The University of Southern Mississippi
The Aquila Digital Community

Master's Theses

Summer 2010

Burrowing Behavior of the Fiddler Crab *Uca panacea* in Relation to Food Availability

Jennifer A. Mraz
University of Southern Mississippi

Follow this and additional works at: https://aquila.usm.edu/masters_theses

 Part of the Marine Biology Commons

Recommended Citation

Mraz, Jennifer A., "Burrowing Behavior of the Fiddler Crab *Uca panacea* in Relation to Food Availability" (2010). *Master's Theses*. 615.
https://aquila.usm.edu/masters_theses/615

This Masters Thesis is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in Master's Theses by an authorized administrator of The Aquila Digital Community. For more information, please contact Joshua.Cromwell@usm.edu.

The University of Southern Mississippi

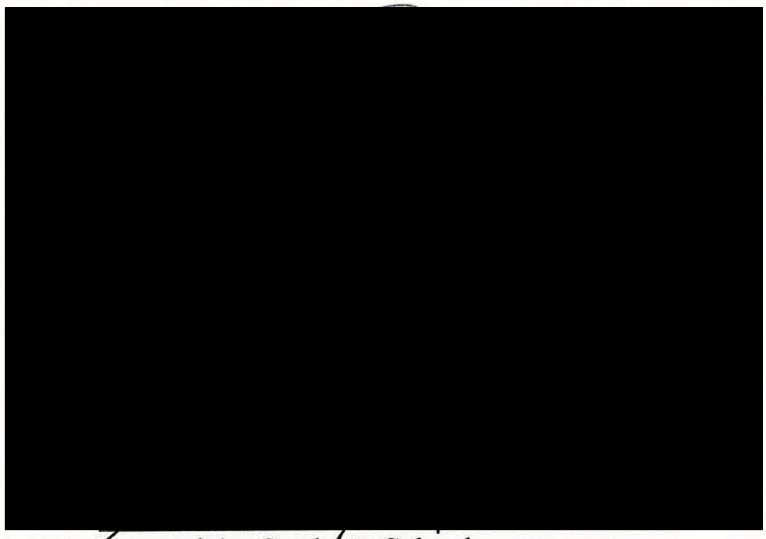
BURROWING BEHAVIOR OF THE FIDDLER CRAB *UCA PANACEA* IN RELATION TO FOOD AVAILABILITY

by

Jennifer Arin Mraz

A Thesis
Submitted to the Graduate School
of The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Master of Science

Approved:



Dean of the Graduate School

August 2010

ABSTRACT

BURROWING BEHAVIOR OF THE FIDDLER CRAB

UCA PANACEA IN RELATION TO FOOD AVAILABILITY

by Jennifer Arin Mraz

August 2010

Much of fiddler crab behavior is regulated by the tides and centers around their burrows. Field and laboratory studies were conducted to assess the effect of food availability on burrowing in the Gulf coast fiddler crab, *Uca panacea*. In the field, crabs were observed for droving behavior through visual observations; evidence for this behavior was assessed further by determining sediment organic content. Although the organic content did increase significantly as distance increased from the edge of the water, fiddler crabs did not exhibit droving behavior at my study site. Field burrows were cast and measured for depth, diameter and volume to determine if burrow size changed as distance increased from the water. Burrow size did not differ significantly based on distance from the water. In the laboratory, males and females were randomly assigned to either low food (0.2% sediment organic content) or high food (1.5% sediment organic content) treatments for a period of 12 d; plaster casts of burrows were measured as above. When male and female results were pooled, there was a significant difference between low and high food treatments in burrow depth, diameter and volume. When crabs were grouped by carapace width into small (8.0-11.0 mm) and large (11.1-15.0 mm) size classes, diameter was the only burrow parameter that differed significantly.

Food availability did affect some aspects of fiddler crab burrowing behavior; understanding what affects burrowing may shed light on fiddler crab importance and impact on ecosystem composition and processes.

ACKNOWLEDGMENTS

I would like to thank my committee, Dr. Patricia Biesiot, Dr. Robert Diehl and Dr. Renae Brodie, for all their support and many, many conversations about my project. I especially thank my adviser Dr. Patricia Biesiot for her support and feedback on the many forms of my research proposal and thesis. Dr. Carl Qualls was always willing to give concise feedback on statistics or processes in JMP; no matter the time of day I would happen to catch him. Dr. Jake Schaefer always gave assistance in wetlab-related matters when needed. Over the years I contacted a few individuals in reference to their fiddler crab work and I thank them for their timely and helpful responses: Dr. Darryl Felder, Dr. Richard Heard, Dr. Shirley Lim and Dr. Steve Borgianini. I thank Harriet Perry for her assistance and for allowing me to use some of her laboratory space in May 2009 at the Gulf Coast Research Laboratory (GCRL), Ocean Springs, MS, USA. Darcie Dennis Graham at GCRL was also very willing to provide assistance and moral support when needed. I thank my two undergraduate assistants: Jessica DeJean for help in preliminary experiments and collections and Cari White for assistance in the field observing fiddler crabs and casting burrows in May 2009. Dr. James Alexander was invaluable for his gracious polyester resin expertise during field burrow casting in May 2009. There were a few individuals instrumental to collecting field samples, organisms and sediment: Laura Anderson, Jaci Smolinsky and Jay Pope. Without these three individuals providing their time, moral and muscular support, this project would not have been successful. I would especially like to thank Jaci Smolinsky and most importantly Laura Anderson for lending an ear to discuss or listen to me talk about aspects of my project whenever I desired.

TABLE OF CONTENTS

ABSTRACT ii

ACKNOWLEDGMENTS iv

LIST OF ILLUSTRATIONS vi

LIST OF TABLES vii

CHAPTER

I. INTRODUCTION 1

II. MATERIALS AND METHODS.....5

Field Site
Assessment of Droving Behavior
Field Burrows
Laboratory Experiment
Data Analysis

III. RESULTS 12

Assessment of Droving Behavior
Field Burrows
Laboratory Experiment

IV. DISCUSSION 18

REFERENCES 26

LIST OF ILLUSTRATIONS

Figure

1. Pictorial Representation of Sediment Sampling Transects. Open Circles (o) Represent Sampled Locations 6

2. Experimental Mesocosm A. Side View; B. Top View Showing the Mesh Enclosure and Water Dish in Place; the Fiddler Crab is Inside its Water Dish 10

3. Wilcoxon Rank Sum Analysis of Percent Organic Content of Sediment along 0.5 m Transects Perpendicular to the Edge of the Water. The Middle Lines Inside Each Box is the Median; the Lines Immediately Above and Below Being the 75^{th} and 25^{th} Percentile (Quartiles), Respectively. Whiskers Mark the 1.5 Interquartile Range; Values Outside the Whiskers are Considered Statistical Outliers. The Same Letters Above the Bars Indicate No Significant Difference in Means 13

LIST OF TABLES

Table

1. Summary Statistics and Wilcoxon Rank Sum Significance Test Results Comparing Field Burrow Parameters to Distance from the Water 14

2. Summary of Wilcoxon Rank Sum Significance Tests of Lab Burrow Parameters between Sexes 14

3. Summary of Wilcoxon Rank Sum Significance Tests of Lab Burrow Parameters between Treatments with Males and Females Pooled.....16

4. Summary Statistics and Wilcoxon Rank Sum Significance Test Results Comparing Crab Parameters between Males and Females Tested in the Lab 16

5. Summary Statistics and Wilcoxon Rank Sum Significance Test Results Comparing Crab Parameters between High Food and Low Food Treatments in the Lab 17

6. Summary Statistics and Wilcoxon Rank Sum Significance Test Results Comparing Carapace Width Size Classes Among Burrow Parameters in the Lab.....17

CHAPTER I

INTRODUCTION

Fiddler crabs, members of the family Ocypodidae and genus *Uca*, inhabit coastline environments in tropical and temperate regions worldwide (Mouton and Felder, 1995). They are selective deposit feeders and scavenge for food such as detritus, algae and bacteria in sediment at the edge of the water (Heard, 1982). Male and female fiddler crabs are morphologically distinct from each other, with males possessing one chela larger than the other whereas females have two small chelae of the same size. Females are capable of using both chelae for foraging whereas males use only the minor chela for foraging; consequently, males must forage faster or for longer periods of time than females (Crane, 1975). The behavior of fiddler crabs is influenced particularly by tidal cycles (Mouton and Felder, 1995). Crabs construct burrows that they plug up and inhabit throughout periods of high tide; they unplug and leave the burrow to feed and court mates during periods of low tide (Wolfrath, 1992). Breeding males remain near their burrow entrance to defend it against wandering males and to court females (Christy, 1982). One courting method commonly used by males is moving the major chela in species specific motions (Heard, 1982) to attract females to inspect his burrow (Christy, 1982). Once the female has accepted a mate, the male uses sand to seal the burrow entrance with both crabs inside. North and South American species of fiddler crabs typically mate in this way whereas in Indo-Pacific and western Pacific species the females defend burrows and mate on the surface (Christy and Salmon, 1984).

The Gulf coast fiddler crab *Uca panacea* is found from the Florida panhandle along the Gulf of Mexico to Texas (Heard, 1982) mainly in sandy habitats with little or

no mud (Powers, 1975). Novak and Salmon (1974) recognized *U. panacea* as a separate species, distinct from its morphologically and behaviorally similar close relative *Uca pugilator*. Since its description, *U. panacea* has been examined with respect to reproductive isolation (Salmon et al., 1978), foraging behavior (Caravello and Cameron, 1987a, 1987b), allocation of time to different activities (Caravello and Cameron, 1991), habitat preference (Powers, 1975; Powers and Cole, 1976; Thurman, 1984), behavior in a nontidal environment (Powers, 1975), color change (Rao and Brannon, 1978), osmoregulation (Thurman, 2002; Thurman, 2003a, 2003b) and molecular systematics (Mangum, 1996; Rosenberg, 2001).

Burrows serve many functions for fiddler crabs: attracting a mate, reproduction, protection from fluctuating environmental conditions and protection from predators (Lim and Heng, 2007). Burrow morphology (e.g., diameter, length, depth, volume) can vary based on the spatial distribution of burrows (Mouton and Felder, 1996; Lim and Diong, 2004). Variability in burrow morphology is also seen between *Uca* species, likely due in part to their varying habitat preferences. Lim and Diong (2004) found that *Uca annulipes* burrows are deeper when located further from the edge of the water. Mouton and Felder (1996) noted the same relationship for *Uca longisignalis* in a salt marsh in Louisiana but not for *Uca spinicarpa*. On the other hand, Bertness and Miller (1984) found that on average *U. pugnax* burrow diameters were larger, depths were shorter and volumes were smaller as the distance from the water increased. To date, burrow dimensions in a tidal environment have not been explored in *U. panacea*.

Fiddler crabs have been known to exhibit droving behavior in response to food availability. Droving is defined by Crane (1975) as the mass movement of crabs from

higher elevated areas to lower elevated areas while the tide ebbs and back to higher elevated areas as the tide flows. Some advantages of this behavior to fiddler crabs have been suggested: they move in groups to reduce the risk of predation (Viscido and Wethey, 2002), minimize individual water loss (Yoder et al., 2005), locate patches of high food availability brought in by the tide (Murai et al., 1983) and locate patches of enough sediment water content to facilitate feeding (Henmi, 1989). In order for droving to be advantageous for feeding in *U. panacea*, two criteria must be met: (1) individuals move as one towards the edge of the water and back towards their burrows with the ebb and flow of the tide; and (2) the sediment organic content is greatest in the area closest to the water and decreases as distance from the water to the burrows increases (Robertson et al., 1980; Murai et al., 1982).

Since fiddler crabs typically forage on nutrients left by the tide, crabs that build burrows closer to the edge of the water potentially could have more food available to them than crabs living further away from the incoming tide (Murai et al., 1983). If more food was available, then crabs could spend less time foraging thereby enabling them to utilize more time and energy on other activities such as building and maintaining burrows. However, crabs with burrows further away from the edge of the incoming tide would have more time to forage for food since their burrows are the first uncovered by the receding tide and the last to be covered by the incoming tide. Based on these observations, fiddler crab burrowing behavior could be influenced by food availability.

The purpose of the present study is to determine: (1) if *U. panacea* forms droves based on food availability; (2) if burrows of male and female *U. panacea* will increase in diameter, depth and volume as distance increases from the edge of the water; and (3) if

fiddler crabs individually isolated in mesocosms in the laboratory will construct and maintain larger burrows if there is a high amount of food available than individuals with a low amount of food available.

CHAPTER II

MATERIALS AND METHODS

Field Site

The study site was the sandy bank (7 m long by 3 m wide) near a bridge over an estuary in a salt marsh along East Beach Drive in Ocean Springs, Mississippi, USA (30°23'56"N; 88°48'57"W). The site is adjacent to an artificially constructed sand beach. The field study was performed at this site and *U. panacea* individuals for the laboratory portion of the study were collected here.

Assessment of Droving Behavior

In summer 2008, large numbers of fiddler crabs were feeding near the edge of the water at the study site (Jennifer Mraz, personal observation), which suggested they may have been droving. During a 10 d period in late May 2009, crabs were observed to determine if they exhibited droving behavior; the study was conducted when the tide was down and during daylight hours (6 – 14 h depending on conditions). Observations for potential droving behavior were also made in the afternoon (2 – 4 h) approximately every two weeks during July – September 2009.

Food availability at the field site was determined by taking sediment cores and assessing them for organic content (Genoni, 1991). Cores of the top 5 mm of sediment were taken during low tide using a PVC pipe (22 mm in diameter). Cores were taken along transects at 0.5 m intervals both perpendicular and parallel to the edge of the water as far as *U. panacea* individuals are found (Fig 1.). Sediment cores were taken on the same days that crab collections were made (see laboratory experiment described below) for a total of five replicate samples for each of the 42 sample locations.

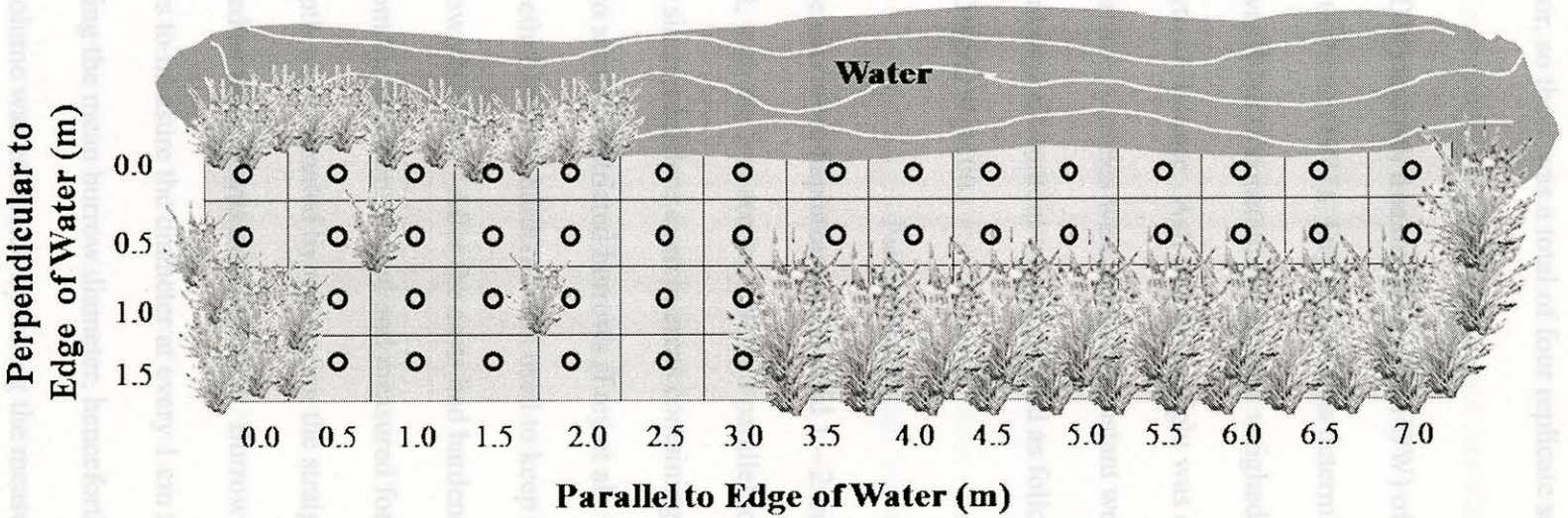


Fig. 1. Pictorial representation of sediment sampling transects. Open circles (o) represent sampled locations.

One sample at the perpendicular 0.5 m, parallel 4.5 m quadrant (see Fig. 1) was discarded due to measuring error, so there was a total of four replicate samples from that one location.

Dry weight (DW) and ash free dry weight (AFDW) of the sediment samples were measured according to Paine (1971). Dry weight was determined using a drying oven at 80°C; the sediment was dried to constant weight and weighed to the nearest 1 mg using a Mettler AJ100 Analytical Balance. Ash free dry weight was determined using a Blue M Box Type Muffle Furnace; samples were dried to constant weight at 500°C and weighed as above. The percent organic content was calculated as follows:

$$\%OC = [(DW - AFDW)/DW]*100.$$

Field Burrows

Burrows to be cast were haphazardly selected 1 – 2 m from the edge of the water within a 2 x 1 m plot, with the 2 m section oriented parallel to the water. Polyester resin was used for casting since it hardens even in areas containing water (Shinn, 1968) and easily flows deep into small constricted burrows (Frey et al., 1973). Approximately 0.19 ml of MEK (methyl ethyl ketone) hardener was used to keep resin from seeping into the sand when poured down burrows. After the casts had hardened for ~10 h, they were removed by hand from the sediment, rinsed and measured for depth, mean diameter and volume. Burrow depth was estimated by measuring the straight line vertical distance of the cast when oriented as when it was in the ground. Burrow diameter was determined using vernier calipers to measure the diameter at every 1 cm interval along the length of the cast and calculating the mean burrow diameter, henceforth referred to simply as burrow diameter. Volume was estimated by taking the measured diameters every 1 cm

along each cast to calculate the volume of each 1 cm section of the cast as a cylinder 1 cm in height and adding all the cylinder volumes together. In previous studies, burrow volume has been estimated using water displacement (see Katz, 1980). However, this method was not used in my study because of the absorptive nature of Plaster of Paris used to make burrow casts in the laboratory experiment (see last paragraph of lab experiment section, p. 10). I chose to use the same method to determine burrow volume regardless of the medium used to make the casts.

Laboratory Experiment

At least 30 *U. panacea* individuals were collected by hand at two week intervals from June through October from the site described above. Collection alternated between selecting only males and selecting only females at each two week interval. Crabs were transported to the University of Southern Mississippi in Hattiesburg, Mississippi, USA, and were individually isolated in large culture dishes with seawater at 15 ppt. The carapace width, carapace length and dorso-ventral thickness (Borgianini, 2008) were recorded for each individual to the nearest 0.1 mm using vernier calipers. Crabs were acclimated to the laboratory in an environmental chamber (Percival Scientific, Model IR-89X; Watlow Control, Series 942) for approximately 3 days without food on a light: dark cycle of 14: 10. Temperature in the chamber was cycled daily between 23°C (at 3 A.M.) and 31°C (at 3 P.M.) to approximate the natural diel temperature cycle in the field. Laboratory temperatures were based on the average low and high temperatures during the summer months over the past ten years at the collection site (EachTown, 2001-2010).

Thirty mesocosms (~68 cm in height) were constructed using two ~19 L (standard 5 gallon) plastic buckets with their tops joined by silicone, duct tape and four metal

brackets (adapted from Genoni, 1991; Fig. 2A). The bottom was cut out of the uppermost bucket and the mesocosm was filled to ~60 cm in height with moist sand (poured through a 2 mm sieve); the sand was obtained from an area adjacent to the crab collection site. At the end of the acclimation period, 30 crabs were randomly assigned to one of two treatments (n = 15 crabs for each of the two treatments) based on values reported by Reinsel and Rittschof (1995): sediment with a high amount of food (~1.5% organic content) or sediment with a low amount of food (~0.2% organic content). Food mixtures comprised sand heated at 500°C for at least 24 h and then allowed to cool; Tetrafauna™ Hermit Crab Meal was added to the sterilized sand at the appropriate concentration to produce the high or low food condition.

During preliminary testing of the mesocosms, almost all crabs constructed burrows along the edge of the container. To keep burrow construction from having an edge effect, a mesh enclosure, 20 cm in diameter and 11 cm in height (Fig. 2B), was constructed from aluminum screening and inverted in the center of each mesocosm; the free edge of the mesh cylinder was buried 1 cm deep. Approximately ~147 ml of the respective food mixture was spread onto the sand surface under the enclosures. This amount represented the area under the enclosure to a depth of ~5 mm, the lowest depth to which fiddler crabs forage in the field (Reinsel, 2004), minus the area of the water dish in the center (6 cm in diameter and 1.25 cm in height). The water dish was filled with ~130 ml of seawater at 15 ppt and replenished daily as needed. Before placing each crab in its respective mesocosm beneath its enclosure, the top sediment was moistened with reverse osmosis water. Crabs were then left in their mesocosms for ~12 days. The top sediment was moistened with reverse osmosis water daily to simulate the moistening of the

sediment by the tide; this is an essential stimulus that induces fiddler crabs to feed (Reinsel and Rittschof, 1995).

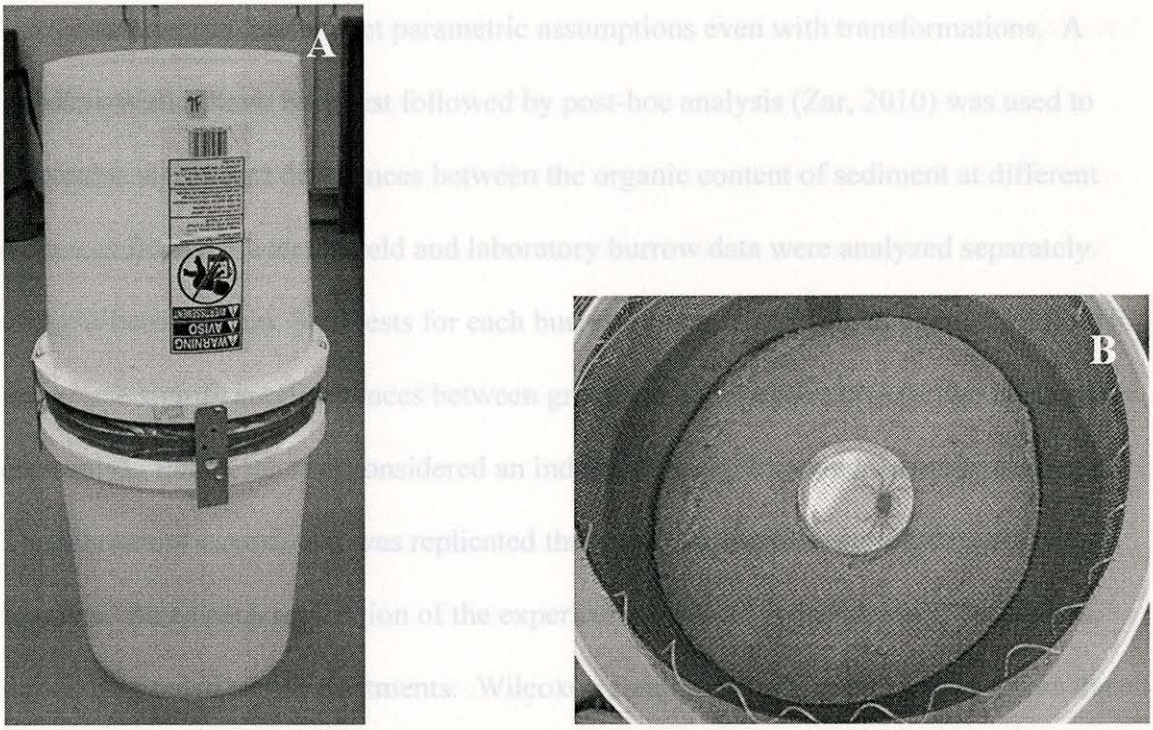


Fig. 2. Experimental mesocosm. A, side view; B. top view showing the mesh enclosure and water dish in place; the fiddler crab is inside its water dish.

At the end of the 12 day experimental period, a cast of each burrow was made using Plaster of Paris at a 1: 0.75 plaster to water ratio; the mixture was poured down any open burrows using a plastic squeeze bottle with ~15 cm of 0.6 cm diameter plastic tubing attached to the tip (Katz, 1980). After 24 h, the upper ~4 cm layer of sand containing the food mixture was removed from each mesocosm , plaster casts were excavated by hand and any remaining crabs were removed. Each mesocosm was then prepared for the next trial by being refilled with moist sand to ~60 cm in height. Casts were measured for the same burrow parameters as described above for the resin casts:

depth, mean diameter and volume. If a crab dug more than one burrow, then the deepest depth was used; diameters were averaged and volumes were summed.

Data Analysis

All data failed to meet parametric assumptions even with transformations. A Kruskal-Wallis Rank Sum test followed by post-hoc analysis (Zar, 2010) was used to determine significant differences between the organic content of sediment at different distances from the water. Field and laboratory burrow data were analyzed separately using Wilcoxon Rank Sum tests for each burrow parameter (depth, diameter, volume) to determine significant differences between groups (and between sexes for the laboratory data only). Each crab was considered an independent replicate and was only used once. The laboratory experiment was replicated three times using males and two times using females. Since each replication of the experiment was run under identical conditions, data were pooled across treatments. Wilcoxon Rank Sum tests were used to assess the relationships between burrow parameters and crab size (carapace length, carapace width, dorso-ventral thickness). For easier comparison and analysis between small and large crabs, crab carapace width was pooled into two size classes (8.0 – 11.0 mm and 11.1 – 15.0 mm) based on the middle two size classes used by Genoni (1991). All analyses were performed using JMP 8 statistical software (SAS) and significance was determined at the 0.05 alpha level.

CHAPTER III

RESULTS

Assessment of Droving Behavior

Over the 10 d observation period in May 2009, fiddler crabs were never observed moving in large groups to forage at the edge of the water. All crabs stayed relatively close to their burrows while foraging. From July to September, more crabs appeared to be foraging than in May, but no mass movement of crabs from one area to another was observed.

Percent organic content (% OC) decreased as distance increased from the edge of the water (Fig. 3). The median % OC at 0.0 m (0.63%) and at 0.5 m (0.55%) were not significantly different from each other but were significantly higher than the % OC at 1.0 m and 1.5 m. The median % OC at 1.0 m (0.36%) and 1.5 m (0.34%) were not significantly different from each other but they were significantly lower than at 0.0 m and 0.5 m.

Field Burrows

Fiddler crab burrows located 1.0 – 1.5 m from the edge of the water had shorter depths, smaller diameters and smaller volumes than burrows located 1.5 – 2.0 m from the edge of the water (Table 1). However, the differences in depth, diameter and volume were not significantly different between the two groups.

Laboratory Experiment

Female fiddler crabs excavated burrows that were larger overall (depth, diameter, volume) than males but none of the differences were statistically significant (Table 2).

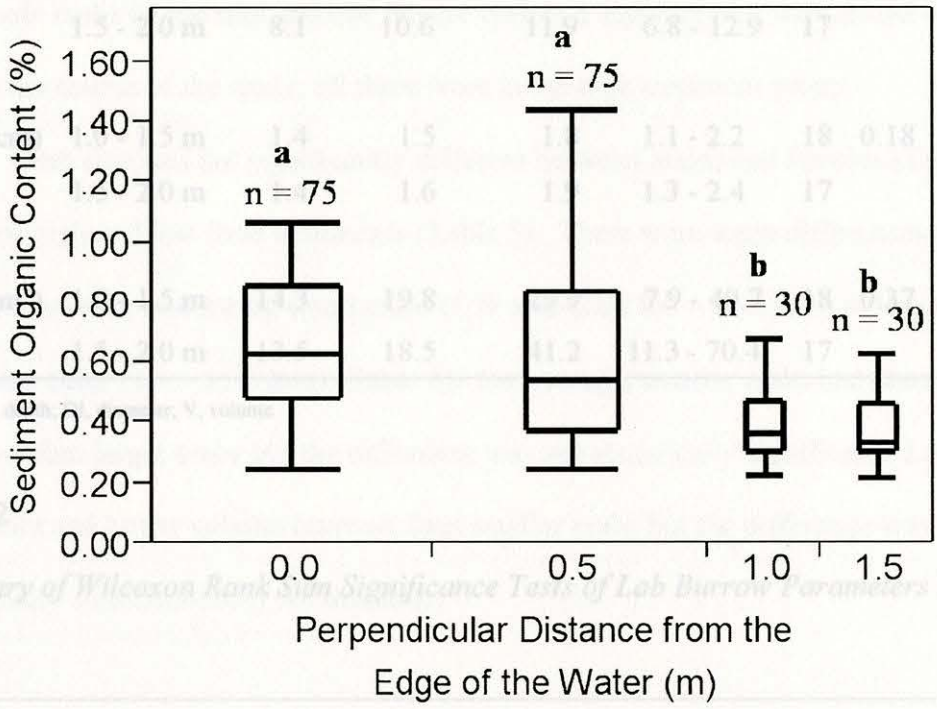


Fig. 3. Wilcoxon Rank Sum analysis of percent organic content of sediment along 0.5 m transects perpendicular to the edge of the water. The middle lines inside each box is the median; the lines immediately above and below being the 75th and 25th percentile (quartiles), respectively. Whiskers mark the 1.5 Interquartile Range; values outside the whiskers are considered statistical outliers. The same letters above the bars indicate no significant difference in means.

Table 1

Summary Statistics and Wilcoxon Rank Sum Significance Test Results Comparing Field Burrow Parameters to Distance from the Water

Burrow Parameter	Distance Interval	25% Quartile	Median	75% Quartile	Range	N	χ^2	*p* - value
DE (cm)	1.0 - 1.5 m	7.6	9.0	10.0	6.4 - 11.7	18	2.02	0.156
	1.5 - 2.0 m	8.1	10.6	11.9	6.8 - 12.9	17		
DI (cm)	1.0 - 1.5 m	1.4	1.5	1.8	1.1 - 2.2	18	0.18	0.668
	1.5 - 2.0 m	1.4	1.6	1.9	1.3 - 2.4	17		
V (cm^3)	1.0 - 1.5 m	14.3	19.8	29.9	7.9 - 40.7	18	0.37	0.541
	1.5 - 2.0 m	13.5	18.5	41.2	11.3 - 70.4	17		

Note: DE, depth; DI, diameter; V, volume

Table 2

Summary of Wilcoxon Rank Sum Significance Tests of Lab Burrow Parameters between Sexes

Burrow Parameter	Sex	25% Quartile	Median	75% Quartile	Range	N	*Z*	*p* - value
DE (cm)	Female	13.4	25.1	43.1	5.9 - 59.6	47	1.45	0.147
	Male	12.2	15.7	33.4	3.3 - 60.4	59		
DI (cm)	Female	1.4	1.8	2.3	1.2 - 3.8	47	1.43	0.152
	Male	1.3	1.6	2.2	1.0 - 2.9	59		
V (cm^3)	Female	34.6	89.5	177.6	12.0 - 351.4	47	1.22	0.221
	Male	27.5	54.5	188.8	2.8 - 417.7	59		

Note: DE, depth; DI, diameter; V, volume

Females and males pooled in the high food treatment excavated burrows that were significantly larger in depth, diameter and volume than crabs in the low food treatment (Table 3). All crabs used in the experiment dug burrows during their 12 d trial period, but the sample size was decreased due to crab burrows not being open at the time of casting or if upon excavation a burrow was found to not be completely filled with plaster. Two male crabs in one trial and one female crab in a separate trial were found dead during the course of the study; all three were in the high treatment group.

Crab size was not significantly different between males and females (Table 4) or between high and low food treatments (Table 5). There were some differences in burrow parameters when comparing small crabs (CW size class 8.0 – 11.0 mm) to large crabs (CW size class 11.1 – 15.0 mm) (Table 6). On average, smaller crabs had deeper burrows than larger crabs but the difference was not statistically significant. Larger crabs had wider and larger volume burrows than smaller crabs but the difference was statistically significant only for diameter.

Table 3

Summary of Wilcoxon Rank Sum Significance Tests of Lab Burrow Parameters between Treatments with Males and Females Pooled

Burrow Parameter	Treatment	25% Quartile	Median	75% Quartile	Range	N	Z	*p* - value
DE (cm)	High	13.5	21.4	45.7	5.4 - 60.4	52	2.32	0.0204*
	Low	10.9	15.6	32.2	3.3 - 51.6	54		
DI (cm)	High	1.4	1.8	2.4	1.2 - 2.9	52	2.24	0.0248*
	Low	1.3	1.6	2.0	1.0 - 3.8	54		
V (cm^3)	High	39.5	92.8	183.0	10.5 - 417.7	52	2.63	0.0085*
	Low	24.5	43.7	112.5	2.8 - 255.4	54		

Note: DE, depth; DI, diameter; V, volume

Table 4

Summary Statistics and Wilcoxon Rank Sum Significance Test Results Comparing Crab Parameters between Males and Females Tested in the Lab

Crab Parameter	Sex	25% Quartile	Median	75% Quartile	Range	N	Z	*p* - value
CW (mm)	Female	9.7	10.4	11.3	8.4 - 14.1	47	0.14	0.886
	Male	9.3	10.5	11.6	8.3 - 14.5	59		
CL (mm)	Female	6.9	7.4	8.1	5.9 - 10.2	47	0.74	0.457
	Male	6.6	7.4	8.4	5.7 - 10.8	59		
DT (mm)	Female	5.3	5.7	6.3	4.7 - 8.2	47	1.16	0.247
	Male	5.0	5.6	6.5	4.4 - 8.0	59		

Note: CW, carapace width; CL, carapace length; DT, dorso-ventral thickness

Table 5

Summary Statistics and Wilcoxon Rank Sum Significance Test Results Comparing Crab Parameters between High Food and Low Food Treatments in the Lab

Crab Parameter	Treatment	25% Quartile	Median	75% Quartile	Range	N	Z	*p* - value
CW (mm)	High	9.8	10.5	11.7	8.3 - 14.5	52	0.98	0.326
	Low	9.4	10.3	11.4	8.3 - 14.1	54		
CL (mm)	High	6.9	7.4	8.4	5.7 - 10.8	52	1.14	0.255
	Low	6.6	7.3	8.1	5.7 - 10.2	54		
DT (mm)	High	5.3	5.7	6.5	4.4 - 8.0	52	0.94	0.348
	Low	5.0	5.7	6.3	4.5 - 8.2	54		

Note: CW, carapace width; CL, carapace length; DT, dorso-ventral thickness

Table 6

Summary Statistics and Wilcoxon Rank Sum Significance Test Results Comparing Carapace Width Size Classes Among Burrow Parameters in the Lab

Burrow Parameter	CW Size Class (mm)	25% Quartile	Median	75% Quartile	Range	N	Z	*p* - value
DE (cm)	8.0 - 11.0	12.4	19.3	42.3	57.7 - 3.3	73	-0.90	0.368
	11.1 - 15.0	12.3	15.7	32.2	60.4 - 5.9	33		
DI (cm)	8.0 - 11.0	1.3	1.6	1.9	2.9 - 1.0	73	3.88	0.0001*
	11.1 - 15.0	1.6	2.1	2.5	3.8 - 1.2	33		
V (cm^3)	8.0 - 11.0	24.9	50.2	132.6	351.4 - 2.8	73	1.91	0.057
	11.1 - 15.0	42.8	89.5	141.1	417.7 - 14.3	33		

Note: CW, carapace width; DE, depth; DI, diameter; V, volume

CHAPTER IV

DISCUSSION

Murai et al. (1982) stated that droving occurred in *Uca vocans vocans* because the organic content near the edge of the water was greater there than around the burrow area; the authors further stated that *Uca lactea perplexa* did not form droves because the organic content around their burrows and near the edge of the water did not differ significantly from each other. Even though the organic content at my field site was higher near the water and decreased towards the burrow area, droving was not observed in *U. panacea*. Caravello and Cameron (1987b) stated *U. panacea* individuals did not form droves at their site; crabs first feed around their burrows and then continue foraging short distances away, which is confirmed by my observations. In my study the organic content closest to the edge of the water may not have been so much higher than near the burrow area that it stimulated droving behavior. Reinsel and Rittschof (1995) studied the droving species *U. pugilator* and determined the average % OC at the edge of the water was 0.22%, in the zone between the edge and the burrows was 0.70%, and around the burrows was 2.90%. In their study, the % OC was more than ten times higher in the area closest to the water than in the burrow zone whereas in my study the % OC near the edge of the water was only about two times as high as in the burrow area.

The nature of my field site could also have accounted for the absence of droving behavior in *U. panacea*. This species prefers sandy habitats with little or no mud (Powers, 1975); however mud was present at my field site at ~3 m from the edge of the water. The area transitions from a sandy, *Spartina alterniflora*, *U. panacea* dominated habitat into muddy, *Spartina patens*, *Distichlis spicata*, *Uca longisignalis* and *Uca*

spinicarpa dominated habitat (Jennifer Mraz, personal observation). Because *U. panacea* inhabits an area so close to the edge of the water, leaving the safety of the burrow area to forage in a large mass closer to the water may not be advantageous. *Uca pugilator* can be found in large open areas and forms large masses in an attempt to decrease the risk of predation (Viscido and Wethey, 2002); this behavior could be more advantageous to a species in that situation than at my study site. Since the area occupied by *U. panacea* at my site was so small, the crabs had a very short distance to transverse to their burrows if startled by a predator.

Other suggested reasons for droving behavior such as sediment water content and reducing individual water loss may also not be relevant for crabs living in a small area. Since the edge of the water was a relatively short distance (maximum of ~3 m) from burrows at my study site, the sediment water content may not have been particularly variable in the sandy area *U. panacea* inhabited. Low population density could have played a role in *U. panacea* not exhibiting droving behavior. There were more *U. panacea* individuals during summer 2008 when my initial observations of possible droving behavior occurred than when I conducted my droving study in spring 2009. Adverse weather conditions on the coast (i.e., Hurricane Ike) in fall 2008 altered the topography of the habitat and also appeared to have affected the density and distribution of fiddler crab and plant species at the field site. Due to the decrease in fiddler crabs, there may have been less competition for space and food in summer 2009, so that droving was not advantageous.

As mentioned above, *U. pugilator* is a droving species whereas *U. panacea* has not been documented to drove. This species specific behavior could be an effect of size.

In their original description of the species, Novak and Salmon (1974) stated male *U. panacea* individuals are not as large as male *U. pugilator*. Larger crabs may have more energetic demands for food than smaller crabs, thus making droving more advantageous to the larger species *U. pugilator*, which typically can be found in large masses (Heard, 1982).

Because fiddler crabs only leave their burrows when the tide is low, there is limited time each day to devote to surface activities such as feeding, finding a mate, and building and maintaining burrows. The Gulf of Mexico experiences diurnal tidal cycles; therefore, crabs further from the edge of the water would have a longer time to conduct day to day activities than crabs closer to the water. Even though there was a tendency in my study for burrows closer to the water to be smaller on average than those further away, the difference in size was not statistically significant. This could be due to the sampling area being limited to 1 – 2 m from the edge of the water; burrows sampled over a wider range perhaps could have shown statistically significant differences in size. For example, Wolfrath (1992) found *Uca tangeri* burrows within a 2 x 3 m sampling area to be 5-8 cm shorter in areas closer to the water than burrows further away located among *Salicornia* spp.; however, this author did not present a statistical analysis of the data so a direct comparison with my data is not possible. Similarly, Klaassen and Ens (1993) found *U. tangeri* burrow depths to increase further away from the water. Mouton and Felder (1996) found *U. longisignalis* burrow depths increased significantly as distance increased along a 15 m long transect from the edge of the water. Lim and Diong (2004) found similar results for *Uca annulipes*; burrows were deeper further from the water. Bertness and Miller (1984) found *U. pugnax* burrows significantly increase in diameter as distance

increased from the edge of the water; they also decrease in depth and volume, though the differences were not statistically significant.

Another possibility for differences in burrow morphology based on distance from the water is that other environmental factors could have a greater affect than food availability, even over small spatial scales. Fiddler crabs tend to build burrows away from the edge of the water to take advantage of the increased stability of the substrate and support offered by vegetation or attached mussels (Bertness and Miller, 1984; Genoni, 1991). By increasing burrow stability, crabs can decrease the cost associated with burrow maintenance (Bertness and Miller, 1984). An individual burrow can be used for long periods of time so stability is important; *Uca tangeri* burrows for example are used for ~3 months before being abandoned (Wolfrath, 1992). These same *Uca tangeri* burrows need to be very stable since the crabs are not active on the surface in winter and neither are a lot of other *Uca* species. *Uca panacea* is not active on the surface in winter when temperatures are less than 20°C (Powers and Cole, 1976). *Uca pugilator* individuals have been reported to be active only when the temperature is greater than 18°C, with 25°C being optimum (Knopf, 1966). When temperatures are below 18°C for long periods, fiddler crabs can lose locomotory function and molting can be stalled (Powers and Cole, 1976); at temperatures high above optimum, fiddler crabs restrict their surface activity to the early hours of the morning and a few hours before sunset. Temperature and vegetation are separately known to be important in regards to fiddler crab behavior, and it has also been suggested they are important to consider together. Powers and Cole (1976) found that compared to non-vegetated areas, areas with clumped vegetation had as much as a 10°C decrease in temperature at the surface. This decrease

in surface temperature would translate to lower temperatures inside burrows in vegetated areas. In their study, *U. panacea* tended to build burrows near vegetation, potentially for burrow temperature regulation.

Fiddler crabs must obtain enough energy through foraging to take care of their burrows since a burrow is essential to the long term survival of individuals. If the sediment organic content is low in the area where fiddler crabs live, crabs may be forced to devote less energy to burrowing because of longer feeding activities. If the sediment organic content is high, crabs should be capable of devoting more energy to burrowing. This trend was seen in my laboratory study; crabs in the high food treatments constructed significantly larger burrows than crabs in the low food treatments. Genoni (1991) suggested crabs would burrow more when less food was available in order to stimulate the growth of microorganisms for them to feed upon, and found this trend to be true for smaller *Uca rapax* crabs. In my study, crabs did not appear to burrow more when less food was available in an effort to increase food availability. Genoni (1991) found on average larger *U. rapax* crabs burrow deeper than smaller individuals. In my study, smaller *U. panacea* crabs dug deeper than larger individuals. This difference in results could be due to the sediment characteristics of the preferred habitat of each species compared to the energetic costs/benefits of moving sediment from deeper depths for smaller versus larger crabs. Other differences in environmental conditions between the preferred habitats of each species could also play a factor. Wolfrath (1992) suggested weather conditions have less of an impact on deeper burrows and that larger burrows preserve the supply of oxygen in them when they are plugged. Lim and Dong (2004) suggested longer burrows aid in temperature regulation.

In my study, female crabs constructed larger burrows than males, although the results were not statistically significant. Genoni (1991) demonstrated *U. rapax* males built deeper burrows than females. Females are regarded as better burrowers than males, with larger males having more difficulty burrowing than smaller males (Bertness and Miller, 1984), presumably because of their larger major chela. Females also tend to build more burrows than males since they are more likely to be displaced from their burrows by males (Bertness and Miller, 1984).

There were some differences in burrow size and food availability in my study between the field site and laboratory experiment. The range and maximum size of burrows cast at the field site (7.9-70.4 cm^3) were much smaller compared to burrows cast in the laboratory experiment (2.8-417.7 cm^3). Crabs at the field site experience tidal inundation on a daily basis, which can disturb the sediment and cause short burrows or the top sections of long burrows to be destroyed. The presence of tidal currents or wave action could be a deterrent for digging large burrows since they risk getting wiped out and would have to be dug again day after day. In the laboratory experiment tidal currents or wave action were not present. The daily addition of water to the sediment surface of mesocosms was not enough to damage burrows; it only provided moisture to stimulate crab feeding. Also, the median levels of organic content found at the field site (high: 0.63%; low: 0.34%) differed from the mean levels of organic content used in the laboratory experiment (high: 1.5%; low: 0.2%). Even though this was the case, the levels of organic content used in the laboratory experiment were not so different as to produce an unnatural burrowing response. Levels of organic content much higher than 1.5% and lower than 0.2% can be found in nature (Reinsel and Rittschof, 1995). Using these more

extreme levels in the laboratory experiment increased the likelihood they would have been interpreted by the crabs as high and low food levels.

Fiddler crabs play an important role in their natural environment. They can be an important dietary item for ghost crabs (Powers, 1975), mud crabs, blue crabs, birds, fishes and raccoons (Teal, 1958). Burrows constructed by fiddler crabs can be shared by breeding mosquitoes, ground spiders and other arthropods (Bright and Hogue, 1972). Hoffman et al. (1984) found deposit feeding by *Uca pugnax* regulates the distribution and amount of meiofauna in the sediment; when crabs were removed, nematodes, segmented worms and meiofaunal crustaceans all increased in abundance. Fiddler crab feeding also encourages decompositional processes by microbial communities (Kristensen, 2008). Fiddler crabs have also been used as an environmental indicator species for examining the ecosystem effects of the mosquito pesticides fenthion and methoprene (Schoor et al., 2000; Stueckle et al., 2008), the antifouling paint compound tributyltin (Weis and Perlmutter, 1987), sewage contamination (Bartolini et al., 2009; Penha-Lopes et al., 2009) and oil spills (Burger and Gochfeld, 1992; Culbertson et al., 2007). Crustaceans have also been recommended to serve as biomarkers for many types of environmental pollution (Fingerman et al., 1998).

Fiddler crab burrows aid in turning over sediment, increasing the availability of nutrients such as phosphorus, nitrogen and iron at the surface (Katz, 1980; Kristensen and Alongi, 2006). The burrows also allow oxygen and water containing nutrients to be more easily accessible to plant roots (Katz, 1980). The bioturbative activities of fiddler crabs have been studied and recognized as important in the overall health of their ecosystems (Kristensen, 2008; Bartolini et al., 2009; Penha-Lopes et al., 2009). Kristensen and

Alongi (2006) determined fiddler crabs and the roots of mangrove saplings have a mutually beneficial relationship resulting in cycling nutrients, increasing food availability and plant growth. In a salt marsh in Georgia, USA, Bertness (1985) determined fiddler crabs and *Spartina* have a mutual relationship as well; burrowing increased production of *Spartina* at intermediate tidal heights, and in lower tidal areas *Spartina* adds structural support to burrows. Fiddler crabs are considered ecosystem engineers because of their foraging and burrow activities affecting the resources available to other organisms in their habitat (Kristensen, 2008). Increasing understanding of what affects fiddler crab burrowing behavior can shed light on the importance and impact of fiddler crabs on ecosystem composition and processes.

REFERENCES

Bartolini, F., Penha-Lopes, G., Limbu, S., Paula, J., Cannicci, S., 2009. Behavioural responses of the mangrove fiddler crabs (*Uca annulipes* and *U. inversa*) to urban sewage loadings: results of a mesocosm approach. Mar. Pollut. Bull. 58(12), 1860-1867.

Bertness, M.D., 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. Ecology 66(3), 1042-1055.

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(3), 211-237.

Borgianini, S.A., 2008. Factors limiting larval dispersal that would impact the distribution of adult populations of the red-joined fiddler crab (*Uca minax* LeConte, 1855) within tidal freshwater habitats of a river dominated estuary. PhD Thesis, The University of South Carolina.

Bright, D.B., Hogue, C.L., 1972. A synopsis of the burrowing land crabs of the world and list of their arthropod symbionts and burrow associates. Contr. Sci. Nat. Hist. 220, 1-58.

Burger, J., Gochfeld, M., 1992. Effects of washing fiddler crabs (*Uca pugnax*) following an oil spill. Environ. Pollut. 77(1), 15-22.

Caravello, H.E., Cameron, G.N., 1987a. Foraging time allocation in relation to sex by the Gulf coast fiddler crab (*Uca panacea*). Oecologia 72(1), 123-126.

Caravello, H.E., Cameron, G.N., 1987b. The effects of sexual selection on the foraging behaviour of the Gulf coast fiddler crab, *Uca panacea*. Anim. Behav. 35(6), 1864-1874.

Caravello, H.E., Cameron, G.N., 1991. Time activity budgets of the Gulf coast fiddler crab (*Uca panacea*). Am. Midl. Nat. 126(2), 403-407.

Christy, J.H., 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). Anim. Behav. 30(3), 687-694.

Christy, J.H., Salmon, M., 1984. Ecology and evolution of mating systems of fiddler crabs (Genus *Uca*). Biol. Rev. Camb. Philos. Soc. 59(4), 483-509.

Crane, J., 1975. Fiddler Crabs of the World (Ocypodidae: genus *Uca*). Princeton University Press, Princeton, New Jersey.

Culbertson, J.B., Valiela, I., Peacock, E.E., Reddy, C.M., Carter, A., Vanderkruik, R., 2007. Long-term biological effects of petroleum residues on fiddler crabs in salt marshes. Mar. Pollut. Bull. 54(7), 955-962.

EachTown. 2001-2010. [Accessed April 2, 2009.] Historical weather for Ocean Springs, Mississippi. http://www.eachtown.com/Mississippi/City/Ocean-Springs;23154/weather_records.html

Fingerman, M., Jackson, N.C., Nagabhushanam, R., 1998. Hormonally-regulated functions in crustaceans as biomarkers of environmental pollution. Comp. Biochem. Physiol. C 120(3), 343-350.

Frey, R.W., Basan, P.B., Scott, R.M., 1973. Techniques for sampling salt marsh benthos and burrows. Am. Midl. Nat. 89(1), 228-234.

Genoni, G.P., 1991. Increased burrowing by the fiddler crabs *Uca rapax* (Smith) (Decapoda: Ocypodidae) in response to low food supply. J. Exp. Mar. Biol. Ecol. 147(2), 267-285.

Heard, R.W., 1982. Guide to Common Tidal Marsh Invertebrates of the Northeastern Gulf of Mexico. Mississippi Alabama Sea Grant Consortium, MASGP-79-004.

Henmi, Y., 1989. Factors influencing drove formation and foraging efficiency in *Macrophthalmus japonicus* (De Haan) (Crustacea: Ocypodidae). J. Exp. Mar. Biol. Ecol. 131(3), 255-265.

Hoffman, J.A., Katz, J., Bertness, M.D., 1984. Fiddler crab deposit-feeding and meiofaunal abundance in salt marsh habitats. J. Exp. Mar. Biol. Ecol. 82(2-3), 161-174.

Katz, L.C., 1980. Effects of burrowing by the fiddler crab, *Uca pugnax* (Smith). Estuar. Coast. Shelf Sci. 11(2), 233-237.

Klaassen, M., Ens, B.J., 1993. Habitat selection and energetics of the fiddler crab (*Uca tangeri*). Neth. J. Sea Res. 31(4), 495-502.

Knopf, G.N., 1966. Observations on behavioral ecology of the fiddler crab, *Uca pugilator* (Bosc). Crustaceana 11(3), 302-306.

Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. 59(1-2), 30-43.

Kristensen, E., Alongi, D.M., 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. Limnol. Oceanogr. 51(4), 1557-1571.

Lim, S.S.L., Diong, C.H., 2004. Burrow-morphological characteristics of the fiddler crab, *Uca annulipes* (H. Milne Edwards, 1837) and ecological correlates in a lagoonal beach on Pulau Hantu, Singapore. Crustaceana 76(9), 1055-1069.

Lim, S.S.L., Heng, M.M.S., 2007. Mangrove micro-habitat influence on bioturbative activities and burrow morphology of the fiddler crab, *Uca annulipes* (H. Milne Edwards, 1837) (Decapoda, Ocypodidae). Crustaceana 80(1), 31-45.

Mangum, C.P., 1996. Subunit composition of polymorphic hemocyanins in the decapod crustaceans: differences between sibling species. Physiol. Zool. 69(3), 568-585.

Mouton, Jr., E.C., Felder, D.L., 1995. Reproduction of the fiddler crabs *Uca longisignalis* and *Uca spinicarpa* in a Gulf of Mexico salt marsh. Estuaries 18(3), 469-481.

Mouton, Jr., E.C., Felder, D.L., 1996. Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. Estuaries 19(1), 51-61.

Murai, M., Goshima, S., Nakasone, Y., 1982. Some behavioral characteristics related to food supply and soil texture of burrowing habitats observed on *Uca vocans vocans* and *U. lactea perplexa*. Mar. Biol. 66(2), 191-197.

Murai, M., Goshima, S., Nakasone, Y., 1983. Adaptive droving behavior observed in the fiddler crab *Uca vocans vocans*. Mar. Biol. 76(2), 159-164.

Novak, A., Salmon, M., 1974. *Uca panacea*, a new species of fiddler crab from the Gulf coast of the United States. Proc. Biol. Soc. Wash. 87(28), 313-326.

Paine, R.T., 1971. The measurement and application of the calorie to ecological problems. Annu. Rev. Ecol. Syst. 2, 145-164.

Penha-Lopes, G., Bartolini, F., Limbu, S., Cannicci, S., Kristensen, E., Paula, J., 2009. Are fiddler crabs potentially useful ecosystem engineers in mangrove wastewater wetlands? Mar. Pollut. Bull. 58(11), 1694-1703.

Powers, L.W., 1975. Fiddler crabs in a nontidal environment. Contrib. Mar. Sci. 19, 67-78.

Powers, L.W., Cole, J.F., 1976. Temperature variation in fiddler crab microhabitats. J. Exp. Mar. Biol. Ecol. 21(2), 141-157.

Rao, K.R., Brannon, A.C., 1978. Color changes induced by peptide derivatives of lysergic acid in the fiddler crab, *Uca panacea*. Comp. Biochem. Physiol. C 59(2), 97-100.

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), 1-17.

Reinsel, K.A., Rittschof, D., 1995. Environmental regulation of foraging behavior in the sand fiddler crab *Uca pugilator* (Bosc 1802). J. Exp. Mar. Biol. Ecol. 187(2), 269-287.

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(1), 67-83.

Rosenberg, M.S., 2001. The systematics and taxonomy of fiddler crabs: a phylogeny of the genus *Uca*. J. Crust. Biol. 21(3), 839-869.

Salmon, M., Hyatt, G., McCarthy, K., Costlow, Jr., J.D., 1978. Display specificity and reproductive isolation in the fiddler crabs, *Uca panacea* and *U. pugilator*. Z. Tierpsychol. 48, 251-276.

Schoor, W.P., Middaugh, D.P., Marcovich, D.T., 2000. Effects of aerially applied fenthion on survival and reproduction of the panacea sand fiddler, *Uca panacea*, in laboratory habitats. Arch. Environ. Contam. Toxicol. 38(3), 327-333.

Stueckle, T.A., Likens, J., Foran, C.M., 2008. Limb regeneration and molting processes under chronic methoprene exposure in the mud fiddler crab, *Uca pugnax*. Comp. Biochem. Physiol. C 147(3), 366-377.

Shinn, E.A., 1968. Burrowing in recent lime sediments of Florida and the Bahamas. J. Paleontol. 42(4), 879-894.

Teal, J.M., 1958. Distribution of fiddler crabs in Georgia salt marshes. Ecology 39(2), 185-193.

Thurman, C.L., 1984. Ecological notes on fiddler crabs of south Texas, with special reference to *Uca subcylindrica*. J. Crust. Biol. 4(4), 665-681.

Thurman, C.L., 2002. Osmoregulation in six sympatric fiddler crabs (genus *Uca*) from the northwestern Gulf of Mexico. Mar. Ecol. 23(4), 269-284.

Thurman, C.L., 2003a. Osmoregulation by six species of fiddler crabs (*Uca*) from the Mississippi delta area in the northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. 291(2), 233-253.

Thurman, C.L., 2003b. Osmoregulation in fiddler crabs (*Uca*) from temperate Atlantic and Gulf of Mexico coasts of North America. Mar. Biol. 142(1), 77-92.

Viscido, S.V., Wethey, D.S., 2002. Quantitative analysis of fiddler crab flock movement: evidence for 'selfish herd' behaviour. Anim. Behav. 63(4), 735-741.

Weis, J.S., Perlmutter, J., 1987. Effects of tributyltin on activity and burrowing behavior of the fiddler crab, *Uca pugilator*. Estuaries 10(4), 342-346.

Wolfrath, B., 1992. Burrowing of the fiddler crab *Uca tangeri* in the Ria Formosa in Portugal and its influence on sediment structure. Mar. Ecol. Prog. Ser. 85, 237-243.

Yoder, J.A., Reinsel, K.A., Welch, J.M., Clifford, D.M., Rellinger, E.J., 2005. Herding limits water loss in the sand fiddler crab, *Uca pugilator*. J. Crust. Biol. 25(1), 141-145.

Zar, J.H., 2010. Biostatistical Analysis. (5th ed.) Prentice Hall, Inc., Upper Saddle River, New Jersey.