Interspecific and intraspecific interactions between fiddler crabs *Minuca pugnax* (mud fiddler) and *Leptuca pugilator* (sand fiddler) influence species' burrowing behavior

Isabelle P. Neylan[a,b,*], Carter S. Smith[a], Erika D. Swanson[c], Stephen R. Fegley[a], Rachel K. Gittman[d]

[a] Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, United States of America
[b] Center for Population Biology, University of California, Davis, CA 95616, United States of America
[c] North Carolina State University, Raleigh, NC 27607, United States of America
[d] Department of Biology and Coastal Studies Institute, East Carolina University, Greenville, NC 27858, United States of America

ARTICLE INFO

ABSTRACT

Species occupying similar habitat and functional niches will necessarily have some external force driving differentiation between them, thus creating complementarity, or otherwise face high competition for resources. In order to fully understand the role of each species in an ecosystem and their contributions to ecosystem function, it is important to understand the nature of these interactions. However, for species that occur in the same spatial niche and appear to occupy redundant functional niches, it is often difficult to distinguish between complementarity and redundancy and therefore to designate the functional role each species plays. We used two co-occurring fiddler crab species that are presumed to be functionally similar, *Leptuca pugilator* (sand fiddler crab) and *Minuca pugnax* (mud fiddler crab), to explore how species interactions may influence burrowing behavior. We ran manipulative mesocosm experiments to assess potential effects of species interactions on the number and location of burrows as well as the burrowing behavior of the crabs. Overall, sand fiddler crabs dug more burrows on average than mud fiddlers across all experiments while mud fiddlers were choosier about the location and sediment type of their burrows, suggesting complementarity in burrowing between the two species. Burrow counts in heterospecific treatments suggest that neither species interfered with nor enhanced burrow creation by the other species. However, increased burrow occupancy by mud fiddlers in the presence of sand fiddlers and aggressive behavior by mud fiddlers toward sand fiddlers suggest that mud fiddler crabs may receive refuge benefits from sand fiddler crabs through antagonistic rather than facilitative interactions. Thus, species-specific habitat use and interspecific interactions are likely influencing the role each species plays as a burrower and marsh ecosystem engineer.

1. Introduction

Complete ecological redundancy occurs when two species co-exist and can each provide the same functional role in the community (Naeem, 2002; Walker, 1992). However, competition is predicted to be highest when species occupy the same part of the niche and use the same resources in space and time (Rosenfeld, 2002); eventually this should lead to the exclusion of one species from the community (The Competitive Exclusion Principle; Hardin, 1960). In theory, ecological redundancy is therefore incompatible with stable coexistence given limited resources, and some factor will inevitably drive the creation of functional differences (Loreau, 2004). However, two species appearing

to occupy the same habitat may in fact be complementary when their functional niches are examined. The functional niche includes factors influencing processes (e.g., habitat modification) rather than just species presence, meaning that two species may exhibit slightly different environmental optima even if co-occupying the same space, leading to complementarity when this new axis is included (Rosenfeld, 2002). Understanding how species function in a community and influence ecosystem processes within the landscape is central to fully understanding the dynamics and ecology of a system and important in managing natural systems.

The role of each species in a community may also play a part in the overall functioning of ecosystems. Whether or not two species are

---

* Corresponding author at: Center for Population Biology, University of California, Davis, CA 95616, United States of America.
  E-mail address: ipneylan@ucdavis.edu (I.P. Neylan).

redundant or complementary can affect the resilience and overall stability of the ecosystem. Having species with overlapping functions can increase the stability of a system to perturbation, as predicted by the Portfolio Effect (Doak et al., 1998) or the Insurance Hypothesis (Yachi and Loreau, 1999). Consequently, while high redundancy and niche overlap may mean higher competition and potential exclusion of one of the species, it may also provide resilience for ecosystems that have lost one of these species.

Fiddler crabs are ideal organisms to study competitive interactions and functional redundancy because they have been well-studied, are found worldwide, and are one of the more abundant macrofauna found in salt marshes, mangroves, and other soft sediment habitats (Bertness and Miller, 1984; Crane, 1975; Teal, 1958). Furthermore, distinct species are often found in close proximity and occupying similar niches. Fiddler crabs are highly social animals displaying herding behavior and burrowing in close proximity to each other, leading to frequent opportunities for interaction and co-occupancy of habitat (Zeil and Hemmi, 2014). Fiddler crabs are also important ecosystem engineers in marsh ecosystems, acting as bioturbators that benefit the marsh plants and supported fauna (Citadin et al., 2016; Gittman and Keller, 2013; Jones et al., 1994; Katz, 1980; Thomas and Blum, 2010; Wang et al., 2010). Burrows can be 10-25 cm deep and play a role in oxygenating and redistributing nutrients in the sediment (Allen and Curran, 1974; McCraith et al., 2003). During a single tidal cycle, fiddler crab foraging and burrowing has been shown to have significant effects on organic content, chlorophyll *a* levels, and meiofaunal density in the sediment (Citadin et al., 2016; Reinsel, 2004; Wang et al., 2010).

Leptuca pugilator (formerly *Uca pugilator*) and *Minuca pugnax* (formerly *Uca pugnax*) are two fiddler crab species known to occupy the same habitat within their overlapping ranges (Allen and Curran, 1974; Colby and Fonseca, 1984; O'Connor, 1993; Teal, 1958) and commonly co-occur in marshes all along the east coast of the United States from Massachusetts to Northern Florida (Bertness, 1985; Reinsel, 2004; Ringold, 1979). *Leptuca pugilator*, commonly known as the sand fiddler crab, typically favors coarser, sandier sediment (Crane, 1975; O'Connor, 1993). *Minuca pugnax*, the mud fiddler, prefers muddier sediment (Aspey, 1978; O'Connor, 1993). These sediment preferences are thought to provide a separation of the species' distributions in a marsh, with sympatry only occurring in marginal areas of habitat consisting of mixed sediment (Allen and Curran, 1974; Colby and Fonseca, 1984; O'Connor, 1993; Teal, 1958). Sand and mud crabs occupy these distinct sediment types in some marshes, such as those in Georgia, with minimal overlap (Teal, 1958). Other marshes, in particular those in North Carolina, however, can have more mixing of fine and coarse sediment without the distinct zonation seen elsewhere (Mattheus et al., 2010; Timmons et al., 2010). While there is still some spatial separation between the two species due to larval settlement and other abiotic factors such as salinity and dominant vegetation, they are observed coexisting in many marshes, including our collection sites where they were observed feeding and burrowing in close (> 10 cm from each other) proximity (Gittman and Keller, 2013; George et al., 2010; O'Connor, 1993; Teal, 1958).

We conducted a series of mesocosm experiments to determine if interactions (intraspecific and interspecific), density, and sediment grain size, influenced species' burrowing frequency, burrowing location, and general behavior. Specifically, we determined i) whether there were differences in the number and location of burrows dug between the two species, ii) whether either species retained their distinct sediment preferences when found co-occurring in mixed sediment, iii) whether there were density-dependent effects on burrowing behavior, and iv) whether burrowing behavior of each species changed in the presence or absence of the other congener. We hypothesized that despite the lack of clear sediment zones in this system, differences in burrowing behavior would emerge. We also predicted that each species would influence the burrowing behavior of the other, creating a biotic rather than the typical abiotic barrier to redundancy.

2. Methods

2.1. Study organisms

We collected female *Leptuca pugilator* (sand) and *Minuca pugnax* (mud) fiddler crabs by hand from two salt marshes: 1) Hoop Pole Creek Clean Water Reserve in Atlantic Beach, NC, USA (34°42′25.12” N, 76°45′1.14” W), which is a 70 × 50 m peninsular marsh predominantly consisting of *Spartina alterniflora* and *Juncus romerianus;* and, 2) the Trinity Center marsh in Pine Knoll Shores, NC, USA (34°41′37.08” N, 76°51′49.68” W), which is an approximately 20 m wide marsh protected by an offshore restored oyster reef and also dominated by *S. alterniflora* and *J. romerianus* as well as *Spartina patens* and *Salicornia* spp. in the higher marsh zone. Both collection sites had similar surface sediments. The marsh surface sediment of Bogue Banks has been described as "muddy very fine sand" (Timmons et al., 2010) and comprised primarily of "fine- and medium-grained sand" (Mattheus et al., 2010). Sites were comprised largely of mixed sediments (where both species were found and collection occurred) along with interspersed patches of mud and sand. All fiddler crabs were collected between August and September 2012 and August and November 2016. We exclusively collected female crabs for these experiments because our primary focus was on burrowing behavior and female fiddler crabs have been found to burrow more often than males in *L. pugilator* and other species of fiddler crabs and without ancillary behaviors that may be confounding (i.e., mate attraction) (Colby and Fonseca, 1984; Hemmi & Zeil, 2003). Crabs were distinguished visually using observable differences in carapace shape and color (Crane, 1975; Hubbard, 2008). All crabs were held in a flow-through water table at UNC Chapel Hill's Institute of Marine Sciences in Morehead City, NC. Filtered saltwater was drawn directly from Bogue Sound. Sediment was collected from Hoop Pole Creek from areas where the crabs were found to co-occur and used as the substrate in the holding tanks for both species. Crabs were only used once and were typically held for < 48 h and never for more than one week.

2.2. Experimental setup

We conducted three, independent experiments to investigate fiddler crab burrowing activity and behavior as follows: 1) mixed sediment trials (referred to hereafter as Mixed trials), with uniformly mixed sediment and low density of crabs (two crabs per tank); 2) low-density trials with two sediment types (fine sediment and coarse sediment) and two crabs per tank (referred to as low-density FC trials); and, 3) high-density trials with two sediment types (fine and coarse) and ten crabs per tank (referred to as high-density FC trials). In each trial, the data collected included the total number of burrows dug, the location of those burrows including sediment type if applicable, and the occupancy of the burrows. For some of the low-density FC trials and mixed sediment trials, a ten-minute video recording of the crab behavior at the beginning of the trial was also captured and analyzed. The natural density of fiddler crabs at Hoop Pole Creek has been documented as approximately 75 crabs per m² (Gittman and Keller, 2013). Therefore, low-density trials were below this average, (approximately 48 crabs per m²) but were the lowest density possible to achieve heterospecific treatments (one crab of each species) while the high-density trials were above naturally occurring average densities, (approximately 242 crabs per m²) but were not unrealistic densities observed in the field. In particular, crabs reach high local densities while herding, a behavior often observed at our field sites and elsewhere (Aspey, 1978; Salmon and Hyatt, 1983; Zeil & Hemmi, 2006).

For sediment preparation, we classified coarse sediment as grain size > 250 μm but < 500 μm, and fine sediment as less than or equal to 250 μm. 250 μm is the cutoff between sediment classified as fine sand and medium sand. We chose to use this threshold because these species typically co-occur in sandy areas more characteristic of the habitat of

the sand fiddler (Aspey, 1978). We therefore wanted to provide two types of sediment that reflected previously documented species' preferences with each half still being accessible to both species. To prepare the two classes of sediments, we collected sediment from Hoop Pole Creek, wet sieved the sediment with a 63-μm mesh, retained the < 62 μm silt and water to be added back to the fine sediment later, and oven dried (at 93.3 °C) sediment retained on the sieve by placing it in an aluminum tray in an oven for 3–5 h. Following oven drying, we placed the sediment in a RoTap with a 500 μm sieve stacked on a 250 μm sieve on top of a collecting tray. We discarded all sediment and debris remaining on the 500 μm sieve, reserved all sediment that remained on top of the 250 μm sieve as coarse sediment, and reserved all sediment in the collecting tray as fine sediment. The retained water used during the wet sieving process was kept in a separate container and set aside undisturbed for 24–48 h to allow the silt/clay fraction to settle. We then removed the supernatant water and added the remaining silt to the fine sediment.

To prepare each experimental tank prior to the low- and high-density FC trials, we used a thin cardboard or plastic divider and filled half the tank with the coarse sediment and half with the fine sediment to 3 cm depth. We found this to be a sufficient sediment depth for crabs to dig and occupy burrows. The sediment was dampened by adding small amounts of filtered sea water until the sediment was thoroughly moistened without having any standing water on the surface. Once the divider was removed, any gaps between the sediment types were closed with a spatula. After each trial, we removed any mixed sediment from the tank and re-sieved it according to the procedure above.

Each trial, within each of the three experiments, consisted of three treatments: one containing only sand fiddler crabs, a second containing only mud fiddler crabs, and a third containing both sand and mud fiddler crabs. All experiments were conducted in 30.5 × 15 × 21 cm glass tanks with internal dimensions of 29.5 cm × 14 cm (for an area of 413cm^2) by 19 cm high. These tanks were wrapped in white paper to ensure that the crabs in one tank could not see crabs in other tanks. Treatments and crabs were randomly assigned to tanks between each trial. In both conspecific and heterospecific treatments, crabs were paired by eye such that sizes were equivalent between the individuals in a tank. Mean carapace length of both species at these sites are approximately 15 mm (Gittman and Keller, 2013).

Prior to each trial, we labeled the crabs on their carapace using a Sharpie® to identify individuals. Once labeled, crabs for each tank were placed into separate plastic cups. Beginning at peak low tide, the crabs were gently released from the cups into the center of the tank to ensure all crabs were introduced simultaneously and in the center of the tank (on the centerline between coarse and fine sediment where applicable) to ensure an unbiased starting location. Following our behavioral observations (described below), all tanks were topped with plastic lids to ensure no crab escaped and covered with a large black trash bag to avoid potential disruptions or effects of ambient light. We chose to start the trials at low tide because fiddler crabs are most active and burrow at this time (Teal, 1958; Bertness and Miller, 1984; Zeil and Hemmi, 2014). While all experiments were conducted indoors, we wanted to accommodate any ingrained timing of behaviors and to allow them a realistic amount of time to create a burrow (Aspey, 1978; Zeil and Hemmi, 2014).We left the tanks undisturbed until the subsequent high tide (~6 h), at which time we uncovered them and recorded the total number of burrows, whether burrows were occupied or unoccupied, burrow location (corner, middle, or side of tank), and burrow sediment type (in the low- and high-density FC tests).

2.3. Mixed sediment trials

To assess burrowing and burrowing behavior in sediment conditions intended to mimic those found naturally within local NC marshes (mixed sand and mud), we conducted a total of ten mixed-sediment trials between August and October 2016. Each trial consisted of three

tanks as described above giving us ten replicates of each treatment. Sediment was collected from the Hoop Pole Creek marsh, coarsely sieved through 500 μm mesh to remove large debris and shell fragments, and then oven-dried or sun dried without separating fine or coarse sediment. The dried sediment was added to each tank to a depth of 3 cm and moistened with salt water as described above.

2.4. Low- and high-density FC trials

To evaluate the effects of fine versus coarse sediment type on burrowing behavior and burrowing location, we conducted separate fine and coarse (FC) sediment experiments twice, in 2012 and in 2016. Low-density FC trials had two crabs per tank and high-density FC trials had ten crabs per tank (i.e., for the high-density trials, one treatment had ten sand fiddler crabs, one had ten mud fiddler crabs, and the third treatment had five sand and five mud). Between August and September 2012, we conducted 11 replicate trials at low-density (2 crabs) and 6 replicates at high-density (10 crabs). From September to November 2016, we conducted another 8 replicate trials at low-density, as well as another 2 trials at high-density. This was a total of 19 low-density and 8 high-density replicates of all three treatments. Trends were consistent when data from 2012 and 2016 were examined separately, but the overall number of burrows was generally higher in 2012 than 2016, potentially because the trials occurred later in the season (August–September vs. September–November) (2012 trials 2.26 ± 0.25; 2016 trials 0.68 ± 0.31 [mean ± SE]), t-test; p < 0.001).

2.5. Behavior videos

For seven of the Mixed trials and five of the low-density FC trials conducted in 2016, we used GoPro cameras to record fiddler crab behavior. Due to the large number of crabs in the high-density FC experiment, no video footage was collected for behavioral analysis. Cameras were positioned directly above the tanks to obtain an aerial view of the crabs. One camera was used to capture the three tanks comprising one trial. The cameras were turned on at the start of each trial and left to record undisturbed for 25 min, which included a 15-min acclimation period (Robertson et al., 1980) and a 10-min behavioral observation period. After 25 min the cameras were turned off and retrieved and the tanks were covered and left undisturbed for the remainder of the trial. Trials in which no video footage was collected also had a 25-min uncovered interval at the beginning of each trial.

We used the program CowLog (Pastell, 2016) to confirm behavior types (described below) and quantify the amount of time each behavior was exhibited. For the low-density FC trials, we also recorded the sediment type (coarse or fine) in which each behavior occurred. Additionally, we recorded when a crab was in a "blind spot" or an area where the camera was not able to capture the crab fully or it was unreasonable to identify a given behavior due to limited visibility. Any crab that was not captured by the camera for > 75% of the observation time was not used in analyses (of 72 crabs observed across all experiments, 7 were excluded from the analysis).

Potential behaviors were established by direct observations of the crabs in the tanks prior to the video trials. Observed behaviors were grouped into four major categories for analysis: Active (roaming and climbing behaviors), Burrow (behaviors involved in making or occupying a burrow), Interact (behaviors that involved the two crabs in the tank touching or invading the other's burrow), and Stand (the crab was standing still and/or feeding). We categorized interactions further as aggressive, neutral, or defensive (Table 1), but we did not analyze these data, as the sample sizes were too low to achieve adequate statistical power and the nature of the interactions meant that the counts were often not independent across crabs (i.e., if one crab is aggressive, the other often responded with a defensive interaction within the same tank).

Table 1
Descriptions of each overall behavior category recorded during video observation periods (active, burrow, interact, or stand). For interactive behaviors, the nature of the interaction (aggressive, neutral, defensive) is also given.

Category	Behavior	Behavior description	Nature of interaction
Active	Roam	Crab actively walking around tank	
	Climb	Crab with legs on glass side of tank attempting to crawl up the side	
Burrow	Burrow	Crab actively digging burrow	
	Occupy Burrow	Crab in burrow	
Interact	Touch	Crabs touching each other without aggressive or defensive behavior	Neutral
	Toward	Crab distinctly advancing toward the other crab	Aggressive
	Crawl	One crab climbing and crawling on top of another crab	Neutral
	Invade	One crab attempting to expel the other crab from its burrow and, when successful, occupying the stolen burrow	Aggressive
	Follow	One crab following the other crab	Aggressive
	Aggressive	A distinct quick action from one crab against another such as grabbing a leg or lunging at them	Aggressive
	Back	One crab retreating from the aggressive action of the other	Defensive
	Face	Both crabs facing each other in close proximity	Neutral
Stand	Stand	Crab standing still	
	Feed	Crab visibly using chelipeds to move sediment to mouth	
	Guard	Crab standing on or near a burrow	

Given the design of the experiment, the two crabs in the conspecific treatment were not considered independent replicates. Therefore, a random number generator was used to select one of the two crabs in each tank to be included in the behavioral analyses (crabs already excluded due to lack of visibility as stated above were automatically not chosen). Three iterations of randomly chosen crabs were analyzed to ensure no individuals were drastically affecting the data. As no major differences were detected, the first round of crabs randomly chosen were used in subsequent analyses.

2.6. Statistical analyses

To address our hypotheses concerning differences in the number and location of burrows between the two species, we used a generalized linear model (GLM) to evaluate the effect of species treatment (i.e., sand fiddler only, mud fiddler only, and both present) on the total number of burrows dug, the sediment type (if applicable), and the location of burrows. Using Akaike's Information Criterion (AIC), we found that a negative binomial distribution provided the best fit across all experiments. For low- and high- density FC trials, our initial generalized linear model found sediment type was not a significant factor. A second GLM with just species treatment and burrow location was conducted (excluding sediment type) and found to better fit the data when the AIC scores were compared. Sediment type was subsequently dropped from the analysis. A likelihood ratio test was used to determine if there were any significant interactions between the variables in the model. When the overall test was significant, we used Tukey's post-hoc tests to determine pairwise differences.

Based on previous literature, we expected that each species of fiddler crab in the low- and high-density FC experiments might exhibit a different sediment preference for burrowing as they are commonly found burrowing in different sediment types in the field and have species-specific burrowing behaviors associated with either mud or sand when a clear sediment type is available (O'Connor, 1993; Teal, 1958). To test this hypothesis explicitly, we conducted a priori comparisons of burrow sediment type (coarse or fine) between the two conspecific treatments in the low- and high-density FC trials, using Welch's two-sample *t*-tests.

To determine whether interspecific interactions change burrowing behavior, we compared the observed number of burrows in the tanks with both species present to the expected number of burrows calculated by taking the average number of burrows in the sand and mud fiddler crab-only treatments. We then conducted separate paired t-tests for each of the three experiments to compare the number of burrows expected in each trial versus the number of burrows observed. These data were log + 1 transformed to meet model assumptions.

To examine potential effects of intraspecific competition, we compared the conspecific treatments of the low-density to the high-density FC trials looking at the number of burrows dug per crab, normalized by the total number of crabs (2 for low-density, 10 for high-density). We then used a Welch's t-test, which controls for the low sample sizes and uneven distribution of trials between the two experiments, and log + 1 transformed the data to satisfy normality assumptions. The tests were run separately for sand and mud fiddlers.

We also examined the occupancy of the burrows at the end of the trials. In many cases, there were more burrows dug at the end of the trial than crabs present in a tank. All burrows were excavated at the end of the trial and crabs were either noted as occupying or not occupying a burrow. We used a chi-squared test for each species with the number of occupied and unoccupied burrows in the presence and absence of the other species to reveal interspecific effects. In conspecific tanks, only one randomly chosen crab per tank (or 5 crabs in the case of high-density trials) was used to keep the sample size consistent between conspecific and congeneric trials.

To detect differences in behavior among treatments from our video footage, we conducted binomial family GLMs on the amount of time spent displaying two of the four behavior categories listed above, Burrow and Interact. These categories were chosen as the most relevant to our questions of interest. For this analysis, we pooled the mixed sediment trials and low-density FC trials, including experiment type as a factor in the analysis. Experiment type (mixed or low-density FC) was not found to be a significant factor in our model for any of the behavioral categories. When results were significant, we used Tukey's post-hoc tests to examine pairwise differences.

A set of planned comparisons were conducted to determine if there was an effect of treatment on sediment preference for the FC trials in our behavior videos. A binomial family GLM was run for each relevant pair of treatments, (sand fiddler in conspecific vs. heterospecific tanks, mud fiddler in conspecific tank vs. heterospecific tanks, and sand fiddler vs. mud fiddler in conspecific tanks) using time spent in coarse sediment as the variable of interest. All tests were run in R version 3.0.2 using the MASS and multcomp packages for the GLMs (Hothorn et al., 2008; Venables and Ripley, 2002).

3. Results

3.1. Burrowing frequency and location

Across all three experiments, we found that sand fiddler crabs (*Leptuca pugilator)* dug more burrows on average than mud fiddler crabs (*Minuca pugnax*). In the mixed trials, the sand fiddler-only treatment had over eight times more burrows on average than the mud fiddler-
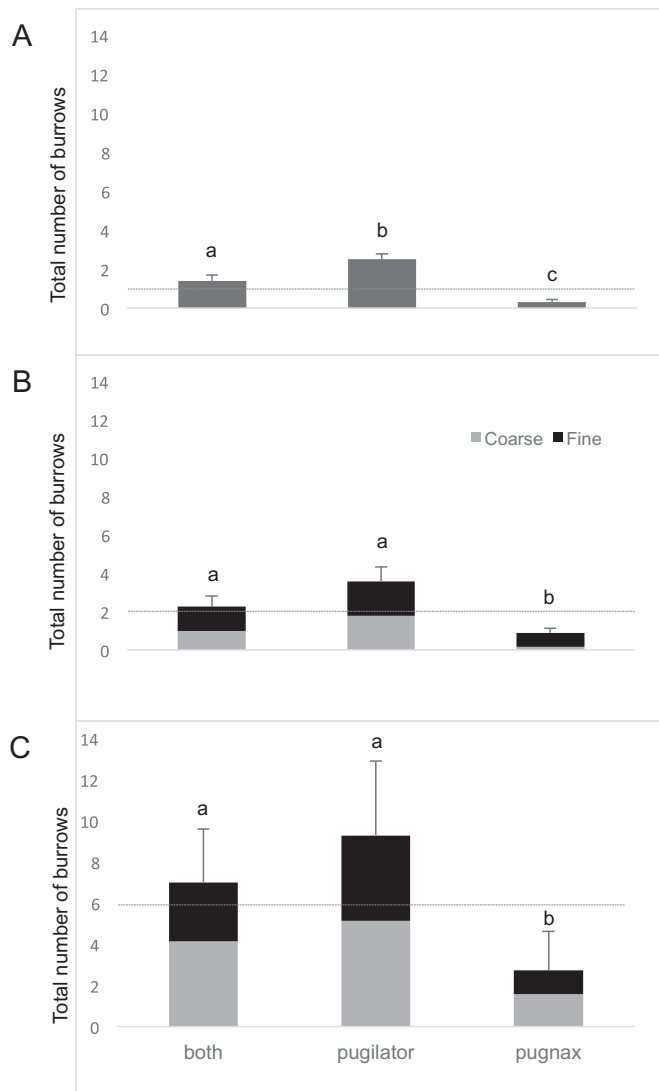
Fig. 1. The mean number of total burrows dug in treatments with *L. pugilator* (sand fiddler) only, *M. pugnax* (mud fiddler) only, and with both species present in the mixed sediment trials (A), the low-density fine vs. coarse sediment trials (B) and the high-density fine vs. coarse sediment trials (C). For fine vs. coarse sediment trials the dark portion of the bar represents the proportion of burrows in fine sediment while the lighter gray portion represents burrows dug in coarse sediment. The dashed horizontal line indicates the expected mean number of burrows dug in heterospecific treatments based on the number dug by each species in conspecific treatments. Letters indicate significant results in Tukey post-hoc analyses within experiments.

only treatment (sand 2.5 ± 0.27; mud 0.3 ± 0.15 [mean ± SE]) and almost twice as many as the treatment containing both species (1.4 ± 0.31; GLM, negative binomial; p < 0.0001; Fig. 1A, Table 3). There was a significant interaction between species treatment and burrow location so post-hoc tests were not run (but see pairwise results discussed below; Table 3). In the low-density FC trials, the sand fiddler dug almost four times more burrows than the mud fiddler (GLM, negative binomial; p < 0.0001; Tukey's post-hoc analysis, p < 0.001). The both species treatment had an intermediate number of burrows between the two conspecific treatments with the number significantly higher than mud fiddler alone (p < 0.01; sand 3.58 ± 0.73; mud 0.89 ± 0.24; Both 2.26 ± 0.55; Fig. 1B, Table 2). For the high-density FC experiments, the sand fiddler dug almost three and a half times more burrows than the mud fiddler (GLM, negative binomial; p < 0.001; Tukey's post-hoc, p < 0.001; sand 9.29 ± 3.62; mud 2.71 ± 1.9), but not significantly more than the both species treatment (p = 0.37; Both 7.0 ± 2.59). There were also significantly more burrows dug when both crabs were present than when the mud fiddler was alone (p < 0.001; Fig. 1C, Table 2). It was common for there to be more than one burrow per crab in treatments that included sand fiddlers.

Additionally, there was a significant difference in the number of burrows in each location (corner, middle, side) for the mixed sediment and low-density FC trials (GLM; negative binomial, mixed p < 0.0001; low-density FC p < 0.0001). Generally, all crabs burrowed more in the corner of the tank than the side of the tank and preferred the sides and corners more than the middle of the tank (Fig. 2, Table 2). For the mixed sediment trials, there was an interaction between species treatment and location (LRT, p < 0.01); therefore, each pairwise combination was examined individually (Fig. 2A, Table 3). Mud fiddler crabs burrowed only in tank corners and never along the sides or in the middle. Most burrows in the low-density FC trials were dug in the corners, followed by along the sides, and lastly in the middle of the tank, although there was not a significant difference between the number of burrows in the corner or along the sides (Fig. 2B, Table 2). For the high-density experiments there was no preference for burrowing in the corner, middle, or side of the tank across treatments (GLM; negative binomial, p = 0.80; Fig. 2C).

The observed number of burrows in the heterospecific treatment was not significantly different than the expected number of burrows calculated from the conspecific treatments in any of the experiments, suggesting no interspecific interactions were affecting burrowing (paired *t*-test; Mixed: p = 1, mean observed = 1.4, mean expected = 1.4; Low-density FC: p = 0.61, mean observed = 2.26, mean expected = 2.13; High-density FC: p = 0.51, mean observed = 7.29, mean expected = 6.0). In the low-density FC trials, the mud fiddler preferred fine sediment to coarse sediment (a priori planned comparison, t(27.6) = −2.38, p = 0.02) while the sand fiddler showed no preference for sediment type (t(27.6) = −0.09, p = 0.93). In the high-density FC trials, neither species exhibited a sediment preference (a priori t-test, sand p = 0.71; mud p = 0.77).

Table 2

Fine vs. coarse low- and high-density trial negative binomial GLM results (given in the left-hand column) and post-hoc analysis results for species treatment and burrow location (right-hand column, given as p-values with significant results (p < 0.05) bolded).

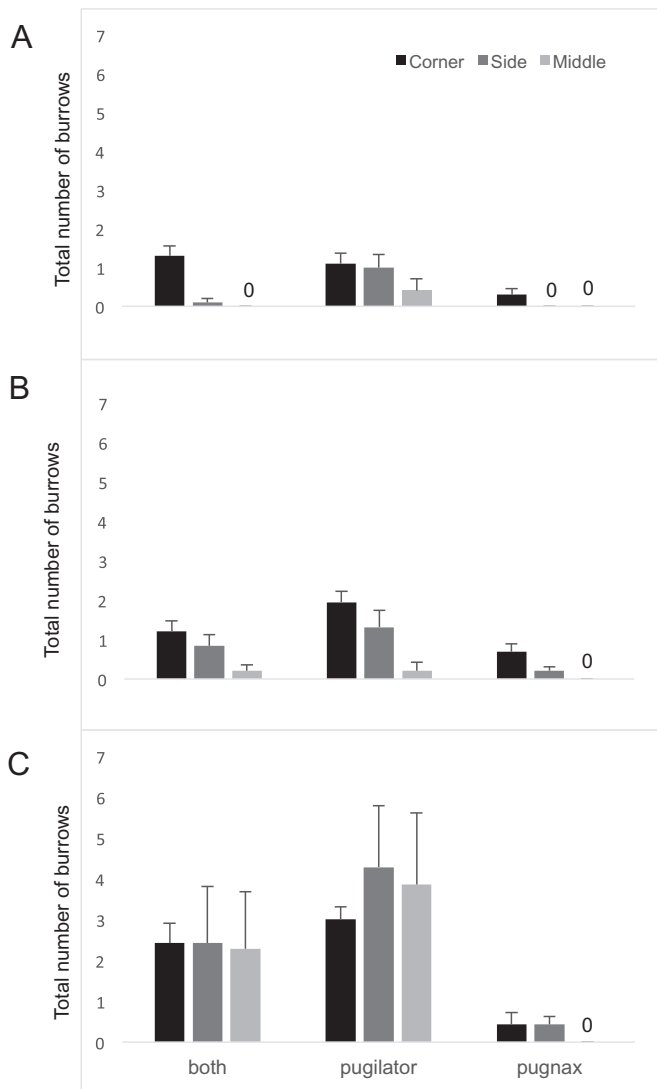| Low-density				High-density			
Species			Post-hoc	Species			Post-hoc
p < 0.001	Sand	Mud	< **0.001**	p < 0.001	Sand	Mud	< **0.001**
		Both	0.199			Both	0.372
	Mud	Both	**0.008**		Mud	Both	< **0.001**
Location				Location			
p < 0.001	Corner	Side	0.067	p = 0.80	Corner	Side	0.909
		Middle	< **0.001**			Middle	0.969
	Side	Middle	< **0.001**		Side	Middle	0.789

Fig. 2. The mean number of total burrows dug in each tank location (corner, side, and middle) in treatments with *L. pugilator* (sand fiddler) only, *M. pugnax* (mud fiddler) only, and with both species present in the mixed sediment trials (A), the low-density fine vs. coarse sediment trials (B) and the high-density fine vs. coarse sediment trials (C).

3.2. Burrow occupancy

In the mixed trials, there was no relationship between the number of burrows occupied by sand fiddlers and the presence or absence of a mud fiddler (chi-squared test, X^2 (1) = 0, p = 1). A relationship was found for the mud fiddler, who did not occupy any burrows in the absence of sand fiddlers, but occupied over half of the burrows (6 out of 10) when a sand fiddler was present (X^2 (1) = 5.9524, p = 0.015) suggesting mud fiddlers may be occupying burrows not built by themselves. In the low-density FC trials, there was no difference in sand fiddler burrow occupancy in the presence or absence of a mud fiddler (X^2 (1) = 0, p = 1), and also no difference for mud fiddler burrow occupancy in the presence of a sand fiddler (X^2 (1) = 0.689, p = 0.407). In the high-density FC trials, there were no significant relationships between the number of burrows occupied and the presence or absence of heterospecifics (X^2 (1) = 1.51, p = 0.220) or mud fiddlers (X^2 (1) = 2.797, p = 0.094).

3.3. Density-dependent effects

We found no significant difference in average number of burrows dug per crab for sand fiddlers (Welch's t-test, p = 0.41; mean low-density per crab = 1.66, mean low-density total = 3.58; mean high-density per crab = 1.11, mean total = 9.29). However, there was a five-fold difference in the average number of burrows per crab when mud fiddlers were in the presence of a high density of conspecifics versus low density (p = 0.02; mean low-density per crab = 0.47, mean total = 0.89; mean high-density per crab = 0.09, mean total = 2.71).

3.4. Behavioral analysis

We found significant differences in the amount of time spent burrowing between treatments (GLM; binomial, p < 0.01, Fig. 3, Table 4). Mud fiddlers in the conspecific treatments burrowed 0% of the time in all trials and spent significantly less time burrowing than any of the other treatments, most notably when compared to sand fiddler crabs in their conspecific treatment (Tukey's post-hoc; p < 0.001) and to other mud fiddlers in heterospecific treatments (p = 0.04). There was no difference in the amount of time sand fiddlers spent burrowing in heterospecific versus conspecific treatments (p = 0.36), nor between the time sand and mud fiddlers spent burrowing in the heterospecific treatment.

Time spent interacting was also significant in our model (GLM; binomial, p = 0.046, Fig. 3, Table 4). This pattern was driven by an increase in the time spent interacting by the sand fiddler in the presence of a mud fiddler (Tukey's post-hoc; sand conspecific – heterospecific, p = 0.021), as well as mud fiddlers interacting more with other mud fiddlers than the sand fiddler with its conspecifics (mud conspecific – sand conspecific, p = 0.02). There was no difference in the time spent interacting between sand and mud fiddlers in the heterospecific tanks (p = 0.380), nor between the mud fiddler in conspecific versus heterospecific tanks (p = 0.79). When the nature of these interactions was examined, we found that in the presence of conspecifics, only two sand fiddler individuals in all trials displayed interactive behavior of any

Table 3
Mixed sediment trials post-hoc analysis pair-wise results for species treatment and burrow location (found to have a significant interaction for this experiment; Species p < .0001; Location p < .0001; Species-Location p < .01). P-values with significant results (p < 0.05) bolded.

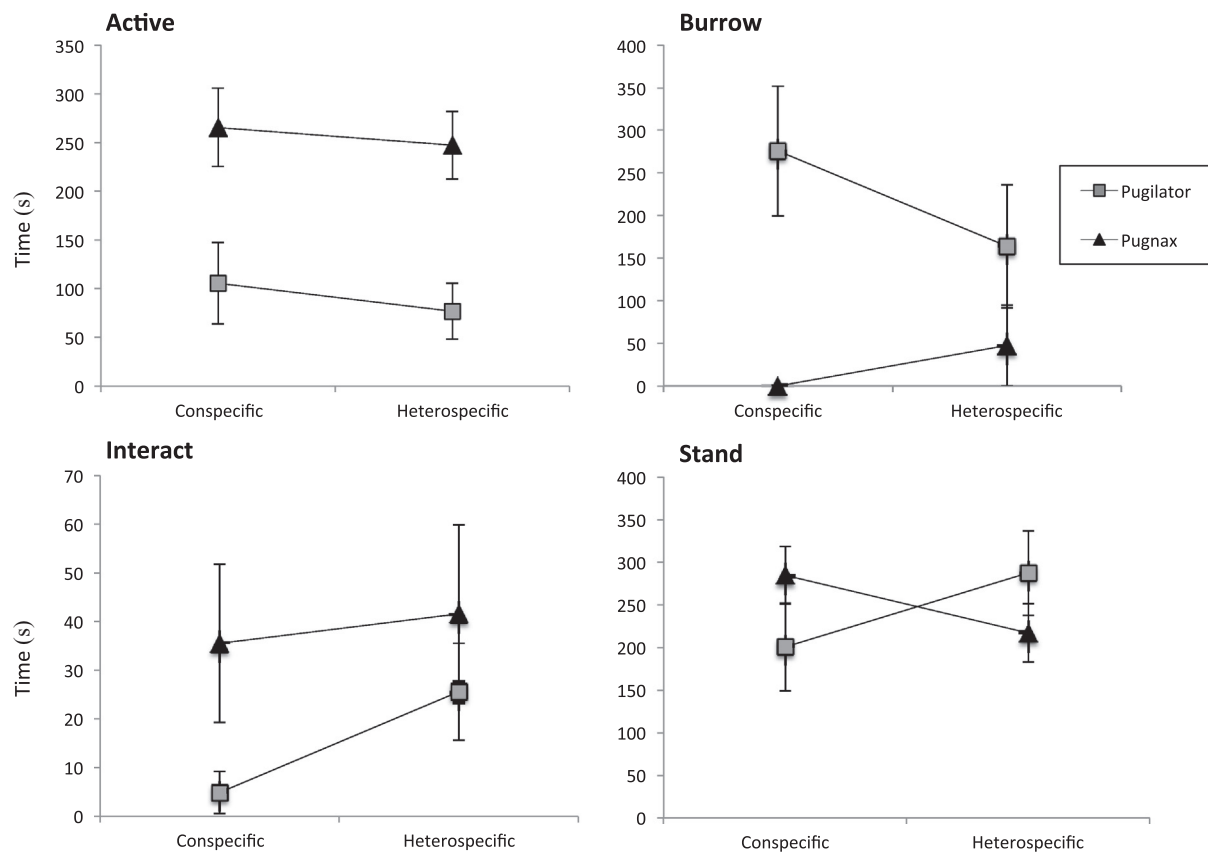|		Pugilator (sand)			Pugnax (mud)			Both		
		Corner	Side	Middle	Corner	Side	Middle	Corner	Side	Middle
Pugilator (sand)	Corner	–								
	Side	0.999	–							
	Middle	0.297	0.508	–						
Pugnax (mud)	Corner	0.149	0.298	0.999	–					
	Side	**0.009**	**0.025**	0.905	0.982	–				
	Middle	**0.009**	**0.025**	0.905	0.982	1.00	–			
Both	Corner	0.999	0.999	0.649	**0.025**	**< 0.001**	**< 0.001**	–		
	Side	**0.025**	0.065	0.982	0.999	0.999	0.999	**0.003**	–	
	Middle	**0.009**	**0.250**	0.905	0.982	1.00	1.00	**< 0.001**	0.999	–

Fig. 3. Behavioral reaction norms for *L. pugilator* (sand fiddler crab) and *M. pugnax* (mud fiddler crab) for each of the four behavior categories (Active, Burrow, Interact, Stand) showing average amount of time each species spent displaying the behavior in the conspecific versus the heterospecific treatment in the mixed sediment and low-density fine vs. coarse sediment trials. Only "burrow" and "interact" were analyzed formally. Note the scales of the y-axes differ, particularly in the "interact" category.

Table 4
Results from the GLM examining the amount of time spent exhibiting burrowing and interacting behaviors in each treatment (*L. pugilator* in the presence of a conspecific (sand), *M. pugnax* in the presence of a conspecific (mud), *L. pugiator* in the presence of *M. pugnax* (sand_both), and *M. pugnax* in the presence of *L. pugilator* (mud_both)) for the mix and fine vs. coarse low-density trials combined. The behavior categories were analyzed separately (p-values given in the left-hand column) and a post-hoc analysis performed when a significant difference was detected (right-hand column). P-values shown with significant results ($p < 0.05$) in bold.

Burrow			
p = **0.003**	Sand	Mud	**< 0.001**
		Sand_both	0.363
	Mud	Mud_both	**0.043**
	Sand_both	Mud_both	0.168
Interact			
p = **0.046**	Sand	Mud	**0.017**
		Sand_both	**0.021**
	Mud	Mud_both	0.788
	Sand_both	Mud_both	0.383

kind and all but one of those interactions was neutral. In contrast, mud fiddlers displayed a higher number of interactions overall in both heterospecific and conspecific treatments. None of the mud fiddler interactions were classified as aggressive in the presence of conspecifics, but were frequently aggressive toward sand fiddlers in heterospecific treatments.

Sand fiddlers in conspecific tanks spent the majority of their time in fine sediment (96.4%). Our GLM revealed that this preference did not carry over to heterospecific tanks (GLM; binomial, $p = 0.04$) where

they appeared to show no sediment preference (50% in fine and 50% in coarse sediment). There was a significant difference between the amount of time spent in coarse sediment between sand and mud fiddlers in conspecific treatments ($p < 0.01$), with mud fiddlers spending about 73% of their time in coarse sediment. Mud fiddlers showed no clear preference in the heterospecific tanks (also 50% fine, 50% coarse) and there was no statistical difference in the amount of time spent in coarse sediment between mud fiddlers in conspecific vs. heterospecific tanks ($p = 0.40$).

4. Discussion

For species to be complementary rather than redundant in an ecosystem, they must use the niche space differently in some way that reduces competition along a resource axis and allows for coexistence. Additionally, their functional contributions to the system should be additive rather than synergistic or antagonistic, which would instead support a facilitative or negative interaction between the species (Loreau, 2004). Our results measuring burrowing frequency support the hypothesis of species complementarity. Across all three experiments, the sand fiddler dug at least three and up to six times more burrows than the mud fiddler. We see these results mirrored in our behavioral data with sand fiddlers spending more of their time burrowing than mud fiddlers, which preferred actively roaming or standing outside of a burrow. When the two species are brought together, the total number of burrows dug was intermediate between the two conspecific treatments, again suggesting an additive rather than antagonistic or synergistic effect. Therefore, in this one measure, it appears there are differences in burrowing habits, at least in our artificial arenas.

Our results for the observed versus expected number of burrows also

supports the complementarity hypothesis. This statistical approach is standard for analyzing species interaction in a substitutive design and in this case was used to determine whether burrowing differed in the presence or absence of the other species (Fraser et al., 1996; Toscano et al., 2010). Based on our results, we can conclude that the number of burrows was not different when individuals were in the presence of conspecifics or heterospecifics. If we had seen fewer than expected burrows, we would have assumed that competition may be occurring and if we had seen more than expected, we would have assumed that one species may be facilitating or enhancing the burrowing of the other. Ultimately, we see that the two species seem to co-occur without influencing each other's burrowing frequency, which is a similar result to Teal (1958).

When looking solely at the total number of burrows dug by the end of a trial, the picture of complementarity is clear. However, when other measures of burrowing behavior are analyzed, a slightly different picture emerges. While sand fiddlers did not show an observable preference between coarse and fine, mud fiddlers did significantly prefer fine sediment as predicted by the literature (O'Connor, 1993; Teal, 1958). In nature, fiddler crabs, particularly mud fiddler crabs who burrow in muddy, poorly structured sediment, preferentially burrow near structured objects such as *Spartina alterniflora* shoots or mussel and oyster shells (George et al., 2010). While both prefer to burrow in corners or along the sides of the tanks over the unstructured middle of the tank, mud fiddlers demonstrated this preference more strongly than sand fiddlers by exclusively burrowing in corners and along sides and never burrowing in the middle of a tank. It is also possible that the discrepancy in number of burrows is due to the speed at which each species burrows. The sand fiddler may be able to make multiple burrows in the same amount of time that a mud fiddler makes one, allowing sand fiddlers to dig in multiple locations before choosing which to occupy. Overall, mud fiddler crabs in our experiments appeared to be more selective about where they chose to burrow.

Further, in our behavioral video analyses, there is evidence that interspecific interactions are affecting burrowing behavior. Sand fiddlers spent less time burrowing in the presence of mud fiddlers and increased the amount of time spent responding to mud fiddlers. Mud fiddlers altered the burrowing behavior of sand fiddlers, likely through interference. These interactions were most often defensive on the part of sand fiddlers while overwhelmingly aggressive by mud fiddlers. Generally, mud fiddlers appear to be more aggressive than sand fiddlers even among conspecifics as seen by the lowered burrowing rate per crab at high densities. Overall, we see the mud fiddler as the aggressor toward sand fiddlers possibly bullying them out of the prime burrow locations that they more strongly prefer (finer sediment near structure). Teal (1958) and Aspey (1978) found a similar negative impact of the mud fiddler on sand fiddlers in their lab and field studies respectively. These antagonistic behaviors by mud fiddler crabs even culminated in instances of mud fiddlers stealing the burrows of sand fiddlers, which we documented twice in our behavioral videos. Given the short duration of the videos, it is reasonable to assume that burrow theft was occurring regularly throughout our trials and that the number of burrows at the end of the trials do not fully reflect the interactions in the interim. The occupancy of burrows at the end of the trials also supports this, possibility with mud fiddlers occupying more burrows in the presence of a sand fiddler than in the presence of only conspecifics, although this pattern was only significant in the low-density FC trials. While the total number of burrows may not be affected, there may be refuge benefits for mud fiddlers at the expense of sand fiddlers that we only observed by recording their interactions.

In nature, fiddler crabs are a highly gregarious species that can occur at high densities in North Carolina (approximately 75 crabs per m^2 on average) (Gittman and Keller, 2013; Zeil and Hemmi, 2014). We examined the potentially important effect of density on each fiddler species' burrowing performance in our high-density trials. Generally, sediment and location preferences broke down in both species at higher

densities meaning that in our space-limited tanks, some amount of scramble or interference competition is most likely occurring in these species for prime burrow locations. We also found that the average number of burrows per crab was lower at higher densities for mud fiddlers and their preference for fine sediment also lessened at high densities, while sand fiddlers were unaffected. It is worth noting that tanks only had four corners and with so many crabs in a confined space, competition over prime spots may be artificially high, leading crabs to settle for suboptimal locations. While this may just be an artifact of our experimental design, based on field observations and the social nature of these crabs, this level of density is not unrealistic, especially when crabs display herding behaviors. Intraspecific and interspecific competition may influence where crabs are able to burrow if prime real estate is limited in nature.

We also only used female crabs, which suited the purposes of this experiment, but may only be giving us half the picture. Male-male competition and differences in biology and physiology of males versus females may also be driving settling patterns in nature. The needs of each sex may differ in where they feed and burrow. For example, male fiddlers possess one enlarged claw that is used in waving displays to attract females. This sexually selected appendage affects their feeding and burrowing efficiency and therefore forces males to compensate by altering their behavior, physiology, and resource use (Caravello and Cameron, 1987; Bywater et al., 2018). Males also spend large portions of their time during mating season attracting mates and digging burrows for those females (Weis and Weis, 2004; Hemmi & Zeil, 2003; Christy, 1982). Therefore, their motivation for burrowing is different than for females and may change seasonally for both sexes.

It appears that while there is niche separation and complementarity at one level, there is also a fair amount of competitive interaction and overlap in this system as well. Many North Carolina marshes have mixed sediments that may not be clearly delineated into mud or sand (Teal, 1958; Timmons et al., 2010). Niche differences could arise from differences in sediment preference (O'Connor, 1993; Teal, 1958), but in our study we only saw a strong preference in mud, not sand fiddlers in where they chose to burrow. Interestingly, we saw contradictory patterns in our behavioral analysis. Sand fiddler crabs in conspecific tanks spent almost all of their time (over 95%) in fine sediment, which is the opposite of what we expected based on the literature and what we find in our own burrowing data. Mud fiddlers in conspecific treatments spent the majority of their time in coarse sediment (another surprising result and in contrast to what we see in their burrowing behavior). These patterns were not observed in the heterospecific tanks with neither species having any clear sediment preference. These results may hint at some other sediment consideration not captured in just burrowing behavior alone. For example, it is possible that fine sediment has higher organic matter and nutrient content, or that it provides better refuge and structure for burrows than the coarser, sandy sediment that may be more open and exposed to predators. These considerations may be particularly important for sand fiddlers who may be excluded from their preferred sediment due to mud fiddler aggression.

Fiddler burrowing is linked to a number of important ecosystem functions and has been shown to promote marsh health by aerating and mixing the sediment (Citadin et al., 2016; Gittman and Keller, 2013; Wang et al., 2010; and others). Differences in burrow number and location could have important implications for how each species functions as a bioturbator and ecosystem engineer in marsh ecosystems; but field data are needed to fully extend the results from this study. Overall, studying these kinds of fine-scale habitat use patterns in co-occurring species could be integral in helping us to better understand the role each species plays in this ecosystem. Both species appear to be important in maintaining bioturbation through their burrowing and ensuring marsh health, but this complementarity may also have implications for the stability of the ecosystem. One species may not be able to fully replace the functioning of the other if removed from the system since their roles are not completely overlapping. Evaluating the

function of each species in a community and evaluating their individual and combined contributions can be challenging. Measuring multiple responses of habitat use and differences in functional niche is important as species interactions are complex and often difficult to untangle, but may affect the ability of each organism to perform critical roles in an ecosystem.

Acknowledgments

References

Allen, E.A., Curran, H.A., 1974. Biogenic sedimentary structures produced by crabs in lagoon margin and salt marsh environments near Beaufort, North Carolina. J. Sediment. Res. 44.

Aspey, W.P., 1978. Fiddler crab behavioral ecology: burrow density in Uca pugnax (smith) and Uca pugilator (Bosc) (Decpoda Brachyura). Crustaceana 34, 235–244.

Bertness, M.D., 1985. Fiddler crab regulation of Spartina alterniflora production on a New England salt marsh. Ecology 66, 1042–1055. https://doi.org/10.2307/1940564.

Bertness, M.D., Miller, T., 1984. The distribution and dynamics of Uca pugnax (smith) burrows in a new England salt marsh. J. Exp. Mar. Biol. Ecol. 83, 211–237. https://doi.org/10.1016/S0022-0981(84)80002-7.

Bywater, C.L., Wilson, R.S., Monro, K., White, C.R., 2018. Legs of male fiddler crabs have evolved to compensate for claw exaggeration and enhance claw functionality during waving displays. Evolution 72, 2491–2502. https://doi.org/10.1111/evo.13617.

Caravello, H.E., Cameron, G.N., 1987. The effects of sexual selection on the foraging behavior of the Gulf coast fiddler crab, Uca panacea. Anim. Behav. 35, 1864–1874. https://doi.org/10.1016/S0003-3472(87). 90079-9.

Christy, J.H., 1982. Burrow structure and use in the sand fiddler crab, Uca pugilator (Bosc). Anim. Behav. 30, 687–694. https://doi.org/10.1016/S0003-3472(82_80139-5.

Citadin, M., Costa, T.M., Netto, S.A., 2016. The response of meiofauna and micro-phytobenthos to engineering effects of fiddler crabs on a subtropical intertidal sandflat. Austral Ecol. 41, 572–579. https://doi.org/10.1111/aec.12346.

Colby, D.R., Fonseca, M.S., 1984. Population dynamics, spatial dispersion and somatic growth of the sand fiddler crab *Uca pugilator*. 16, 269–279.

Crane, J., 1975. Fiddler Crabs of the World: Ocypidiae: Genus Uca. Princeton University Presshttps://doi.org/10.1515/9781400867936.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D., 1998. The statistical inevitability of stability-diversity relationship in community ecology. Am. Nat. 151, 264–276. https://doi.org/10.1086/286117.

Fraser, S., Gotceitas, V., Brown, J.A., 1996. Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Can. J. Fish. Aquat. Sci. 53, 305–314. https://doi.org/10.1139/f95-183.

George, S.B., Carlson, M.D., Regassa, L.B., 2010. Shell use by juvenile fiddler crabs Uca pugnax and U. pugilator. J. Exp. Mar. Biol. Ecol. 396, 35–41. https://doi.org/10.1016/j.jembe.2010.09.014.

Gittman, R.K., Keller, D.A., 2013. Fiddler crabs facilitate Spartina alterniflora growth, mitigating periwinkle overgrazing of marsh habitat. Ecology 94, 2709–2718. https://doi.org/10.1890/13-0152.1.

Hardin, G., 1960. The competitive exclusion principle. Science 131 (3409), 1292–1297. https://doi.org/10.2307/1705965.

Hemmi, Jan M., Zeil, Jochen, 2003. Burrow surveillance in fiddler crabs II. The sensory cues. Journal of Experimental Biology 206 (22), 3951–3961. https://doi.org/10.1242/jeb.00636.

Hothorn, Torsten, Bretz, Frank, Westfall, Peter, 2008. Simultaneous Inference in General Parametric Models. Biometrical Journal 50 (3), 346–363.

Hubbard, C.R., 2008. Comparison of Invasive and Non-invasive Techniques for Measuring Fiddler Crab Density in a Salt Marsh. Electronic Theses and Dissertations. vol. 737. https://digitalcommons.georgiasouthern.edu/etd/737.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. In: Ecosystem Management. Springer New York, New York, NY, pp. 130–147. https://doi.org/10.1007/978-1-4612-4018-1_14.

Katz, L.C., 1980. Effects of burrowing by the fiddler crab, Uca pugnax (smith). Estuar. Coast. Mar. Sci. 11, 233–237. https://doi.org/10.1016/S0302-3524(80)80043-0.

Loreau, M., 2004. Does functional redundancy exist? Oikos 104, 606–611. https://doi.org/10.1111/j.0030-1299.2004.12685.x.

Mattheus, C.R., Rodriguez, A.B., McKee, B.A., Currin, C.A., 2010. Impact of land-use change and hard structures on the evolution of fringing marsh shorelines. Estuar. Coast Shelf Sci. 88 (3), 365–376. https://doi.org/10.1016/j.ecss.2010.04.016.

McCraith, B.J., Gardner, L.R., Wethey, D.S., Moore, W.S., 2003. The effect of fiddler crab burrowing on sediment mixing and radionuclide profiles along a topographic gradient in a southeastern salt marsh. J. Mar. Res. 61, 359–390.

Naeem, S., 2002. Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments. Ecology 83, 2925–2935. https://doi.org/10.1890/0012-9658(2002)083[2925:DTIODO]2.0.CO;2.

O'Connor, N.J., 1993. Settlement and recruitment of the fiddler crabs Uca pugnax and U. pugilator in a North Carolina, USA, salt marsh. Mar. Ecol. Prog. Ser. 93, 227–234.

Pastell, M., 2016. CowLog – cross-platform application for coding behaviours from video. J. Open Res. Softw. 4. https://doi.org/10.5334/jors.113.

Reinsel, K.A., 2004. Impact of fiddler crab foraging and tidal inundation on an intertidal sandflat: season-dependent effects in one tidal cycle. J. Exp. Mar. Biol. Ecol. 313, 1–17. https://doi.org/10.1016/j.jembe.2004.06.003.

Ringold, P., 1979. Burrowing, root mat density, and the distribution of fiddler crabs in the eastern United States. J. Exp. Mar. Biol. Ecol. 36, 11–21. https://doi.org/10.1016/0022-0981(79)90097-2.

Robertson, J.R., Bancroft, K., Vermeer, G., Plaisier, K., 1980. Experimental studies on the foraging behavior of the sand fiddler crab Uca pugilator (Bosc, 1802). J. Exp. Mar. Biol. Ecol. 44, 67–83. https://doi.org/10.1016/0022-0981(80)90102-1.

Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98, 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x.

Salmon, M., Hyatt, G.W., 1983. Spatial and temporal aspects of reproduction in North Carolina fiddler crabs (Uca pugilator Bosc). J. Exp. Mar. Biol. Ecol. 70 (1), 21–43. https://doi.org/10.1016/0022-0981(83). 90146–90146.

Teal, J.M., 1958. Distribution of fiddler crabs in Georgia salt marshes. Ecology 39, 185–193. https://doi.org/10.2307/1931862.

Thomas, C., Blum, L., 2010. Importance of the fiddler crab Uca pugnax to salt marsh soil organic matter accumulation. Mar. Ecol. Prog. Ser. 414, 167–177. https://doi.org/10.3354/meps08708.

Timmons, E.A., Rodriguez, A.B., Mattheus, C.R., DeWitt, R., 2010. Transition of a regressive to a transgressive barrier island due to back-barrier erosion, increased storminess, and low sediment supply: bogue banks, North Carolina, USA. Mar. Geol. 278, 100–114. https://doi.org/10.1016/J.MARGEO.2010.09.006.

Toscano, B.J., Fodrie, F.J., Madsen, S.L., Powers, S.P., 2010. Multiple prey effects: agonistic behaviors between prey species enhances consumption by their shared predator. J. Exp. Mar. Biol. Ecol. 385, 59–65. https://doi.org/10.1016/J.JEMBE.2010.01.001.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, Statistics and Computing. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387-21706-2.

Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18–23. https://doi.org/10.1046/j.1523-1739.1992.610018.x.

Wang, J.Q., Zhang, X.D., Jiang, L.F., Bertness, M.D., Fang, C.M., Chen, J.K., Hara, T., Li, B., 2010. Bioturbation of burrowing crabs promotes sediment turnover and carbon and nitrogen movements in an estuarine salt marsh. Ecosystems 13, 586–599. https://doi.org/10.1007/s10021-010-9342-5.

Weis, J.S., Weis, P., 2004. Behavior of four species of fiddler crab, genus Uca, in Southeast Sulawesi, Indonesia. Hydrobiologia 523, 47–58. https://doi.org/10.1023/B:HYDR.0000033093.84155.1d.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc. Natl. Acad. Sci. 96, 1463–1468. https://doi.org/10.1073/pnas.96.4.1463.

Zeil, Jochen, Hemmi, Jan M., 2006. The visual ecology of fiddler crabs. Journal of Comparative Physiology A 192 (1), 1–25.

Zeil, J., Hemmi, J.M., 2014. Nervous systems and control of behavior. In: Nervous Systems and Control of Behavior, pp. 484–505.