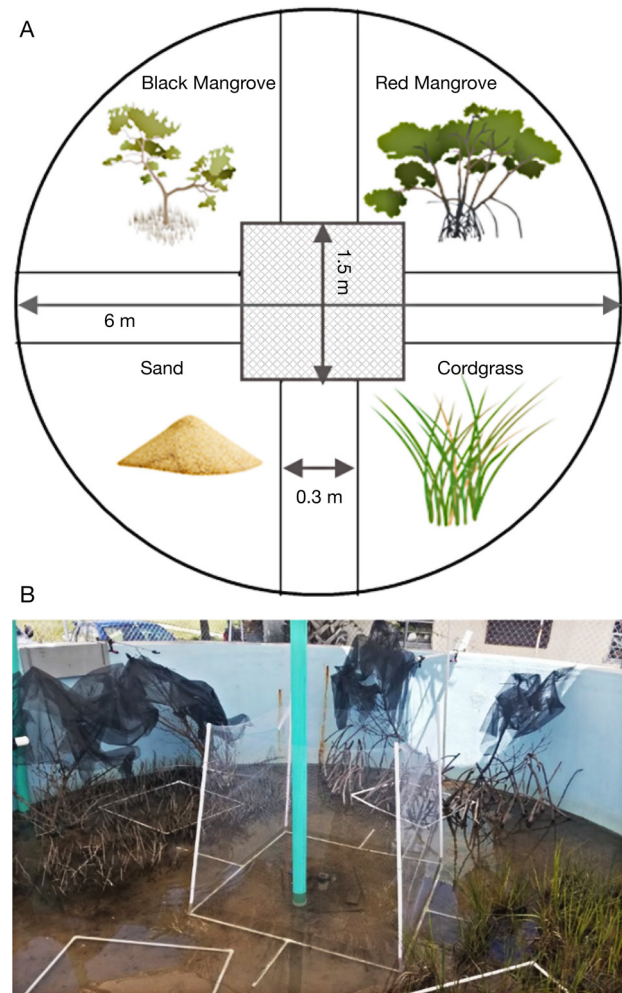

Fig. 1. (A) Birds-eye view of mesocosm design: sub-divided circular arena with 4 equal sections randomly assigned to 4 habitat types, clockwise from top left: *Avicennia germinans* (pneumatophores), *Rhizophora mangle* (prop roots), *Spartina alterniflora* (tillers) and sand. (B) Picture of the mesocosm at Whitney Laboratory, St. Augustine, Florida, USA

~15 m⁻². Vegetation and sand were acclimated in the mesocosm for 3 wk before trials began. GoPro cameras were fitted to the top of the mesocosm, one in each vegetation type, and focused downward over a 1 m² PVC quadrat that was haphazardly placed within the habitat type between trial dates. To contain the predator fish during predator trials, we installed a 1.5 m² PVC cage with 2 cm mesh-diameter monofilament fishing net in the center for the mesocosm. To discourage visits by predatory birds, a canopy was suspended over the mesocosm.

For each trial, the mesocosm was stocked with either 30 *Fundulus heteroclitus* (mummichog) or *F. majalis* (striped killifish) (both ~6–9 cm in length), collected locally from the Matanzas River. The fun-

dulids were fed ad libitum in a holding tank prior to being released to acclimate to the mesocosm for 24 h before the start of the trial. For each fish species, 5 replicate trials were performed.

Each trial consisted of 3 stages, each lasting for 4 h: pre-predator, predator present, and post-predator, with the pre-predator stage starting when light availability was sufficient (~07:00–08:00 h) to obtain video footage. During the pre-predator stage, only the fundulid species were in the mesocosm. During the predator-present stage, a predatory fish, *Sciaenops ocellatus* (~48–66 cm in length), was introduced into the 1.5 m^2 mesh cage at the center of the mesocosm (Fig. 1). The predator was held in a separate holding tank prior to the trial where it was starved for 24 h to standardize feeding history and hunger level, and individuals were exchanged between trials (Hulthén et al. 2015, Vinterstare et al. 2023). The predator was then removed for the post-predator stage. All animal collection, holding, and experimental procedures were approved under the University of Florida IACUC #201810308.

During each predation stage, 15 min of video footage was recorded per hour in each habitat type, resulting in a total of 60 min of footage per predation stage, habitat type, and trial. Footage was analyzed to record prey fish habitat use, habitat fidelity, and schooling behavior. Habitat use, an important indicator of which habitats the fish would likely use in nature, was measured with 2 metrics: the total number of fish that entered the quadrat within each habitat per 15 min video (cumulative number of fish) and the total amount of time (in minutes) all fish spent in each habitat quadrat per 15 min video (cumulative time). Because individual identification of each fish was not possible, each fish that entered the habitat was treated as a new individual (Coppola et al. 2021). Therefore, cumulative counts of fish entries per 15 min video can be higher than the 30 fish stocked in the mesocosm.

Time per entry was used as a measure of habitat fidelity, or the duration a fish would remain within a habitat after entering. Habitat fidelity is an indicator of the cost of switching habitats, either because of differences in food availability, predation protection, or other risk factors (Switzer 1993, Bouillon et al. 2011). Habitat fidelity is of particular interest in our study, as fundulids have been shown to have small home ranges (Abraham 1985, Nelson et al. 2014, Jensen et al. 2019). Fidelity is an important metric to pair with the cumulative number of fish per habitat because if habitat fidelity is high, a given fish will move into and out of a habitat less frequently, poten-

tially resulting in a lower number of fish recorded entering each habitat.

Since some fish respond to predators by forming schools and increasing school size, all fish entries were categorized as 'schooling' for fish entering the quadrat as a group (≥2 fish) (Godin & Morgan 1985). To determine fish dependence on schooling behavior for increased predator detection and protection, schooling attributes were characterized as the percent of fish within a habitat that were schooling and the average size of the school in each respective habitat and predation stage combination. To determine if being a part of a school affected habitat use, time per entry (habitat fidelity) was also compared for both individual and schooling fish. We analyzed habitat fidelity for individuals and schools separately because schools would have an elevated time per entry, as all else being equal, time per entry in each habitat was calculated from the entry time of the first fish and the exit time of the last fish in a school.

All videos were analyzed by the lead author and volunteer citizen scientists. To maintain consistency among reviewers, the lead author gave all citizen scientists the same training and reference materials. All instances of unclear school sizes or entry and exit times were flagged by citizen scientists and reviewed by the lead author. If there were still discrepancies, another reviewer would analyze the video. If a consensus was not reached after 3 independent reviews, the lead author would make the final decision. The lead author also reviewed 10% of unflagged citizen scientists' entries to ensure uniformity. There was no significant difference in fish counts (*t*-test; $t = 0.06$, df = 46, p = 0.95) or recorded times ($t = 0.375$, df = 46, p = 0.70) coded by the citizen scientists and the lead author.

All data were analyzed using SAS 9.4. All variables for each species (i.e. cumulative time in habitat, time per entry, time per entry for schooling and individual fish, cumulative number of fish, average school size, percentage of fish in schools) were analyzed using a generalized linear mixed model using a negative binomial distribution (White & Bennetts 1996, Lindén & Mäntyniemi 2011, Looby et al. 2021). All data were linearized and transformed using the Laplace method. In all models, habitat and predation stage were treated as fixed effect variables, and trial was treated as a random effect. Fish species were not compared in the same model because the trials lacked temporal independence (i.e. we did not randomize the sequence of the mummichog and killifish trials). For all statistical analyses, the significance level was set at $\alpha = 0.05$.

3. RESULTS

3.1. Habitat use and fidelity

Killifish habitat use, measured as the cumulative number of fish in each habitat (Fig. 2A) and the cumulative time spent in each habitat (Fig. 2B), was similar across predation stages and habitats (Table 1). However, killifish habitat fidelity (time per entry) was approximately 2 times higher for cordgrass, averaging 15 s entry^{-1} across all predation stages, compared to the black and red mangrove habitats, which were similar and averaged only 6–8 s entry^{-1} across stages (habitat $p = 0.026$; Fig. 2C, Table 1). Killifish habitat fidelity (time per entry) was intermediate in the sand and indistinguishable from any of the other habitats, with an average time of 9–10 s entry^{-1} across all predation stages (habitat $p = 0.026$; Fig. 2C, Table 1).

Predation stage did not influence any of the mummichog habitat use or fidelity metrics; however, mummichog cumulative time per entry and time per entry did vary across habitats (Fig. 3A, Table 2). In particular, this species spent about twice as much time in the black mangrove (average of 1:55–3:00 min per stage) and cordgrass (average of 1:50–3:45 min per stage) compared to the red mangrove (average of 0:57–1:56 min per stage) habitat. Mummichog habitat fidelity was intermediate in sand (average of 0:58–2:01 min per stage) and similar to the other habitat types (habitat $p = 0.03$; Fig. 3B, Table 2). Similarly, the habitat fidelity of individual mummichogs (time per entry) was highest in the black mangrove (average of 0:12–0:19 min per entry) and cordgrass (average of 0:11–0:14 min per entry) compared to the red mangrove (average of 0:05–0:03 min per entry) or sand habitat (average of 0:04–0:03 min per entry) (habitat $p = 0.03$; Fig. 3C, Table 2).
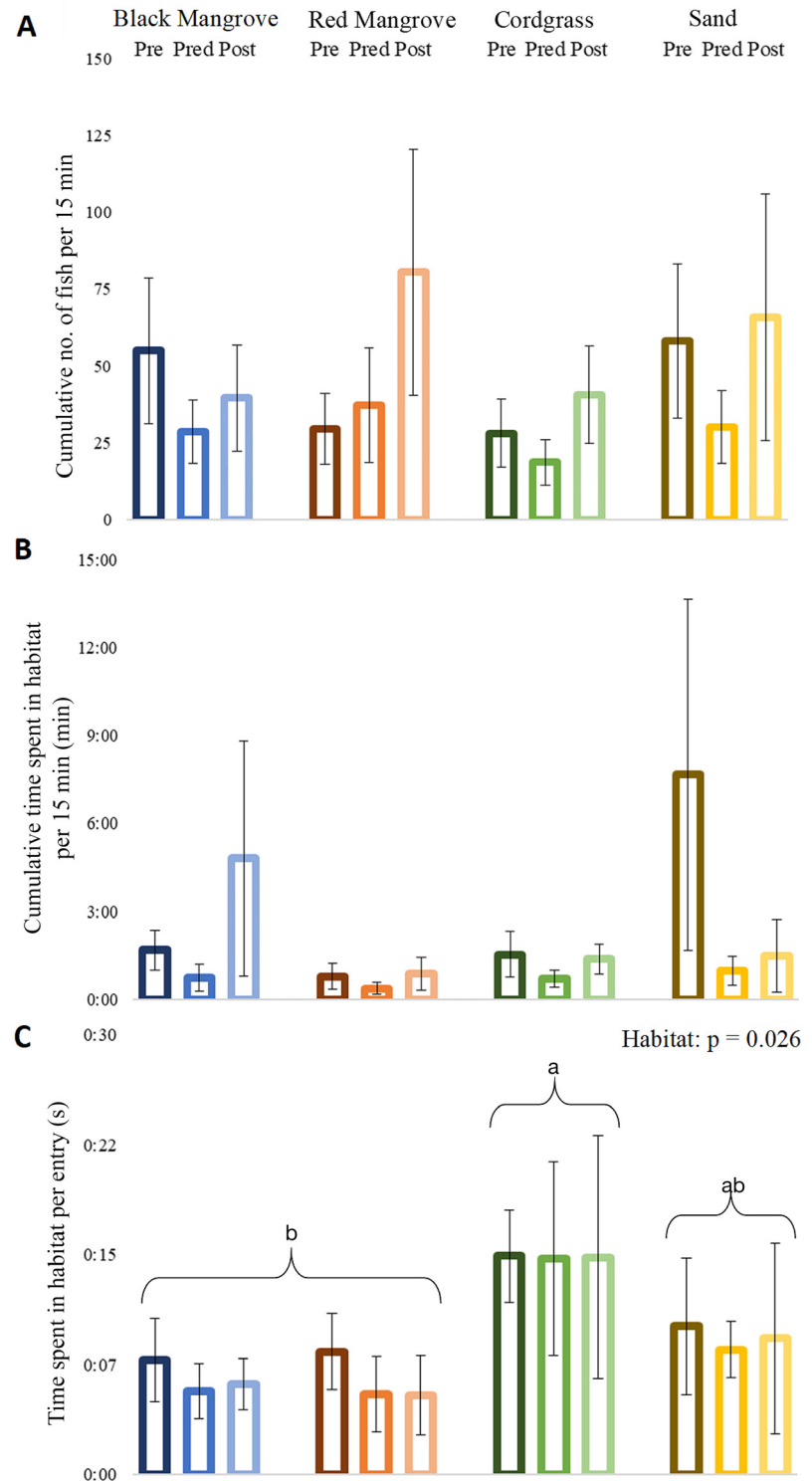

Fig. 2. Overview of *Fundulus majalis* (striped killifish) habitat use and fidelity as measured by (A) cumulative number of fish entering each habitat quadrat during a 15 min time period, (B) cumulative time spent in each habitat per 15 min, and (C) time spent in each habitat and stage per entry. Each trial consisted of 3 stages, pre-predator (pre), predator present (pred), and post-predator (post). Habitat type is indicated by chart color: black mangrove: blue; red mangrove: orange; cordgrass: green; sand: yellow. Error bars: ±SEM. Different lowercase letters above the bars indicate significant differences

Table 1. Results of generalized linear mixed model for cumulative time, cumulative number of fish, and time per entry for the *Fundulus majalis* (striped killifish) trials. Significant p-values are in **bold**

		df	F	p
Cumulative time	Stage	2	1.19	0.32
	Habitat	3	0.95	0.42
	Habitat × stage	6	0.97	0.46
Cumulative no. of fish	Stage	2	2.2	0.13
	Habitat	3	1.03	0.39
	Habitat × stage	6	0.48	0.81
Time per entry	Stage	2	0.24	0.79
	Habitat	3	3.41	**0.03**
	Habitat × stage	6	0.04	0.99

3.2. Schooling attributes

Killifish demonstrated high schooling (>85%) across all habitats and predation stages (Fig. 4A). However, the percentage of individuals schooling in response to predation stage differed across habitats (habitat × stage $p < 0.01$; Fig. 4A, Table 3). In both the sand and red mangrove habitats, killifish schooling increased by 2% from the pre-predator to the predator-present stage. In the post-predator stage, schooling then decreased by 3% in the sand but remained the same in the red mangrove habitat. In the black mangrove habitat, schooling decreased from the pre-predator (93%) to predator-present stage (89%) and then increased again in the post-predator stage (93%). In contrast, percent schooling in the cordgrass habitat remained consistent across all predation stages (95–96%).

The effect of predation stage on killifish school size also varied across habitats (habitat × stage $p < 0.01$; Fig. 4B, Table 3). In the black mangrove and sand habitats, school size shifted in opposite directions in response to predation stage. Killifish formed 33% larger schools in the black mangrove habitat during the predator-present stage than the pre- and post-predator stages; however, in the sand habitat, killifish formed 33 and 50% smaller schools in the predator-present than the pre-predator and post-predator stages, respectively (habitat × stage $p < 0.01$;
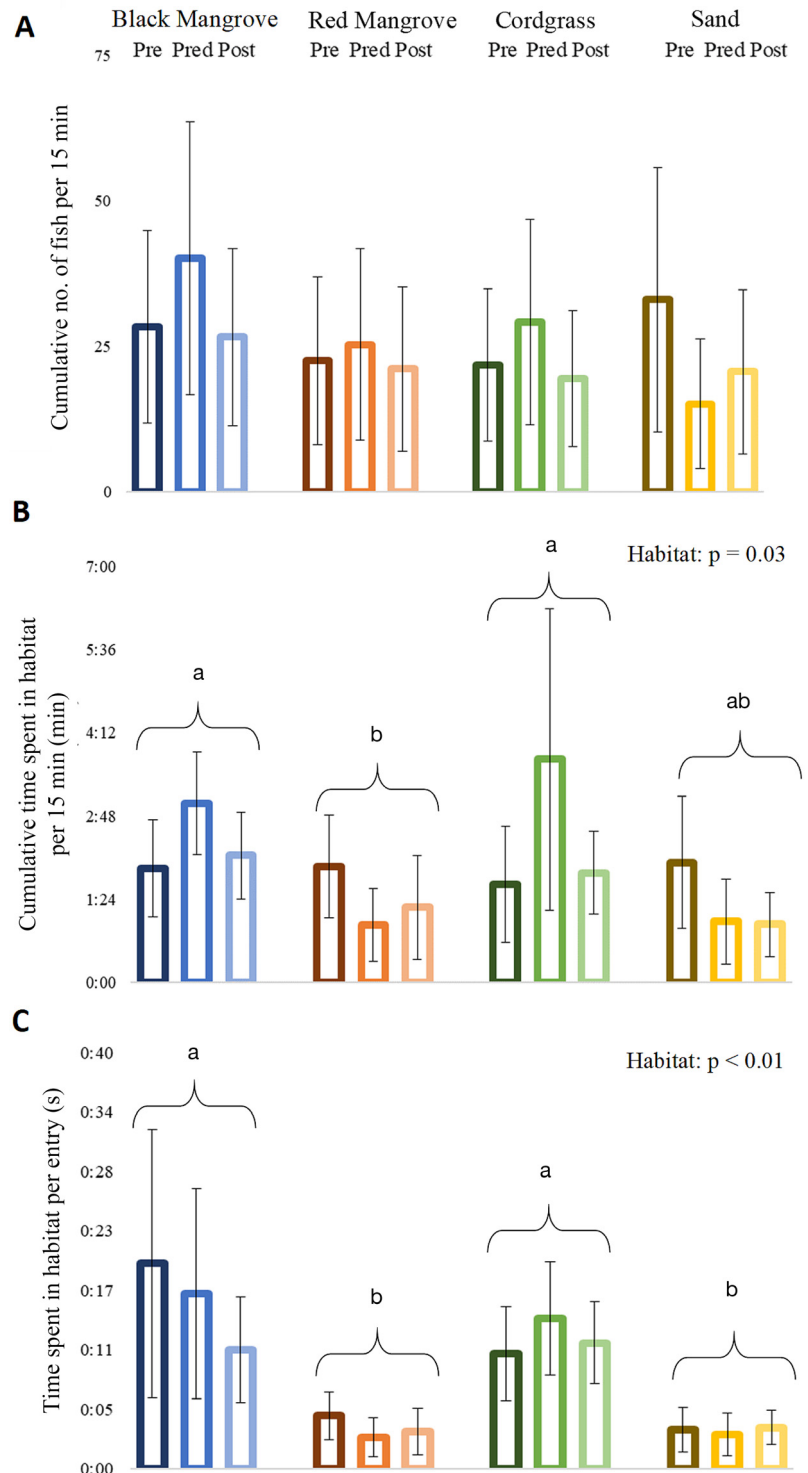

Fig. 3. Same as Fig. 2, but for *Fundulus heteroclitus* (mummichog)

Fig. 4B). School size did not vary with predation stage in the red mangrove or cordgrass habitats. Across all trials, average school sizes ranged from a minimum of 6 to a maximum of 14 fish.

Table 2. Results of generalized linear mixed model for cumulative time, cumulative number of fish, and time per entry for the *Fundulus heteroclitus* (mummichog) trials. Significant p-values are in **bold**

		df	*F*	p
Cumulative time	Stage	2	1.11	0.34
	Habitat	3	3.63	**0.02**
	Habitat × stage	6	0.64	0.70
Cumulative no. of fish	Stage	2	0.29	0.74
	Habitat	3	0.68	0.57
	Habitat × stage	6	0.38	0.88
Time per entry	Stage	2	0.17	0.85
	Habitat	3	3.41	**<0.01**
	Habitat × stage	6	0.04	0.93

Killifish schools and individuals exhibited similar habitat fidelity across predation stages (Fig. 4C,D, Table 3). The significant differences in habitat fidelity for all fish entries (Fig. 2C) was likely lost because of increased within-group variability resulting from the decreased sample size.

Similar to killifish, the percentage of mummichogs schooling was high across all habitat and predation stages (>60%) and differed in response to predation stage across habitats (habitat × stage p < 0.01; Fig. 5A, Table 4). In the black mangrove, the percentage of mummichog schooling in the pre-predator stage was 18 and 16% higher than in the predator-present and post-predator stages, respectively. Similarly, within the sand, mummichog schooling was 27 and 37% higher in the pre-predator than the predator-present and post-predator stages, respectively. In the red mangrove and cordgrass, in con-
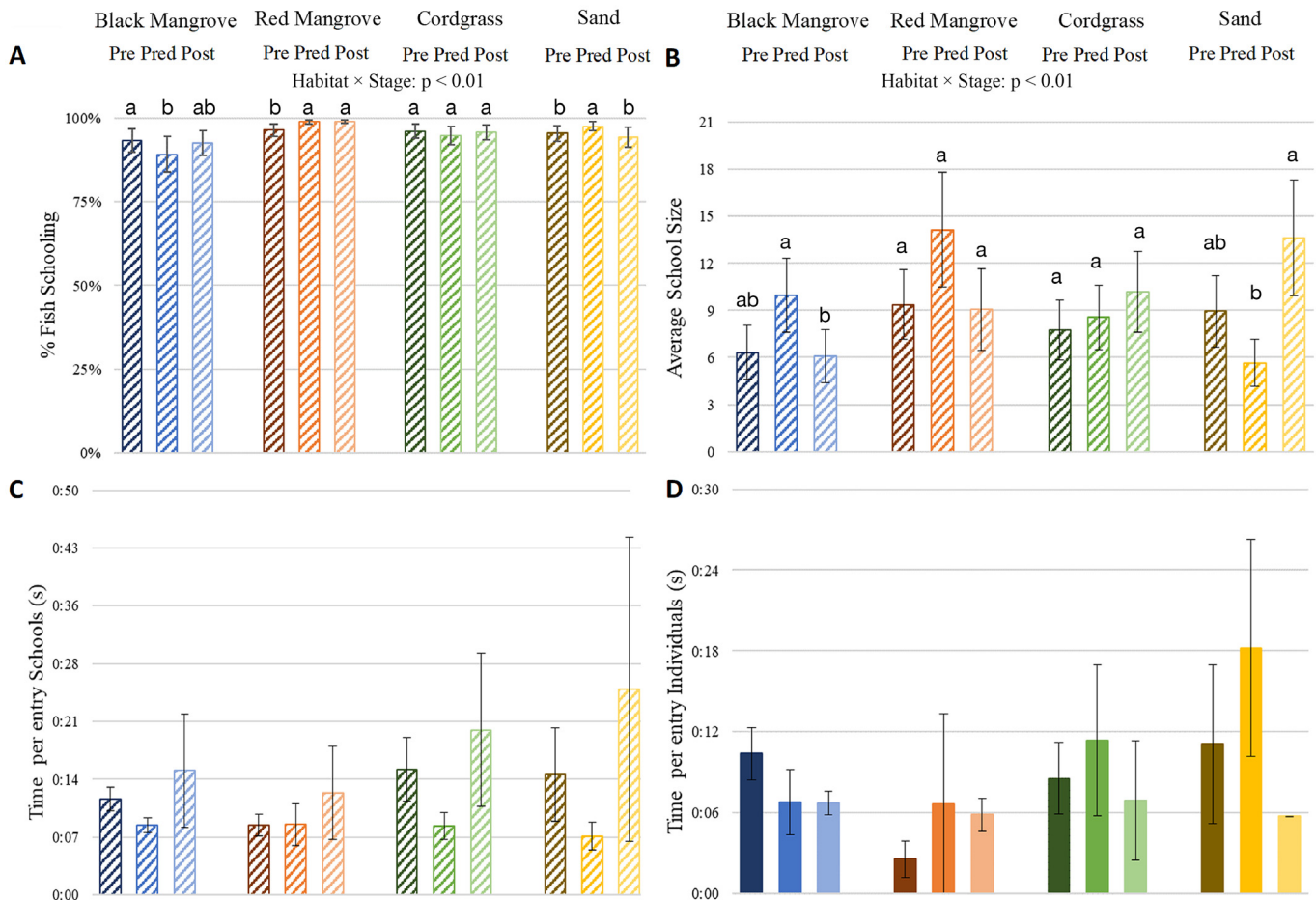

Fig. 4. Overview of *Fundulus majalis* (striped killifish) schooling, indicating (A) the percent of fish of observed in schools, (B) average size of schools, and (C) time that schools and individuals spent in each habitat and stage per entry. Each trial consisted of 3 stages, pre-predator (pre), predator present (pred), and post-predator (post). Habitat type is indicated by chart color: black mangrove: blue; red mangrove: orange; cordgrass: green; sand: yellow. Solid bars: fish observed entering as an individual; patterned bars: fish observed entering as a part of a school. Error bars: ±SEM. Different lowercase letters above bars indicate significant differences

Table 3. Results of generalized linear mixed model for the percentage of fish schooling, school size, and time per entry for schools, as well as time per entry for individuals in the *Fundulus majalis* (striped killifish) trials. Significant p-values are in **bold**

		df	*F*	p
% of fish schooling	Stage	2	3.24	0.40
	Habitat	3	46.38	**<0.01**
	Habitat × stage	6	10.43	**<0.01**
School size	Stage	2	0.94	0.40
	Habitat	3	2.23	0.10
	Habitat × stage	6	3.45	**0.01**
Time per entry (schools)	Stage	2	1.84	0.13
	Habitat	3	1.03	0.39
	Habitat × stage	6	0.33	0.91
Time per entry (individuals)	Stage	2	3.00	0.08
	Habitat	3	2.67	0.08
	Habitat × stage	6	0.94	0.49

trast, the percentage of fish schooling was similar in the pre-predator and predator-present stages, and 9 and 20% lower in the final, post-predator stage in the red mangrove and cordgrass, respectively (habitat × stage p < 0.01; Fig. 5A, Table 4).

Mummichog school sizes varied between the pre- and post-predator stages, with considerably larger school sizes occurring during the pre-predator than post-predator stage in all habitats (stage p = 0.032; Fig. 5B). School sizes in the predator-present stage were intermediate and not significantly different than either pre- or post-predator stages in any habitat (Fig. 5B). Average mummichog school sizes were relatively low within all habitat and predation stage combinations, ranging from 2–7 fish, compared to the killifish, which ranged from 6–14 fish. Similar to killifish, neither schools of mummichogs nor individuals varied in their habitat fidelity across predation stages (Fig. 5C,D, Table 4), and significant differences in habitat fidelity for fish entries (Fig. 2C) were absent when partitioned by schooling versus individuals (Table 3).
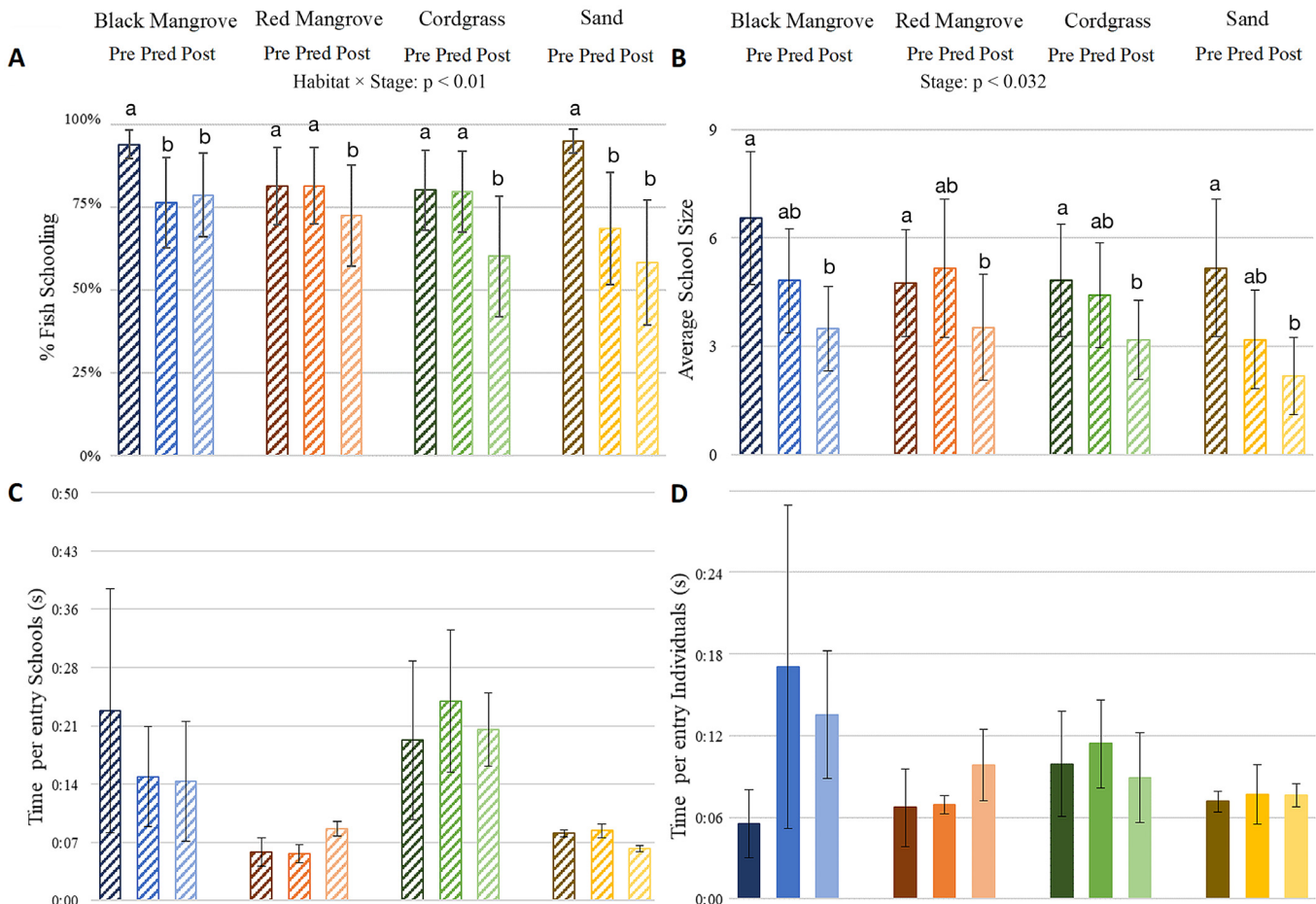

Fig. 5. Same as Fig. 4, but for *Fundulus heteroclitus* (mummichog) schooling

Table 4. Results of generalized linear mixed model for the percentage of fish schooling, school size, and time per entry for schools, as well as time per entry for individuals in the *Fundulus heteroclitus* (mummichog) trials. Significant p-values are in **bold**

		df	*F*	p
% of fish schooling	Stage	2	76.91	**<0.01**
	Habitat	3	15.34	**<0.01**
	Habitat × stage	6	16.77	**<0.01**
School size	Stage	2	3.98	**0.03**
	Habitat	3	0.83	0.49
	Habitat × stage	6	0.3	0.93
Time per entry (schools)	Stage	2	0.15	0.13
	Habitat	3	0.10	0.39
	Habitat × stage	6	0.50	0.91
Time per entry (individuals)	Stage	2	0.70	0.86
	Habitat	3	0.57	0.96
	Habitat × stage	6	0.60	0.80

4. DISCUSSION

In this replicated mesocosm study, we affirmed that mummichogs utilized structurally complex habitats; however, in contrast to our hypotheses, we discovered that their habitat use was not limited to the familiar cordgrass environment nor did it increase during the predator-present stage. Instead, mummichogs made use of cordgrass and black mangrove at similar levels during all predation stages, indicating that for mummichogs, in the presence or absence of predators, black mangrove may be an adequate habitat substitute for cordgrass as this foundation species migrates north. As hypothesized, killifish did show an affinity for cordgrass and sand habitats; however, their cumulative use of these habitats was not substantially different from that of the 2 mangrove species. Killifish showed a very high degree of schooling overall, but the percentage of fish schooling was highest in the more open sand and red mangrove habitats, particularly while the red drum predator was present, suggesting that this species may utilize behavioral avoidance strategies over the use of complex refugia habitats for predator protection. Collectively, the generally subtle differences in habitat use observed in the killifish trials may indicate that like the mummichogs, killifish habitat use and predator avoidance strategies may be minimally affected by the transition of cordgrass to mangroves.

Neither fish species drastically changed its habitat use or schooling patterns based on predator pres-

ence, and we postulate that the perceived threat of predation by both prey species was low in the presence of the red drum predator in our study. This may have arisen in our mesocosm because the abundance and variety of predators (e.g. birds) is typically higher in natural systems than it was within our experiment, or because detection of the predator by the prey fish was low. Since fish, including fundulids, often use visual cues from predators, periods of inactivity by the red drum may have habituated the fundulids to its presence, thus decreasing its perceived threat (Welch & Colgan 1990). An inability of the red drum to feed on the prey fish could have also negated the potential for chemical detection of the predator, as some fundulids have been shown to increase antipredator behavior in response to skin extract from conspecifics, mimicking a recent and successful predator attack (Hoare et al. 2004). With some fish responses to predators being continuous rather than binary, such as increasing antipredator schooling behaviors with increasing predation threat, low density or detection of predators within our study may have resulted in a low predator response by prey fish (Hager & Helfman 1991, Svensson et al. 2000). If we had increased the perceived threat, patterns in antipredator responses may have been further elucidated. It is also important to note that within this study we measured non-consumptive predator effects on habitat use by the study species. Although these species demonstrated a limited behavioral response to the presence of the predator, alluding to a similar level of perceived predation threat, this may not be representative of actual predation risk. Further experimentation is needed to elucidate changes in consumptive effects of predators with shifting vegetation. Striped killifish did not use any one particular habitat type over another; the only metric differing between habitats was habitat fidelity, measured as the time per entry metric (Fig. 2C). Killifish showed the highest fidelity to cordgrass and trended towards elevated fidelity to sand, where they are known to feed (Harvey 1998). These patterns suggest that killifish may preferentially use these familiar habitats. This may be a result of decreased feeding ability in more structurally complex habitats, including those formed by mangroves, as killifish are visual predators and may have a decreased ability to catch prey in complex habitats. For example, striped killifish capture twice as many amphipods in bare environments than in more complex macroalgae (Drake et al. 1995). Within our study, sand was the least complex of the habitats, devoid of any structure. Comparing the complexity of

mangroves and saltmarsh vegetation is difficult since the complexity of an environment can involve multiple attributes, including shading, color variation, stem density, stem height, surface area, and perimeter length (McGarigal & Marks 1995, Cocheret de la Morinière et al. 2004, Willis et al. 2005, Kjernsmo & Merilaita 2012). However, for the stem density parameter, black mangrove pneumatophores within our study (based on densities and the surrounding St. Augustine area) were greater than cordgrass tiller or red mangrove prop root densities (Walker et al. 2019). Similar complexity patterns have also been reported in other areas, with higher densities and areal stem cover (the product of mean stem area and stem density) at black mangrove compared to cordgrass sites in the Louisiana mangrove–saltmarsh ecotone (Caudill 2005). Within the ecotone, black mangrove may thus be considered the most complex intertidal habitat, followed by cordgrass, with red mangrove being the least complex of the vegetated environments. This suggests that killifish may spend considerable time in 'risky' (i.e. structurally simple) but food-rich environments such as sand to fulfill their nutritional needs. Of note, we did not quantify prey availability in our mesocosm, so we cannot definitively resolve the potential role of food availability across habitat types in mediating fish behavior. However, we anticipate that prey availability was low across habitats because of the significant time it took to set up the tanks — a period of stress that likely killed many benthic prey — as well as the lack of benthic habitat availability, with shallow sand used to cover the concrete base of the tank and mangrove plants.

The schooling behaviors of the killifish observed in this study support the hypothesis that this species may utilize riskier feeding habitats and schooling in place of using refugia habitats for predator protection. Killifish heavily utilized schooling, with >85% of individuals schooling in all habitats and predation stages (Fig. 4A). Killifish also did not decrease their use of less complex sand and red mangrove habitats after the introduction of the predator (Fig. 2) but did increase their percent schooling within these habitats during the predator-present stage (Fig. 4A). This suggests that they responded to an increased perceived predation threat with increased schooling behavior rather than movement into more structured habitats. While the relatively low difference (80 vs. 100% schooling) and no obvious response to the predator with increased school sizes or differences in habitat fidelity based on schooling (Fig. 4) may not appear ecologically significant, this effect may be amplified in larger population sizes than the 30 fish used in each trial of our study. Owing to their lack of overall use of one habitat over another, affinity for schooling, and their known affinity for foraging in sand habitats, killifish may be able to adapt to the changing coastal vegetation if their dietary needs are met by foraging in the sand habitats, as the vegetative structure is of secondary importance. However, killifish did trend towards having the highest fidelity to cordgrass vegetation, which indicates that they may still use this moderately complex habitat for feeding or other essential activities.

Conversely, we found that mummichogs are more likely to use habitats that have a complex structure, whether it is the resident cordgrass or the more recently established black mangrove. Mummichogs spent significantly more cumulative time in and had the highest fidelity to the cordgrass and black mangrove habitats (Fig. 3B,C). This is particularly interesting since the mummichog diet is largely composed of saltmarsh prey with less known about their ability to feed on mangrove-derived prey (Kneib et al. 1980). This may indicate that, unlike killifish, mummichogs are more likely to utilize habitats based on complexity than environments they are known to feed in (i.e. refuge ability). This is supported by the mummichogs' decreased use of anti-predator schooling behavior, which is more beneficial in open environments, relative to the striped killifish. Although the majority of individuals of this species were found within schools, mummichogs displayed a lower percentage of schooling and had smaller school sizes than killifish (Figs. 4A, & 5A,B). Moreover, unlike killifish, mummichogs also did not increase schooling or school size in any habitat in response to the predator (Fig. 5A,B).

However, mummichogs did not seem to use red mangroves to the same degree as the other habitats. We speculate that this could be because red mangroves represent the most novel or recent of the habitats, with very few established stands of red mangroves occurring in St. Augustine, where our prey fish were collected. The thicker, less uniform shapes of red mangrove prop roots may be a poor mimic of the familiar cordgrass structure compared to the thinner, more stem-like structure of black mangroves. The complexity of red mangroves in our study was also low, with the lowest stem density of the 3 vegetated mesocosm sections. However, surveys of prop root densities in mature South Florida stands report densities up to 45 stems m^{-2}, compared to the 15 stems m^{-2} in our mesocosm. Diameters of mature prop roots have also been reported to be up

to 4.9 cm, far larger than cordgrass blade widths (0.7–0.9 cm) and black mangrove pneumatophore diameters (0.5–0.6 cm) measured within our study (Thayer et al. 1987). Red mangroves, which occupy the lower to mid-intertidal range (compared to black mangroves, which occupy the mid-high intertidal), can support a diverse community of fouling marine epibionts on their prop roots which could further increase their complexity (Ellison et al. 1996, Duke et al. 1998). Studies of mangroves in southern Florida have found that there was a succession pattern of fish colonization in mangroves, with mature stands having higher fish diversity than newly restored forests (Barimo & Serafy 2003). Together, this body of work and our results suggest that fish species that utilize complex coastal vegetation, including mummichogs, could adapt to the transition to mangroves as the forests mature and become more complex.

Mummichog use of mangroves may also be dependent upon whether mangroves can support their dietary needs. Field experiments have shown that mummichog diets cannot be sustained by subtidal food sources alone, with feeding in the intertidal marsh being essential to maintaining populations of this species and 44% of their body carbon composition being derived from the cordgrass food web (Weisberg & Lotrich 1980, Hughes & Sherr 1983, Weisberg 1986). However, in our study, we found similar use of black mangrove and cordgrass environments in all predator stages, which may indicate that mummichogs may use black mangroves for activities such as feeding even when predator protection is not needed. As opportunistic feeders, with a broad diet of polychaetes, copepods, algae, insects, larval fish, and others, mummichog populations may derive sufficient substrate and food resources from mangroves (although see note above indicating that we did not explicitly measure the distribution of prey in our mesocosms to explore these mechanisms) (Kneib 1986). Future research will be needed to determine if black mangroves can support mummichog populations to a similar degree as cordgrass environments and disentangle the relative importance of structural versus dietary factors in facilitating this abundant nekton species.

For both species, additional research with field surveys should verify whether the observed patterns from our mesocosm experiments extend to the natural environment. Our study lacked the differentiated food resources found in natural habitats and instead focused on the effects of habitat structure. Our study was also constrained to mesocosm characteristics such as decreased size of habitats and non-natural

substrates. Although the large size of our mesocosm allowed for a fairly realistic representation of the patchy, highly mixed creeks in the St. Augustine region, fidelity to habitats could change with increasing homogeneity or larger patch sizes, as well as with a more natural density and diversity of food and predators found in the field. Surveys of habitat use of these fish species in the region could test how the habitat use patterns observed in our experiment contribute to natural patterns in settings with differentiated food resources and monotypic stands of habitat along creeks.

5. CONCLUSIONS AND FUTURE DIRECTIONS

Our findings suggest that both killifish and mummichogs may be able to adapt to the changes in structure from marsh to black mangrove (and possibly red mangrove) vegetation if other habitat needs can still be met. One need that may warrant further consideration is the ability of mangrove environments to support the diets of these species. Given that both species have broad, omnivorous diets, it is possible that dietary impacts to populations could be minimal, with resilience to dietary changes already having been shown in mummichogs (Currin et al. 2003, Goto & Wallace 2011). Further studies examining the wider ecological implications of dietary shifts in these tidally transient species are also needed. Saltmarsh vegetation has been shown to have greater bioavailability to local food webs than mangroves in multiple mangrove–saltmarsh ecotones, including Louisiana, China, and Australia (Perry & Mendelssohn 2009, Feng et al. 2015, Jinks et al. 2020). If the less bioavailable mangroves result in an increase in mummichogs and killifish dependence on non-intertidally derived food resources, it could reduce their role in terrestrial and marine food web connectivity (Nyunja et al. 2009).

In addition to the effects of changing structure on use and predator avoidance examined in adult fish in our study, structural differences between the 2 vegetation types may be more influential to the success of mummichogs and killifish at younger life stages. In particular, juvenile and egg stages might be more dependent on the cordgrass environment than adults. Mummichogs and killifish deposit their eggs in the intertidal and juvenile mummichogs spend the first 6–8 wk exclusively on the marsh surface, making them susceptible to conditions within the vegetation at low tide that are not experienced by adult mummichogs (Able & Castagna 1975, Taylor et al.

1977, 1979, Jones et al. 1978, Abraham 1985). With vegetation structure influencing the temperature and humidity of the marsh surface at low tide, structural changes may affect the desiccation threat to pre-adolescent killifish and mummichogs (Powers & Cole 1976). Similarly, humidity, temperature, and light conditions can influence surface algae growth, which is a particularly important food source for juvenile mummichogs (Kneib 1986, Whitcraft & Levin 2007). A survey of diatoms at the mangrove–saltmarsh ecotone in northeast Florida found significantly higher diatom levels in saltmarsh creeks than in mangrove-lined creeks; therefore, the transition to mangroves may result in a greater impact on the diet of juvenile mummichogs than adults (Walker et al. 2019).

Besides the structural attributes of coastal vegetation examined in our study, other characteristics such as tidal inundation levels (i.e. water depth on the wetland surface during high tide) will also influence nektonic species' use of these environments as habitat. In our study, we maintained a uniform water height within all our habitats. However, in nature, red mangroves occupy a lower intertidal range than black mangroves or cordgrass (Duke et al. 1998). The lower tidal position increases the hydroperiod, duration, and depth of flooding within this habitat and is an important factor in determining the length of time and number of species that use the intertidal (Jones et al. 1978). Although neither species largely used the red mangrove habitat within our study, the longer hydroperiod would increase the amount of time that this habitat would be available to prey species and may have an overall greater influence on their use of these environments than their structure alone.

Although there are still many facets to explore to determine the effect of mangrove migration on striped killifish and mummichogs, our study fills some of these knowledge gaps by shedding light on their habitat use and schooling strategies. We can conclude that mummichogs utilize the structurally complex habitats of cordgrass and black mangroves at similar levels. Killifish, on the other hand, seemed to show less affinity for structure and only a slight affinity towards habitats in which they are known to feed. They also potentially utilized schooling to a higher degree in more open environments in the presence of a predator, implying that they prioritize social cues and behavioral avoidance of predators over the use of refugia habitat. These findings suggest that both species may be amenable to the conversion of coastlines to mangroves, with killifish relying on schooling for predator avoidance and foraging

in sand environments, and mummichogs utilizing black mangroves to the same degree as cordgrass environments. Mummichogs spent more time in the structure of black mangrove and cordgrass and used red mangroves the least, suggesting that as climate trends continue and red mangrove stands expand into higher latitudes, mummichogs may be negatively impacted if increased forest maturity does not result in higher-quality habitat. Given the observed behavioral flexibility of both species towards range-expanding foundation species, we hypothesize that this amenability to new intertidal vegetation may confer increased resilience in climate-altered ecosystems for the highly connected food webs that killifish and mummichogs are embedded within.

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