FACTORS INFLUENCING THE DISTRIBUTION OF CLAPPER RAILS IN MISSISSIPPI'S TIDAL MARSHES

by

SCOTT ANDERSON RUSH

(Under the Direction of Robert J. Cooper)

ABSTRACT

For many of the marsh birds that inhabit the tidal ecosystems of the northern Gulf of Mexico, such as the Clapper Rail (*Rallus longirostris*), little information exists on habitat use, reproduction and response to prey availability. Further, natural and human-induced processes continue to act upon these estuarine ecosystems. During the four year period 2005 to 2008, I studied the spatial and reproductive ecology of Clapper Rails in tidal marshes of the northern Gulf of Mexico. Through application of occupancy models, reproductive metrics, radio-telemetry and chemical tracers I provide an evaluation of factors that influence the spatial, reproductive and trophic ecology of Clapper Rails within these tidal systems. Projections from occupancy models indicate that Clapper Rails occupied much of the area surveyed (71%). However, small-scale habitat alteration such as the loss of emergent marsh and increased cover of the halophyte *Juncus roemerianus* may influence future distributions of these birds.

Tidal marsh habitat is characterized by periodic tidal flooding, a condition that has shaped many aspects of the Clapper Rail's reproductive ecology. Clapper Rails may limit nest loss to tidal flooding by placing nests in structurally complex habitat. Further, that as tidal height increases within a breeding season the size (volume) of Clapper Rail eggs increased and clutch size decreased, relative to the date of nest initiation. Thus, evidence suggests that Clapper Rails pursue an adaptive trade-off that mitigates the loss of productivity due to tidal flooding and the mortality of recently hatched young, tied to a seasonal increase in predation pressure.

Moreover, physiochemical conditions differ between the marine and freshwater estuaries studied. Radio-telemetry and chemical tracers (carbon and nitrogen stable isotopes and egg yolk lipid concentrations) provided evidence that prey availability influences the movement and distribution of Clapper Rails as well as their subsequent allocation of resources to reproduction.

Collectively, these findings indicate that Clapper Rail populations are spatially and temporally dynamic. Conservation initiatives developed for this species and similar tidal marsh-dependent organisms should account for variation in population drivers that can act at multiple spatio-temporal scales.

INDEX WORDS: carbon isotope, $\delta^{13}C$, $\delta^{15}N$, egg, lipids, marsh bird, nest, nitrogen isotope, northern Gulf of Mexico, occupancy model, tidal marsh, trophic, *Rallus longirsotris*, *Uca*.

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“The eye of the trilobite tells us that the sun shone on the old beach where he lived; for there is nothing in nature without purpose, and when so complicated an organ was made to receive the light, there must have been light to enter it.”

– Jean Louis Rodolphe Agassiz, Geological Sketches, 1870

Now, with that said, let me add that through the evolution of my education I am slowly learning, not through great bounds but at a labored pace, one particular construct: correlation does not definitively imply causation. As example, unlike the trilobite’s vision these words are here, not through an act of mine but by the guidance of others. Forgive if I forget but of the many, let me pay tribute to a few. I am deeply grateful for the assistance and friendship of Jenny Albrecht Booth, Jacquelyn Brush, Sandra Ellis, Brant Faircloth, Gretchen Grammar, Charles “Dusty” Reeve, Eric Soehren, Scott Somershoe and Jake Walker. To Dave Zabriskie and the Woodreys, you granted me safe harbor after the storm and I am indebted. John Carroll, Sara Schweitzer and Sean McGregor - thank you. Past and present members of the Cooper Lab have had a huge influence on where this research has taken me, particularly Brady Mattsson, Kirk Stodola and Rua Mordecai. Along the way numerous mentors have transformed the way I look at ecological problems. To this end, I am of course indebted to my committee members: Bob Cooper, Mark Woodrey, Aaron Fisk and Chris Romanek and to all others who have all been extremely supportive and influential in my overall approach to research. On a more personal note: Christine, your undying love and intrepid spirit will always be, and has been for so long a lighthouse in an ocean often fogged by darkness. Piranga, although I've never seen you swim, and for that matter, I'm not sure you can, your vision in the waters kept me near to home. Yes, even when you flooded the bathroom. Mom and Dad, what can I say that would be fitting enough to highlight all you have done and all you have given? Albeit not nearly enough, however, these words are yours.

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"The continents themselves dissolve and pass to the sea, in grain after grain of eroded land. So the rain that rose from it return again in rivers. In its mysterious past it encompasses all the dim origins of life and receives in the end, after, it may be, many transmutations, the dead husks of that same life. For all at last returns to the sea – to Oceanus, the ocean river, like the ever flowing stream of time, the beginning and the end."

– Rachel Carson, The Sea Around Us, 1951

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

PREFACE

Currently more than 40% of the nation's coastal wetlands have been claimed for agriculture, or drained and altered for human occupancy (Horwitz 1978, Nixon 1982, Weinstein and Kreeger 2000, Glenn et al. 2006, Greenberg et al. 2006). Organisms that inhabit these tidal marshes are uniquely adapted and exhibit distinct ecological traits that have allowed them to persist in what can often be harsh environments (Dunson and Travis 1994, Greenberg and Maldonado 2006). Not surprisingly, with the loss of tidal marsh habitat, the majority of vertebrate species endemic to these ecosystems are currently considered threatened, endangered, or are of heightened conservation concern (Greenberg et al. 2006).

The research presented here was originally premised to assess the applicability of the Clapper Rail (*Rallus longirostris*) as an indicator of the health of the tidal marshes of the northern Gulf of Mexico. Although Clapper Rails have been shown to provide valuable indication of tidal marsh "health" (Novack et al. 2005), from our research we have also found, that in some ways, this species may be relatively resistant to habitat change and alteration. In the pages that follow we identify some of these metrics, correlations with localized and landscape-level processes, and how this species is responding and may respond to future conditions. Generally, we draw relevance to what

Clapper Rails can tell us about the ecology of marsh birds, and more-broadly, tidal marsh ecology and implications for anticipated environmental change within these ecosystems.

TIDAL MARSHES: ECOLOGY AND IMPORTANCE

Estuarine intertidal marshes form the interface between the sea and the land and can be viewed as transition zones between freshwater and marine aquatic systems (Dardeu et al. 1997). Cowardin et al. (1979) formally defined estuaries as "deep-water tidal habitats and adjacent tidal wetlands which are usually semi-enclosed by land, but have open, partially obstructed, or sporadic address to the open ocean and in which water is at least occasionally diluted by freshwater runoff from the land." This transition between sea and land results in a spectrum of abiotic and biotic forces that shape biological and physical communities (Dardeu et al. 1992, Moore 1992). Consequently, tidal marshes are valued for both their high levels of productivity as well as their buffering capacity against coastal storm events, such as hurricanes (Stone et al. 1997, Day et al. 2007).

Historically, the tidal wetlands of the northern Gulf of Mexico were considered to be some of the most productive ecosystems in the world (Boesch and Turner 1984, Houde and Rutherford 1993). Tragically, these tidal estuaries are now acted on by multiple stressors, affecting both their structure and function (Justić et al. 1995, Jackson et al. 2001, Mutsert 2008). For example, the northern Gulf of Mexico is vulnerable to sea level rise, flooding and erosion (Hammar-Klose and Thieler 2001, Day et al. 2008). Coupled with human alteration, these forces have lead to the continued loss of these ecosystems (Turner 1997, Shirely and Battaglia 2006, Day et al. 2008, Stedman and Dahl 2008). Although the coastline of the northern Gulf of Mexico claims 41% of the United

State’s coastal wetlands, historical changes within these ecosystems represent over 80% of the nation’s wetland losses (Dahl 1990).

Despite these alarming changes, forces that have structured the northern Gulf of Mexico’s tidal ecosystems have also shaped the ecology and behaviors of endemic organisms (Greenberg et al. 2006). Birds are included among these unique organisms.

MARSH BIRDS

The term “marsh bird” describes species that inhabit and depend on emergent wetlands. North American marsh birds inhabit wetlands typically characterized by a well-developed zone of emergent vegetation, and hydrologic conditions that may be uniquely associated with each species’ distribution (Eddleman et al. 1998). However, by definition ‘marsh birds’ include a broader array of species some North American representatives include King Rail (*Rallus elegans*), Clapper Rail, Virginia Rail (*Rallus limicola*), Sora (*Porzana carolina*), Black Rail (*Laterallus jamaicensis*), Yellow Rail (*Coturnicops noveboracensis*), American Bittern (*Botaurus lentiginosus*), Least Bittern (*Ixobrychus exilis*), Pied-billed Grebe (*Podilymbus podiceps*), Limpkin (*Aramus guarauna*), American Coot (*Fulica americana*), Purple Gallinule (*Porphyrula martinica*), and Common Moorhen (*Gallinula chloropus*) (Conway 2005). Although the diversity of North America’s marsh birds is broad, it may be matched by the unique and colorful colloquialisms given to many of these species. Such names as ‘Thunder Pumper’, ‘Marsh Hen’, ‘Pull-doo’ and ‘Hell Diver’ are among the few that may be more commonly used or, at least identifiable (American Bittern, Clapper Rail, American Coot, and Pied-billed Grebe, respectively). However, as assertive and unique as their names may be, many marsh birds are reclusive and are often heard more frequently than seen, a behavior that has earned the descriptor ‘secretive’.

Although additional information is mentioned in the following chapters, I would like to begin to draw focus on a few of the ecological and life history traits of a particular marsh bird, the Clapper Rail. Physically, the Clapper Rail has a laterally compressed body, stature that may have given rise to the phrase “thin as a rail”. The Clapper Rail’s large feet and long webless toes allow it to easily walk on the soft mud characteristic of its wetland haunts. Clapper Rail feathers contain the pigment eumelanin which is tied to the expression of greater black and grayish coloration in the dorsal contour feathers (Greenberg et al. 2006) and has been suggested to serve as camouflage, blending effectively with tidal marsh soils (Greenberg and Droege 1990). Although both Clapper Rails and their freshwater counterpart the King Rail (*Rallus elegans*) have salt glands, the morphology of the Clapper Rails’ glands may be the product of a longer evolution to tidal marsh environments (Olson 1997). Located in depressions in the skull that are just above the eyes, these glands enable birds to exude condensed salts from their bodies (Gill 1995). Although the size and functionality of this gland may be environmentally conditioned in Clapper Rails, the osteological structure surrounding the gland arguably represents a genetically-linked adaptation to salt marsh environs (Olson 1997).

At the time of writing, the phylogenetic separation of King Rail from Clapper Rail continues to be debated (Chan et al. 2006). By name, however, Clapper Rails and King Rails have been separated since the Reverend John Bachman persuaded John James Audubon that the smaller, darker birds of coastal estuaries (Clapper Rail) were distinct from the larger, more reddish birds (King Rail) more frequently identified with freshwater systems (Meanley 1969). The geologic forces responsible for the creation of many of North America's tidal marshes have been suggested to have also helped separate King and Clapper Rails and their typical habitats (Olson 2006). Ironically, what could have separated these species may also leave them imperiled. That is, the processes of sea-level rise and the loss of coastal and freshwater marsh leaves the status of tidal marsh in question, heralding significant impacts on both Clapper and King Rails (Eddleman and Conway 1998, Hunter et al. 2006, Cooper 2008).

Despite continued and often dismal projections of wetland loss and alteration, conservation actions may be acting in favor of the future of these marsh bird species. Specifically for the marsh birds of the northern Gulf of Mexico, development of conservation initiatives (Hunter et al. 2006, Cooper 2008), advancements in monitoring techniques (Conway 2008), and tidal marsh restoration (Day et al. 2005, Rozas and Minello 2007, Day et al. 2007) continue to slow the deleterious effects of coastal degradation and add depth to our understanding of the ecology and life history strategies employed by many of these unique organisms.

OVERVIEW OF THE REMAINING CHAPTERS

In Chapter 2 (Occupancy of select marsh birds within tidal marshes of the northern Giulf of Mexico: current estimates and projected change) we provide an overview of the distributions of Clapper Rails, and other marsh bird species, within northern Gulf of Mexico tidal marshes. This chapter sets the stage for many of the topics covered in the subsequent chapters such as the dynamic processes that may influence Clapper Rail distributions within these tidal systems, now and in the future.

In Chapter 3 (Variations in the nesting habits of Clapper Rails in response to tidal marsh habitat along the northern Gulf of Mexico), we dig deeper into Clapper Rail ecology by examining the interplay between this species' breeding ecology and biotic and abiotic forces that dominate tidal estuaries. The influence of the tidal marsh environment on Clapper Rail ecology and productivity are reoccurring themes throughout this dissertation.

Although previous studies have quantified Clapper Rail diet composition (*references in* Eddleman and Conway 1998), inferences drawn from these studies may have biased source contributions. Stable isotope analysis has proven to be a powerful tool for the study of avian trophic relationships in coastal ecosystems. In Chapter 4 (Clapper Rail diet composition and egg resources vary across two hydrologically dynamic estuarine ecosystems), we apply stable isotope analysis to examine the trophic composition of Clapper Rails in two northern Gulf of Mexico tidal marshes.

The substance of Chapter 5 (Impacts of food and predators on Clapper Rail movements in coastal Mississippi, USA) focuses on relationships between the Clapper Rails' distributions, habitat and food resources. The distributions of fiddler crabs, the dominant prey type of Clapper Rails within the tidal estuaries of the northern Gulf of Mexico, trophic ecology and governance of Clapper Rail distributions are focal topics covered in the remaining chapters.

In Chapter 6 (Variation in Clapper Rail egg volume and clutch size: insights into reproductive strategies and life history), we explore reproductive tradeoffs and Clapper Rail life history strategies. This chapter provides a complement to Chapter 2 but provides a theoretical basis, backed by quantitative evidence exploring Clapper Rail life history adaptations for breeding in tidal estuaries.

Through the chemical tracers and models employed in Chapter 7 (Linking localized habitat to spatial distributions and reproductive parameters of Clapper Rails through trophic ecology), we provide evidence of trophic links between Clapper Rails and habitat. Here we explore further the spatial influences that habitat and fiddler crab distributions exert on Clapper Rails. Relationships between fiddler crabs and Clapper Rail reproductive metrics provide the cornerstone of Chapter 8.

Constructs provided in Chapter 8 (Hydrologic conditions and predator-prey dynamics structure Clapper Rail populations in two northern Gulf of Mexico estuaries) work predominantly off foundations laid in Chapter 7. However, rather than focus on localized habitat effects, as a unifying agent, we provide evidence watershed-level conditions influence Clapper Rail populations through trophic ecology and reproduction.

Chapter 9 (Conclusion) synthesizes the results from Chapters 1–8.

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CHAPTER 2

OCCUPANCY OF SELECT MARSH BIRDS WITHIN TIDAL MARSHES OF THE NORTHERN GULF OF MEXICO: CURRENT ESTIMATES AND PROJECTED CHANGE[1]

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[1] Rush, S. A., E. C. Soehren, M. S. Woodrey, C. Graydon, and R. J. Cooper. Submitted to *Wetlands*, 8/10/2008.

ABSTRACT

Among the forces listed as influential to the state of northern Gulf ecosystems are sea-level rise, human development and habitat alteration. While predictive models have been applied to project the interactions between habitat modification and population estimates for some estuarine species, the scope of many of these assessments is limited to single species, leaving projections of the future of estuarine ecosystems unclear. Predictions of ecosystem change may be furthered by focusing on a suite of species, such as the marsh birds that inhabit these ecosystems. During 2004 and 2005, we conducted point count surveys within the estuarine systems of Alabama and Mississippi to assess whether small-scale wetland habitat characteristics and a broader scale metric of human development influenced the site occupancy of several marsh bird species: Clapper Rail (*Rallus longirostris*), Common Yellowthroat (*Geothlypis trichas*), Least Bittern (*Ixobrychus exilis*), Marsh Wren (*Cistothorus palustris*), and Seaside Sparrow *(Ammodramus maritimus*). On the basis of current habitat, we project change in species occupancy based on several scenarios. Projections indicate that small-scale habitat alteration through loss of emergent marsh and increased cover of the halophyte *Juncus roemerianus* may be most influential to the distribution of these species. Thus, continued alteration of existing conditions coupled with sea-level rise will likely have a significant impact on the distribution of this group of marsh bird species as well as the integrity of their habitat.

KEYWORDS: anthropogenic modification, habitat, *Juncus roemerianus*, salinity, sea-level rise, *Spartina alterniflora*.

INTRODUCTION

Within the southern United States' tidal marshes, recent changes in the distribution of plant communities have been related to environmental stress, sea level rise and increased herbivory (Visser et al. 2002, McKee et al. 2004, Silliman et al. 2005). Noted among the suite of environmental stressors acting upon estuaries are reduction of freshwater inflow and a subsequent landward increase in salinity (Brinson and Christian 1999, Gibson and Najjar 2000, Visser et al. 2002, Higinbotham et al. 2004, McKee et al. 2004). Collectively, drought-induced stress and herbivory have been blamed for mass die-backs of *Spartina alterniflora* (Loisel.) (Silliman et al. 2005) resulting in extensive loss of vegetation and a marked inland shift of polyhaline marsh (Visser et al. 2002, McKee et al. 2004). Additionally, shifting salinity regimes and tidal submergence, both factors resulting in reduced freshwater inflow and sea level rise, are linked to the conversion of emergent marsh to patches of open water (Day et al. 1995, Dunton et al. 2001, Visser et al. 2002). Hydrologic conditions as related to climactic extremes can act in concert with sea-level fluctuations and anthropogenic development, altering coastal vegetation and tidal marsh ecosystems (Turner 1997, Greenberg et al. 2006a, Lee et al. 2006, Xu and Wu 2006, Field and Mortech 2007). Predicting the response of estuarine ecosystems to environmental change requires predictive modeling done at varying spatial scales using carefully chosen metrics (Costanza et al. 1990, Day et al. 1995, McFadden et al. 2007). Mechanistic models for evaluating disturbance effects would enable resource managers to understand the implications of disturbance regimes and processes that extend beyond the wetland being managed (Silliman and Bertness 2004, Johnson et al. 2007, Wilcox and Xie 2007, Kelly et al. 2008).

The application of predictive models has provided information regarding changes in habitat and population estimates for some estuarine species, many of which have been shown to be effective indicators of tidal marsh ecosystem integrity (Morris et al. 1990, Peterson et al. 2000, DeLuca et al. 2004, Shriver et al. 2004, Mitchell et al. 2006, Rozas et al. 2007, Purcell et al. 2008). Marsh birds might be especially useful as indicators of tidal marsh ecosystem integrity because, among other favorable attributes, they tend to occupy higher trophic levels and are relatively easy to survey (DeLuca et al. 2004). Early indications are that many species of birds associated with tidal marsh ecosystems may already face population declines or compromised habitat availability (Eddleman et al. 1988, Pashley et al. 2000, Erwin et al. 2006). Thus, further loss or alteration of available habitat can have direct impacts on future population trends (Pashley et al. 2000) and development of predictive models addressing species response to changing conditions is critical to their effective conservation (Greenberg et al. 2006a). The aims of this study were to address habitat associations for several species of marsh birds within tidal marshes along the northern Gulf of Mexico. Specifically, our objectives were to (1) examine the importance of vegetation, marsh structure, and localized human alteration on several species of marsh birds within tidal marshes of the northern Gulf of Mexico, (2) assess the effects of these variables on species occupancy across this landscape, and (3) provide predictions of species occupancy change based on scenarios of potential habitat change.

STUDY AREA AND METHODS

SURVEY AREA − In Alabama our study area was in the tidally-influenced marshes that occur along the shoreline of Baldwin and Mobile counties (Fig. 2.1). Saline emergent marshes used in this study were characterized primarily by dominant stands of either *Juncus roemerianus* (Scheele) or *Spartina alterniflora*. Marshes were located fringing the mainland coastline, islands and inlets of lower Mobile Bay. These marshes were regularly inundated by tidal flooding and were characterized by a meso to polyhaline salinity regime. Brackish emergent marshes were typically characterized by one or several combinations of *Typha domigensis* (Pers.), *Sagittaria lancifolia* (L.), *Cladium jamaicense* (Crantz), *Peltandra virginica* (L.), *Phragmites australis* [(Cav.) Trin. ex Steud.], or other less frequently encountered dominants occurring in the lower portion of the Mobile-Tensaw River Delta (Fig. 2.1).

Our study area in Mississippi included two estuarine systems, the Pascagoula River Marsh Coastal Preserve and Grand Bay National Estuarine Research Reserve, both of which are in Jackson County (Fig. 2.1). Emergent marsh of the oligohaline and mesohaline Pascagoula River Marsh Coastal Preserve was dominated by *J. roemerianus*, *S. alterniflora*, *S. cynosuroides* [(L.) Roth] and *S. lancifolia* while the polyhaline Grand Bay site was dominated by *J. roemerianus* and *S. alterniflora*. This habitat is further described in Eleuterius (1972).

FIELD METHODS AND HABITAT CLASSIFICATION − Following the sampling methodology described in the North American Marshbird Monitoring Protocol (Conway 2008) and Conway and Droege (2006) we conducted marsh bird surveys at 109 locations in Alabama and 118 locations in Mississippi. Survey locations were selected based on accessibility and inclusion of dominant habitat types represented within this estuarine landscape. We used call playback for Clapper Rails (*Rallus longirostris* Boddaert), and Least Bitterns (*Ixobrychus exilis* Gmelin) while detections of Marsh Wren (*Cistothorus* *palustris* Wilson), Seaside Sparrow (*Ammodramus maritimus* Wilson) and Common Yellowthroat (*Geothlypis trichas* L.) were through passive detections only. Marsh bird surveys were conducted in Alabama during 2004 and in Mississippi during 2005. All survey points were at least 400 m apart and two replicate surveys were conducted at each survey point. Survey periods were structured to allow greater than 2 weeks between surveys at each survey point. Initial surveys were conducted after 27 Mar but prior to 23 June. The second survey was conducted after 15 June but before 6 August. During each survey, the presence of our focal species was recorded only if they were detected within 100 m of the survey point. Within both Alabama and Mississippi all surveys were conducted by one of four surveyors, i.e., two surveyors in Alabama and two surveyors in Mississippi. For analysis, we placed surveyors in one of two experience categories, which was subsequently encoded using a dichotomous variable in our analysis.

The level of localized anthropogenic habitat modification was measured using National Agricultural Imagery Program (2005, 1 m raster coverage) and geographic information systems (GIS) software ArcGIS and ArcView (Environmental Systems Research Institute, Redlands, California). We calculated the percent of area that had been anthropogenically modified within 500 m of each survey point. Our selection of a 500 m radius buffer was based on similar studies that found that avian diversity decreased relative to the level of anthropogenic modification at this scale (Findlay and Houlahan 1997, DeLuca et al. 2004, Shriver et al. 2004). We did not differentiate types of development (i.e., low density housing, agriculture, etc.), but treated all identifiable development as similar (hereafter referred to as DEVELOPMENT). We caution the reader that variables measured within a 500 m radius of each survey point may lack independence because survey points were sometimes less than this distance apart.

To quantify marsh structure and the composition of vegetation we established two concentric circles, one of 200 m and one of 50 m, encircling each survey point. Within each 200 m radius circle we calculated the linear length of emergent marsh vegetation edge (EDGE), the percent area comprised of emergent vegetation (AREA), and a measure of INTERSPERSION defined as edge density, a measure of the interface between vegetation and water defined as the ratio of EDGE to AREA (Rehm and Baldassarre 2007). Within 50 m of each survey point we estimated the percent cover of major vegetation types. Visual inspection indicated dominant cover types were represented by one of three species, *J. roemerianus*, *S. alterniflora* and *S. cynosuroides*, reflecting a salinity gradient. However, the distributions of these three species may be related through interactions of environmental factors and competition (Stibling 1997, Pennings et al. 2005). Collinearity analysis suggested significant negative correlations among *S. alterniflora* and *S. cynosuroides* (Pearson $r = -0.21$, $p = 0.001$), and *J. roemerianus* and *S. cynosuroides* (Pearson $r = -0.27$, $p < 0.001$). To avoid multicollinearity, and because *J. roemerianus* was present at a greater number of sample locations than either *Spartina* spp., we used only *J. roemerianus* (hereafter JUNCUS) to represent the salinity gradient.

MODELING SPECIES DISTRIBUTIONS − We focused on five marsh bird species: (1) Clapper Rail, (2) Least Bittern, (3) Seaside Sparrow, (4) Marsh Wren and (5) Common Yellowthroat (*Geothlypis trichas* L.). Focus was given to these five species because occupancy rates were high enough to provide efficient estimates of habitat association (MacKenzie et al. 2002), and because they are believed to represent a range of salinities in their respective habitat associations within tidal marsh ecosystems. For each species we developed models to address the influence of covariates on occupancy.

Occupancy modeling can be conceptualized by considering three probabilities for each species during each survey (1) the probability that the survey site is occupied by the focal species (ψ), (2) the conditional probability that, given the focal species occupies the survey site, it used that precise location during the survey period, and (3) the conditional probability, given the focal species occupies the survey site and was detected by the surveyor (MacKenzie et al. 2002). In the present study only two replicate surveys were conducted at each site, and while the inclusion of additional survey events can provide more robust occupancy estimates (MacKenzie et al. 2005), the geographic breadth of this study and time constraints made additional surveys impractical. Occupancy models were estimated using the single season, single species models in program PRESENCE (Program PRESENCE 2.1, MacKenzie et al. 2006). We initiated model development with the inclusion of covariates within the detection portion of each model (MacKenzie et al. 2002). We then developed models for each species derived from our *a priori* hypotheses.

MODEL DEVELOPMENT AND HYPOTHESES OF SPECIES OCCUPANCY − We began analysis by considering potentially important covariates for detection. Of primary interest was the influence of observer (OBSERVER), which was treated as a survey-specific covariate by pooling data collected in Mississippi and Alabama. Preliminary analysis from this system also showed that detections of Clapper Rails, Seaside Sparrows and Marsh Wrens were influenced by tidal height (Rush et al. *in press*). Therefore, all models for Clapper Rail, Seaside Sparrow and Marsh Wren incorporated TIDE and OBSERVER as covariates to detection and all models for Common Yellowthroat and Least Bittern included OBSERVER. Further, because our sampling was distributed across two years, we investigated year as a nuisance variable to detection. Results indicated detection did not vary significantly among years so, as a covariate, year was not considered further.

Next, we considered important covariates for estimating occupancy. For passerines (Seaside Sparrow, Marsh Wren and Common Yellowthroat) we anticipated that the percent of cover of emergent marsh within 200 m of each survey point would relate positively with occupancy. Clapper Rails (Eddleman and Conway 1998, S. Rush unpublished data) and Least Bitterns are believed to preferentially use marsh edge, or exhibit preference for habitat characterized by a complex pattern of interspersion of water and emergent vegetation (Rehm and Baldassarre 2007). Therefore, when developing models we included INTERSPERSION as a covariate for these two species.

Vegetation associations in tidal marshes often reflect salinity gradients, and we chose vegetative covariates accordingly. Clapper Rails and Seaside Sparrows occupy tidal marsh habitat characterized by the presence of large patches of *S. alterniflor*a and *J. roemerianus* (Post and Greenlaw 1994, Eddleman and Conway 1998). Throughout their range, Marsh Wrens can be found in tidally influenced habitat (Kroodsma and Verner 1997) and are believed to prefer JUNCUS habitat situated along tidal creeks (Kroodsma and Verner 1997). While Common Yellowthroats are typically associated with wetland habitat, associations are largely with freshwater communities (Guzy and Ritchison 1999). Similarly, Least Bitterns (Gibbs et al. 1992) are less common within higher salinity habitat. Thus, for each species we included JUNCUS as a covariate in the construction of occupancy models. Marsh birds have been shown to respond negatively to various forms of anthropogenic disturbance within the landscape surrounding estuarine systems (DeLuca et al. 2004, Shriver et al. 2004, Mitchell et al. 2006, Purcell et al. 2008). Therefore, we included DEVELOPMENT in our models, with the expectation of a negative relation to each species' occupancy. Additionally, for each species we included a model with no factors (NULL model) and a model that contained all factors (the global model: GLOBAL). Although "null models" can be developed without covariates, our prior knowledge of several factors that have influenced the detection of marsh birds within this system (Rush et al. *in press*) led us to include OBSERVER and TIDE in the null models developed for Clapper Rail and Seaside Sparrow, and OBSERVER in the null models for Common Yellowthroat and Marsh Wren (MacKenzie et al. 2006).

ASSESSMENT OF MODEL FIT − We assessed model fit using procedures outlined by *Burnham and Anderson (ĉ: 2002) and found it to be adequate for all models.* Akaike's Information Criterion (AIC, Akaike 1973) was then used to compare models based on log-likelihood values (Burnham & Anderson 2002) and estimated model fit based on values of AIC, the number of parameters (K), and the deviance (Dev). Models were ranked and compared using ΔAIC and AIC weights, where ΔAIC estimates the relative difference between the top ranked model and each other model, and AIC weights measure the weight in favor of the model given the data. Models with $\Delta\text{AIC} \leq 2$ were considered to be equally parsimonious. However, if models differed by only one predictor variable, we then based model selection on model deviance with the better supported model having the lower deviance. When comparing a more complex model a to a simpler, less parameterized model b, we employed information-theoretic evidence ratios (ER = AIC weight of model *a* / AIC weight of model *b*) to quantify the relative support of model *a* versus model *b* (Burnham and Anderson 2002*).* We applied model averaging to estimate occupancy and detection if several models were found to fit the data equally well. Parameter estimates were weighted by the Akaike weight of the associated model and we calculated mean covariate values and unconditional variance estimates to account for uncertainty in model selection (Burnham and Anderson 2002). For each parameter we report 95% confidence intervals based on the unconditional variance. Parameters were interpreted as significant if the confidence intervals around the parameter estimates did not contain zero.

As a diagnostic tool, prior to analysis we randomly divided our data set, selecting 25% to set aside as an independent data set for use in model validation, and using the remaining 75% of the data set aside for model development (R 2.7.1, R Development Core Team 2008). For each species, and applying the 25% of the data set aside for model validation we combined data for both survey periods to produce a composite history of presence and absence for each survey site. These data were then used to address the predictive performance of the best supported model where we plotted sensitivity values (the proportion of observations where the model correctly predicts a presence) against false positive values (1 − specificity, or the proportion of observations where the model correctly predicts an absence) to fit a relative operating characteristic (ROC) curve (Proc Logistic: Zweig and Campbell 1993, Pearce et al. 2001). The ROC curve provides a graphical approach to the assessment of each model's discrimination capacity, where perfect discrimination is represented when the area under the ROC curve (AUC) equals 1 (Zweig and Campbell 1993, Pearce et al. 2001). Conversely, a model with no discrimination capacity has an AUC equal to 0.5. Values of AUC from 0.5 to 0.7 were judged as representing ‘low’ model accuracy while values between 0.7 and 0.9 were considered to have ‘good’ accuracy, indicating that the model had reasonable discrimination ability (Swets 1988, Manel et al. 2001).

PREDICTING CHANGES IN SPECIES OCCUPANCY RELATIVE TO HABITAT CHANGE − Our predictive models of species response to habitat change were developed based on the following assumptions: 1) Current population trends and demographics suggest continued anthropogenic development of the northern Gulf of Mexico (Adams et al. 2004, Yáñez-Arancibia and Day 2004). 2) Increased development adjacent to and within the estuarine landscape and alteration of estuarine systems within the Gulf of Mexico, through sea-level rise and natural and human induced habitat change, will lead to reductions in AREA (Roach et al. 1987, Johnston et al. 1987, Day et al. 1995, Dunton et al. 2001, Visser et al. 2002, McFadden et al. 2007), loss of freshwater marsh habitat (Visser et al. 2002, McKee et al. 2004, McFadden et al. 2007), and an increase in the extent of meso and polyhaline salt marsh (increase in JUNCUS: Visser et al. 2002, McKee et al. 2004). 3) We expect future habitat trends to result in reduced INTERSPERSION within these tidal systems (Delaney et al. 2000, Rehm and Baldassarree 2007).

For each species, we applied the significant model-averaged parameter estimates, derived from our occupancy models, to predict species occurrence relative to projections of localized disturbance by incorporating point estimates and associated unconditional variance estimates in a logistic regression analysis (R 2.7.1, R Development Core Team 2008). We evaluated the response of each species to habitat change at several proportional increments (e.g., 5%, 10%, 20%, and 30%). Under the different scenarios habitat metrics were assumed to change equally across the landscape. For the logistic model, we applied model-averaged covariates, using a normal distribution to calculate the mean and variance for each covariate. We then used these covariates to generate a single value of occupancy. This process was repeated 1000 times to generate point and variance estimates for each species' occupancy under each predicted level of habitat change. We applied the methods of Efron (1981) to our bootstrap variance estimates to calculate 95% confidence intervals for occupancy predictions. Because model estimates were on the logit-scale we back-transformed estimates to proportions to facilitate interpretation of the effect sizes (Kutner et al. 2005, MacKenzie et al. 2006).

RESULTS

The accuracy of the top-scoring model (AUC ≥ 0.7) differed between species with the most supported model for Seaside Sparrow and Clapper Rail showed good model accuracy, while models developed for Least Bittern, Marsh Wren and Common Yellowthroat all showed low accuracy (Table 2.1). Naïve occupancy estimates, derived from the NULL models, ranged from 31% for Common Yellowthroat to 71% for Clapper Rail (Table 2.2).

For each species, top models included the covariate JUNCUS (Table 2.1), while model-averaged parameter estimates indicated significant associations between JUNCUS for all species except Marsh Wren (Table 2.2). Clapper Rails and Seaside Sparrows, species most frequently associated with salt marsh habitat, exhibited positive relationships between JUNCUS and occupancy (Table 2.2). Seaside Sparrow occupancy related positively to AREA and was the only species to exhibit a significant relationship between occupancy and DEVELOPMENT (Table 2.2). For Marsh Wren, evidence ratios revealed that a model containing DEVELOPMENT received 1.6 times more support than the less parameterized model that included the additive effects of JUNCUS and AREA only (Table 2.1). Evidence ratios indicated that the occupancy of Clapper Rails also related positively to INTERSPERSION (Table 2.2).

Our results indicate that predicted change in habitat characteristics associated with the tidal marshes of the northern Gulf of Mexico could have an impact upon the distribution of each of our study species (Table 2.3). However, for most species, the directional effect of habitat change on occupancy was not clear until the magnitude of habitat change exceeded 20% of present conditions. As examples, an increase in JUNCUS may lead to higher occupancy rates by both Seaside Sparrow and Clapper Rail, but the potential for continued DEVELOPMENT and the loss of INTERSPERSION could reduce the presence of each species, respectively (Fig. 2.2, 2.3). Similarly, for Least Bittern, Marsh Wren and Common Yellowthroat marsh loss and alteration may ultimately lead to reductions in occupancy (Table 2.2). However, we found a large variation in the bootstrapped predictions developed from our logistic regression models (Table 2.2), suggesting uncertainty in the degree to which alteration of tidal marsh habitat may be influential to these species. Here, our results suggest that the site occupancy response of Least Bitterns to increased JUNCUS and that of Clapper Rails to decreased INTERSPERSION may range from no change in occupancy to a fairly substantial loss of their presence (46% and 75%, respectively).

DISCUSSION

Alteration and loss of habitat has been posited as one of the primary factors influencing conservation of tidal marsh bird species (Gibbs, et al. 1992, Post and Greenlaw 1994, Kroodsma and Verner 1997, Eddleman and Conway 1998, Guzy and Ritchison 1999). Further, within the northern Gulf of Mexico studies suggest habitats and species assemblages will change considerably over the coming decades (Forbes and Dunton 2006, Day et al. 2008) with marsh birds included among the organisms expected to be influenced by these changes (Greenberg et al. 2006a). Our results indicate that redistribution of habitat within the tidal marshes of the northern Gulf of Mexico will negatively influence the occupancy of several marsh bird species. Based on our predictions, such as habitat change and reductions in physical marsh structure, the presence of Marsh Wren, Common Yellowthroat and Least Bittern will decrease. Conversely, we expect that Clapper Rails and Seaside Sparrows will exhibit heightened occupancy relative to current habitat distributions.

As demonstrated elsewhere, the species we studied are associated with habitat that represented opposite ends of the salinity gradient present within the tidal systems of the northern Gulf of Mexico. Specifically, our results suggest that Clapper Rails and Seaside Sparrows are more likely to occur in habitats with higher salinity (as reflected in the variable JUNCUS), and Least Bittern and Common Yellowthroat are more likely to occur in oligohaline and mesohaline habitats within tidal systems (Gibbs et al. 1992, Post and Greenlaw 1994, Kroodsma and Verner 1997, Eddleman and Conway 1998, Guzy and Ritchison 1999). Marsh Wrens are known to occupy emergent marshes of varying salinities (Kroodsma and Verner 1997), so the largely equivocal results for salinity effects on this species was not surprising. As with most species that inhabit tidal marsh systems, any model predicting occurrence must take salinity into account; indeed, any species for which this is not the case would likely be a poor indicator of tidal marsh ecosystem integrity.

Loss of emergent marsh habitat through conversion to open water can result from both reduced accretion, loss of vegetation and increased inundation (Day et al. 2005). Additionally, change in the location of isohalines, either upstream or downstream, can affect areas where favorable salinity conditions overlay favorable shoreline or bottom features that are influential to productivity (Sklar and Bowder 1998). Thus, the implications of marsh loss may be experienced through trophic cascades and disruption of relays to adjacent systems (Kneib 2000, Hughes 2004, Valiela et al. 2004, Stevens et al. 2006, Rountree and Able 2007). Alteration in hydrological flows and inundation may result in a redistribution of tidal wetland plant communities with reciprocal restriction in the extent of freshwater plant communities (Bradley et al. 1990, Spalding and Hester 2007).

The ultimate long-term effects of habitat change for both Clapper Rail and Seaside Sparrow may not be as straight forward as predicted by our models. For example, Clapper Rails have been shown to exhibit nest height plasticity in an effort to avoid nest loss from tidal flooding (Storey et al. 1988, Eddleman and Conway 1998). Clapper Rails nesting within estuarine systems lacking structurally diverse habitat could face higher levels of nest loss due to flooding (Erwin et al. 2006). Under conditions of rising sea-level, the larger spectrum of structurally diverse vegetation types may be replaced by the less diverse assemblage of salt tolerant species, as narrowed estuarine systems may face higher tidal amplitudes (Odum 1988). Seaside Sparrows use habitat characterized by higher salinity but may not nest in areas dominated by *J. roemerianus* (Post and Greenlaw 1994). Instead, this species tends to prefer the short form of *S. alterniflora*, apparently for its structural diversity, which is thought to help conceal nests (Post and Greenlaw 1994, Brawley et al. 1998, Greenberg et al. 2006b). The distribution of *J. roemerianus*, as exhibited by Pennings et al. (2005) and supported by the correlations in our habitat evaluation, may be restricted to areas exhibiting a specific suite of habitat characteristics, which include middle to lower salinity environments. On the other hand, the spatial distribution of *S. alterniflora* may be competitively excluded to low marsh environs, characterized by high salinity and low topography (Mendelssohn and Batzer 2006). Therefore, within the tidal marshes of the northern Gulf of Mexico Seaside Sparrows may only exhibit increased occupancy if physical changes in the estuarine landscape facilitate an increase in the distribution of *S. alterniflora*. For both Clapper Rails and Seaside Sparrows, predicted linear relationships of occupancy may not translate directly to future population trends as these relationships depend upon the physical structure of the tidal marsh environment (Erwin et al. 2006).

Of our focal species, only Seaside Sparrows showed a predictable response to localized human disturbance (Fig.2.3). In the northeastern coast of the United States, Shriver et al. (2004) found Seaside Sparrows showed a positive relationship between occupancy and salt marsh size. Unlike the tidal wetlands examined by Shriver et al. (2004), which tend to be discrete, isolated systems, tidal marshes of the northern Gulf of Mexico represent a more continuous system (Dardeau et al. 1992). Thus, our finding of a negative response between Seaside Sparrow occupancy and the percent of localized human disturbance also may be a reflection of the size of habitat available. Because dynamic processes may be specific to individual marshes, extrapolation to, and comparisons of, the response of individual species to habitat availability and change, even on a small geographic scale, must be approached with a high level of caution (Erwin et al. 2006). Still, application of information gained through this type of exercise may lay the structure of the adaptive framework within which conservation initiatives can be developed (Ruth et al. 2003, Williams 2003).

Restricting human alteration of tidal marsh topography through dredging and development may help limit temporally acute perturbations and habitat change, allowing species-habitat relationships to adapt over broader time scales. Also, as presented in our study, lack of an effect for DEVELOPMENT should not be interpreted to mean that there are not potential negative effects of coastal development on the majority of our focal species. Development can act alone or synergistically to affect tidal ecosystems. For example, if sea level rise predictions are borne out, then in-shore habitats will experience an increase in salinity, but coastal development may limit areas where species associated with meso and oligohaline marshes can thrive. Again, conservation initiatives that promote preservation of suitable habitat or connectivity of different marsh systems, allowing species to adapt to changing conditions, would seem to be a prudent action (Hulme 2005).

In this study, we have attempted to show potential changes in the occupancy of several species of marsh birds under several possible habitat change scenarios. But acceptance of these findings must be tempered. Studies aimed at identifying species occupancy often face resource allocation choices affecting the spatial distribution of survey effort and the number of replicate surveys that can be conducted. These trade-offs can influence the precision of occupancy estimates (MacKenzie et al. 2006). As our study was restricted to only two replicate survey events this limited number of replicate surveys may be reflected in the precision of each species-specific occupancy estimate and subsequent predictions of occupancy response to habitat change (Tables 2.2 and 2.3). Additionally, for each of our focal species, estimates of AUC indicate that models developed for only Clapper Rail and Seaside Sparrow showed good accuracy. However, for species with models indicating low accuracy, measures may be more reflective of our limited sample sizes (25% of the data) towards this assessment rather than the strength of model predictions developed using the majority of the data (Guisan et al. 2007). Our models assume marsh bird species exhibit linear responses between habitat and occupancy. However, alterations of tidal marsh habitat may not occur along linear scales (DeLuca et al. 2004, Burkett et al. 2006) and current predictions of the scale of environmental change accompany high levels of uncertainty (McFadden et al. 2007). Thus, redistribution of both habitat and the occupancy of associated fauna may not occur as directly as predicted.

Recent studies indicate the habitats and species assemblages of the tidal estuaries of the northern Gulf of Mexico will change considerably over the coming decades (Forbes and Dunton 2006, Day et al. 2008). As evidenced in our study, the potential for divergent ecological effects among species should be taken into account in planning for wetland management. Continued monitoring of multiple marsh bird species and their habitat needs is critical to furthering our understanding of their ecology and assessment of their response to future conditions within estuarine systems.

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TABLE 2.1. *A priori* candidate models explaining variation the distributions of several marsh bird species according to vegetation, marsh structure and localized anthropogenic modification. AUC is a metric of model selection optimality. Only candidate models with ΔAIC≤ 6 are shown (Richards 2008).

Species	Occupancy	Detection	AIC	ΔAIC	w_i	*AUC*
Seaside Sparrow	JUNCUS + AREA + DEVELOPMENT	OBSERVER + TIDE	225.04	0.0	0.98	0.85
Clapper Rail	JUNCUS + INTERSPERSION	OBSERVER + TIDE	364.71	0.0	0.66	0.81
	JUNCUS + INTERSPERSION + DEVELOPMENT	OBSERVER + TIDE	366.19	1.48	0.31	0.83
Least Bittern	JUNCUS	OBSERVER	330.34	0.0	0.67	0.63
	JUNCUS + INTERSPERSION	OBSERVER	331.81	1.50	0.32	0.65
Marsh Wren	JUNCUS + AREA + DEVELOPMENT	OBSERVER + TIDE	256.57	0.0	0.62	0.69
	JUNCUS + AREA	OBSERVER + TIDE	257.57	1.00	0.38	0.68
Common Yellowthroat	JUNCUS + AREA	OBSERVER	242.31	0.0	0.49	0.70
	JUNCUS + AREA + DEVELOPMENT	OBSERVER	244.1	1.79	0.20	0.69

w_i Indicates AIC weight or relative support of evidence for this model

TABLE 2.2. Naïve occupancy estimates and directional response of several marsh bird species to habitat metrics measured in tidal marshes of the northern Gulf of Mexico. Naïve estimates derived from the NULL or least parameterized model. Coefficient estimates represent non-transformed covariates.

Species	Naïve occupancy estimate mean, 95% CI	Variable	Estimated coefficient, (95% CI)
Seaside Sparrow	54%, 38 to 70%		
		Intercept	-1.42 (-2.41, 0.52)
		JUNCUS	3.41 (0.16, 6.66)
		AREA	4.84 (0.94, 8.74)
		DEVELOPMENT	-17.25 (-34.46, -0.04)
Clapper Rail	71%, 64 to 78%		
		Intercept	-7.08 (-13.53, -0.63)
		JUNCUS	8.98 (3.86, 14.1)
		INTERSPERSION	2.48 (0.72, 4.24)
Least Bittern	71%, 42 to 100%		
		Intercept	1.60 (-3.44, 6.64)
		JUNCUS	-6.72 (-11.52, -1.92)
Marsh Wren	37%, 27 to 47%		
		Intercept	-0.77 (-2.48, 0.94)
		AREA	4.65 (1.75, 7.55)
Common Yellowthroat	51%, 33 to 68%		
		Intercept	1.05 (-0.44, 2.54)
		JUNCUS	-3.22 (-6.14, 0.3)

TABLE 2.3. Predicted magnitude of change in species occupancy based on bootstrapped estimates and back-transformed to %2 . using logistic transformation. For each species' predicted directional response indicated with (+) indicating an anticipated increase in area occupied under predicted habitat change and (–) a decrease.

		Predicted change in measured habitat metrics			
		5%	10%	20%	30%
Species	Habitat characteristic (Predicted direction of change)	Predicted species response Mean change in area occupied (95% CI)			
Seaside Sparrow	JUNCUS (+)	+2% (+1 to + 2%)	+4% (+2 to 4%)	+8%, (+4 to 8%)	+11% (+5 to 12%)
	AREA (−)	−2% (−1 to −3%)	−3% (−2% to −5%)	−10% (−4% to −11%)	−14% (−7% to −16%)
	DEVELOPMENT (+)	−2% (−1 to −2%)	−4% (−1 to −4%)	−8% (−3 to −10%)	−11% (−5% to −17%)
Clapper Rail	JUNCUS (+)	+5% (+2 to 10%)	+10% (3 to 20%)	+20% (+6 to 39%)	+31% (+10 to 75%)
	INTERSPERSION (−)	−1% (0 to −5%)	−2% (0 to −9%)	−4% (0 to −17%	−6% (0 to −25%)
Least Bittern	JUNCUS (+)	−2% (0 to −8%)	−3% (0 to −17%)	−7% (0 to −33%)	−10% (0 to −46%)
Marsh Wren	AREA (−)	−2% (−1 to −5%)	−4% (−2 to −9%)	−8% (−3 to −17%)	−13% (−5 to −22%)
Common Yellowthroat	JUNCUS (+)	−1% (0 to −3%)	−2% (0 to −8%)	−5% (−1 to −12%)	−7% (−1 to −18%)

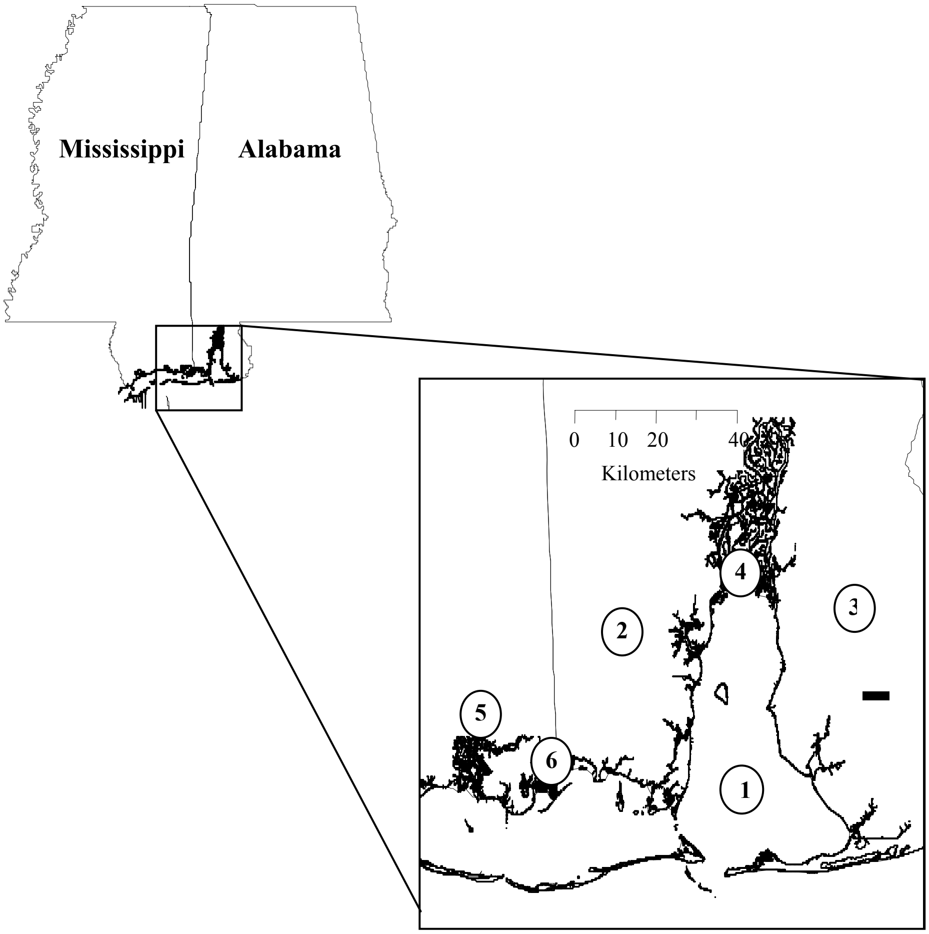

FIGURE 2.1. Study area in northern Gulf of Mexico with dominant geographic areas identified. Point 1) indicates Mobile Bay, 2) Mobile County, 3) Baldwin County, 4) Mobile-Tensaw River Delta, 5) Lower Pascagoula River Coastal Preserve, and 6) Grand Bay National Estuarine Research Reserve.

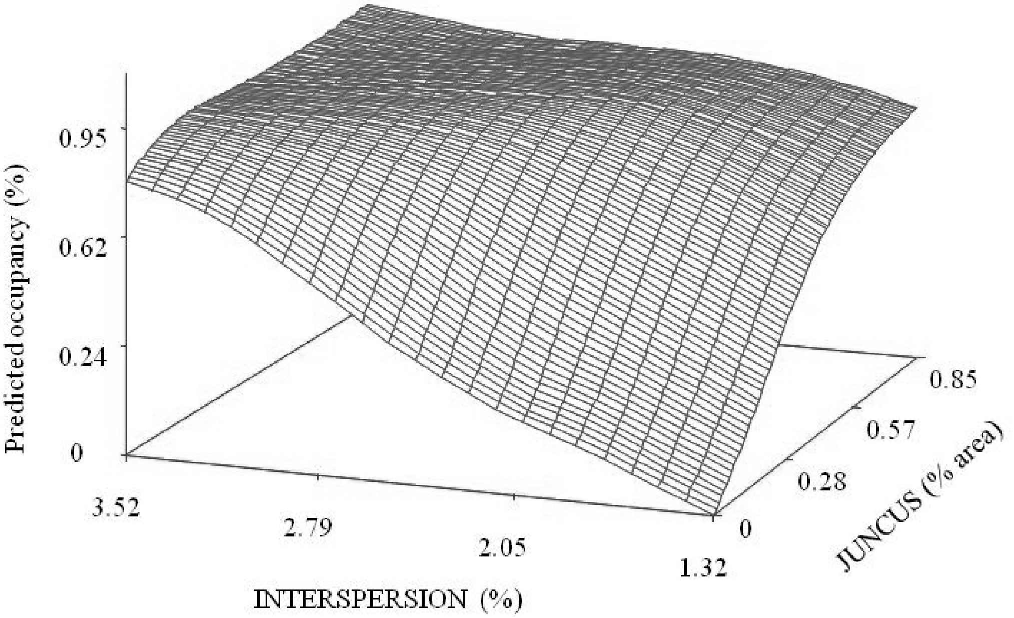

FIGURE 2.2. Predictions of Clapper Rail occupancy within tidal marshes of the northern Gulf of Mexico relative to both INTERSPERSION (edge density or a measure of the interface between vegetation and water) and JUNCUS (the proportion of cover by *Juncus roemerianus*) measured within 50 m of marsh bird survey points. Occupancy predictions were developed using logistic regression incorporating model-averaged covariates generated using Program PRESENCE.

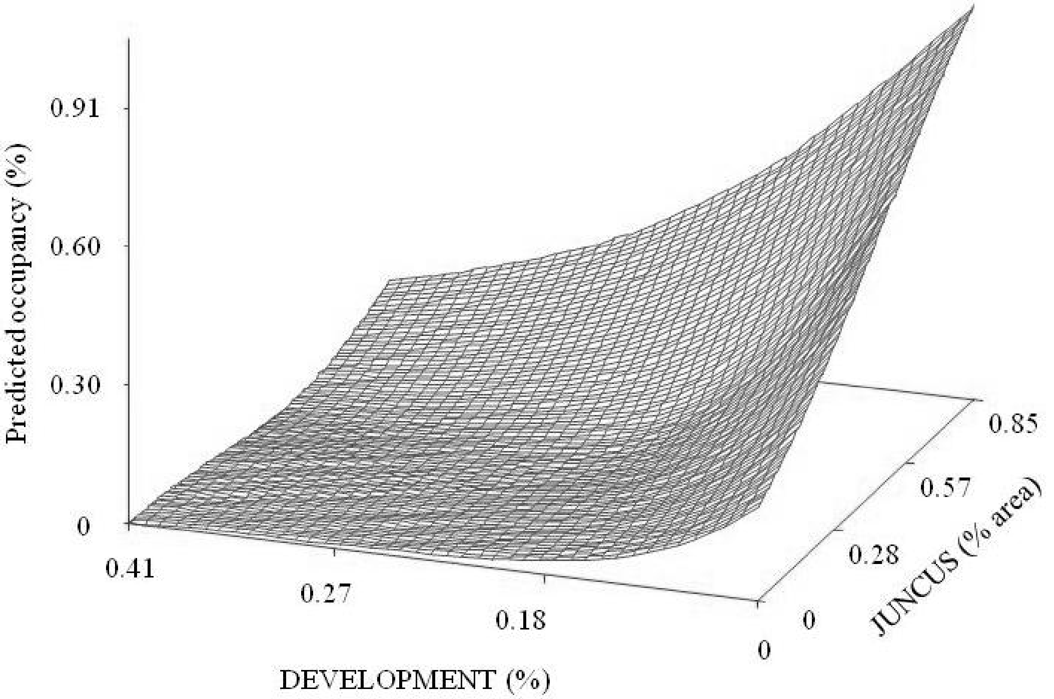

FIGURE 2.3. Predicted occupancy of Seaside Sparrows within tidal marshes of the northern Gulf of Mexico relative to DEVELOPMENT (the proportion of anthropogenic modification within 500 m of marsh bird survey points) and JUNCUS (the proportion of *Juncus roemerianus* cover measured within 50 m of survey points). Occupancy predictions were developed using logistic regression incorporating model-averaged covariates generated using Program PRESENCE.

CHAPTER 3

VARIATION IN THE NESTING HABITS OF CLAPPER RAILS IN RESPONSE TO TIDAL MARSH HABITAT[1]

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[1] Rush, S. A., M. S. Woodrey, and R. J. Cooper. To be submitted to *Condor*.

ABSTRACT

For many species of marsh bird, such as the Clapper Rail (*Rallus longirostris*), information on both demography and general life history remains limited. To document nest success and address potential habitat differences across tidal systems of the northern Gulf of Mexico we monitored 74 active nests of Clapper Rails within the Pascagoula River Marsh Coastal Preserve (a freshwater-dominated estuary) and the Grand Bay National Estuarine Research Reserve (a marine-influenced estuary) in coastal Mississippi from 2005 to 2007. We measured the height of each Clapper Rail nest and during 2006 we sampled vegetation at 40 active Clapper Rail nests and 40 random locations and measured a series of three habitat features at each location: (1) distance to nearest tidally-influenced body of water, (2) average height of vegetation, and (3) density of vegetation. Overall, Clapper Rail nests experienced relatively high daily survival rates (0.97-0.99) with the majority of nest loss apparently the result of tidal flooding. Clapper Rail nest sites were more structurally complex relative to random locations and were associated with a greater diversity of vegetation. The results of this study suggest that where structurally diverse habitat was available, Clapper Rails exhibited nest height plasticity as a mechanism to avoid nest loss from tidal flooding and that habitat alteration as a result of factors such as sea level rise may lead to lower nest success.

KEYWORDS: flooding, habitat diversity, *Juncus roemerianus*, marsh bird, nest success, nest height, *Rallus longirostris*, sea level rise.

INTRODUCTION

Tidal marshes are dynamic environments where terrestrial and oceanic ecosystems abut (Adams 1990, Pennings and Bertness 2001). This transition between sea and land results in a spectrum of abiotic and biotic forces that shape biological and physical communities (Pennings and Callaway 1992, Brewer 2003, Pennings et al. 2005a, Mitchell et al. 2006, Wang et al. 2007). For instance, the frequently flooded polyhaline (salinity >18 ppt., Cowardin et al. 1979) salt marshes of the Gulf Coast are characterized by a relatively low richness of vascular plant species as compared with the mesohaline (salinity 5-18 ppt., Cowardin et al. 1979) and oligohaline (salinity <0.5 ppt., Cowardin et al. 1979) tidal marshes that occur further inland (Eleuterius 1972, Odum 1988, Visser et al. 1998). Further, many of the organisms that inhabit these tidal marshes are uniquely adapted to persist in what can often be harsh environments (Dunson and Travis 1994, Greenberg and Maldonado 2006). Included among these organisms is the Clapper Rail (*Rallus longirostris*).

The Clapper Rail is a secretive marsh bird that inhabits coastal tidal marshes throughout the United States and Northern Mexico. Throughout much of this species' range, evidence suggests that tidal flooding is a primary factor that influences nest loss (Eddleman and Conway 1998). In response, Clapper Rails express an array of behaviors that are thought to help mitigate nest loss to tidal flooding. Nesting Clapper Rails have been shown to retrieve eggs displaced from the nest (Pettengill 1938, Kosten 1982) and eggs submerged in water can remain viable for short periods of time (Kozicky and Schmidt 1949, Oney 1954). Furthermore, evidence collected from east coast tidal marshes suggests Clapper Rails increase the height of their nests to avoid nest flooding during changing tidal conditions (Adams and Quay 1958, Storey et al. 1988). For other geographic areas, however, relationships between Clapper Rail nest success, nest height, habitat structure and diversity remain unexplored (Jackson 1983, Storey et al. 1988, Gaines et al. 2003).

To examine interactions between habitat and Clapper Rail breeding biology, we evaluated nest survival and nest site characteristics in several tidal estuaries situated within the northern Gulf of Mexico. Specifically, our objectives were to (1) describe the structure of Clapper Rail nests in two distinctly different tidal marsh systems typical of the northern Gulf Coast, (2) provide the first estimates of daily nest survival for Clapper Rails breeding along the northern Gulf of Mexico, and (3) determine if nest survival is related to habitat and if so, what mechanisms might be driving observed differences.

Along the northern Gulf of Mexico tidal height maximums increase throughout the Clapper Rail's breeding season (Stout 1984). As per Storey et al. (1988) and Eddleman and Conway (1998), we hypothesized that over the course of the breeding season Clapper Rails adjusted their nest height in response to increased tidal height. Therefore, nest success would correlate positively with date of nest initiation. Specifically, within our study system this relationship may have applied to the oligo- and mesohaline marsh of the Pascagoula where habitat diversity allows for plasticity in nest height. Conversely, for the Clapper Rails that nested within the structurally less complex habitat of the polyhaline salt marsh of Grand Bay, nest success would correlate negatively with date of nest initiation. When comparing Clapper Rail nests with randomly chosen locations, we did not expect to find a significant difference in the distance to tidal influence, a hypothesis premised on Clapper Rail's nesting in structurally complex and diverse habitat (Meanley 1985). Within Gulf Coast tidal marshes the structure and diversity of the emergent vegetation may be more spatially variable than in east coast tidal marshes (Kunza and Pennings 2008). To conceal the nest from predators and to provide sufficient support for the nest, Clapper Rails appear to choose nest sites characterized by dense cover (Storey et al. 1988). Therefore, we hypothesized that the density of cover would translate directly to stem density and that Clapper Rail nest sites will be characterized by higher stem counts than control sites.

STUDY AREA AND METHODS

STUDY AREA – During April-August 2005-2007, we located and monitored active Clapper Rail nests in the Pascagoula River Marsh Coastal Preserve (hereafter Pascagoula, 30º 25'N, 88º 34'W) and the Grand Bay National Estuarine Research Reserve (hereafter Grand Bay, 30º 20'N, 88º 24'W), both of which are located in Jackson County, Mississippi (Fig. 3.1). Emergent marsh of the oligohaline and mesohaline Pascagoula site is dominated by *Juncus roemerianus*, *Spartina alterniflora*, *S. cynosuroides* and *Sagittaria lancifolia* while the polyhaline Grand Bay site is dominated by *J. roemerianus*, with *S. alterniflora* found in narrow bands along the marsh and water interface. Both sites are influenced by irregular micro-tides (< 1 m: Dardeu et al. 1992), experience warm vernal climates with a mean summer temperature of 27˚C and average monthly summer precipitation of 16 cm. Following the definition of Cowardin et al. (1979), the Pascagoula is truly estuarine, subject to heightened tides and fluctuations in river flow (Eleuterius 1972), but the polyhaline tidal marsh system of Grand Bay receives oceanic input and is not directly associated with riverine discharge.

NEST SEARCHING AND CLASSIFICATION. – During 2005 to 2007 we located Clapper Rail nests by systematically searching locations on foot where adults had been heard calling (Adams and Quay 1958). We attempted to allocate equal portions of time to searching along the marsh edge and through the marsh interior. Search patterns often incorporated multiple searchers walking in parallel and were most often structured along linear transects running both parallel and perpendicular to the shoreline. When a nest was discovered we recorded its location (using a handheld GPS unit: Trimble GeoXT, Trimble Navigation Limited) and aged all eggs using methods outlined in Rush et al. (2007). We focused our searches for active nests only. Our decision to focus only on active nests was made for several reasons. Firstly, Clapper Rails may build nests that are not used during the incubation period (Eddleman and Conway 1998, Gaines et al. 2003). Therefore, inference based on, or incorporating these inactive nests may not provide appropriate metrics of reproductive ecology. Additionally, in the absence of observing the construction of a nest, or if the eggs in a nest had not been aged, then it was not possible to determine when the nest was built. Once located, attempts were made to check the status of each nest (active/inactive) every 2-3 days until the nest was deemed to have produced at least one chick (assessed by observation) or the eggs and/or nest was destroyed. When a nest was found destroyed we determined whether nest loss was due to depredation or flooding.

NEST PLACEMENT − During 2006 we recorded the following measurements for each nest: (1) height (cm) of the nest platform above the marsh surface, measured from the nest rim to the ground, (2) height (cm) of vegetation within 10 cm of the nest, averaged from one measurement collected from each cardinal direction, (3) distance (m) to nearest tidal influence (tidal creek or tidal pool), and (4) the number of stems of each species of vegetation within a 0.25 m^2 frame placed over each nest. We defined a tidal creek as a body of water that floods and drains with tidal fluxes and forms a connection between the marsh and open water through which sediment, nutrients and fauna are exchanged (Dardeau et al. 1991, Gaines et al. 2003). Similarly, we defined a tidal pool as an area that floods during high tide but may be isolated during low tides (Gaines et al. 2003). We chose a 0.25 m^2 frame because it is approximately 12% larger than the average diameter of Clapper Rail nests in this study (mean diameter: 552, SE: 42.1 cm^2). To quantify stem counts the sampling frame was placed over the nest and positioned downward to ground level. To expose all stems, after positioning the sampling frame and before conducting stem counts, we removed all tidal wrack or nest material from the frame. Stems were then repositioned to ensure that all stems within the sampling frame were counted and the total number of stems was tallied by species. Additionally, we selected a random location within 50 m of each nest site to characterize areas not used for nesting by Clapper Rails. Random locations were chosen using a random numbers table to select a compass bearing and distance ≤ 50 m from the paired nest site. We selected the 50 m cutoff in order to minimize the effects of the differences in habitat structure that can occur over large spatial scales, particularly in freshwater-dominated estuaries (Moore 1992, Bertness and Pennings 2000). A radius of 50 m centered on each nest site also equates to the core use area of Clapper Rails within these systems (S. A. Rush unpubl. data). At each random location we measured the average vegetation height (cm), distance (m) to the nearest tidally influenced body of water, and total stem count by species within the 0.25 m^2 sampling quadrat.

MODEL COVARIATES − We applied statistical analyses to compare habitat measurements collected at Clapper Rail nests with measurements collected from random sites and to contrast Clapper Rail nest site habitat characteristics between our two study areas. In the coastal salt marshes of the northern Gulf Coast the presence of *J. roemerianus* has been shown to correlate negatively with the presence of *S. alterniflora* (Pennings et al. 2005b). In response, and to avoid multicollinearity, we used total stem count only in our analysis.

STRUCTURE OF NESTING HABITAT − To statistically compare habitat metrics collected from Clapper Rail nests and control sites we developed a series of logistic regression models (PROC GENMOD, SAS Institute, Cary, North Carolina). For each model the dependent variable was whether habitat measurements were obtained from a nest (coded as '1') or a control site (coded as '0'). Habitat measurements were also contrasted by study site. The beta diversity of vegetation at nest and control locations was calculated for each study area using Whittaker's formula (Whittaker 1972).

For both study sites we assessed the strength of relationships between nest height, tidal height and date of nest initiation. We calculated the probable date the nest was initiated based on the estimated age of the nest when first discovered (Rush et al. 2007). Linear models were used to evaluate nest height relative to the estimated date of nest initiation (PROC GLM, SAS Institute, Cary, North Carolina), where tidal height was regressed against Julian date (PROC GLM, SAS Institute, Cary, North Carolina). Daily tidal maximums were obtained from a monitoring station located within each of our study systems (NOAA 2004, NOAA 2008). Due to limitations in data availability, for the

Pascagoula we supplemented available measurements with tidal predictions (NOAA 2008).

MODELING DAILY NEST SURVIVAL – In order to compare the nest success of Clapper Rails between our two study sites we pooled data for 2005 to 2008 (51 nests for the Pascagoula site and 23 nests for Grand Bay site) and used Nest Survival models Program MARK (White and Burnham 1999) to estimate nest success. This procedure allowed us to model nest success as a binomial process based on encounter histories developed for each nest. Each encounter history was coded with five pieces of information: 1) date nest was discovered, 2) last day the nest was known to be active, 3) last day a nest was checked, 4) fate of the nest, and 5) number of nests that shared the same encounter history. We calculated the number of days in each encounter history relative to the earliest date that a nest was discovered. Within Program MARK we constructed models using the design matrix tools and the logit-link function.

ASSESSING MODEL FIT − When modeling, a typical initial step involves testing the fit of the most saturated model (i.e., the model containing all explanatory variables and interactions of interest) by calculating the variance inflation factor ($\hat{c}$) and then adjusting for any lack of fit. For nest survival models however these adjustments are not possible because the models are saturated and $\hat{c}$ cannot be identified (Dinsmore et al. 2002). So, only when modeling Clapper Rail nesting habitat did we develop the most saturated model and test for model fit. To create the most parsimonious models we developed and examined combinations of independent variables based on covariates included in our *a priori* hypotheses. To evaluate nest success we generated a list of 5 candidate statistical models. This list included a model with no factors (NULL model) and a model that contained all factors. We followed a similar approach for the analysis of nest habitat, in turn generating 6 candidate models. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Akaike 1974, Burnham and Anderson 2002) to compare models based on log-likelihood values (Burnham and Anderson 2002) and estimated model fit based on values of AIC_c, the number of parameters (*K*), and the deviance (Dev). Models were ranked and compared using ΔAIC_c and AIC_c weights, where ΔAIC_c estimates the relative difference between the top ranked model and each other model, and AIC_c weights measure the weight in favor of a model given the data. Models with $\Delta AIC_c \leq 2$ were considered to fit the data equally well. However, if two models differed by only one predictor variable then we based model selection on model deviance with the better-supported model as that with the lower deviance. Parameter estimates were weighted by the Akaike weight of the associated model and we calculated unconditional variance estimates to account for uncertainty in model selection. For each parameter we report 95% confidence intervals based on the unconditional variances. Estimated predictors were considered significant if the associated confidence interval did not contain zero.

RESULTS

Over the 3 years of this study we located and monitored the fate of 76 Clapper Rail nests (54 nests from the Pascagoula site and 22 nests from Grand Bay site). For these nests, the average clutch size was 7.84 (95% CI: 7.3 – 8.4) eggs. Generally, the probability of nest loss was low with only 10 nests lost at the Pascagoula site and 5 nests lost at the Grand Bay site. Of these, 42% at the Pascagoula appeared to be the result of flooding, compared with 75% of the nest loss at Grand Bay. During 2006 Clapper Rail nest height increased over the breeding season at the Pascagoula (nest height (cm) = 36.13 + 0.36 [SE = 0.03]*JULIAN) but not at Grand Bay (Fig. 3.2).

Our results provide evidence that Clapper Rails nested within structurally and floristically diverse habitat whereas the beta diversity of vegetation was higher among nest sites than control points (Pascagoula: 0.93 vs. 0.54 and 0.75 vs. 0.22, Grand Bay, respectively). Among models used to compare the physical attributes of nest habitat and control points, the most saturated model was found to be the best supported (Model 1, Table 3.1: ($\hat{c}$ = 1.04). Habitat metrics suggest that Clapper Rail nests were located in taller vegetation and that stem counts were higher among nest locations than paired control sites (Table 3.2). However, estimates did not indicate that Clapper Rail nests were located closer to tidally influenced waterways than paired control locations (Table 3.2).

The best-supported model of Clapper Rail nest success did not include site-specific differences (Table 3.3: Model 1). However, this model and a model with nest success varying by site and date of nest initiation received similar levels of support (Table 3.3, Model 2). The model that included the interaction of date and site received 2.4 times more support than the model that considered site alone (Table 3.3, Model 2). Model averaged parameter estimates indicate Clapper Rails experienced similar mean daily nest survival at both study sites (Pascagoula: 0.99 ± 0.01, Grand Bay: 0.98 ± 0.01, Table3. 4). A positive relationship was apparent between Clapper Rail nest success and the date of nest initiation at the Pascagoula, but confidence intervals suggest this relationship was ambiguous for Grand Bay (Table 3.4).

DISCUSSION

Similar to studies conducted along the Atlantic and Pacific Coasts of the United States (Eddleman and Conway 1998), we found that Clapper Rails nesting on the northern Gulf Coast experience a relatively high rate of nest success, which may translate to high reproductive productivity. Given an average daily nest success of 98.5% (95% CI: 97.5% to 99%), a typical incubation period of 24 days (Rush et al. 2007), and an average clutch size of 7.84 eggs, the data suggest productivity of approximately 4 to 7 young per nest attempt.

The results of our study and those of others (Storey et al. 1988, Gaines et al. 2003) provide evidence that Clapper Rails nest in structurally diverse habitat when it is available. Clapper Rails are found in tidal marshes throughout much of North America (Eddleman and Conway 1998), yet within these systems habitat features can often vary across relatively small spatial scales (Eleuterius 1972, Odum 1988, Adams 1990, Bertness and Pennings 2000, Pennings and Bertness 2001). Here we compared the structure and diversity of habitat used by nesting Clapper Rails within two contrasting tidal systems of the northern Gulf Coast. Paralleling the observations of Eleuterius (1972), we found greater diversity of vegetation at the Pascagoula site than at Grand Bay. Although the vegetation at Clapper Rail nest sites had higher plant species diversity than paired control sites, the lower diversity and structure of the nesting habitat at Grand Bay is suggestive that Clapper Rails nesting within similar polyhaline tidal marshes of the northern Gulf Coast Grand Bay may experience a tradeoff between plasticity of nest height to avoid flooding and maintenance of an adequate level of cover to conceal the nest (Storey et al. 1988, Gaines et al. 2003). For Clapper Rails nesting at Grand Bay, we anticipated that as tidal height increased over the breeding season restrictions in the diversity of nesting habitat could translate into higher levels of nest loss from either flooding or from predation (Reinert 2006). However, we did not find a significant directional relationship to support this hypothesis. However, while overall nest loss at Grand Bay was low, our small sample size may have restricted the statistical power to assess relationships such as directional effects between nest loss and date of nest initiation. Continued and expanded monitoring of the breeding ecology of Clapper Rails may help to further elucidate relationships between Clapper Rail nest success and habitat across an array of tidal systems.

Narrow, shallow-bottomed estuaries such as the Pascagoula generally experience higher tidal amplitudes relative to the broader, low-lying topography of marine-dominated estuaries such as Grand Bay (Odum 1988). Clapper Rails and other marsh birds that nest within freshwater-dominated estuarine systems may be able to minimize nest loss by raising the height of their nest above flood levels (Greenberg et al. 2006, Reinert 2006). However, within marine-influenced estuarine systems, which often lack structural diversity, these species likely face compromises in nest placement mediating nest loss due to flooding and predation (Erwin et al. 2006, Greenberg et al. 2006). The rate of sea level rise is predicted to increase over the next century (Overpeck et al. 2006), altering the hydrologic and salinity regimes of coastal wetlands (Day et al. 2000a, 2000b, Spalding and Hester 2007). Within oligo and mesohaline estuaries such as the Pascagoula, increased salinity may lead to reduced plant species diversity, and consequently reduced habitat diversity and structure (Dardeu et al. 1992, Pennings and Bertness 2001). Continued high spring tides within polyhaline marsh systems, such as the

Grand Bay estuary, suggest that throughout their range Clapper Rails and other marsh-nesting birds will face higher levels of nest loss due to flooding, and thus could serve as a primary indicator of climate change effects in coastal tidal marsh systems (Reinert et al. 2006, Takekawa et al. 2006, Wilson et al. 2007).

Previous studies have provided limited information on relationships between Clapper Rail nest success and habitat (Eddleman and Conway 1998), and to date we know of no other study that has provided estimates of Clapper Rail nest success along North America's Gulf Coast. Thus, our research provides the first detailed study of the relationship between nest habitat and Clapper Rail nest success along the northern Gulf Coast. As our study suggests, Clapper Rails may face estuary-specific pressures that can mediate nest success. Despite the apparently high levels of nest success, fledgling Clapper Rails may face high levels of mortality (Duhsé 1988) that ultimately influence population structure. Additional research focused on the Clapper Rail's reproductive ecology and post-fledgling period are needed to evaluate the potential impacts of sea level rise and habitat alteration on this species. Similar research focused on other marsh bird species is strongly encouraged. Only by broadening our understanding of the potential impacts of sea-level rise and habitat change will we be able to begin to develop a proactive, effective conservation strategy for marsh birds and the tidal marshes of the northern Gulf of Mexico.

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TABLE 3.1. Candidate models to explain habitat variation between Clapper Rail nest sites and control sites at two study sites in coastal Mississippi. Models are ranked by second order Akaike's Information Criterion (AIC$_c$). Also included are model weight (w_i), and the number of estimable parameters (K).

Model number	Model	AIC$_c$	ΔAIC$_c$	w_i	K	Deviance
1	SITE[c] + HEIGHT[d] + DISTANCE[a] + TOTAL[b] + SITE * HEIGHT	100.13	0	0.86	8	82.12
2	DISTANCE	104.64	4.51	0.09	2	100.52
3	TOTAL	107.99	7.86	0.02	2	103.86
4	SITE + HEIGHT + TOTAL + SITE * HEIGHT[e]	108.01	7.88	0.02	7	92.48
5	SITE + HEIGHT + SITE * HEIGHT	108.19	8.06	0.02	6	95.08
6	NULL[e]	110.17	10.04	0.00	1	108.14

[a] Distance to closest tidally-influenced water (measured in m)

[b] Total stem count of vegetation within 0.25m^2

[c] Study site comparison

[d] Height of vegetation above marsh surface

[e] Intercept only model, no covariates

TABLE 3.2. Metrics describing habitat differences between Clapper Rail nests and random control points.

			Habitat measurements (mean, 95% CI)	
Model covariate	Study site	*n*	nests	Control
HEIGHT	Pascagoula	25	141.19, 137.92 to 144.46	123.52, 107.92 to 139.12
	Grand Bay	15	91.64, 79.57 to 103.71	70.85, 57.52 to 84.18
TOTAL	Pascagoula	25	269.92, 216.65 to 323.19	180.4, 141.31 to 219.49
	Grand Bay	15	243.57, 192.62 to 294.52	145.2, 85.42 to 204.98
DISTANCE	Pascagoula	25	5.85, 1.35 to 10.35	12.92, 8.86 to 16.98
	Grand Bay	15	22.27, 16.78 to 27.76	22.43, 16.53 to 28.33

HEIGHT the height of vegetation above the marsh surface (cm)

TOTAL stem count of vegetation within $0.25m^2$

DISTANCE the distance to closest tidally-influenced water (m)

TABLE 3.3. Candidate models to explain Clapper Rail nest success at two study sites in coastal Mississippi. Models are ranked by second order Akaike's Information Criterion (AIC_c). Also included are model weight (w_i), and the number of estimable parameters (K).

Model number	Model	AIC_c	ΔAIC_c	w_i	K	Deviance
1	NULL[a]	117.41	0	0.43	1	115.415
2	SITE[b] + JULIAN[c] + SITE * JULIAN	117.54	0.13	0.40	4	109.50
3	SITE	119.32	1.91	0.16	2	115.30
4	SITE + JULIAN	126. 96	9.55	0.01	3	120.93
5	JULIAN	127.89	10.48	0.01	2	123.88

[a] Intercept only model, no covariates

[b] Study site comparison

[c] Julian date

TABLE 3.4. Number of Clapper Rail nests monitored (*n*), mean daily nest survival rates (Nest survival) and covariate estimates for the effect of date of nest initiation on nest success (Effect of nest initiation) for Clapper Rails nesting at two study sites in coastal Mississippi. For nest success and date of nest initiation numbers represent mean, 95% confidence interval. Nest initiation date indicates Julian date with 1 Apr denoting day 1.

Parameter	Study Site	
	Grand Bay	Pascagoula
n	22	54
Nest survival	0.98, 0.96 to 0.99	0.99, 0.98 to 1.00
Effect of nest initiation date	0.0004, -0.01 to 0.01	0.01, 0.05 x 10^2 to 0.02

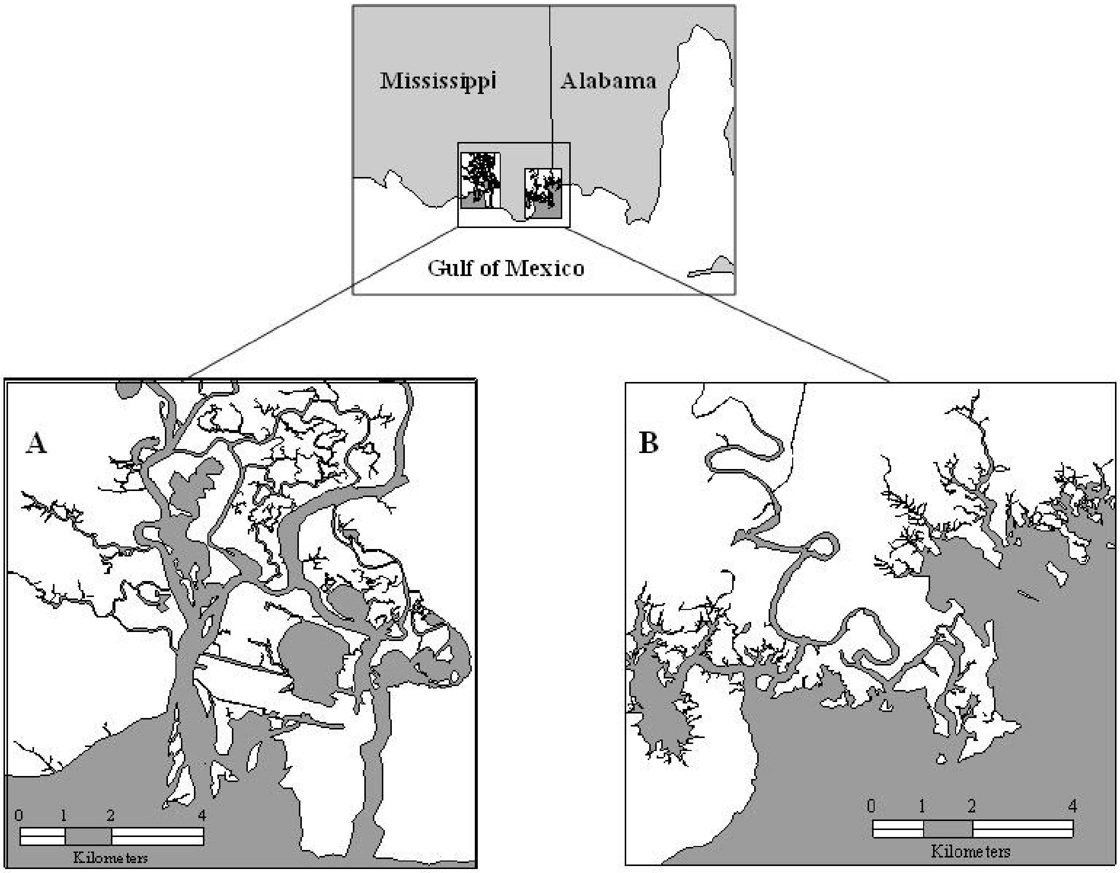

FIGURE 3.1. Location of study area in coastal Mississippi: A) Pascagoula River Marsh Coastal Preserve (Pascagoula) and B) the Grand Bay NERR (Grand Bay).

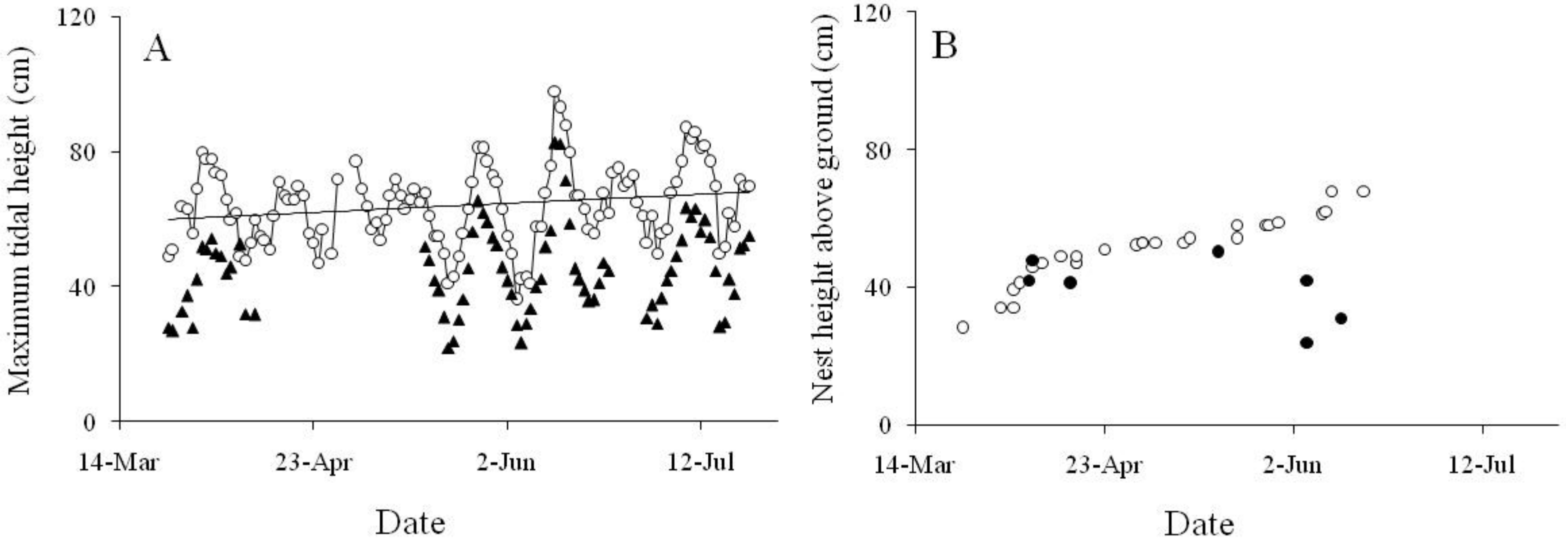

FIGURE 3.2. Height of Clapper Rail nests relative to tidal height in two estuaries in coastal Mississippi: Panel A denotes tidal height relative to mean low water (MLW). Circles represent tidal height data collected at Grand Bay (NOAA 2004) while triangles represent tidal height data collected at the Pascagoula River (NOAA 2008, Station Number: 8741533). In some instances tidal data were limited for the Pascagoula (denoted by black bars indicating predicted tidal maximums above MLW: NOAA 2006). The solid black line represents a linear model fit to data from Grand Bay illustrating an increase in mean tidal maximums by date: (Tidal maximum) = 59.86 + 0.07*(Julian date), $F_{1,114} = 4.86$, $P = 0.03$, where 24 March 2006 was considered as Julian date 1. Panel B shows height of Clapper Rail nests at Grand Bay (solid circles) and at the Pascagoula (open circles) relative to the date of nest initiation.

CHAPTER 4

CLAPPER RAIL DIET COMPOSITION AND EGG RESOURCES VARY ACROSS TWO HYDROLOGICALLY DYNAMIC ESTUARINE ECOSYSTEMS[1]

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[1] Rush, S. A., J. A. Olin, A. T. Fisk, M. S. Woodrey and R. J. Cooper. To be submitted to *Oecologia*.

ABSTRACT

Much of North America's tidal marsh habitat has been significantly altered by both natural and man-made processes. Thus, there is a need to understand the trophic ecology of organisms endemic to these ecosystems. We applied carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis, along with isotope mixing models, to egg yolk, liver and muscle tissues of clapper rails (*Rallus longirostris*) and their likely prey items to explore variation in trophic niche and diet composition in this important marsh bird in two northern Gulf of Mexico tidal marshes that are river (Pascagoula) and ocean (Grand Bay) dominated. Stable isotope values of, and mixing model results for, muscle, liver and egg yolk showed a tighter association to fiddler crabs (*Uca longisignalis*), a wider trophic niche and significant dependence on grasshoppers in the river-dominated estuary. Clapper rails from the ocean-dominated estuary had a narrower trophic niche width and appeared to be utilizing marine resources, particularly, based on modeling of liver stable isotope values. Variation in stable isotope values between egg yolk and liver/muscle in both systems suggests that endogenous resources are important for egg production in clapper rails. Gulf fiddler crabs provided the majority of resources for egg production in clapper rails in the river-dominated estuary but may be less important to egg production in rails from the ocean-associated estuary. These results demonstrate that diet composition, prey source and niche-width of clapper rails can vary significantly across different estuaries and appear to be influenced by hydrological conditions.

KEYWORDS: carbon, C3 plant, C4 plant, egg, fiddler crab, liver, mixing model, muscle, nitrogen, northern Gulf of Mexico, stable isotope analysis, *Uca longisignalis*.

INTRODUCTION

Evidence collected from the southern United States' tidal marshes suggests that drought, sea level rise, and nutrient loading have already altered many biological interactions in these complex ecosystems (Visser et al. 2002, McKee et al. 2004, Silliman et al. 2005, Livingston 2007). Tidal estuaries are unique environments where a distinct array of physical and chemical properties can vary over relatively short time periods (Dardeau et al. 1992) and small distances (Mannino and Montagna 1997). Predicting the response of estuarine ecosystems to changing environmental conditions is therefore challenging, as it necessitates understanding interactions among several trophic levels and multiple nutrient sources (marine, freshwater and terrestrial) (Boesch and Turner 1984, Costanza et al. 1990, Day et al. 1993, McFadden et al. 2007, Moody and Aronson 2007). Because they are relatively well studied, birds have been used to measure ecological conditions and evaluate the impacts of environmental change within tidal estuaries (Shriver et al. 2004, DeLuca et al. 2004, DeLuca et al. 2008).

An often cited rationale for the use of birds as ecosystem indicators is that most species occupy a relatively high trophic position; environmental conditions that affect basal productivity and physio-chemical process can therefore affect marsh bird distributions from the "bottom up" (Novak et al. 2005, DeLuca et al. 2008). However, for some of these species information on diet composition remains largely ancillary (based on gut content analysis, and cast pellets), a situation particularly true for the Clapper Rail (*Rallus longirostris*). Despite limited understanding of the Clapper Rail's diet, this species has been suggested as an indicator of tidal marsh ecosystem integrity (Novak et al. 2005) for example, as bioindicators of contaminant dynamics through food webs

(Rodriguez-Navarro et al. 2006, Cumbee et al. 2008). And although studies focused on analysis of stomach contents have identified fiddler crabs (genus *Uca*) as the Clapper Rail's principle prey item within northern Gulf of Mexico estuaries (Heard 1982a, citations in Eddleman and Conway 1998), gut content analysis tends to be biased towards foods that are harder to digest, such as crab carapaces (Sarda and Valladares 1990). Further, the analysis of gut contents provides only a snapshot of the diet of the consumer at the time it was collected. To overcome these shortcomings, stable isotope analyses can provide additional validation to gut content analysis and a more robust evaluation of diet and trophic niche (Mariano-Jelicich et al. 2008).

Stable isotope analyses have proven to be a powerful tool for the study of avian trophic relationships in coastal ecosystems (Michener and Schell 1994, Evans Ogden et al. 2005, Inger and Bearhop 2008). This approach is based on the principle that the ratios of heavier to lighter isotopes, expressed for carbon as ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), depend on 1) the isotopic composition of its food resources, and 2) isotopic fractionation during food assimilation (DeNiro and Epstein 1978, 1981). For carbon, there appears to be little (i.e., approx. 1%) or no change in $\delta^{13}C$ between trophic levels (Hobson and Welch 1992). Carbon isotopes have therefore been applied as indicators of primary production in studies of food webs (DeNiro and Epstein 1981, Peterson and Fry 1987, Post 2002). Specifically with reference to temperate estuarine systems, marine organic matter and carbon from plants that use the C_4 photosynthetic process are enriched in ^{13}C ($\delta^{13}C$ marine: -18 to -22‰, C_4 plants: -6 to -19‰) relative to carbon sourced from C_3 plants and terrestrial sources, which are typically more depleted ($\delta^{13}C$ of C3 plants: -23 to -30‰), (Smith and Epstein 1971, Sullivan and Moncreiff 1990, Créach et al. 1997, Winemiller et al. 2007). For nitrogen, a $\delta^{15}N$ enrichment of 2-4% between producers and consumers appears typical (Peterson and Howarth 1987, Michener and Schell 1994, Hobson et al. 2002). Thus, a shift in $\delta^{15}N$ between a consumer and its food provides an approximate indication of trophic level (Post 2002). Also, animal tissues are synthesized and replaced at different rates, and the isotopic composition generally reflects the diet of the animal at the time the tissues were synthesized (Haramis et al. 2001, Rubenstein and Hobson 2004, Hobson et al. 2005). Therefore, by selecting several tissues with varying replacement rates researchers can gain insight into the animal's diet and variation in diet that can occur over different time scales (Inger and Bearhop 2008). For instance, the composition of avian eggs and livers are typically reflective of recent contributions to the bird's diet while tissues such as muscle can provide information reflecting slightly longer periods of time, averaging several weeks to months (Hobson and Clark 1992a, Rubenstein and Hobson 2004).

To identify the relative importance of fiddler crabs, to Clapper Rails we analyzed $\delta^{13}C$ and $\delta^{15}N$, and used stable isotope mixing models in Clapper Rails and potential prey items collected from two tidal marshes in northern Gulf of Mexico. By analyzing liver, muscle and egg yolks of the Clapper Rails, we could assess temporal aspects of diet selection and determine the origin of resources used for egg production. Finally, because the two systems we examined varied in the hydrologic characteristics (river versus ocean dominated), we could assess the influence of important environmental variables on feeding and egg production in Clapper Rails.

STUDY AREA AND METHODS

STUDY AREA − Our study area consisted of two estuarine systems in Jackson County, Mississippi, USA: Pascagoula River Marsh Coastal Preserve (hereafter Pascagoula, 30º 25'N, 88º 34'W) and the Grand Bay National Estuarine Research Reserve (hereafter Grand Bay, 30º 20'N, 88º 24'W) (Fig. 4.1). The emergent marsh of the oligohaline and mesohaline Pascagoula is dominated by *Juncus roemerianus*, *Spartina alterniflora* and *S. cynosuroides* while the polyhaline Grand Bay is dominated by *J. roemerianus*, with *S. alterniflora* found in narrow bands along the marsh and water interface. Both estuaries were influenced by irregular tides of small amplitude (<1 m Dardeu et al. 1992), a warm subtropical climate with mean summer temperature of 27˚ C, and average monthly summer precipitation of 16 cm. Within each estuary, hydrographic conditions and salinity are primarily influenced by precipitation, tidal flux and prevailing winds, patterns that are usually relatively stable during the summer when weather conditions are less variable. The Pascagoula site was subject to heightened tides and fluctuations in river flow (Eleuterius 1972), but the polyhaline tidal marsh system of Grand Bay received oceanic input and was not directly associated with riverine discharge.

SAMPLING – Within both estuaries and during Jan to Aug 2006, we collected pectoral muscle, liver and egg yolk samples from Clapper Rails (see Table 4.1 for sample sizes). All samples were placed in ice in the field and stored frozen upon return to the laboratory. Only a single egg was removed from any nest, and collections were approximately equal along the marsh edge and through the marsh interior. Concurrent with egg collections, and based on trophic evidence provided in Eddleman and Conway

(1998), we collected samples of dominant food items along with samples of the culms of dominant vegetation (Table 4.1). Prey items were obtained from within a 50 m radius circle surrounding each nest location, a distance based on the mean home range of birds within these systems (S. Rush unpubl. data), and keyed to species (Heard 1982b). Additionally, the percent aerial cover of dominant vegetation types within 50 m of each nest site was estimated visually (methods described in Conway 2008). Prey items included the gastropods (*Neretina usnea* and *Littorina irrorata*), bivalves (*Geukensia demissa* and *Rangia cuneata*; Bishop and Hackney 1987, LaSalle and de la Cruz 1985), tettigoniid grasshoppers (Parsons and de la Cruz (1980), the blue crab (*Callinectes sapidus*) and the gulf fiddler crab (*Uca longisignalis*; Mouton and Felder 1996). All materials were placed in individual plastic bags and frozen within several hours of collection.

STABLE ISOTOPE ANALYSIS – Clapper Rail tissues and prey items were freeze-dried and subsamples of soft tissues were used for isotope analysis. Exoskeleton or other calciferous tissues were avoided as these may bias ratios of carbon isotopes (Currin et al. 1995). In most cases multiple representatives of each prey item were obtained from each nest site. In this case, all samples of the same species were homogenized to obtain a single sample reflecting that prey source at that nest site. Lipids were extracted from all samples using a 2:1 ratio of Chloroform / Methanol (Bligh and Dyer 1959). Supernatant and solids were poured through glass filter paper (Whatman Ashless Filter Paper, Whatman International Ltd., Kent, UK) to separate the supernatant and weighed to determine lipid contents.

Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were measured using a Delta Plus isotope-ratio mass spectrometer (ThermoFinnigan, San Jose, CA, USA) coupled with an elemental analyzer (Costech, Valencia, CA, USA, analytical precision ± 0.15‰). Stable isotope ratios are expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation: $\delta^{13}C$, $\delta^{15}N = [R_{smpl}/R_{strd} - 1] X 10^3$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. Pee Dee Belemnite and atmospheric nitrogen were used as the isotope standards of carbon and nitrogen respectively. The analytical precision (standard deviation) for $\delta^{15}N$ was 0.14 and for $\delta^{13}C$ was 0.05 based on analysis of NIST standards sucrose ($n = 13$) and ammonium sulphate ($n = 13$) run during the analysis of the samples for this study.

Several metrics were used to explore relationships between diet and habitat. Eggs from each of the two populations were graphed in the $\delta^{13}C$−$\delta^{15}N$ niche space and niche width was measured independently for each population. The measure of niche breadth that we employed was based on the total area of convex hull (TA) measured against a subset of individuals from each population (Cornwell et al. 2006). The TA encompasses the smallest convex polygon bounding this sub-set of individuals in the $\delta^{13}C$ and $\delta^{15}N$ niche space and is a measure of niche width, reflecting variation along both the $\delta^{13}C$ and $\delta^{15}N$ niche dimensions (Layman et al. 2007). Convex hull areas were calculated using *chplot* (Vidmar and Pohar 2005) implemented in the statistical package R (Version 2.7.1: R Development Core Team 2008). Linear relationships (*glm* in R) between the $\delta^{13}C$ of Clapper Rail egg yolks and the proportion of C_3 plants within 50 m of each nest site were used as an additional metric to evaluate relationships between Clapper Rail diet and habitat.

The proportional contribution of each prey item to the Clapper Rail’s diet was evaluated using mixing models run in the programs Isosource and MixSIR (Inger and Bearhop 2008), computational programs that can provide estimates of the relative contributions of diet sources to an organism (Phillips and Gregg 2003, Moore and Semmens 2008). For all modeled contributions we assumed the isotopic discrimination factors reported by Hobson et al. (1995) and Hobson and Clark (1992b; δ^{13}C: -0.1 ± 0.5‰ for egg yolk, 0.3 ± 0.4‰ for muscle and -0.4 ± 1.0‰ for liver; and δ^{15}N: 3.1 ± 0.4‰ for egg yolk, 1.4 ± 0.1‰ for muscle and 2.7 ± 0.1‰ for liver). Isosource calculates feasible combinations (in 1% increments) of primary producer isotope signatures, δ^{13}C and δ^{15}N, that explain observed consumer isotope signatures. All combinations of food-source contributions summing to 100% were examined in increments of 1%. IsoSource outputs are presented as a range of all feasible solutions indicating the minimum and maximum contributions for each food source that were consistent with isotope mass balance (Urton and Hobson 2005, Inger et al. 2006). MixSIR uses a Bayesian framework, designed to estimate the probability distributions of source contributions to a mixture, while explicitly accounting for uncertainty with multiple sources, fractionation, and isotope signatures. Using uninformative priors and estimates of uncertainty associated with mixing model inputs, each MixSIR model ran for 10×10^6 iterations, resulting in convergence on the posterior source contributions of the different prey items of the diet of the Clapper Rail. The maximum importance ratio was below 0.001, suggesting that our models were effective in estimating the true posterior density (Moore and Semmens 2008). IsoSource outputs are reported here as median and 1-99th percentile range of solutions (Benstead et al. 2006), and only stable isotope data for samples collected and presented in this paper were used. Results of the MixSIR models are presented as median and the 5th and 95th credibility intervals. For all other analyses and unless otherwise specified, parameter estimates are presented as means and 95% confidence intervals.

RESULTS

Values of $\delta^{13}C$ showed a continuum from enriched values in C_4 grasses (*Spartina sp.*) to depleted values in C_3 grasses (Table 4.1). In general, $\delta^{13}C$ values were depleted in prey species and Clapper Rail egg yolk from the Pascagoula site compare to Grand Bay; exceptions were the muscle and liver values of the Clapper Rails. Nitrogen stable isotope values were generally enriched in the Pascagoula system compared with Grand Bay (Table 4.1); exceptions were again the muscle and liver values of the Clapper Rails. As expected, $\delta^{15}N$ was lowest in the primary producers, the salt marsh grasses, increased in invertebrates, and were highest in the muscle and liver of the Clapper Rails (Table 4.1; Fig. 4.2). All other prey organisms examined exhibited $\delta^{13}C$ values between, and $\delta^{15}N$ values greater, than those of the C_3 and C_4 plants (Fig. 4.2). The ranges of both $\delta^{13}C$ and $\delta^{15}N$ were larger among Clapper Rail egg yolks collected at the Pascagoula than from Grand Bay (Fig. 4.3). The total area of the convex hull (TA) was over 3 times larger for the Pascagoula (98.84) than Grand Bay (30.96), indicating Clapper Rails had a wider trophic niche within the Pascagoula estuary (Fig. 4.3). Mirroring primary production, the $\delta^{13}C$ of Clapper Rail egg yolks collected from the Pascagoula indicated a strong negative relationship relative to the proportion of C_3 plants within 50 m of each nest site, although this relationship was not observed in the Grand Bay egg yolks (Pascagoula: $\beta = -0.10$, SE = 0.02, Grand Bay: $\beta = 0.27$, SE = 0.24: Fig. 4.4).

Stable isotope mixing models, Isosource and MixSIR, revealed that the contribution of each prey source to the Clapper Rail varied among estuaries and tissues, and for certain tissues and sites between the two mixing models. Model estimates of diet composition of the Clapper Rail egg yolks and pectoralis muscles from the Pascagoula identified that the gulf fiddler crab comprised the vast majority of the Clapper Rails' diet (Isosource estimate: 37 to 74%, MixSIR estimate 57 to 87%: Table 4.2). In contrast, estimates derived for Grand Bay were much more variable. Isosource models developed for Grand Bay indicated that the source contribution of gulf fiddler crabs to Clapper Rail egg yolk ranged from 0 to 39%. Isosource models for the muscle did not converge. Estimates derived from MixSIR models showed that the source contribution of gulf fiddler crabs to Clapper Rail egg yolk and pectoral muscle from the Pascagoula ranged from 57 to 87% with a similar contribution at Grand Bay (56 to 99%), (Table 4.2). Models focused on the isotopic ratios measured in Clapper Rail livers revealed strong contrasts among estuaries. MixSIR models developed for the Pascagoula suggested a source contribution of fiddler crabs of 60 to 79%, while at Grand Bay the contribution of gulf fiddler crabs was estimated to have been relatively negligible (0.1 to 7%, Table 4.2).

DISCUSSION

The results of our isotopic analyses provide evidence that the diet of Clapper Rails differed between estuaries and across time scales. Supporting earlier evaluations based largely on stomach content analysis (citations in Eddleman and Conway 1998), our mixing models results indicated that fiddler crabs comprised the dominant prey item of Clapper Rails breeding within these estuaries. For the Pascagoula, the river-associated estuary, $\delta^{13}C$ and $\delta^{15}N$ of egg yolks, liver and pectoral muscle samples provided evidence that Clapper Rails maintain a similar diet during both the winter and the breeding season (Table 4.2). Although egg yolk and pectoral muscle results from Grand Bay, an ocean-dominated estuary, indicated a dominance of the gulf fiddler crab in the Clapper Rail's diet, evidence from liver samples suggests greater seasonal variation in this species' diet selection, variation that could not be explained by differences in fiddler crab stable isotope values. Taken together, the carbon and nitrogen estimates from the eggs and livers suggest that during the summer the diet of Clapper Rails at the Pascagoula was influenced by C_3 primary productivity, but during the winter, marine contributions were less influential to the Clapper Rail's diet (Table 4.1). As an additional indication of the trophic link between C_3 primary productivity and the Clapper Rail's diet, our results indicated that at the Pascagoula the $\delta^{13}C$ of Clapper Rail egg yolks related negatively with the aerial cover of C_3 macrophytes within 50 m of each nest site. Countering the Pascagoula, the diet of Clapper Rails at Grand Bay appeared to have strongly mirrored marine sources during the summer but shifted to a C_3-based trophic pathway during the winter (Table 4.1, Fig. 4.4).

The Pascagoula and Grand Bay estuaries are physiographically distinct systems and some of these characteristics may explain differences in the isotopic ratios measured in the livers of Clapper Rails. Within the southeastern United States, the magnitude of nutrient input entering into estuarine systems depends strongly on riverine discharge and therefore can vary seasonally (Dardeu et al. 1992). Owing to lower tidal levels and an increase in northerly winds, marsh surfaces experience greater exposure during the winter months (Day 1973, Hackney and de la Cruz 1982, Stout 1984). Paralleling seasonal precipitation and tidal differences, greater nutrient loading occurs during January through

May (Odum et al. 1979). Estuaries strongly influenced by hydrologic conditions may reflect this seasonal difference in their basal productivity, a chemical signal notable in higher trophic levels (Eldridge and Cifuentes 2000, Kaldy et al. 2005, Sierszen et al. 2006). Further, Grand Bay is largely characterized by *J. roemerianus*, while habitats of the Pascagoula reflect a mix of *S. cynosuroides* and *J. roemerianus*. The biomass of fungal decomposers and edaphic algae was found to be highest on *J. roemerianus* during the fall and winter months, a relationship that is contrary to similar primary productivity on *S. alterniflora* (Sullivan and Moncreiff 1988, Newell 2001). Therefore, a seasonal shift of consumer tissue isotope ratios to a more depleted state may reflect this seasonal source of basal productivity. Although we did not sample all sources of primary productivity within each estuary, Sullivan and Moncreif (1990) reported a $\delta^{13}C$ of -21‰ for edaphic algae sampled from an estuary geographically proximate to our study area. Although this ratio is below that identified for Clapper Rail tissues collected at Grand Bay, the isotopic difference between eggs produced during the summer, and liver and muscle tissues developed during the winter, may indicate a combination of increased terrestrial input and a shift in source primary productivity within this estuary.

Despite these differences, carbon and nitrogen stable isotope values indicated several similarities between the two estuarine systems examined. Although the $\delta^{13}C$ of the C_3 plant *J. roemerianus* was depleted in C^{13}, and samples collected from the Pascagoula were slightly more so than those from Grand Bay (Table 4.1), all were within the range (-23 to -30‰) reported for C_3 terrestrial plants (Smith and Epstein 1971). Carbon isotope ratios of the marine bivalves (*G. demissa* and *Rangia* sp.) were relatively depleted within both estuaries, providing evidence that C_3 plants, or marine carbon sources, constituted a greater contribution of the diets of these species (Table 4.1). Evidence indicates that tettigoniid grasshoppers preferentially fed on C_4 plants but also included some C_3 plants in their diets, reflected in the lighter isotopic ratio (Parsons and de la Cruz 1980; Table 1). Unlike grasshoppers, periwinkle snails do not directly consume large quantities of plant material (Silliman and Bertness 2002). Rather, these snails graze predominately on fungus and the senescent materials of *S. alterniflora* (Silliman and Zieman 2001). Subsequently, their $\delta^{13}C$ often incorporates signatures of both sources (Kemp et al. 1990, Currin et al. 1995). However, our $\delta^{15}N$ results indicate that the periwinkles' diet may have varied between the Pascagoula and Grand Bay. The $\delta^{15}N$ of periwinkles collected from the Pascagoula indicated a greater consumption of *Spartina* than at Grand Bay. Increased nitrogen concentrations can positively influence the consumption of *Spartina* by periwinkles and higher nitrogen concentrations, originating from terrestrially-derived sources, may explain the greater proportion of *Spartina* in the diet of periwinkles within the Pascagoula estuary (Silliman and Zieman 2001). The $\delta^{13}C$ of blue crabs varied considerably among samples from the Pascagoula, reflecting the habitat heterogeneity within this estuary (Table 4.1), (Bucci et al. 2007). Deposit-feeding fiddler crabs ingest vascular plant detritus, bacteria and algae, and like blue crabs, their isotopic signature can also reflect dominant habitat types (Montague 1980, Dye and Lasiak 1986). For instance, Sullivan and Moncreif (1990) noted that the isotopically depleted $\delta^{13}C$ of fiddler crabs reflected the dominance of *J. roemerianus* within a Mississippi tidal system. Despite the reflection of habitat in the $\delta^{13}C$ of these tidal marsh consumers, dominant habitat types may not imply optimal trophic conditions (Levin et al. 2006, Whitcraft and Levin 2007). The detritus of dominant macrophytes can vary in nutritional quality and may not be efficiently used by consumers (Haines and Hanson 1979, Enriquez et al. 1993, Kreeger and Newell 2000, Gratton and Denno 2003). Limited availability of alternative nutrient sources can lead to trophically depauperate ecosystems, although biogeochemical processes such as nutrient cycling and hydrology can help maintain trophic complexity within these tidal marsh ecosystems (Kreeger and Newell 2000, Valiela et al. 2004, Zheng et al. 2004, McKellar et al. 2007). Here, nitrogen has proven to be a key nutrient structuring these ecosystems (McFarlin et al. 2008).

Because salt marshes can receive large inputs of terrestrial nitrogen sources, estuarine nitrogen pools can vary over relatively small spatial and temporal scales (Cifuentes et al. 1988, Hoffman and Bronk 2006, McFarlin et al. 2008). These divergent nutrient pools can provide an explanation for variation in δ^{15}N observed within trophic levels (Créach et al. 1997). Within the context of our study we found a significant level of variation in the δ^{15}N values of the three trophic levels identified within each estuary. Along with aforementioned differences in source nutrient pools, this variation can be reflective of several physiological and chemical processes. For instance, nitrogen isotope ratios can change through fractionation processes during the decomposition of detritus and primary production, source dietary materials, the tissue sampled and the physical condition of the organism (Robbins et al. 2005, Kempster et al. 2007). In general, the Clapper Rail’s egg yolks and liver tissue should reflect the elemental composition of materials assimilated over a relatively short time period, which can range from several days to several weeks (Hobson 1995, Hobson and Clark 1992a, Hobson et al. 2000). In contrast, isotopic turnover rates in muscle tissue can take longer and reflect a diet ingested several weeks to several months previous (Hobson and Clark 1992a).

The physiochemical properties experienced within estuarine systems can affect the richness and abundance of estuarine organisms and the ecology of consumers (Valiela et al. 1997, Duffy et al. 2005). The lower tidal amplitudes and greater plant species diversity experienced within fresh and brackish marshes generally support a more diverse assemblage of consumer organisms (Moore 1992). This diverse assemblage creates a broad and complex food web within these ecosystems (Odum 1988, Moore 1992, Odum et al. 1995). Our results indicated that Clapper Rails breeding within the riverine Pascagoula estuary experienced a wider trophic niche than counterparts at the marine-dominated Grand Bay (Fig. 4.3). This difference was primarily evident as a reduction in the diversity of basal resources supporting the food web reflected by the reduction in the $\delta^{13}C$ measured in the Clapper Rail eggs (Fig. 4.2). Maintenance of heterogeneous energy pathways can act to stabilize food webs and consumer populations (Kreeger and Newell 2000, Rooney et al. 2006). Communities structured around species-poor food webs may be more vulnerable to habitat change (Borrvall et al. 2001, Jonsson et al. 2006). This variation can extend non-linearly to other trophic levels (Bruno and O'Connor 2005). Such structuring from the 'bottom-up' has direct implications for estuarine communities that include species such as the Clapper Rail (DeLuca et al. 2008).

Tidal marsh communities face continued pressures such as habitat alteration (Greenberg et al. 2006). Understanding the impacts of these changes on organisms such as the Clapper Rail necessitates a better understanding of the ecological interactions between these organisms and their environment. Efforts to better understand interactions such as trophic ecology will not only enhance predictions of their response to environmental change but also strengthen their application as metrics of tidal marsh integrity.

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TABLE 4.1. Stable isotope ratios of Clapper Rail tissues and prey items, mean (95% CI). *n* denotes number of nest sites sampled in each estuary.

		Pascagoula			Grand Bay	
Species / Tissue	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$
Clapper Rail						
Egg yolk	28	-21.05	9.32	8	-18.58	8.95
		(-23.27 to -19.17)	(7.69 to 10.94)		(-20.46 to -16.69)	(7.51 to 10.39)
Liver	5	-18.84	7.17	6	-24.80	10.28
		(-21.13 to -16.55)	(6.48 to 7.85)		(-26.8 to -22.8)	(8.66 to 11.91)
Pectoral muscle	5	-19.41	8.62	8	-23.30	9.79
		(-23.47 to -15.36)	(7.97 to 9.27)		(-24.35 to -21.59)	(8.33 to 11.71)
Spartina sp.	18	-13.31	4.84	3	-13.81	3.21
		(-13.67 to -12.96)	(3.63 to 6.06)		(-14.22 to -13.4)	(0.72 to 5.7)
J. roemerianus	23	-27.34	4.61	7	-25.33	2.53
		(-27.97 to -26.71)	(2.93 to 6.30)		(-26.32 to -24.33)	(2.21 to 4.22)

olive nerite	22	-20.88	7.37	0		
		(-21.87 to -19.89)	(6.86 to 7.87)		—	—
marsh periwinkle	8	-20.0	6.49	8	-15.6	3.84
		(-21.84 to -18.81)	(5.88 to 7.11)		(-17.28 to -13.93)	(3.38 to 4.29)
ribbed mussel	2	-26.0	6.21	8	-22.63	6.71
		(-27.19 to -24.83)	(5.79 to 6.63)		(-24.08 to -21.17)	(5.5 to 7.92)
common rangia	14	-26.29	7.19	1		
		(-27.41 to -25.17)	(6.62 to 7.75)		-27.42	6.79
tettigoniid grasshoppers	10	-19.04	6.42	3	-17.81	5.6
		(-21.1 to -16.98)	(5.4 to 7.44)		(-19.57 to -16.05)	(5.41 to 5.78)
blue crab	3	-22.74	6.28	3	-15.25	5.58
		(-27.48 to -18.0)	(4.79 to 7.76)		(-17.01 to -13.49)	(5.41 to 5.76)
gulf fiddler crab	14	-20.73	4.96	8	-21.22	5.9
		(-21.25 to -20.21)	(4.57 to 5.35)		(-23.27 to -19.17)	(3.93 to 7.86)

TABLE 4.2. Proportion of prey items contributing to carbon and nitrogen stable isotopes signatures in different tissues of Clapper Rails using Isosource (mean; minimum and maximum) and MixSIR (50%; 5−95%). Modeling results for Clapper Rails and prey species collected from the Pascagoula and Grand Bay in 2006. *dnc* denotes that the model did not converge.

Estuary	Tissue	Model /Prey	*gulf fiddler crab*	*olive nerite*	*marsh periwinkle*	*ribbed mussel*	tettigoniid grasshoppers	*blue crab*	*common rangia*
Pascagoula	Yolk	Isosource	61.9 (55 – 73)	2.8 (0 – 17)	9.1 (0 – 42)	1.1 (0 – 8)	21.8 (0 – 38)	2.5 (0 – 16)	0.8 (0 – 6)
		MixSIR	79 (70 – 87)	3 (0.2 – 11)	3 (0.2 – 11)	1.7 (0.1 – 6.4)	3.9 (0.3 – 14)	2.5 (0.2 – 10)	1.8 (0.1 – 6.7)
	Liver	Isosource	*dnc*	*dnc*	*dnc*	*dnc*	*dnc*	*dnc*	*dnc*
		MixSIR	69 (60 – 79)	3.7 (0 – 13.8)	4.3 (0 – 15.6)	3.2 (0 – 11.8)	4.8 (0 – 18.2)	4.1 (0 – 16.3)	2.9 (0 – 11.3)
	Muscle	Isosource	47 (37 – 74)	3.7 (0 – 13)	11.8 (0 – 58)	1.5 (0 – 11)	31.4 (0 – 61)	3.3 (0 – 22)	1.1 (0 – 9)
		MixSIR	67 (57 – 77)	3.7 (0 – 15.1)	4.2 (0 – 15.5)	3.3 (0 – 12.4)	4.9 (0 – 19.4)	4.6 (0 – 19.4)	3.3 (0 – 12.7)

Grand Bay	Yolk	Isosource	10 (0 – 39)	—	3 (0 – 12)	17 (0 – 42)	16 (0 – 63)	46 (15 – 70)	8 (0 – 26)
		MixSIR	64 (56 – 73)	—	7.2 (0.5 – 28)	0.8 (0.1 – 3.3)	1.8 (0.1 – 7.7)	22 (2.6 – 36)	0.5 (0 – 2.2)
	Liver	Isosource	*dnc*	—	*dnc*	*dnc*	*dnc*	*dnc*	*dnc*
		MixSIR	1.6 (0.1 – 7)	—	1.3 (0.1 – 5.3)	84 (71 – 93)	1.7 (0.1 – 7.3)	1.4 (0.1 – 5.5)	7.4 (0.7 – 21)
	Muscle	Isosource	*dnc*	—	*dnc*	*dnc*	*dnc*	*dnc*	*dnc*
		MixSIR	95 (88 – 99)	—	0.3 (0.1 – 0.6)	0.3 (0.1 – 1.4)	0.2 (0 – 1)	1.5 (0 – 6.0)	1.5 (0.3 – 11)

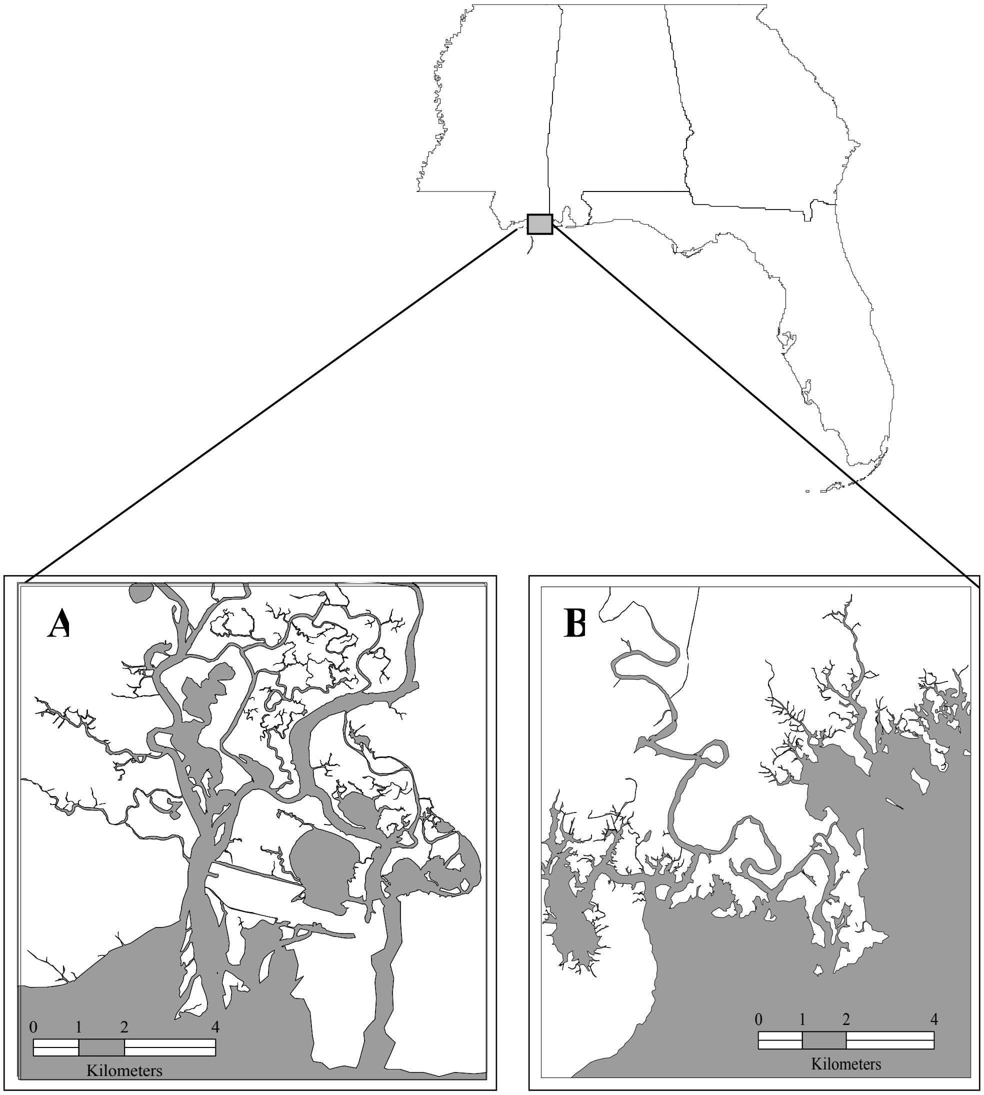

FIGURE 4.1.Study locations within Jackson County, Mississippi. Panel A shows the river-dominated Pascagoula Marsh Coastal Preserve (Pascagoula) and panel B is the Grand Bay National Estuarine Research Reserve (Grand Bay).

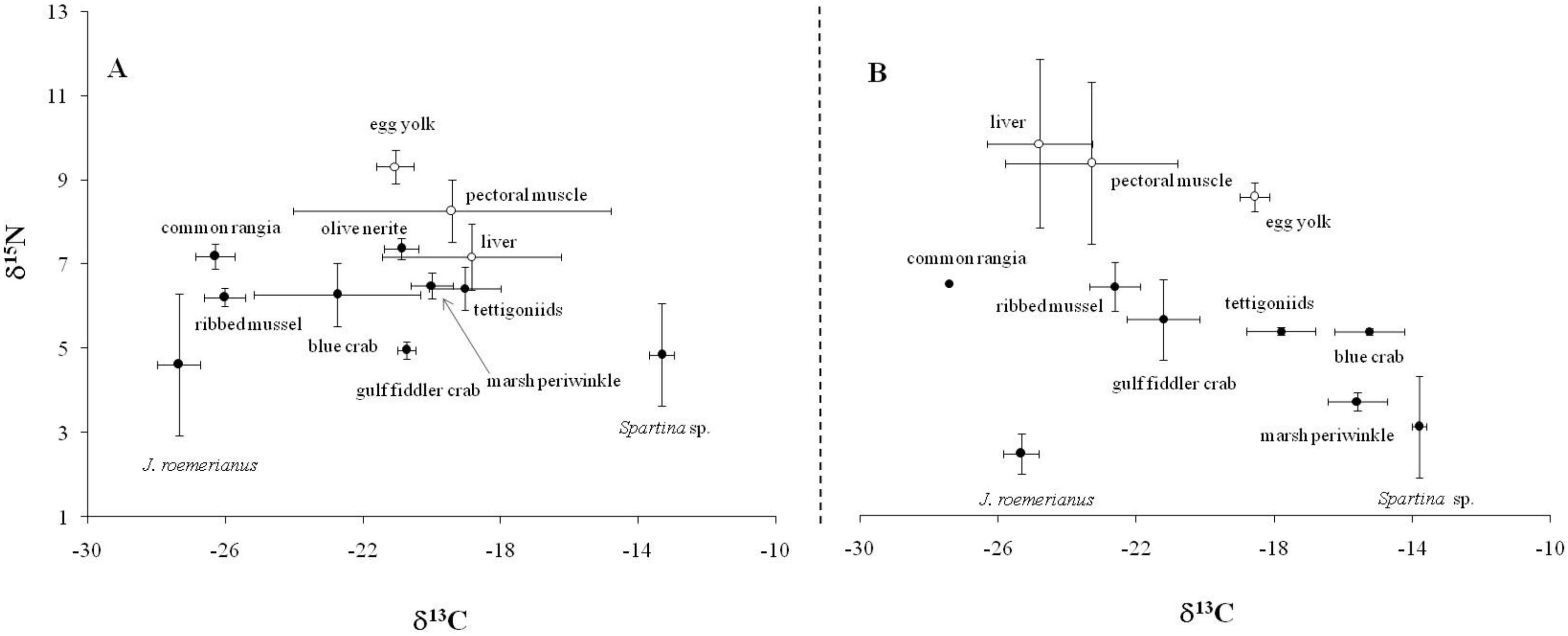

FIGURE 4.2. δ^{13}C and δ^{15}N values of Clapper Rail egg yolks and anticipated diet components in two northern Gulf of Mexico tidal marshes. Panel A represents the Pascagoula and B Grand Bay. Error bars reflect mean ± 1 SD. Open circles represent Clapper Rail tissues and filled circles, potential prey items. Potential assimilation of carbon sources by consumers is indicated by the degree of alignment among taxa relative to the x-axis while trophic level is reflected in the position on the y-axis.

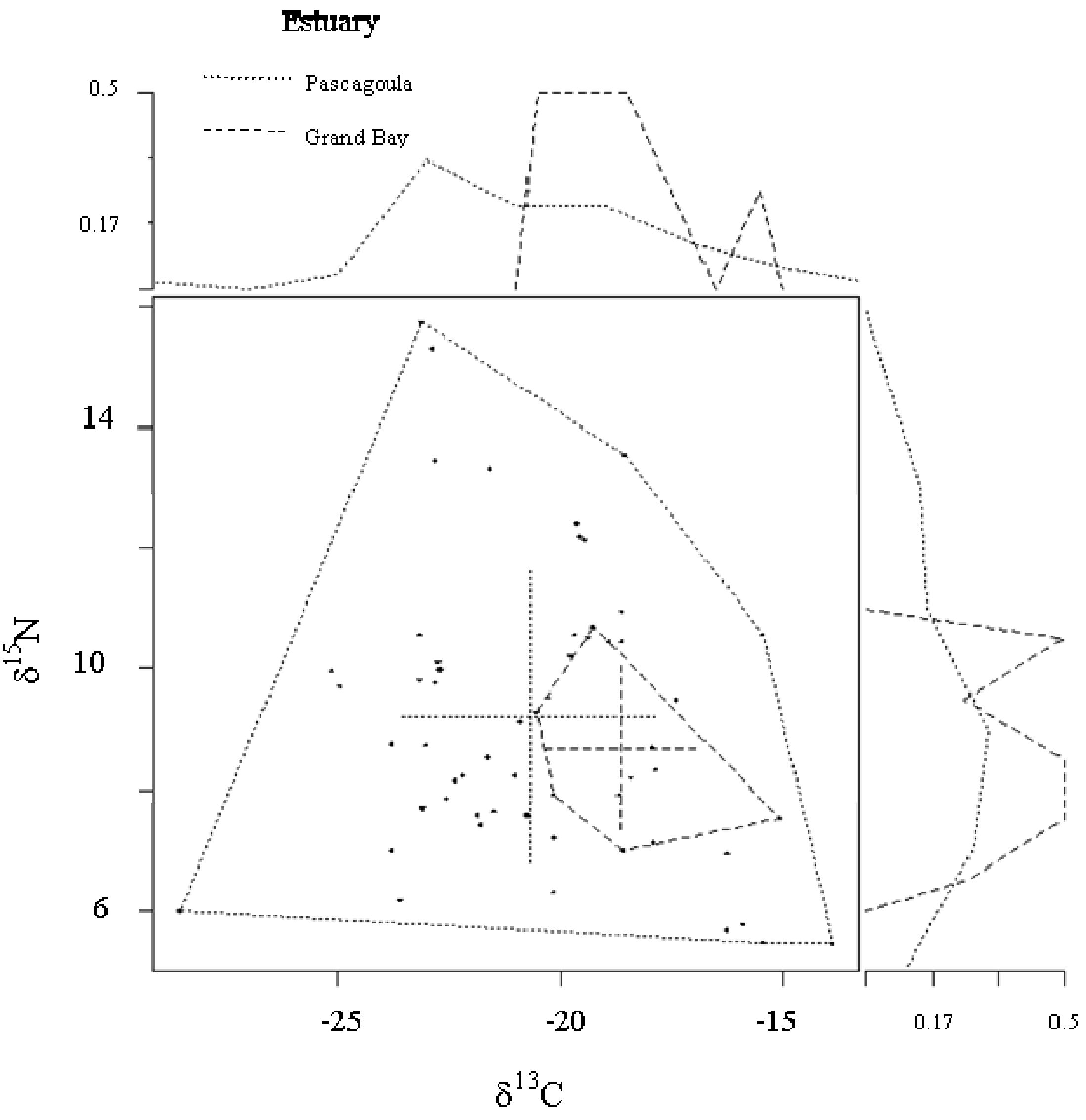

FIGURE 4.3. Convex hull plot depicting Clapper Rail trophic niche in two northern Gulf of Mexico estuaries. Inner plot represents trophic niche based on carbon and nitrogen isotope ratios measured in egg yolks (black circles) during 2006 with polygons representing 95% confidence intervals. Symbols in the outer plot represent marginal densities reflecting trophic niche probability mass.

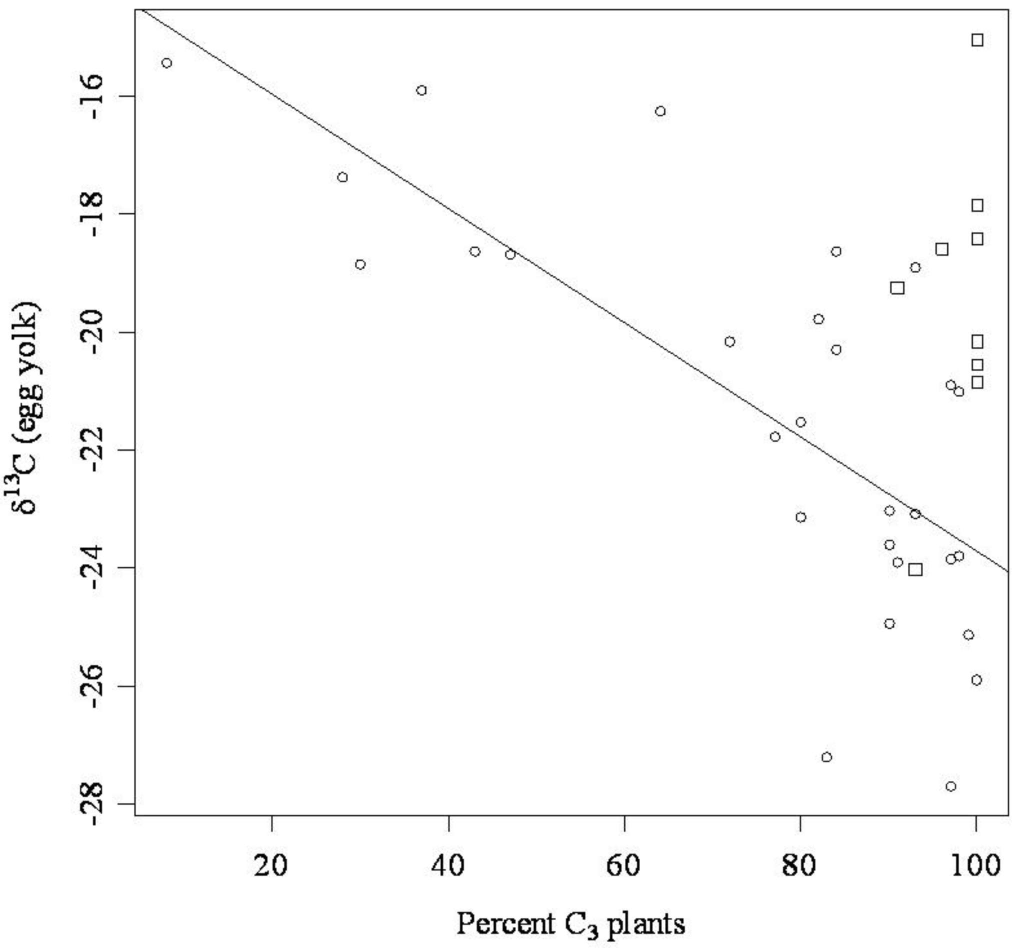

FIGURE 4.4. Relationship between the $\delta^{13}C$ of Clapper Rail egg yolks relative to percent aerial coverage of C_3 plants within 50 m of Clapper Rail nests. Circles denote measurements obtained from Clapper Rail nests at the Pascagoula and squares represent nests at Grand Bay. Fitted line indicates relationship for Pascagoula.

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CHAPTER 5

IMPACTS OF FOOD AND PREDATORS ON CLAPPER RAIL MOVEMENTS IN COASTAL MISSISSIPPI, USA[1]

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[1] Rush, S. A., R. Mordecai, M. S. Woodrey, and R. J. Cooper. To be submitted to *Waterbirds*.

ABSTRACT

One explanation for the declines of some marsh bird species is the loss and modification of tidal marsh habitat. This may be particularly true for the northern Gulf of Mexico where the geographic scale of tidal marsh habitat continues to be altered from its historic extent. For many of the marsh birds that inhabit these tidal ecosystems little information exists on habitat use, particularly in relation to movement and response to prey availability. In this study we used radio-telemetry to investigate home range size, movement patterns and response of Clapper Rails (*Rallus longirostris*) to prey availability within tidal marshes in coastal Mississippi. Mean fixed kernel 95% home range for breeding Clapper Rails was 1.56 ha ± SE 0.55 with a 50% core use area 0.19 ha ± SE 0.17, which are estimates similar to those obtained throughout this species' range. The extent of Clapper Rail movements was negatively correlated with density of fiddler crab burrows. We found Clapper Rails' use of marsh edge decreased relative to tidal height but use of this habitat type may be restricted during the first few weeks of the parental-care period when adults are caring for recently fledged young. Collectively these results illustrate the importance of edge and interior marsh habitats and may provide an explanation for the variation in Clapper Rail densities found within and between tidal marsh systems.

KEYWORDS: core area, edge, fiddler crab, home range, parental care, tide.

INTRODUCTION

For many marsh bird species, little data exist relating daily and seasonal movements to habitat use. Despite this limitation, evidence suggests that many of these species may be experiencing significant population declines, which could be due to fewer individuals within available habitat (Tate 1986, Eddleman et al. 1988, Conway et al. 1994), habitat loss (Conway and Droege 2006, Greenberg et al. 2006), or both. For these species, the development of effective conservation plans necessitates the collection and application of information relating habitat use and availability and population demographics (Conway et al. 1994, Conway 2006, Conway and Droege 2006). This relationship could be particularly relevant for the marsh birds that inhabit tidal marshes along the northern Gulf of Mexico, where the loss of tidal marsh habitat continues at a relatively high rate (Eddleman et al. 1988, Day et al. 2000, McFadden et al. 2007).

Research on the breeding biology of one species of marsh bird, the Clapper Rail (*Rallus longirostris*), has focused on nesting habitat, reproductive success, movement, and diet (Eddleman et al. 1988, Eddleman and Conway 1998). Although this research has been formative in guiding our current understanding of marsh bird ecology significant gaps remain in our knowledge of many basic concepts such as habitat use and the underlying forces that influence the distributions of this secretive marsh bird (Eddleman and Conway 1998). Specifically lacking is information on Clapper Rail home range and movement during the breeding season, including relationships between movements and prey availability, and habitat use during the post-fledging period (Eddleman and Conway 1998).

Gut content analysis and observational evidence suggest that within tidal marshes of the northern Gulf of Mexico Clapper Rails feed on an array of different animal and plant materials, with fiddler crabs (*Uca spp.*) being a primary food item both in volume consumed and occurrence in stomach contents (Roth 1972, Heard 1982, Eddleman and Conway 1998, S. Rush unpubl. data). As fiddler crabs are the primary prey for Clapper Rails along the northern Gulf Coast of Mexico, models of optimal foraging and territory size predict that the density of prey and their availability to a predator should be important factors influencing the predator's home-range and movement patterns (McNab 1963, Schoener 1968, Schoener 1983, Jenkins 1981, Mace and Harvey 1983, Newton 1998). We hypothesized that the size of a Clapper Rail's home range will be negatively correlated with the relative abundance of fiddler crabs within the tidal marshes of the northern Gulf of Mexico. However, we know of no studies that have addressed relationships between Clapper Rail movements and fiddler crab availability.

Within tidal marshes edge habitat has been identified as a habitat critical for fostering diversity and faunal development (Levin and Talley 2000, Minello et al. 2004). For many species the structural diversity inherent to edges may provide protection from predation pressure and a pathway for energy flow between abutting habitats (Eddleman and Conway 1998, Peterson et al. 2000, Bologna and Heck 2002 Gaines et al. 2003,). Clapper Rail chicks are altricial and leave the nest within 48 hours of hatching. While adult Clapper Rails remain with their young for the first few weeks post-fledging, the young are subject to predation pressure (Eddleman and Conway 1998). Because Clapper Rail chicks are highly mobile and difficult to monitor, little is known about their movements and habitat use during the post-fledging period. Although relationships between the age of fledgling Clapper Rails and marsh edge remain relatively unexplored (Meanley 1969), evidence suggests that fledglings of the Clapper Rail's freshwater congener the King Rail (*Rallus elegans*), associate with marsh edge (Meanley 1969). The relationship between King Rail young and marsh edge may provide some insight into the behavior of Clapper Rail young during their early development. However, contrasts among the ecosystems occupied by these two species, and varying threats to the future of those ecosystems (Turner 1997, Mulholland et al. 1998), raises the question of whether information obtained for one species can be extrapolated to the other.

Within tidal marsh systems tidal wrack - deposits of material washed ashore during storm events - may form linear boundaries of higher elevation along shorelines and edges of emergent marsh (Tolley and Christian 1999). The higher elevations of these wrack deposits may serve Clapper Rail adults and young as refugia during periods of high tide and or escape from predators (Eddleman and Conway 1997). Whether use of marsh edge and wrack deposits provides evidence that supports these structures as critical components of Clapper Rail habitat needs further study. Specifically, does use of marsh edge depend on fledgling age, and is the proximity of the adult relative to the edge of the emergent vegetation influenced by tidal height (Meanley 1969)?

In an effort to better understand the ecology and habitat use of Clapper Rails within tidal marshes along the northern Gulf Coast of Mexico, we used radio-telemetry to track individual Clapper Rails to examine aspects of their breeding biology that have not been studied in detail. Specifically, our objectives were to (1) estimate home range size and assess movement patterns during the breeding season, (2) examine the relationship between fiddler crab density and Clapper Rail home range size, and (3) relate movements of adults during the post-fledging period to fiddler crab density, fledgling age and tidal cycle.

STUDY AREA AND METHODS

STUDY AREA – Our study area comprised two estuarine systems in coastal Jackson County, Mississippi, USA: 1) the Pascagoula River Marsh Coastal Preserve (hereafter Pascagoula, 30º 25'N, 88º 34'W) and 2) the Grand Bay National Estuarine Research Reserve (hereafter Grand Bay, 30º 20'N, 88º 24'W) (Fig. 5.1). The oligohaline to mesohaline emergent marsh of the Pascagoula is dominated by *Juncus roemerianus*, *Spartina alterniflora*, *S. cynosuroides* and *Sagittaria lancifolia*, while the polyhaline Grand Bay site is dominated by *J. roemerianus*, with *S. alterniflora* found in narrow fringes along the water interface. Both estuaries experience irregular mico-tides (<1 m: Dardeu et al. 1992), warm vernal climates with mean summer temperature of 27˚ C, and average monthly summer precipitation of 16 cm. By the definition of Cowardin et al. (1979), the Pascagoula is considered truly estuarine, subject to heightened tides and fluctuations in river flow (Eleuterius 1972), while the polyhaline tidal marsh of Grand Bay receives oceanic input and is not directly associated with riverine discharge.

During May to July 2006 and 2007 we captured Clapper Rails in mist nets placed at nests**.** During 2006 we trapped 10 Clapper Rails (2 birds at Grand Bay and 8 birds on the Pascagoula) and during 2007 we trapped 12 Clapper Rails (4 birds at Grand Bay, 8 birds on the Pascagoula). All birds were radio-marked (see below) and released at trap sites. To date, estimates of Clapper Rail home range have not addressed the potential for differential movement between sexes. Since a reliable method to morphologically sex Clapper Rails does not exist (Eddleman and Conway 1998), we collected a small amount of blood (ca. 0.2 ml) from each bird captured during 2007 so that individuals could be sexed chromosomally following the methods of Griffiths et al. (1998). Blood was collected from the leg vein using a 1-ml syringe and stored in absolute ethanol (0.5ml), at room temperature prior to analysis.

We radio-tagged Clapper Rails with 6 g radio transmitters (model RI-2C, Holohil Systems Ltd., Carp, Ontario, Canada). On average, Clapper Rails weigh 280 g (Eddleman and Conway 1998), so the weight of the transmitter relative to mass of the adults was expected to be roughly 2% and not expected to interfere with daily activities. We attached the transmitters to the birds' back between the wings using a backpack harness (Haramis and Kearns 2000). Overall handling time of birds once they were removed from the net was ≤ 15 min. All trapping and handling procedures followed the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Gaunt and Oring 1997) and an Animal Welfare Protocol Statement at Mississippi State University (Protocol #07-013 to Mark S. Woodrey).

HOME RANGE AND MOVEMENT – We located radio-marked Clapper Rails 1 to 7 times per week. Consecutive locations collected from a single bird were always ≥ 24 hours apart (once per tidal cycle), following the protocol of White and Garrott (1990). The locations of all radio-tracked Clapper Rails were determined by approaching the bird on foot, using a portable telemetry receiver (Lotek Wireless Inc., Newmarket, Ontario, Canada) coupled with a 3-element hand-held Yagi antenna (Telonics Corporation, Mesa, AZ, USA), to pinpoint the position of the individual rail. Clapper Rail locations were recorded using a handheld Global Positioning System (Trimble GeoXT, Trimble Navigation Limited, Sunnyvale, CA, USA). In an effort to ensure the independence of sample points for each bird only one location was taken per 24-hour period with all tracking conducted during daylight hours. In addition, we varied our tracking sessions to sample across the tidal range.

We first tested whether individuals exhibited site fidelity in the paths of their movement. We used the 'site fidelity test,' an extension of the Monte Carlo random walk test using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView GIS 3.3 (ESRI 1996). To accurately reflect the random walk distribution we ran 1000 simulations for each bird (Hooge and Eichenlaub 1997). The starting point for each simulation was the nest location, where the bird had been trapped. For each bird we calculated the mean squared distance from the center of activity (harmonic mean) and the linearity of the path. These values respectively measure dispersion (R^2) and direction of the movement (L). Each bird's movement path was compared with the ranked values of the random walks to test for statistical differences in these metrics.

We estimated home range for individuals using the fixed kernel method (Worton 1989) of the animal movement extension of ArcView (Hooge and Eichenlaub 1997). We applied least squares, cross validation to select the smoothing parameter. We selected the least squares, cross validation smoothing parameter because it is reported to be the most accurate (Bogner and Baldassarre 2002). We calculated both the 95% utilization distribution, which we refer to as "home range," and the 50% utilization distribution, the "core area" for each bird (Bogner and Baldassarre 2002). Calculations were made only for individuals with ≥ 30 locations (Seaman et al. 1999).

MOVEMENTS RELATIVE TO PREY – The abundance of fiddler crabs can vary by habitat type (Rader 1984, Mouton and Felder 1996). To estimate the number of fiddler crabs associated with each Clapper Rail nest we conducted burrow counts within 3 weeks of the success or failure of a Clapper Rail nest. We used burrow counts to provide a relative index of fiddler crab abundance because this method has been applied elsewhere and is considered appropriate for that purpose (Mouton and Felder 1996, Macia et al 2001). Burrow counts were conducted by counting all fiddler crab burrows within 0.25 m^2 quadrats (Mouton and Felder 1996). For each radio tagged Clapper Rail we conducted 10 burrow counts at 10 locations, a total of 100 counts, within 50 m of each nest/trap site. We used 10 counts per nest location because a preliminary analysis of variation in burrow counts indicated this number of samples minimized variation of the mean number of burrow counts among points while also minimizing sampling effort (S. Rush unpubl. data). Count locations were determined through the use of a random numbers table to select both distance from the nest site and compass bearing. All counts were conducted within 1hr of mean low tide and were restricted to areas not submerged during the count period.

To test the influence of fiddler crab abundance on Clapper Rail home range we conducted a linear mixed effects model (LME), fit with the Laplace approximation, and analyzed in the statistical package R ((Bates and Sarkar 2007, R Development Core Team 2008). Application of the LME allowed us to control for a lack of independence among samples (i.e., multiple fiddler crab burrow counts at each nest). For each nest we treated the harmonic mean (distance from the center of activity, in our case the nest) as the response term to a normal error structure in which the crab count was treated as a fixed effect. Only estimates from Clapper Rails tracked during 2007 that had $\geq$ 10 locations were included in this analysis. Additionally, we constrained this analysis to include only those individuals that exhibited site fidelity (Spencer et al. 1990) expressed as neither significant dispersion (R^2) nor significant linearity (L) (Hooge and Eichenlaub 1997). For the parameter estimates from the fitted LME, we report the mean ± 1 SE.

MOVEMENTS OF ADULTS WITH YOUNG – Using ArcGIS 9.1 (ESRI 2005) and digital orthorectified 1-m resolution imagery of the study site (National Agricultural Imagery Program 2007), we plotted Clapper Rail telemetry locations. Telemetry locations were coded using a binary categorical system denoting locations within 10 m of the marsh edge as “1” and locations > 10 m from the edge as “0.” We defined marsh edge using definitions applied in Minello et al. (2003) and accepted a delineation point of 10 m relative to the edge of the vegetation at mean low tide after visual inspection of our study systems indicated the majority of tidal wrack deposits occurred within this space. We measured tidal height as the difference (in minutes) between the time an individual was located and the time of predicted high tide for that day using tide tables (NOAA 2007) based on the nearest tide monitoring station (methods described in Rush et al. *in press*). To evaluate the influence of age (i.e., adult vs fledgling) and tidal height on edge habitat use we used hierarchical logistic regression with a random intercept to account for within-subject dependence. We fit models using Markov chain Monte Carlo (MCMC) in the Bayesian software package WinBUGS (Spiegelhalter et al. 2007). For the random intercept we used a normal prior for the mean, with a mean of 0 and variance of 5, and a uniform prior (0,4) for the standard deviation (Gelman 2006). A normal prior with a mean of 0 and a variance of $1\text{x}10^6$ was used for all priors. Each model was run for 100,000 MCMC iterations with a burn-in of 1,000 and ensured that the model estimates converged using the Raftery and Lewis diagnostic (Raftery and Lewis 1992a, Raftery and

Lewis 1992b) with the default parameters in CODA (Plummer et al. 2006). Candidate models were compared using the Deviance Information Criterion (DIC, Spiegelhalter 2002) and DIC weights (Burnham and Anderson 2002). In hierarchical models, the number of parameters can be a poor estimate of model complexity. DIC, unlike the Akaike Information Criterion (AIC), directly estimates model complexity (p_D) and was developed to compare hierarchical models (Spiegelhalter 2002).

RESULTS

During 2006 and 2007 we radio marked 22 adult Clapper Rails. However, for the majority of birds tag retention time was relatively low. Only 8 birds yielded ≥ 30 locations / bird and the site fidelity test rejected the null hypothesis for 7 of the 8 individuals. Analyses indicated that the movement paths of these seven individuals were more constrained than random movement paths (Monte Carlo simulation, $n = 1000$, $P < 0.05$) demonstrating site fidelity. These 7 individuals (2 birds from Grand Bay and 5 birds from the Pascagoula) were used to calculate estimates of both home range and core area. However, of these birds, the effective application of genetic markers to identify sex proved limited. In total the sex of only two individuals could be identified; both were male. As a result, subsequent analyses of Clapper Rail movement do not account for specific differences that may be attributable to sex.

MOVEMENTS OF ADULTS − Clapper Rail home range and the size of the core areas varied considerably among the 8 birds tracked. Mean home range size was 1.56 ha ± 0.55 (range = 0.35-5.0 ha, $n = 8$), and mean core area was 0.19 ± 0.17 (range = 0.06-0.53 ha, $n = 8$). Six individuals tracked during 2007 had ≥ 10 locations and exhibited a high level of site fidelity. For these six birds, our fitted model indicated that the length of the Clapper Rail's random walks decreased relative to fiddler crab abundance (n = 6 nests, coefficient = -0.007 ± 0.003).

MOVEMENTS OF ADULTS WITH YOUNG – The model representing an age and tidal height interaction received strong support as the best model (w_{DIC}=0.88, Table 4.1). There was a positive interaction ($8.40E^{-05} \pm 6.18E^{-05}$) between age and tidal height, suggesting that during low tide the proportion of time spent near the marsh edge increased with fledgling age, while remaining relatively constant at high tide (Fig. 5.2).

DISCUSSION

MOVEMENTS OF ADULTS – Our estimate of Clapper Rail home range (1.56 ha) was considerably larger than estimates derived from birds in Louisiana (0.53 ha, Sharp 1976, and 0.02 ha, Roth et al. 1976), but close to estimates derived from other geographic locations within this species' range (Eddleman and Conway 1998). These geographic differences may reflect variation in habitat quality and prey availability. Clark and Lewis (1983) suggested that Clapper Rails preferentially use habitat on the basis of two primary mechanisms, the presence of emergent vegetation and, to a lesser degree, the presence of fiddler crabs. Our results for rails along the northern Gulf Coast support these suggested mechanisms as well as demonstrate the importance of edge habitat for other taxa found within estuarine systems (Minello 1999, Rozas and Zimmerman 2000, Kneib 2003). Further, our data indicate that during the breeding season, the movement of Clapper Rails was negatively correlated with the number of fiddler crab burrows found near the nest site. Although further research aimed at identifying factors affecting the demographics and distributions of Clapper Rail populations (Eddleman et al. 1988) is greatly needed, our results suggest that during the breeding season, areas associated with high densities of fiddler crabs may translate to smaller Clapper Rail home ranges, possibly explaining the observed intra- and inter-estuary differences in this species' densities.

Studies examining sex-specific patterns of habitat use by marsh bird species are sorely needed, and would prove valuable to marsh bird conservation and the evaluation of survey techniques (Weller 1988, Reed 2004). However, among many species morphological similarities between the sexes make identification difficult, if not impossible. Although our application of Griffiths et al.'s (1998) chromosomal sexing technique met with limited success, this or similar techniques (Caetano and Ramos 2008) may prove worthwhile to this venture. As an example in our study, the two sexed birds were both identified as males. Both sexes of Clapper Rail are known to incubate the nest (Oney 1954, Eddleman and Conway 1989), and it has been noted that females perform the majority of diurnal incubation, taking over from the male at dawn (Eddleman and Conway 1998). In our study we captured all Clapper Rails within 4 hours of dawn with both sexed individuals captured within 3-4 hrs after sunrise. Although our trapping methods may have disrupted the behavior of nesting Clapper Rails in this study, additional studies incorporating markers of both parents may provide interesting information regarding the temporal incubation budget for this species along the northern Gulf of Mexico.

MOVEMENTS OF ADULTS WITH YOUNG − Both observational and telemetry-based studies of Clapper Rail foraging behavior indicate this species makes extensive use of emergent marsh edge, specifically during periods of low tide (Clark and Lewis 1983, Meanley 1985, Zembal and Fancher 1988). However, none of these studies addressed the movement of adults during the parental care period. In general, our results suggest

Clapper Rails tend to move towards marsh edge as tide waters recede (Clark and Lewis 1983, Meanley 1985, Zembal and Fancher 1988). Further, we found that the proportion of time Clapper Rails spent within 10m of a marsh edge varied with both tidal height and age of their young. During high tides, Clapper Rails with young tend to spend proportionately equal periods of time in the internal marsh and within 10m of the marsh edge. But during periods of low tide, depending on the age of their young, adults appear to shift their foraging towards marsh edge. For approximately the first two-weeks after the young fledge, Clapper Rail adults use of marsh edge does not differ with tidal height (Fig. 5.2). After 5 to 6 weeks post-fledging, which is considered by some to be the end of the parental-care period (Adams and Quay 1958, Zembal and Fancher 1988), adult Clapper Rails spend significantly more time within 10 m of the marsh edge at low tide.

We hypothesized that within the first few weeks of parental care Clapper Rails may limit use of marsh edge during the low tides to reduce predation risk for their young. Although the consequences of predation pressure on habitat use by Clapper Rail chicks has not been studied previously (Eddleman and Conway 1998), we expect fledgling mortality to be high along the northern Coast of the Gulf of Mexico where predators such as raccoons (*Procyon lotor*), Great Blue Herons (*Ardea herodias*) (both known predators of adults (Eddleman and Conway 1998)), and Black-crowned and Yellow-crowned Night-Herons (*Nycticorax nycticorax* and *Nyctanassa violacea,* respectively) are common in tidal marsh habitats. This suite of predatory species makes extensive use of marsh edge and inter-tidal zones, especially during low tides, and may have been influential in structuring the behavior of Clapper Rails relative to habitat (Butler 1992, Davis 1993, Watts 1995).

BROADER ECOLOGICAL IMPLICAITONS – Collectively, our results are drawn from a population of Clapper Rails along the northern Gulf of Mexico only and we would expect behavioral variation to occur across Clapper Rails' wide geographic range because of differences in marsh types (e.g., riverine-dominated versus marine-influenced, in marsh vegetation, flooding regimes, and a myriad other regional differences in marsh characteristics). Specifically, during low tide within our study area, the tidal marsh edge is essentially an abrupt transition between emergent marsh vegetation and inter-tidal mud flats. This characteristic facilitated the delineation of our 10 m marsh edge in our sites, however, this marsh/intertidal ecotone may not be as well-defined, and may not match the marsh characteristics of habitats used by Clapper Rails, throughout their range (Eddleman and Conway 1998). Additionally, while gut content analysis and observational data collected throughout the Clapper Rail's range suggest similarities in diet, principal food items may differ geographically (Heard 1982, Eddleman and Conway 1998). Understanding the factors that structure marsh bird behaviors and how they may vary spatially and temporally will benefit the development of management strategies critical for to their effective conservation.

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TABLE 5.1. Model selection results for the effect of age of young (Age) and tidal height (Tide) on the proportion time spent in edge habitat. Models are ordered by the difference in Deviance Information Criterion (ΔDIC) and DIC weights (*w*DIC). Superscripts of (+) or (–) indicate the direction of the estimate and (*) indicates 95% credible intervals (Bayesian confidence intervals) that do not overlap zero. pD is the estimate of model complexity.

Model	ΔDIC	*w*DIC	pD
Age * Tide $^{(+)*}$	0.00	0.88	9.90
Age $^{(+)*}$	4.70	0.08	9.85
Tide $^{(+)*}$	6.26	0.04	8.18
Null	113.67	0.00	14.13

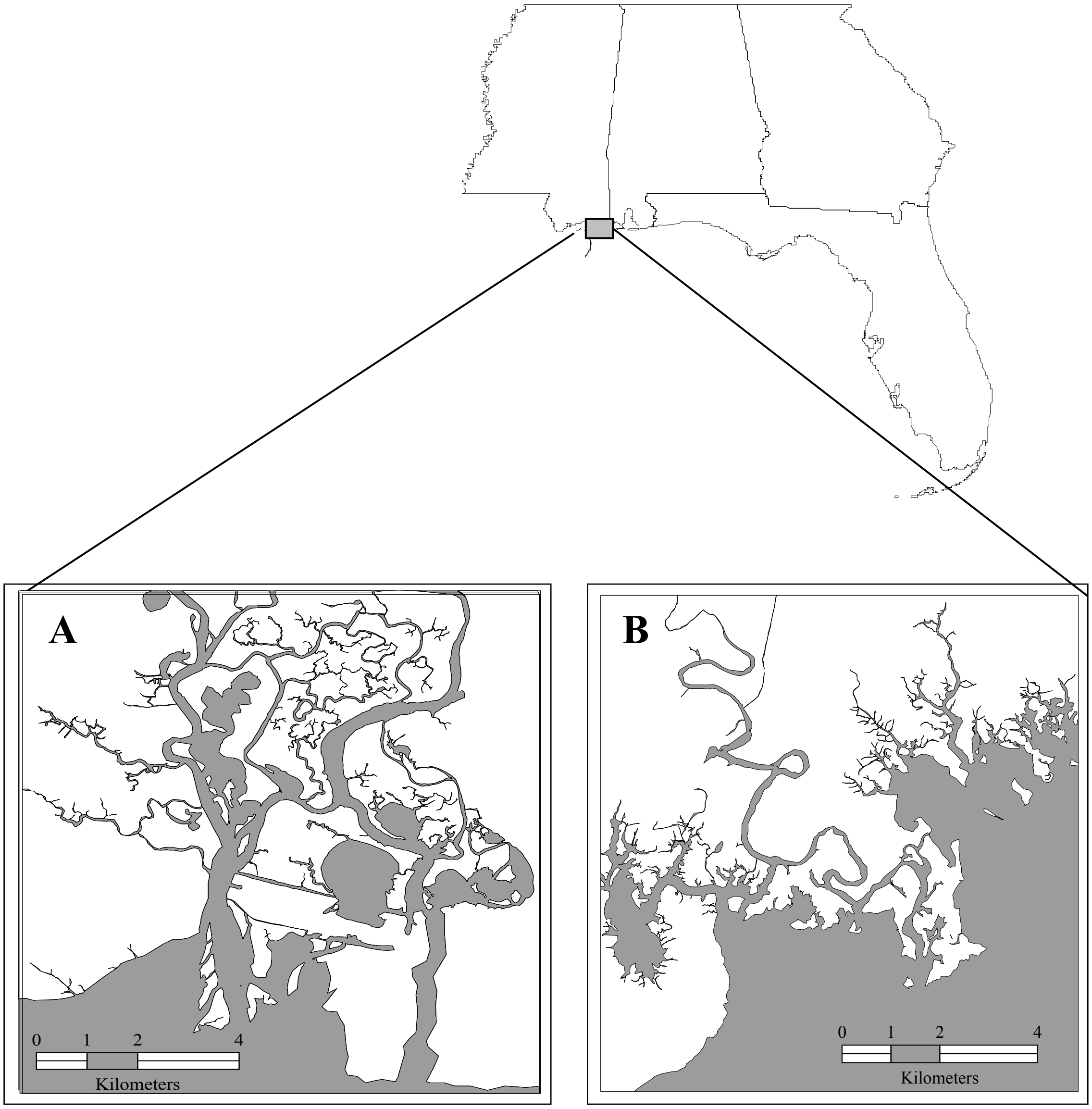

FIGURE 5.1. Study locations within Jackson County, Mississippi. Panel A shows the Pascagoula Marsh Coastal Preserve (Pascagoula) while panel B is the Grand Bay National Estuarine Research Reserve (Grand Bay).

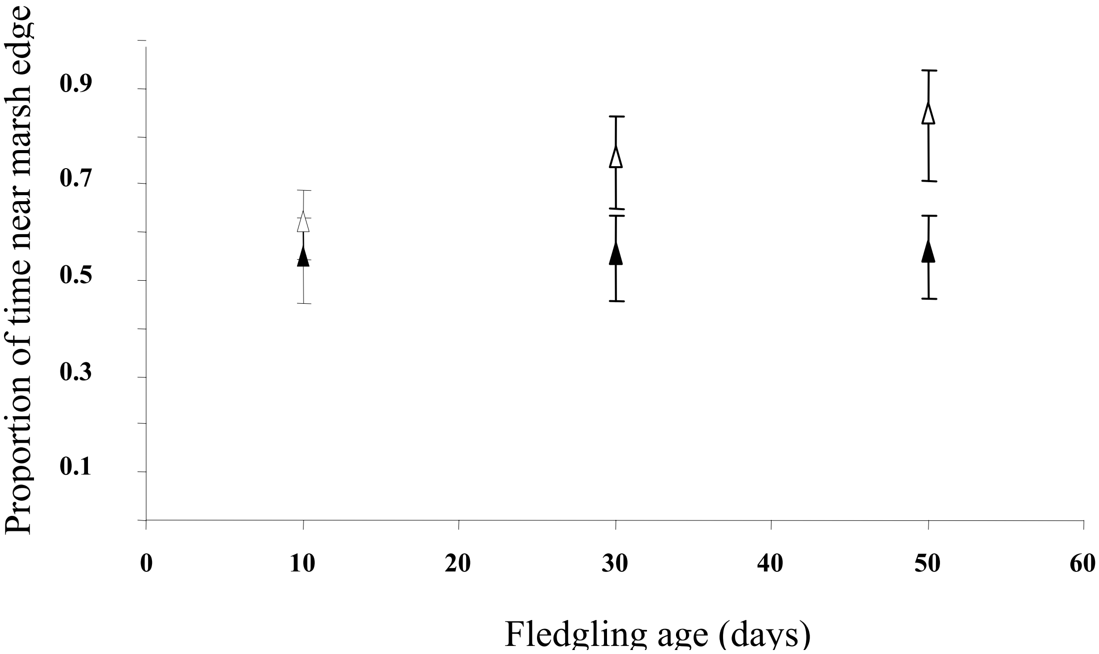

FIGURE 5.2. Interactive effect of fledgling age and tidal height on the proportion of time spent within 10 m of a marsh edge. For simplicity, only predictions for three ages are shown. Open triangles represent low tide (373 min from high tide) and solid triangles represent high tide (10 min from high tide). Error bars indicate 95% credible intervals (Bayesian confidence intervals).

CHAPTER 6

VARIATION IN CLAPPER RAIL EGG VOLUME AND CLUTCH SIZE: INSIGHTS INTO REPRODUCTIVE STRATEGIES AND LIFE HISTORY[1]

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ABSTRACT

Studies evaluating the influence of the environment on reproductive strategies remain relatively limited, owing in part to habitat complexity. Tidal marsh systems are relatively simple and may therefore provide a unique opportunity to study avian reproductive strategies. Here we analyzed variation in egg and clutch size in the Clapper Rail (*Rallus longirostris*) on the basis of four years of data collected from northern Gulf of Mexico tidal marshes. Mean egg volume increased and mean clutch size decreased relative to the Julian date of nest initiation. Within clutches egg volume did not change relative to laying sequence however, nitrogen isotope analysis indicated that the $\delta^{15}N$ of the last egg laid varied from the first egg laid by an average of 2.09 ‰. This result suggests that females may not alter resource allocation within a laying sequence but do draw upon somatic energy reserves during clutch formation. Among larger clutches (> 10 eggs), hatching success decreased relative to clutch size. For Clapper Rails, differences in egg volume and clutch size may represent trade-offs between productivity and a nidifugous life history strategy.

KEYWORDS: adaptive response, clutch size, $\delta^{15}N$, egg volume, estuary, Gulf of Mexico, nitrogen isotope, nutrient allocation.

INTRODUCTION

Reproduction is a nutrient-demanding process and physiological limitations during egg development may have marked effects on reproductive output and egg size (Monaghan et al. 1998, Nager et al. 2000, Nager et al. 2001, Visser and Lessells 2001). Plasticity in clutch size and the volume of eggs may relate to parental investment strategies and constraints (Slagsvold et al. 1984, Roff 1992, Williams 1994, Hipfner et al. 2003, Saino et al. 2004), and can directly influence life history traits such as egg composition (Carey et al. 1980, Ricklefs 1984, Arnold 1989, Reynolds et al. 2003), nest success (Reed et al. 1999, Fontaine and Martin 2006), hatchling size (Briskie and Sealy 1990, Williams 1994) and survival (Galbraith 1988, Grant 1991). Studies addressing egg size have shown that within a population, variation in egg and clutch size can be explained partly by genetic (Birkhead 1984) and ecological factors such as ambient temperature (Hargitai et al. 2005, Pendlebury and Bryant 2005), food and nutrient availability (Valkama et al. 2002, Bidwell and Dawson 2005, Kontiainen et al. 2008), habitat and territory quality (Potti 1993, Carey 1996, Potti 2008), female mass (Carey 1996, Nol et al. 1997), population density (Perrins and McCleery 1994, Both et al. 2000) and predation pressure (Fontaine and Martin 2006). These factors may influence variation in egg size within a population (Ojanen et al. 1981, Nilsson and Svenson 1993), although they appear to exert less force on variation within an individuals' clutch (Christians 2002). Though few studies have examined variation in both clutch and egg size between wild separate populations within the same geographic area, egg production may also depend on ambient conditions and, as a result, provide valuable information on the proximate causes of habitat related differences in the productivity of these species. Thus, understanding how factors shape the reproductive ecology of wild birds is critical to our ability to predict their response to changing environmental conditions (Greenberg et al. 2005, Visser et al. 2008).

Studies evaluating the influence of environment on reproductive strategies remain relatively limited, owing in part to environmental complexity (Hargital et al. 2005, Ball and Ketterson 2008). Tidal marsh systems may provide a unique opportunity to study avian reproductive strategies. Tidal marshes are relatively simple systems, typically dominated by a limited number of plant species and having simple trophic structure (Bertness and Ewanchuk 2002, van de Koppel et al. 2005). The diversity and structure of tidal marsh habitats are influenced by physio-chemical processes such as tidal flooding and salinity (Pennings et al. 2004). Despite relatively simple vegetation structure, birds nesting within tidal systems still face adaptive compromises in nest structure, placement, and the timing of reproduction. One such organism, the Clapper Rail (*Rallus longirostris*), is a secretive marsh bird that inhabits coastal tidal marshes throughout the United States and Northern Mexico. Throughout its range the Clapper Rail has developed several adaptations to facilitate breeding within tidal marshes (Eddleman and Conway 1998). For example, within the tidal marshes of the northern Gulf of Mexico, recent evidence suggests Clapper Rails exhibit nest height plasticity as a mechanism to avoid nest loss from tidal flooding (S. Rush unpubl. data).

Within estuaries, Clapper Rails feed on an array of plant and animal materials with fiddler crabs, which we associated with more saline conditions, comprising the primary prey source (Roth 1972, Heard 1982a, Eddleman and Conway 1998). Fiddler crab distributions can vary over relatively small spatial scales (Mouton and Felder 1996, Behum et al. 2005). It is not known whether a Clapper Rail's reproductive output mirrors fiddler crab distributions and can differ along salinity or habitat gradients. Specifically, do more saline environments provide higher quality food that in turn can be transferred to progeny?

For birds such as the Clapper Rail, reproduction is a nutrient-demanding process (Carey 1996). Physiological limitation during egg development may have marked effects on productivity and may have served as the basis of certain life history strategies (Monaghan et al. 1998, Nager et al. 2000, Nager et al. 2001, Visser and Lessells 2001, Bond et al. 2007). For instance, Greenberg and Droege (2006) suggested that relative to their freshwater counterpart, the King Rail (*Rallus elegans*), the Clapper Rail's clutch size is often smaller owing to reduced seasonality of resources or as a response to this species' high level of nest loss (McDonald and Greenberg 2006). Birds facing resource limitations may employ several strategies to meet these demands; one strategy is to store nutrients prior to breeding that can subsequently be invested into reproduction (Drent and Daan 1980, Jönsson 1997, Meijer and Drent 1999). These somatic nutrient stores are known as endogenous reserves. Alternatively, assimilation of locally available food sources can support reproduction. These nutrient sources are known as exogenous resources (Drent and Daan 1980, Jönsson 1997, Meijer and Drent 1999). Analysis measuring ratios of nitrogen stable isotopes ($\delta^{15}N$) has been used to directly trace nutrient allocation for reproduction (Hobson et al. 2000, 2005, Klaassen et al. 2001, Gauthier et al. 2003). This method uses naturally occurring stable isotope signatures in the environment as a means of identifying nutrient sources for egg formation. Comparison of egg volume across clutches and differences in $\delta^{15}N$ between eggs should reveal whether

Clapper Rails are able to assimilate nutrient resources of a magnitude needed to support consistent egg formation within a clutch, or if the mobilization of endogenous nutrient reserves during clutch formation occurs (Gauthier et al. 2003).

Clapper Rails are known to lay multiple clutches of eggs per nesting season (Eddleman and Conway 1998). For most birds, parental investment in offspring may decrease over the course of the breeding season, typically translating into smaller clutches or decreased hatching success as the season progresses (Rowe et al. 1994). If Clapper Rails reduce parental investment across the breeding season then we would expect a decrease in clutch size in relation to the date of nest initiation. Also, if clutch size does decrease between the first and subsequent clutches of the breeding season, does egg size or hatching success also differ with clutch size or between clutches? We combined nitrogen stable isotopes and reproductive metrics to draw inferences as to whether hatching success related to laying sequence, nutrient provisioning, or egg size. Additionally, and to explore environmental and physiologic relationships structuring Clapper Rail reproductive strategies, we examined variation in Clapper Rail clutch size and the volume of their eggs within and between two separate estuarine systems in coastal Mississippi, and within-season variation in the volume of Clapper Rail eggs and clutch size. We also discuss how this research addresses broader ecological implications explaining life history strategies and provide suggestions for further studies.

STUDY AREA AND METHODS

STUDY AREA – Our study area was two estuarine systems in coastal Jackson County, Mississippi, USA: 1); the Pascagoula River Marsh Coastal Preserve (hereafter Pascagoula, 30º 25’N, 88º 34’W) and 2) the Grand Bay National Estuarine Research

Reserve (hereafter Grand Bay, 30º 20’N, 88º 24’W) (Fig. 6.1). The approximately 4500 ha of the oligohaline to mesohaline emergent marsh of the Pascagoula is dominated by *Juncus roemerianus*, *Spartina alterniflora*, *S. cynosuroides* and *Sagittaria lancifolia*, while the approximately 7000 ha of the polyhaline Grand Bay site is dominated by *J. roemerianus*, with *S. alterniflora* found in narrow fringes along the water interface. Both estuaries experience irregular mico-tides (<2 m: Dardeu et al. 1992), warm vernal climates with mean summer temperature of 27˚ C, and average monthly summer precipitation of 16 cm. By the definition of Cowardin et al. (1979), the Pascagoula is considered truly estuarine, subject to heightened tides and fluctuations in river flow (Eleuterius 1972), while the polyhaline tidal marsh of Grand Bay receives oceanic input and is not directly associated with riverine discharge.

SAMPLE AND DATA COLLECTION − During March to August of 2006 − 2008, coinciding with the known breeding period of Clapper Rails in coastal Mississippi, active Clapper Rail nests were located through systematic searches of locations where adults had been heard calling or by walking through suitable nesting habitat. At each nest location (using a handheld GPS unit: Trimble GeoXT, Trimble Navigation Limited), clutch size was recorded and eggs were aged using methods detailed in Rush et al. (2007). Nests that contained an incomplete clutch (based on estimates relative to other nests monitored at a similar time) or were found before the initiation of incubation (the eggs were cool to the touch) were monitored every two to three days until clutches were completed. Starting in 2007, egg volumes were measured using methods outlined in Rush et al (*in review*).

To identify relationships between clutch size, egg volume and hatching success, in 2007 and 2008, permanent ink markers were used to label the three youngest eggs in Clapper Rail nests (n = 13, clutch size mean: 7.9, SE: 0.48). All eggs were labeled relative to the order in which they were laid to provide information relating laying sequence to hatching success. Additionally, during 2008 the youngest and oldest eggs were collected from three Clapper Rail nests, all with clutches of relatively equal size (mean: 7.3; Table 5.1). Nests were continually monitored until the nest successfully fledged young or was determined to have failed. For standardization purposes, we approximated the date of nest initiation for each nest, assuming Clapper Rails lay one egg per day and begin incubation before clutch completion (Meanley 1985). Thus, to estimate the date of nest initiation we back-calculated from our estimate of nest age, determined when the nest was first located, to derive an approximate date of nest initiation.

In this study we did not individually mark adult Clapper Rails. Although the lack of individually-marked birds prohibited our ability to evaluate whether the same female was associated with nests within and between breeding seasons, we believe the majority of the nests used in this study represent independent samples. Evidence such as distances between nests and the within-breeding season site fidelity of radio-tagged adults supports our rationale (Eddleman and Conway 1998, S. Rush unpubl. data).

STABLE ISOTOPE ANALYSIS − Clapper Rail eggs were frozen within a few hours of collection. Once frozen, eggshells were removed and eggs were freeze-dried. Egg yolks were separated from the albumen and individual yolks homogenized. Lipids were extracted from the yolk using a 2:1 ratio of Chloroform / Methanol (Bligh and Dyer 1959). Here, samples were immersed in a volume of solvent three to five times greater than sample volume, mixed for 30 s, and left undisturbed for 24 hrs. Supernatant and solids were poured through glass filter paper (Whatman Ashless Filter Paper, Whatman International Ltd., Kent, UK) to separate the supernatant and weighed to determine lipid contents. Mass balance equations were then used to determine the proportion of lipid in each sample.

Stable isotope ratios of nitrogen ($\delta^{15}N$) were measured using a Delta Plus isotope-ratio mass spectrometer (ThermoFinnigan, San Jose, CA, USA) coupled with an elemental analyzer (Costech, Valencia, CA, USA; analytical precision ± 0.15‰). Stable isotope ratios are expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation: $\delta^{15}N = [R_{smpl}/R_{strd} - 1] \text{ X } 10^3$, where $R = {}^{15}N/{}^{14}N$. Atmospheric nitrogen was used as the isotope standard of nitrogen. The analytical precision (standard deviation) for δ15N was 0.14 and for $\delta^{13}C$ was 0.05 based on analysis of NIST standards sucrose ($n = 13$) and ammonium sulphate ($n = 13$).

For our analysis we contrasted $\delta^{15}N$ between first and last eggs. Here, enrichment in $\delta^{15}N$ values, indicated by a shift towards higher $\delta^{15}N$ values, would suggest a greater proportion of the egg yolk is comprised of somatic energy reserves, therefore indicating either catabolism or mobilization of endogenous nutrient reserves during egg formation (Hobson 1995).

STATISTICAL ANALYSIS – Shapiro-Wilks tests and normality plots indicated clutch size and egg volume data were approximately normally distributed. During the three years of this study all Clapper Rail nests were located after 1 April. To standardize estimated clutch initiation dates among years, we treated 1 April as Julian date 1 for each year. Variation in clutch size (as the dependent variable) was then compared against

Julian date for our two focal estuaries, and among the 3 years of this study using linear mixed models (LMEs), fitted to a normal error structure, in the R package *lme4* (Bates and Sarkar 2007). To examine variation in egg volume among sources (Flint et al. 2001), by date of clutch initiation, and within clutches (i.e., between first and last eggs layed), LMEs were fitted with the function *lmer* and the variance of egg volume was contrasted among: 1) years, 2) study systems, and 3) nests. Here, nests were treated as random grouping variables, eggs were treated as nested within clutches, and both year and study system were treated as random intercepts. Likelihood ratio tests (Karrell et al. 2008) indicated little benefit from inclusion of the additional effects of year and study system (χ^2_5 = 1.25, P = 0.94) and, therefore, we did not include these additional nested effects when modeling egg volume by clutch initiation date. We followed a similar procedure when modeling clutch size. Using the *lme4* package in R (Bates and Sarkar 2007), we modeled clutch size relative to Julian date and treated the three years of our study as nested within the two study systems. Model fit was assessed using residual plots. Parameter estimates were developed using the function *mcmcsamp* in the R package *lme4* (Bates and Sarkar 2007) by first generating a Markov Chain Monte Carlo (MCMC) sample from the posterior distribution of each parameter estimate. We then computed the Bayesian highest posterior density (HPD) 95% confidence intervals of the MCMC sample for each parameter estimate using the function *HPDinterval* in *lme4* (Bates and Sarkar 2007).

RESULTS

CLUTCH SIZE AND HATCHING SUCCESS − Over the 3 years of this study clutch size was determined for 60 Clapper Rail nests. Contrasts of model intercepts indicated that clutch size did not differ between Grand Bay and the Lower Pascagoula (Grand Bay *n* = 18, mean = 10.42, SE = 1.04, Lower Pascagoula *n* = 42, mean = 10.11, SE = 0.57). At both sites clutch size decreased over the breeding seasons (β_{Julian} = -0.05, 95% CI: -0.03, -0.08: Fig. 6.2). Comparison of clutch sizes recorded for the subset of nests that contained un-hatched eggs (*n* = 11 nests versus 28 nests where all eggs hatched) indicated that the probability of at least one Clapper Rail egg not hatching increased relative to the size of the clutch ($\beta_{\text{Clutch Size}}$ = 1.10, SE = 0.43: Fig. 6.3).

Among Clapper Rail nests where the three youngest eggs had been marked (*n* = 13), nine nests successfully fledged young, two nests were depredated and two nests appeared to have been washed out by tides. Among the nine nests that successfully fledged young, three nests (clutch sizes of 7, 11 and 12) contained one unhatched egg, all among the three youngest eggs in each clutch.

EGG VOLUME − A relatively small proportion of the overall variation in egg volumes occurred between sample years (13%) and even less between our study systems (<1%). A much greater portion of the variation was found between nests (53%) and within individual clutches (33%). We did not find that egg volume decreased within the estimated laying sequence ($F_{1, 11}$ = 2.23, *P* = 0.16), but relative to estimated date of clutch initiation, egg volume increased over the breeding season (β_{Date} = 0.03, 95% CI: 0.01, 0.04: Fig. 6.4). Egg yolk δ^{15}N was higher in the last egg compared to first egg laid (mean difference: 2.09 ‰, 95% CI: 0.29, 3.83, Table 5.1), but we did not find that egg volume differed within clutches, between the first and last egg laid (coefficient = 0.57, 95% CI: -0.13, 1.27).

DISCUSSION

Generally, hypotheses that account for changes in avian clutch size and egg volume within breeding seasons can be separated into two types, ‘proximate’ and ‘ultimate’ explanations (Murphy 1986, Rohwer 1992). Here, proximate explanations pose that constraints acting on the volume of avian eggs and clutch size relate to habitat quality or the availability of resources to females during clutch formation. On the other hand, ultimate explanations suggest that temporal placticity in clutch size and egg volume is an adaptive effort aimed at the maximization of fitness (Murphy 1986). Our results suggest that, for Clapper Rails breeding within the tidal marshes of the northern Gulf of Mexico, clutch size and egg volume relate both with proximate and ultimate factors, but ultimate factors may have a stronger influence.

For Clapper Rails breeding within the estuarine systems of the northern Gulf of Mexico and much of the eastern United States, tidal flooding is one of the primary factors influencing nest loss (Eddleman and Conway 1998, Rush et al. unpubl. data). In response, Clapper Rails have been found to express an array of behaviors that are thought to mitigate nest loss to tidal flooding. Nesting Clapper Rails have been shown to retrieve eggs displaced from the nest (Pettengill 1938, Kosten 1982) and eggs submerged in water can remain viable for short periods of time (Kozicky and Schmidt 1949, Oney 1954). Also, Clapper Rails nesting in habitat prone to tidal flooding may be more likely to build ramps on their nests (Eddleman and Conway 1998). These ramps may facilitate a parent’s ability to return eggs to the nest. Clapper Rails may also increase nest height to avoid nest flooding during changing tidal conditions (Adams and Quay 1958, Storey et al. 1988). This broad suite of behaviors and adaptations seemingly aimed at reducing the loss of nests through flooding suggests another question - could temporal variation in Clapper Rail clutch size also be an adaptation to mitigate loss of productivity due to tidal flooding?

Here, Clapper Rails have larger clutches early in the breeding season, a behavior that may hedge against partial nest loss (Kozicky and Schmidt 1954, Eddleman and Conway 1998). Within some tidal marsh habitats an increase in nest height may also help alleviate these pressures (Rush et al. unpubl. data). However, early in the breeding season, the height of vegetation may restrict nest height. Thus, where nest height is limited, larger clutches may aid against nest loss from flooding. When eggs are washed from the nest larger clutches may be advantageous as they can increase the probability that at least partial clutches can be returned to the nest, a behavior that would increase fitness probability, at least more than if a nest was completely lost.

An alternative explanation is that the production of eggs is an energy demanding activity and that continued egg production necessitates the mobilization of endogenous resources or the continued acquisition of energy from the environment (Rowher 1992, Weathers and Sullivan 1993, Ganter and Cooke 1996, Sandercock et al. 1999). A decreased clutch size across the breeding season may reflect depletion in resource availability (Nager 2006). Our δ^{15}N results suggest that Clapper Rails laying a full clutch of eggs rely on the mobilization of somatic energy reserves (Table 1) and that during egg production the intake of exogenous sources of energy may not offset the energetic costs of reproduction. However, it is possible that these results may be affected by temporal differences such as prey availability.

Early in the breeding season the physiological constraints imposed by developing larger clutches may interact with laying order, thereby depleting the amount of resources that remain available for allocation to the last egg laid. For the developing embryo, limited resources may prove influential and reduce its hatching probability. Here, among the 39 Clapper Rail nests monitored in this study, 28% of the nests had at least one egg that did not hatch. Among these nests we found that unhatched eggs were some of the last eggs laid. Further, in each case unhatched eggs were found to contain what appeared to be fully developed embryos. These observations indicate that nutrient pools were substantial enough to foster embryonic development, at least to the observed stage. However, without further study it remains uncertain whether this mortality resulted specifically from nutrient limitations, as several aspects of the Clapper Rail's reproductive ecology suggest that nutrient availability may play only a minor part in influencing hatching success.

Within clutches, Clapper Rail eggs hatch asynchronously, producing nidifugous chicks (Eddleman and Conway 1998). Chicks first to hatch remain in the nest for a short period of time (typically < 2 days) before being lead from the nest site by one parent (Eddleman and Conway 1998). During this time, the other parent continues to incubate the remaining unhatched eggs and brood newly-hatched chicks (Eddleman and Conway 1998). A strategy of asynchronous hatching may result in this second parent leaving the nest with older chicks before the last egg has successfully hatched. Thus, adult Clapper Rails caring for large broods may move from the nest before the last egg hatches, leaving the remaining egg exposed. Although the embryo within this remaining egg may be fully developed, in the absence of parental care it can succumb to exposure before hatching.

Because larger clutches were more likely at the beginning of the breeding season, hatching probability may be reduced then (Fig. 6.3). This effect may explain the mortality of chicks within partially pipped eggs (Kozicky and Schmidt 1949).

The size and age of a breeding Clapper Rail may also be posited as explanations for increase egg volume and decreased clutch size relative to Julian date. While we did not measure size, mass or age of the adult birds associated with each nest, other studies focused on several other species suggest that larger or older adults may lay larger eggs (Christians 2002). For Clapper Rails, however, we do not believe that differences in adult size or age provide a universal explanation for the observed differences in egg volume and clutch size. For any particular species, the age and size of an adult typically explain only a small amount of the variation in clutch size (Carey 1996, Christians 2002). Therefore, correlates of these metrics with egg volume remain relatively obscure. Second, breeding phenology would need to be biased towards the individuals that produce larger eggs breeding later in the season. This is an unlikely relationship since Clapper Rails are known to lay multiple clutches within a breeding season (Blandin 1963, Meanley 1985, Eddleman and Conway 1998). We believe a better explanation may be simply that the volume of Clapper Rails eggs increases over the breeding season.

While uncommon among birds, an increase in egg volume across a breeding season has been identified in several species (citations in Christians 2002). One possible explanation for this change is that predation pressure may be tied to the release of several hormones associated with reproduction and development (Schwabl et al. 2007). While none of the hormones examined by Schwabl et al. (2007) illustrated a linear correlation between predation pressure and egg volume, these relationships may differ among nonpasserine species such as Clapper Rails. Generally, larger eggs produce larger offspring (Alisauskas 1986, Rhymer 1988). Larger offspring develop more quickly and thus have an advantage in evading predation (Grant 1991, Carey 1996). Predation pressure may be increased for Clapper Rail chicks that hatch later in the breeding season when the abundance of some key predatory species has been increased via recruitment (Davis 1993, Watts 1995). Differences in Clapper Rail clutch size and egg volume may represent an adaptive balance between the loss of nests through tidal flooding of early nests, increased predation pressure later in the breeding season (Fig. 6.5), and to a lesser extent, the availability of exogenous resources.

Clapper Rails have been shown to feed primarily on fiddler crabs (genus *Uca*: Heard 1982), an organism with distributions that can vary at relatively small temporal and geographic scales (Teal 1958, O'Connor and Epifanio 1985, Behum et al. 2005, Godley and Brodie 2007, Jimenez and Bennett 2007). Limited variation in Clapper Rail clutch size and egg volume measured between our two study sites could imply that 1) Clapper Rail egg volume and clutch size may not be strongly influenced by prey availability, or 2) the distribution of fiddler crabs may not vary considerably across the estuarine systems in our study. While evidence collected by Mouton and Felder (1996) provides some support for the later explanation, our egg volume and clutch size results suggest that for Clapper Rails, the total volume of reproductive output declines across the breeding season. As an example, point estimates derived from our model (Fig. 6.5) indicate that clutch volume for nests initiated on Julian date 1 and clutch volume for nests initiated on Julian date 60 differ by approximately 43cc, the equivalent of two Julian date

1eggs. Whether this difference in reproductive output mirrors temporal differences in the prey abundance and availability within these tidal systems warrants further study.

Within other geographic areas annual differences in the distribution and abundance of some fiddler crab species has been shown to occur (Godley and Brodie 2007). However, we currently know of no studies that have addressed seasonal relationships in fiddler crab abundance within the tidal marshes of the northern Gulf of Mexico. Therefore, studies focused on inter-annual predator-prey interactions between Clapper Rail and fiddler crabs within these tidal systems are needed. This type of study, coupled with research examining the rate of development and survival of Clapper Rail fledglings relative to egg volume and clutch size, will help further evaluate the existence of an adaptive reproductive balance between nest success and fledgling survival and prove key to advancing our understating of life-history evolution.

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TABLE 6.1. Values of $\delta^{15}N$ in egg yolks of first laid and last eggs laid in Clapper Rail clutches within two estuarine systems in coastal Mississippi, USA (identified in Fig. 6.1). First and last laid eggs were identified using methods detailed in Rush et al. (2007). The estimated date of clutch initiation is a Julian date calibrated using 1 April 2008 as day 1.

System	Nest	Estimated date of clutch initiation (Julian)	Clutch size	$\delta^{15}N$ First egg laid	$\delta^{15}N$ Last egg laid
Pascagoula	CRB	62	7	6.81	10.48
Pascagoula	UB	64	7	9.98	10.53
Grand Bay	BAI	54	8	7.48	9.54

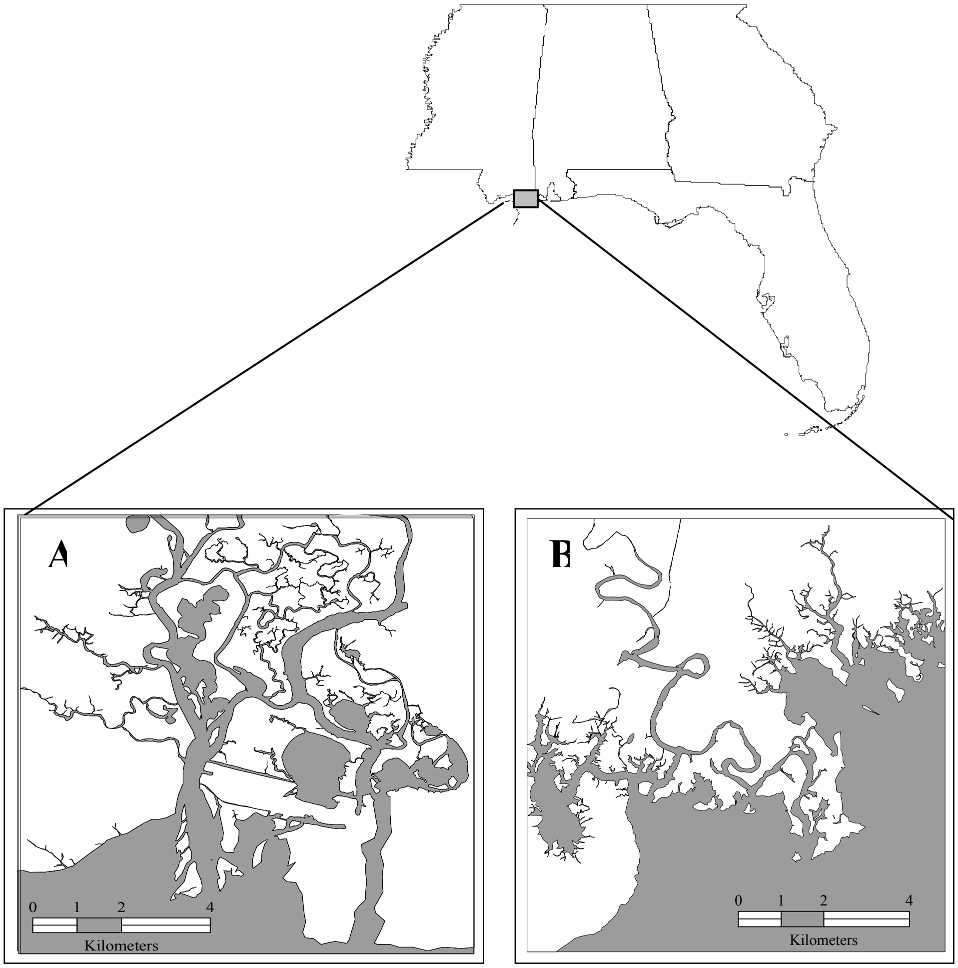

FIGURE 6.1. Study locations within Jackson County, Mississippi. Panel A shows the Pascagoula Marsh Coastal Preserve (Pascagoula) while panel B is the Grand Bay National Estuarine Research Reserve (Grand Bay).

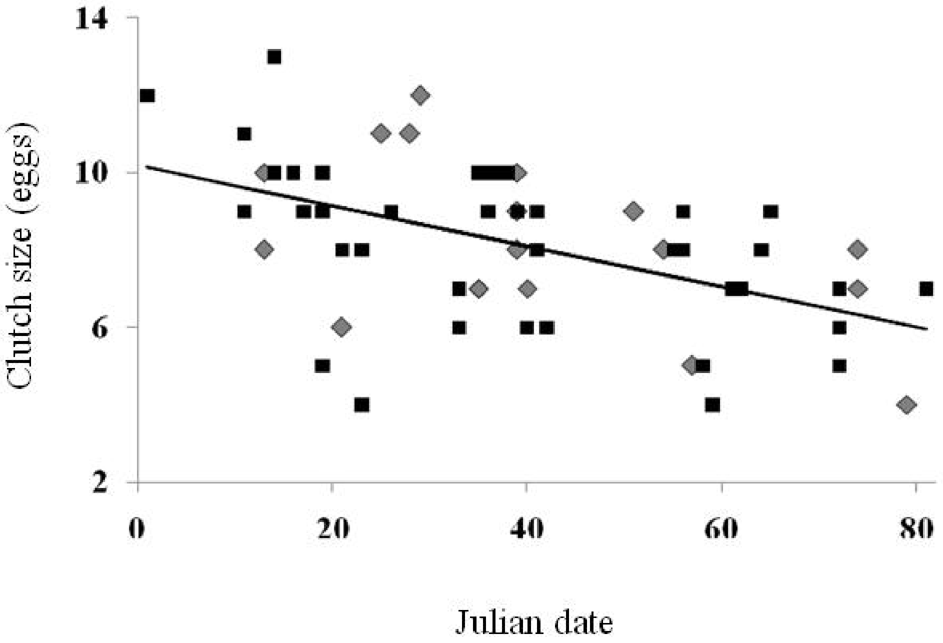

FIGURE 6.2. Clapper Rail clutch size by Julian date measured in two coastal estuaries. Gray diamonds represents Clapper Rail eggs measured at the Grand Bay while black squares represent measured at the Lower Pascagoula. Julian date calibrated with 1 April represented by date 0. Black line represents mean trend between date and clutch size.

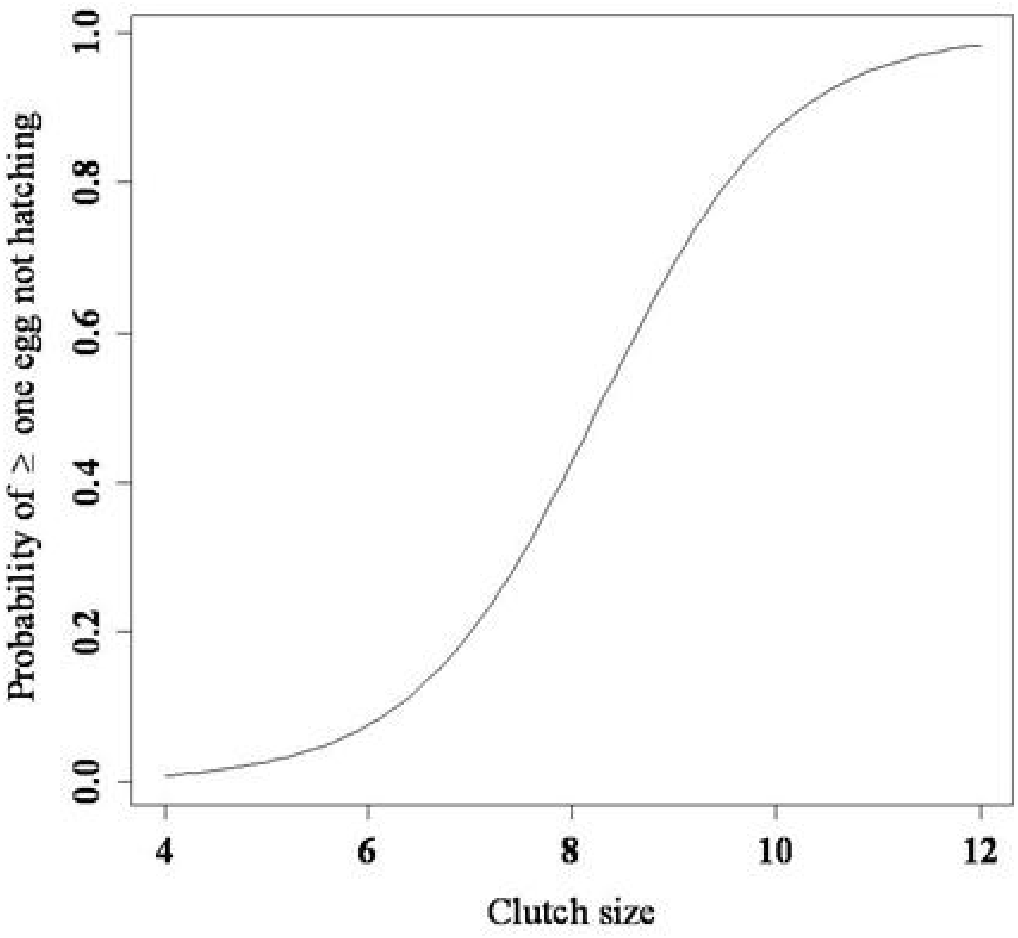

FIGURE 6.3. Probability of at least one egg not hatching relative to clutch size for Clapper Rail nests in coastal Mississippi. Open circles represent individual nests. Multiple nests of like clutch sizes were found. Therefore, each circle may represent multiple nests. Overall, of the 28 nests modeled, 11 nests were found with one egg that did not hatch. The black line represents relationship between clutch size and probability of at least one egg not hatching as predicted using logistic regression,

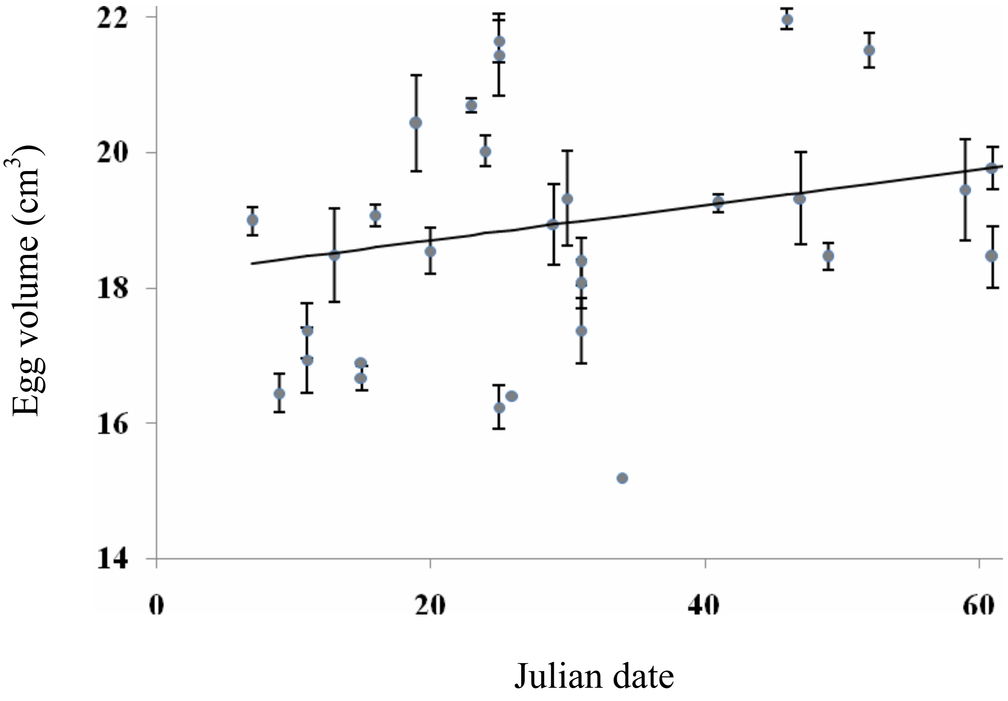

FIGURE 6.4. Relationship between Clapper Rail egg volume and Julian date of nest initiation among nests within two estuarine systems in coastal Mississippi, USA. Gray circles represent individual nests (*n* = 30) while error bars indicate mean ± one standard error. Black line represents mean trend between date and egg volume.

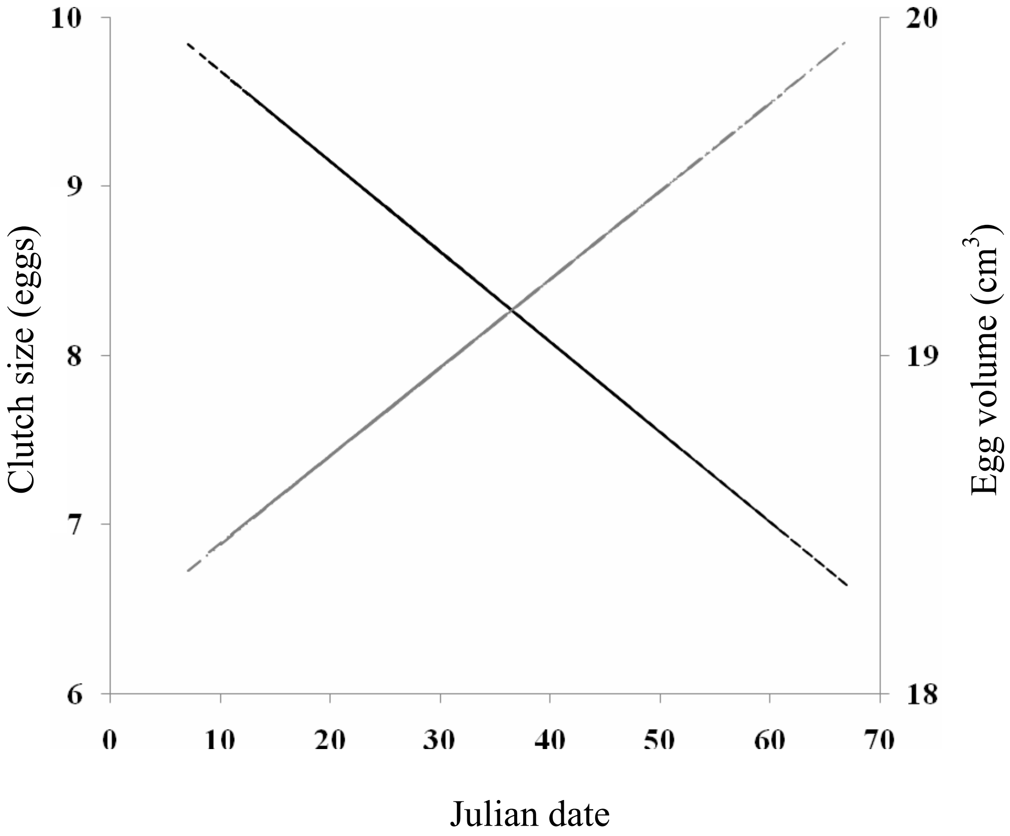

FIGURE 6.5. Clapper Rail productivity by Julian date among nests within two estuarine systems in coastal Mississippi, USA. Julian date calibrated with 1 April represented by date 1. Black line represents mean trend between date and clutch size and gray line represents relationship between egg volume and Julian date.

CHAPTER 7

LINKING LOCALIZED HABITAT TO SPATIAL DISTRIBUTIONS AND REPRODUCTIVE PARAMETERS OF CLAPPER RAILS THROUGH TROPHIC ECOLOGY[1]

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[1] Rush, S. A., A. T. Fisk, M. S. Woodrey, and R. J. Cooper. To be submitted to *Estuaries and Coasts*.

ABSTRACT

As interfaces between aquatic and terrestrial systems, the tidal marshes of the northern Gulf of Mexico support a high abundance of organisms. Recent changes in physical and chemical attributes of these ecosystems have resulted in, and portend significant alteration to, habitat and energy flows. However, predicting the response of these estuaries to changing conditions is challenged by limited understanding of complex interactions between primary production, consumers and predators. To elucidate energy flows within these estuarine systems we examined trophic interactions between primary producers (*Spartina alterniflora*, *S. cynosuroides*, and *Juncus roemerianus*), a primary consumer (*Uca longisignalis*) and a secondary consumer (Clapper Rails (*Rallus longirostris*)). Lipid concentrations and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios indicated relatively strong trophic links between *U. longisignalis* and primary production. Here, small-scale habitat differences may have governed the spatial distributions of *U. longisignalis*. In turn, the abundance of *U. longisignalis* influenced the spatial dynamics of breeding Clapper Rails and was linked to the concentration of lipids and $\delta^{13}C$ in their eggs. Our findings illustrate how the distributions of predators can be defined by the spatial arrangement of primary producers and consumers within these tidal estuaries. Further, based on this simple three-level trophic system, our findings provide evidence that small changes in emergent tidal marsh habitat can significantly affect the flow of energy across multiple trophic levels.

KEYWORDS: carbon isotopes, Gulf of Mexico, marsh bird, *Rallus longirostris*, *Uca longisignalis*

INTRODUCTION

Estuaries are productive systems supporting a high diversity and abundance of plants and animals (Beck et al. 2001). Complex interactions between biotic and abiotic factors structure the distributions of organisms trophic interactions, predator-prey dynamics and subsequent energy flow within these systems (Stephens and Bertness 1991, Frederick and Loftus 1993, Callaway and King 1996, Travis 1996, Nomann and Pennings 1998, Beck et al. 2001, Behum et al. 2005). Evidence collected from the southern United States' tidal marshes suggests that drought, sea level rise and increased herbivory may have already altered many biological interactions, leaving the future of these estuarine systems uncertain (Visser et al. 2002, McKee et al. 2004, Silliman et al. 2005). However, predicting the response of these estuaries to changing environmental conditions is challenging as it necessitates understanding interactions between primary production, predators and their prey (Boesch and Turner 1984, Costanza et al. 1990, Day et al. 1993, McFadden et al. 2007, Moody and Aronson 2007).

Within estuarine intertidal zones many bird species prey on organisms such as epibenthic and benthic invertebrates (Warren 1985, Piersma 1987, Watts 1988, Frix et al 1991). Important among these are sediment-dwelling invertebrates such as fiddler crabs (genus *Uca*: Teal 1958, Crane 1975, Thurman 2003a), with distributions influenced by an array of biotic and abiotic conditions (Peterson and Turner 1994, Mouton and Felder 1995, Levin and Talley 2000, Thurman 2003b, Behum et al. 2005, Godley and Brodie 2007). In turn, the spatial arrangement of fiddler crab populations can structure predator distributions (Watts 1988, Peterson and Turner 1994, Ribiero et al. 2003, Ribeiro et al. 2004, Valiela et al. 2004, Hemmi et al. 2006).

Facilitative interactions between fiddler crabs and emergent macrophytes, such as *Spartina alterniflora*, have been shown (Kerwin 1971, Montague 1980, Montague 1982, Bertness 1985, Gribsholt et al. 2003). Burrows created by fiddler crabs help to enhance primary productivity (Bertness 1985, Daleo et al. 2007) and macrophytes can provide refugia from predation and ambient conditions such as heat and dessication (Teal 1958, Normann and Pennings 1998, Bortolus et al. 2002). Evidence collected within the northern Gulf of Mexico suggests that detrital materials from emergent plants and benthic microalgae may also provide the primary food sources for fiddler crabs (Sullivan and Moncreiff 1990). However, the chemical structure of senescent plant materials may differ by species of origin and can shape energy flows at fundamental levels (Burkholder 1956, Teal 1962, Cruz and Gabriel 1974, Montague 1980, Bushaw-Newton et al. 2008).

The Clapper Rail is a medium-sized marsh bird that inhabits the tidal estuarine habitats of the northern Gulf of Mexico, feeding on an array of plant and animal materials with fiddler crabs comprising its primary prey source (Roth 1972, Heard 1982a, Eddleman and Conway 1998). For birds such as the Clapper Rail, reproduction is a nutrient-demanding process (Carey 1996) and physiological limitation during egg development may have marked effects on productivity (Monaghan et al. 1998, Nager et al. 2000, Nager et al. 2001, Visser and Lessells 2001). Consequently, one effect of habitat change may be linked through the redistribution of primary production and fiddler crabs, ultimately affecting Clapper Rail reproduction and the distribution of breeding adults.

Stable isotope analyses have proven to be a powerful tool for the study of trophic relationships in coastal ecosystems (Michener and Schell 1994). This approach is based on the principle that the ratios of heavier to lighter isotopes, expressed for carbon as $\delta^{13}C$

and nitrogen as $\delta^{15}N$, depend on 1) the isotopic composition of its food resources, and 2) isotopic fractionation during food assimilation (DeNiro and Epstein 1978, 1981). For carbon, there appears to be little (i.e., approx. 1%) or no change in $\delta^{13}C$ between trophic levels (Hobson and Welch 1992). Therefore, carbon isotopes have proven useful as indicators of primary production in studies of food webs (DeNiro and Epstein 1981, Peterson and Fry 1987, Post 2002). For nitrogen, a $\delta^{15}N$ enrichment of 2-4% between producers and consumers appears typical (Peterson and Howarth 1987, Michener and Schell 1994, Hobson et al. 2002). Thus, a shift in $\delta^{15}N$ between a consumer and its food provides an approximate indication of trophic level (Post 2002).

Here, we examined energy flow from primary producers (emergent marsh macrophytes), to a primary consumer (fiddler crabs), and a secondary consumer (Clapper Rail), within several estuarine systems in the northern Gulf of Mexico. We used lipid concentration, carbon and nitrogen stable isotopes, and occupancy models to assess the influence of nutrient acquisition by, and distributions of, Clapper Rails. Specifically, we asked (1) Does basal production influence diet and metabolite composition of fiddler crabs? (2) Do fiddler crab distributions influence the occurrence of Clapper Rails? If so, (3) are variations in habitat and fiddler crab abundance reflected in the metabolite composition of Clapper Rail eggs? We discuss how this research approaches broader ecological implications of habitat change and energy flow within these tidal ecosystems and provide suggestions for further studies.

STUDY AREA AND METHODS

STUDY AREA − Our study area consisted of two estuarine systems in coastal Mississippi, USA. These two systems were: 1) the Pascagoula River Marsh Coastal

Preserve (hereafter Pascagoula, 30º 25’N, 88º 34’W) and, 2) the Grand Bay National Estuarine Research Reserve (hereafter Grand Bay, 30º 20’N, 88º 24’W), both of which are located in Jackson County (Fig. 7.1). The emergent marsh of the oligohaline and mesohaline Pascagoula is dominated by *Juncus roemerianus*, *Spartina alterniflora*, *S. cynosuroides* and *Sagittaria lancifolia* while the polyhaline Grand Bay is dominated by *J. roemerianus*, with *S. alterniflora* found in narrow bands along the marsh and water interface. Both estuaries are influenced by irregular tides of small amplitude (<1 m Dardeu et al. 1992), warm vernal climates with mean summer temperature of 27˚ C, and average monthly summer precipitation of 16 cm. Following the definition of Cowardin et al. (1979), the Pascagoula site was subject to heightened tides and fluctuations in river flow (Eleuterius 1972), but the polyhaline tidal marsh system of Grand Bay received oceanic input and was not directly associated with riverine discharge.

PREDATOR / PREY DISTRIBUTIONS − During 2008, we followed the North American Marshbird Monitoring Protocol (Conway 2008, Conway and Droege 2006) and conducted marsh bird surveys at 35 locations at the Lower Pascagoula and 35 locations at Grand Bay. All survey points were at least 400 m apart, four replicate surveys were conducted at each survey point, and all surveys were conducted by one observer. Survey periods were structured to allow greater than 2 weeks between surveys. Initial surveys were conducted later than 1 April but prior to 9 May with the fourth and final survey conducted after 17 June but before 26 June. We used call playback to facilitate the detection of Clapper Rails and only recorded individuals if detected (heard or seen) within 200 m of a survey point.

An often-used metric of fiddler crab abundance is the burrow count, where the number of burrows observed within a specified area is quantified and used as a measure of relative abundance (Mouton and Felder 1996, Macia et al 2001, Ribeiro et al. 2005). During 2006, employing burrow counts, we enumerated all open fiddler crab burrows ≥ 5 mm in diameter, within a 0.5 X 0.5 m sampling frame placed at 10 random locations within 50 m of 9 Clapper Rail nests. Count locations were identified using a random numbers table to select a compass bearing and distance from the nest site. We used a cutoff of 50 m from each nest site based on mean home range size of the Clapper Rail (S. Rush unpublished data). All counts were conducted within 1 hr of mean low tide and were restricted to areas not submerged during the count period. All counts were made within 2 hrs of low tide during the period 3 April to 5 May 2008. Additionally, during 2008, we counted fiddler crab burrows at 35 locations where Clapper Rail surveys had been conducted within the Lower Pascagoula and 35 survey sites at Grand Bay. For each count the dominant vegetation type (i.e., species with coverage of > 50% of the frame) was recorded.

Samples of fiddler crabs and plants were collected from each estuary for use in carbon and nitrogen stable isotope analysis. Approximately 10 crabs were collected *ad libidum* from 10 sites within each estuary. Crabs were washed with saline water and keyed to species (Heard 1982b). At each location culms and leaves were collected from a macrophyte known to use the C_3 photosynthetic process (*J. roemerianus*) and two species known to use the C_4 process (*S. alterniflora,* and *S. cynosuroides*). All crab and plant samples were placed on ice and returned to the lab where they were immediately frozen. Crabs were sorted on the basis of sex and size within one month of collection. Size was defined as carapace width, a metric comprised of 4 categories (10-14, 15-19, 20-24, and 25-29 mm).

TROPHIC ECOLOGY − During April to July 2006, 2007 and 2008 we located active Clapper Rail nests by systematically searching locations on foot where adults had been heard calling (Adams and Quay 1958) or by walking through suitable nesting habitat and allocating equal portions of time to searching along the marsh edge and through the marsh interior. Once a nest was located, all eggs were aged using floatation methods outlined in Rush et al. (2007). Incomplete clutches (identified by additional eggs observed in the nest over subsequent visits) were aged by back-calculation based on the number of eggs in the clutch and assuming incubation began once the penultimate egg was laid. A single egg was collected from each nest. During 2006, the percent aerial cover of dominant vegetation types within 50 m of each nest site was estimated visually (methods described in Conway 2008).

All Clapper Rail eggs, fiddler crabs and vegetation samples were freeze-dried to remove moisture and subsamples of egg yolk were collected from each egg. We focused on egg yolk as this tissue provides the primary food source for the developing embryo and has been shown to represent an adult's diet during egg formation (Hobson 1995, Carey 1996). Sub-samples of tissue were also collected from the cephalothorax of each fiddler crab with attempts made to avoid sampling the exoskeleton or other calciferous tissues as these may bias ratios of carbon isotopes (Currin et al. 1995, Yokoyama et al. 2005). Lipids were extracted from Clapper Rail eggs and fiddler crabs using a 2:1 ratio of Chloroform / Methanol (Bligh and Dyer 1959). Samples were immersed in a volume of solvent three to five times greater than sample volume, mixed for 30 s, and left undisturbed for 24 hrs. Supernatant and solids were poured through glass filter paper (Whatman Ashless Filter Paper, Whatman International Ltd., Kent, UK) to separate the supernatant and mass balance equations were used to determine the proportion of lipid in each sample.

Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were measured using a Delta Plus isotope-ratio mass spectrometer (ThermoFinnigan, San Jose, CA, USA) coupled with an elemental analyzer (Costech, Valencia, CA, USA, analytical precision ± 0.15‰). Stable isotope ratios are expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation: $\delta^{13}C$, $\delta^{15}N = [R_{smpl}/R_{strd} - 1] \times 10^3$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. Pee Dee Belemnite and atmospheric nitrogen were used as the isotope standards of carbon and nitrogen, respectively. The analytical precision (standard deviation) for δ15N was 0.14 and for $\delta^{13}C$ was 0.05 based on analysis of NIST standards sucrose (*n* = 13) and ammonium sulphate (*n* = 13).

STATISTICAL ANALYSIS − An organisms' habitat distribution and habitat use can be evaluated through the collection of binary presence/ absence data. However, imperfect detection of the organism (when the probability of detection is < 1), can lead to bias in estimates of habitat use (MacKenzie et al. 2006, Royle and Dorazio 2008). When the frequency of the nonoccurrence of the focal organisms is large, the data may not fit standard distributions such as the normal or binomial. To accommodate these circumstances, occupancy models can be structured to incorporate a zero-inflation parameter (Welsh et al. 1996, MacKenzie et al. 2006, Royle and Dorazio 2008). Using the statistical package R, zero-inflated models were used to explore relationships between the relative density of fiddler crab burrows and the probability that a survey site was occupied by a Clapper Rail. Here, the detection of a Clapper Rail was treated as a categorical variable, characterized by ‘1’ if during a survey a Clapper Rail was detected at each survey site, and ‘0’ if not. To mirror habitat associations that occur at the scale of a Clapper Rail’s home range, the dataset was restricted to individuals detected within 50 m of each survey point (S. Rush unpubl. data). The detection of Clapper Rails was modeled as a binomial process evaluated over the four replicate surveys. Clapper Rail occupancy, estimated among sites, was evaluated relative to the abundance of fiddler crab burrows measured at each survey site.

We applied several techniques to explore the trophic ecology of fiddler crabs and Clapper Rails. Specifically for fiddler crabs, we evaluated the strength of relationships between fiddler crab burrow density and dominant vegetation type, and correlations between tissue-lipid concentration and the δ^{13}C of the tissues. We examined relationships between lipid concentrations in fiddler crabs and tissue δ^{13}C using linear mixed models (LMEs) fitted to a normal error structure. Initially, both size and sex were treated with random intercepts. However, likelihood ratio tests indicated that size alone provided substantially better fit and was retained in further modeling (χ^2_2 = 6.01, p = 0.5).

We also used LMEs to explore Clapper Rail trophic ecology. We modeled relationships between lipid concentration in Clapper Rail egg yolks, the δ^{13}C of the egg yolks (a reflection of diet at the time of egg formation: Hobson 1995), and the density of fiddler crab burrows proximate to each nest. We began by controlling for the age of the egg (number of days post-laying), estimated at the time the egg was collected. We then applied a three-level mixed model, a process that enabled us to identify the proportion of variance in Clapper Rail egg yolk lipid concentrations at three levels (nest, estuary, and year). Within each estuary, we modeled egg yolk lipid concentration as a function of nest-level predictors plus a random error:

$$Y_{ijk} = \pi_{0jk} + \pi_{pjk}\alpha_{ijk} + e_{0ijk}$$

where Y_{ijk} is the concentration of lipids in an egg collected from nest *i* in estuary *j* and year *k*. Further, π_{0jk} is the intercept for estuary *j* in year *k*, α_{ijk} is a nest characteristic that predicts the effect of egg age on mean yolk lipid concentration, π_{pjk} are the corresponding estuary level characteristics that indicate the direction and strength of the association between each nest characteristic, a_p, and the outcome in estuary *jk*, and e_{0ijk} is a level-1 random effect representing the deviation of lipid concentrations measured in an egg sampled from nest *ijk* from the predicted concentration based on the estuary –level model. These residual nest effects were assumed to be normally distributed with a mean of 0 and a variance σ^2. Variation among estuaries within years was modeled, with each estuary effect, π_{pjk} as:

$$\pi_{pjk} = \beta_{p0k} + \sum_{q=1}^{Q_P} \beta_{pqk} X_{qjk} + r_{pjk}$$

where β_{p0k} is the intercept for year *k* in modeling the estuary effect π_{pjk}, X_{qjk} is an estuary characteristic used as a predictor of the estuary effect π_{pjk}, β_{pqk} is the coefficient representing the direction and strength of the association between estuary characteristic X_{qjk} and π_{pjk}. Lastly, r_{pjk} is a level-2 random effect that represents the deviation of estuary *jk*'s level-1 coefficient, π_{pjk}, from its predicted value based on the estuary-level model. Similarly, each level-3 “outcome” may be predicted by some year-level characteristic.

$$\beta_{pqk} = \gamma_{pq0} + \sum_{s=1}^{S_{pq}} \gamma_{pqs} W_{sk} + u_{pqk}$$

Similar to other levels, γ_{pq0} is the intercept term, W_{sk} is a year characteristic used as a predictor for year effect, γ_{pqs} is the corresponding level-3 coefficient, and u_{pqk} is the level-3 random effect.

Our model partitioned the total variability in the outcome Y_{ijk} into three compartments: (level 1) among nests within estuaries, σ^2; (level 2) among estuaries within years, τ_π; and (level 3) among years, τ_β. This process allowed us to estimate the proportion of variation in egg yolk lipid concentrations within estuaries, among estuaries within years, and among years (Raudenbush and Bryk 2002).

We applied the estimated covariate relationship between egg age and lipid concentration to standardize estimates of lipid concentrations among nests. Standardized concentrations were then applied in a general linear model to evaluate interactions between 1) yolk lipid concentrations and carbon isotope ratios, and 2) yolk lipid concentrations and the relative density of fiddler crab burrows estimated for each Clapper Rail nest. Linear relationships between model residuals and δ^{13}C were evaluated for data collected over the three years of the study while models relating yolk lipid concentrations with fiddler crab burrow densities were limited to data collected during 2007.

All LMEs were developed on a normal error structure, estimated with the statistical package R, (version 2.7.1: *lmer*, R Development Core Team 2008), and maximum likelihood (Bates and Sarkar 2007). Both fixed effects and random effects were counted as parameters (Skrondal and Rabe-Hesketh 2004). Models were compared using Akaike's Information Criterion (AIC: Akaike 1973). We considered the model with the lowest AIC as the best-fit model, although only if it was less, by two units or more, than the simpler models in which it was nested (Burnham and Anderson 2002, Richards 2008). The strength of support for each model was also evaluated using Akaike weights (w_i), where Akaike weight indicates the relative plausibility of a given model within a set of candidate models (ΔAIC: Burnham and Anderson 2002). Data were log-transformed or arc-sine square-root transformed to meet normality assumptions when necessary. Model fit was assessed by visually inspecting normality plots of the residuals. All analyses were conducted in R, version 2.7.1. Except where indicated, we report parameter means and 95% confidence intervals.

RESULTS

PREDATOR / PREY DISTRIBUTIONS − All fiddler crabs were identified to a single species (*Uca longisignalis*); however, the distribution of this species' burrows varied within and between estuaries. The mean density of fiddler crab burrows at Pascagoula sites was 9.56 m^2 (95% CI: 6.88. 12.2), compared with 31.44 m^2 (95% CI: 29.52, 33.32) at Grand Bay. At Grand Bay the density of fiddler crab burrows was higher in locations dominated by *S. alterniflora* (37.32 burrows m^2 (95% CI: 29.8, 44.84), than in habitat dominated by *J. roemerianus* (27.44 burrows m^2, 95% CI: 21.52, 33.4). However, at the Pascagoula, there was no difference in burrow densities between locations dominated by *J. roemerianus* (4.48 burrows m^2 (95% CI: 3.52, 5.48) or *S. cynosuroides* (4.76 burrows m^2 95% CI: 3.48, 6.04)). Variation in the mean density of fiddler crab burrows was higher between our two study sites (Grand Bay: 79%, Pascagoula 76%) than within survey sites (Grand Bay: 21%, Pascagoula 24%).

Although the best supported model of Clapper Rail occupancy (NULL Model, Model 1, Table 7.1), did not indicate that occupancy differed relative to the mean density of fiddler crab burrows, or by estuary, a similar level of support was given to a more complex model that included individual site effects (Model 2, Table 7.1). Parameter estimates derived from this model identified Clapper Rail occupancy was higher at Grand Bay (0.52, 95% CI: 0.18, 0.82) than Pascagoula (0.15, 95% CI: 0.03, 0.50), but related positively to the density of fiddler crab burrows at the Pascagoula only (estimate = 1.17, 95% CI: 0.90, 1.43).

TROPHIC ECOLOGY − The $\delta^{15}N$ of the primary producers was generally greater at the Pascagoula site than Grand Bay, although the differences were only statistically significant for *J. roemerianus* (Table 7.2). As expected, the $\delta^{13}C$ of *J. roemerianus* (*n* = 26) a species that uses the C_3 photosynthetic process, was – 26.62 (95% CI: -27.08, -26.16), while the C_4 plants *S. alterniflora* and *S. cynosuroides* were much lower (-13.97, 95% CI: -14.08, -13.85, Table 7.2). There was some evidence that values of $\delta^{13}C$ differed between estuaries, although the difference was only statistically significant for *J. roemerianus* where $\delta^{13}C$ was more depleted at the Pascagoula (Table 7.2). Fiddler crab $\delta^{13}C$ and $\delta^{15}N$ were not substantially different among size classes or sex (Table 7.2), but differences between estuaries were apparent for both isotopes. The $\delta^{13}C$ of *U. longisignalis* were more negative at the Pascagoula than at Grand Bay (Pascagoula: -22.70, 95% CI: -23.68, -21.71, Grand Bay: -18.66, 95% CI: -19.27, -18.06) while $\delta^{15}N$ were higher for Pascagoula (Pascagoula: 6.44, 95% CI: 5.96, 6.91, Grand Bay: 4.51, 95% CI: 4.04, 4.98).

The concentration of lipids in fiddler crab tissues appeared to vary by diet. The best-supported model ($\delta^{13}C$: Table 7.3) indicated a polynomial relationship best explained tissue-based lipid concentrations relative to $\delta^{13}C$ (Fig. 7.2). Both $\delta^{13}C$ and $\delta^{15}N$ were relatively consistent among Clapper Rail eggs across years but differed between sites (Table 7.4), although lipid concentrations varied at several scales. Variance decomposition revealed that the greatest proportion of variation in egg yolk lipids was within estuaries (60%), while a smaller proportion was apparent among years (40%), and a negligible proportion (< 0.01%) among estuaries within years. As expected with embryonic development (Carey 1996), the proportion of lipids in Clapper Rail egg yolks decreased relative to the age of the egg (estimate = -0.003, 95% CI: -0.001, -0.004). Although a linear relationship was not evident between yolk lipid concentrations and the $\delta^{13}C$ of the yolk sample (estimate: 0.002, 95% CI: -0.006, 0.009), lipid concentrations were positively related to the density of fiddler crab burrows within 50 m of Clapper Rail nests (estimate = 0.10, 95% CI: 0.02, 0.22, Fig. 7.3).

DISCUSSION

Tidal marshes of the Gulf of Mexico can experience contrasting gradients of physical and chemical properties, processes that influence the distributions of an array of organisms (Stephens and Bertness 1991, Callaway and King 1996, Travis 1996, Nomann and Pennings 1998, Moody and Aronson 2007). In our study fiddler crabs comprised a single species, *U. longisignalis*, with burrow densities approximately 2 times greater at Grand Bay than at the Pascagoula. Despite large-scale differences, there was considerably greater variation in the distribution of burrows within survey sites and at Grand Bay between habitat types. Because *U. longisignalis* distributions can be influenced by substrate and salinity (Genoni 1985, Mouton and Felder 1996), this variation may be governed by habitat differences and can in turn influence the distributions of other organisms including Clapper Rails.

Although the null model was the best-supported model of Clapper Rail occupancy, similar support was given to the model that related Clapper Rail occupancy to the density of fiddler crab burrows, as study site-specific (Table 7.1). This null model does not imply that in the absence of fiddler crabs Clapper Rails will occupy a site, only that fiddler crab density may not provide substantial support as an explanation of Clapper Rail occupancy. In fact, the similarly-supported site-specific model indicated that at the Pascagoula, Clapper Rail occupancy increased with the density of fiddler crab burrows. The mean density of fiddler crab burrows at the Pascagoula was similar to the minimum estimated for Grand Bay, where no such relationship was evident. The difference in the relationships between fiddler crab burrows and Clapper Rail occupancy between these estuaries provides evidence that a threshold effect may exist in the density of fiddler crab burrows, below which Clapper Rail occupancy decreases. Our results indicate that habitat shifts that affect the spatial distribution of *U. longisignalis* can also influence predators such as Clapper Rails. Similar bottom-up effects have been shown for a variety of estuarine organisms and can extend over several trophic levels and spatial scales (Wainright et al. 2000, Seitz and Lipcius 2001, Seitz et al. 2003, Valiela et al. 2004, Moody and Aronson 2007).

The $\delta^{13}C$ of the primary producers *Spartina* spp. and *J. roemerianus* showed slight differences between estuaries but fell within ranges reported previously for our study area (Sullivan and Moncrieff 1990). In contrast, some differences in the $\delta^{15}N$ of these primary producers were noted among species and estuaries. At Grand Bay, the δ^{15}N of *S. alterniflora* was considerably higher than that of *J. roemerianus*. And while the δ^{15}N of *J. roemerianus* differed among estuaries, the δ^{15}N of *Spartina* spp. was relatively consistent. These differences are not unexpected because within an estuary, source pools of nitrogen can vary at relatively minor scales, reflecting natural variation or anthropogenic inputs (Pruell et al. 2006), directly influencing basal productivity (Bucci et al. 2007, McFarlin et al. 2008). However, hydrological conditions can also act as principle drivers of the distributions of primary productivity within estuarine systems (Jassby et al. 1995, Visser et al. 2002, Higinbotham et al. 2004). Shifting salinity regimes and tidal submergence are linked to the conversion of emergent marsh to patches of open water or non-vegetated substrate (Day et al. 1993, Dunton et al. 2001, Visser et al. 2002). Hydroperiod can also act in concert with sea-level fluctuations and anthropogenic development altering coastal vegetation and the physic-chemical properties of tidal marsh habitat (Turner 1997, Brinson and Christian 1999, Higinbotham et al. 2004, Xu and Wu 2006, Field and Mortech 2007).

Within both the Pascagoula and Grand Bay, the δ^{13}C of the fiddler crab *U. longisignalis* was closer to C_3 than C_4 plants (Table 7.3). In a study of estuarine trophodynamics, Currin et al. (1995) found that *S. alterniflora* and benthic microalgae were primary components of *U. pugnax*'s diet. Although we did not measure the δ^{13}C of benthic microalgae, earlier research conducted in proximity to our study area suggests that the δ^{13}C of benthic microalgae is -20.6 (Sullivan and Moncrieff 1990). Assuming this δ^{13}C remained true for benthic microalgae during the period of our study, this source of primary production could have provided a considerable dietary source for *U.*

longisignalis. Select nutritional properties of the emergent macrophytes *J. roemerianus* and *S. alterniflora* limit their use as a readily accessible nutritional source available to most tidal marsh invertebrate consumers (Kreeger and Newell 2000). Rather, in order to obtain requisite nutrients, invertebrates ingest additional sources of primary production (Kreeger and Newell 2000). Our models indicate that despite these relationships, the lipid concentrations of the fiddler crab *U. longisignalis* were highest when tissue-based $\delta^{13}C$ differed from that of benthic microalgae. Assimilation of emergent macrophyte materials by consumers may play a role in nutrient dynamics such as lipid acquisition and production (Richoux and Froneman 2008). Further research examining relationships between dietary sources and benthic macroinvertebrates would provide valuable information towards our understanding of energy exchanges within estuarine systems.

Absence of a direct relationship between lipid concentration in Clapper Rail egg yolks and the yolk's $\delta^{13}C$ may indicate that localized primary productivity does not directly influence this reproductive metric. Rather, a relationship between the abundance of fiddler crab burrows and amount of egg yolk lipid was more strongly supported (Fig. 7.3). Thus, variation in fiddler crab density occurring at small-spatial scales may be reflected in Clapper Rail egg yolk lipid concentrations. For birds such as the Clapper Rail, physiological limitations during egg formation and embryonic development may have marked effects on offspring survival and development (Monaghan et al. 1998, Nager et al. 2000, Nager et al. 2001). Increased lipid concentrations may benefit developing embryos and hatched young through survival and fitness (Williams 1994), effects that influence future populations.

Within coastal wetlands, the alteration of physio-chemical processes and habitat is expected to continue throughout the next century (Day et al. 2000a, b, Overpeck et al. 2006, Spalding and Hester 2007). The results of this study suggest that these changing conditions will no doubt influence distribution of primary production and subsequently the populations of higher trophic levels. Understanding these changing processes will aid in the development of proactive conservation strategies for the northern Gulf of Mexico.

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TABLE 7.1. Zero-inflated Poisson regression models predicting Clapper Rail site occupancy. ESTUARY indicates one of two estuarine systems in coastal Mississippi, and CRABS is a measure of the relative density of fiddler crab burrows. NULL represents an unparameterized, intercept only model.

Model	Model terms	AIC	ΔAIC	w_i	Deviance	K
1	NULL	402.5	0	0.39	-196.3	5
2	CRABS + ESTUARY + ESTUARY * CRABS	403.3	0.8	0.27	-193.6	8
3	ESTUARY	404.5	2.0	0.14	-196.3	6
4	CRABS	404.5	2.0	0.14	-196.3	6
5	ESTUARY + CRABS	406.5	4.0	0.05	-196.2	7

[a] Difference in AIC values compared to the best-supported model

[b] Akaike weight (Burnham and Anderson 2002).

[c] Number of parameters in the model.

TABLE 7.2. $\delta^{13}C$ and $\delta^{15}N$ of select components of two estuarine ecosystems in coastal Mississippi. Isotope ratios reflect samples collected during 2008. Values represent mean (95% CI) and *denotes sample sizes too small to quantify appropriate estimates of variance.

		Grand Bay			Pascagoula	
Species	n	$\delta^{13}C$	$\delta^{15}N$	n	$\delta^{13}C$	$\delta^{15}N$
Spartina spp.	11	-14.03 (-14.19 to -13.87)	4.89 (3.93 to 5.85)	5	-13.82 (-13.92 to -13.72)	5.75 (4.34 to 10.09)
Juncus roemerianus	16	-25.81 (-26.59 to -25.03)	2.90 (2.41 to 3.39)	10	-27.75 (-28.42 to -27.08)	4.52 (3.66 to 8.18)
Uca longisignalis male	27	-18.38 (-19.07 to -17.69)	4.38 (3.77 to 4.99)	21	-22.87 (-24.07 to -21.67)	6.34 (5.77 to 12.11)
Female	14	-19.21 (-20.39 to -18.03)	4.77 (4.06 to 5.48)	6	-22.09 (-23.62 to -20.56)	6.77 (5.95 to 12.72)
size class						
10 – 14 mm	14	-18.33 (-18.87 to -17.79)	4.83 (4.29 to 5.36)	8	-21.93 (-23.00 to -20.85)	6.49 (5.79 to 7.19)
15 – 19 mm	15	-18.97 (-20.21 to -17.73)	4.52 (3.66 to 5.37)	12	-22.08 (-23.88 to -20.29)	6.66 (5.87 to 7.45)
20 −24 mm	12	-18.66 (-19.78 to -17.55)	4.15 (3.32 to 4.97)	5	-24.39 (-25.91 to -22.87)	6.10 (5.00 to 7.20)
25 – 29 mm	0	---	---	2	-25.23*	5.72*

TABLE 7.3. Relative plausibility of linear mixed effects models relating lipid concentrations in tissues of the fiddler crab *Uca longisignalis*. Tissues sampled from individuals categorized by sex. To account for variation among sampling points and estuaries, models were developed with random intercepts and common slopes. NULL represents an unparameterized, intercept only model and $\delta^{13}C$ represents the carbon isotope ratio of the tissue. Models evaluated using Akaike's Information Criterion (AIC)

Model terms	AIC	ΔAIC[a]	w_i[b]	Deviance	K[c]
$\delta^{13}C + (\delta^{13}C)^2$	-145.6	0	0.78	-155.6	5
$\delta^{13}C$	-142.1	3.5	0.13	-150.1	4
NULL	-141.3	4.3	0.09	-147.3	3

[a] Difference in AIC values compared to the best-supported model

[b] Akaike weight (Burnham and Anderson 2002).

[c] Number of parameters in the model.

TABLE 7.4. $\delta^{13}C$ of Clapper Rail egg yolks collected from within in two estuarine ecosystems in coastal Mississippi.

System	Year	*n*	$\delta^{13}C$ (mean ± SE)	$\delta^{15}N$ (mean ± SE)
Grand Bay	2006	8	-18.39 ± 0.44	8.26 ± 0.36
	2007	4	-19.67 ± 0.95	8.05 ± 0.62
	2008	5	-20.08 ± 0.85	7.77 ± 0.26
Pascagoula	2006	27	-20.86 ± 0.54	8.49 ± 0.40
	2007	12	-22.13 ± 0.46	10.29 ± 0.30
	2008	5	-22.13 ± 0.72	10.61 ± 0.78

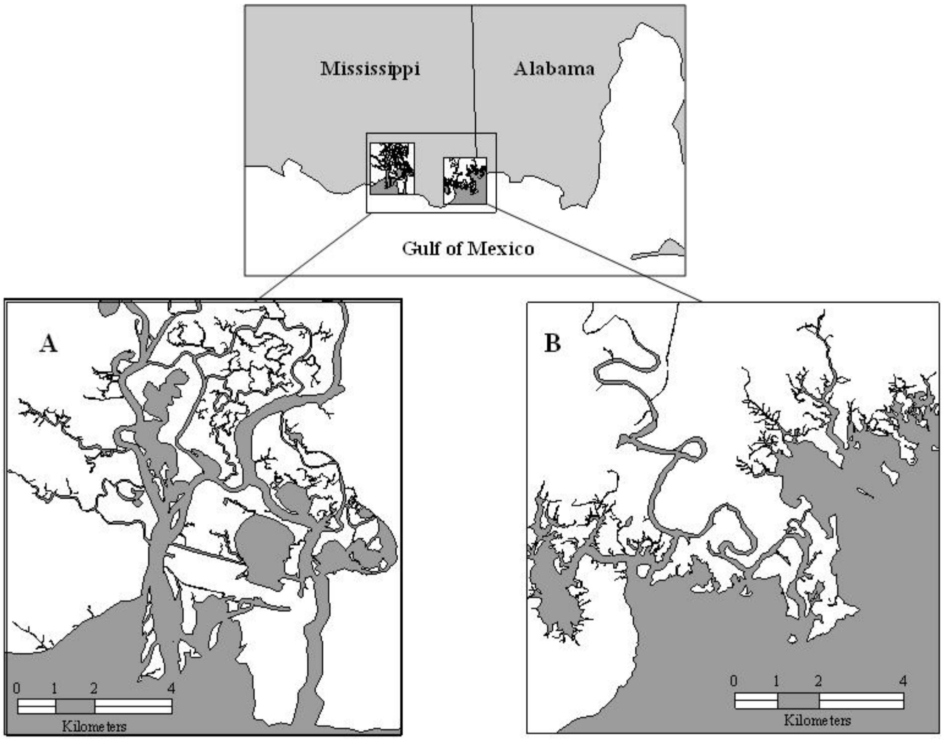

FIGURE 7.1. Study areas within Jackson County, Mississippi. Panel (A) shows the Pascagoula River (B) shows Grand Bay.

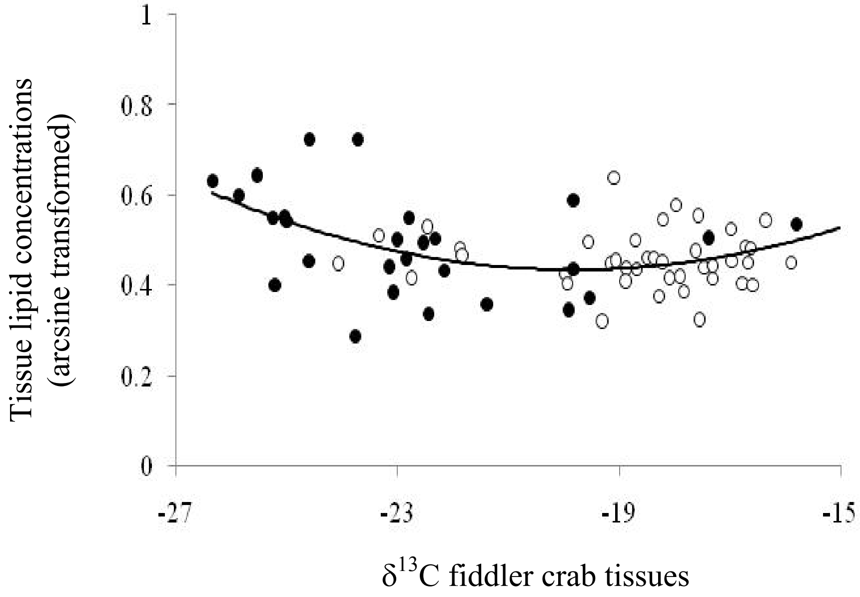

FIGURE 7.2. Lipid concentrations measured in fiddler crab tissues relative to tissue δ13C. Filled circles denote samples collected from the Pascagoula and open symbols reflect samples obtained from Grand Bay. Solid line represents best-fit second-order polynomial equation.

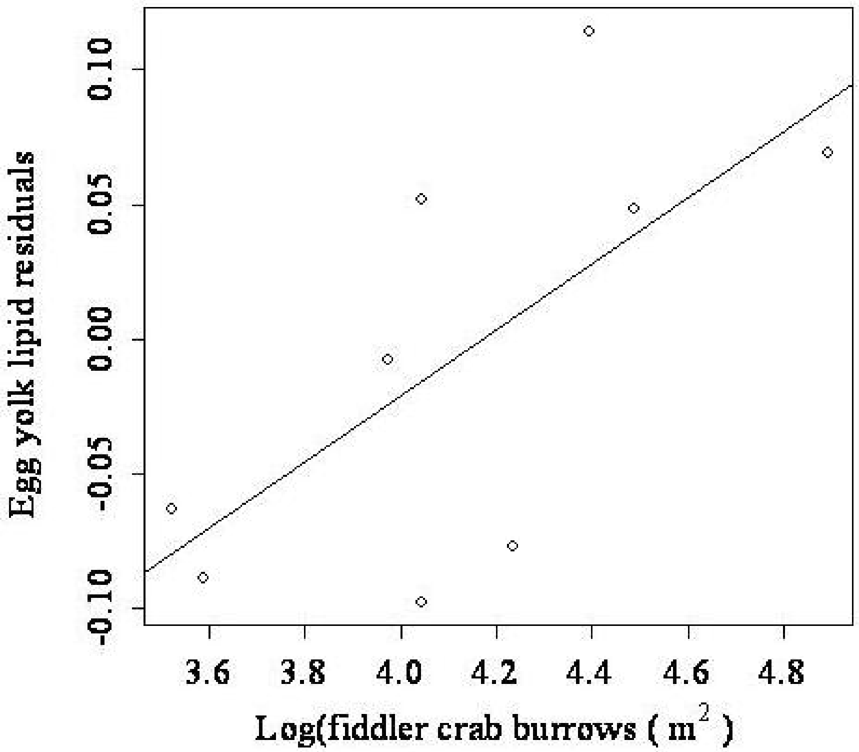

FIGURE 7.3. Relationship between proportion of lipids in Clapper Rail egg yolks and the density of fiddler crab burrows within 50 m of Clapper Rail nest sites. Lipid concentrations have been corrected for the incubation stage of the Clapper Rail egg at the time the egg was collected and the residuals are plotted.

CHAPTER 8

HYDROLOGIC CONDITIONS AND PREDATOR-PREY DYNAMICS INFLUENCE CLAPPER RAIL POPULATIONS FROM THE BOTTOM-UP [1]

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[1] Rush, S. A., A. T. Fisk, M. S. Woodrey, and R. J. Cooper. To be submitted to *Aqueous Goodness*.

ABSTRACT

Tidal estuaries of the northern Gulf of Mexico are inhabited by a rich assemblage of marsh bird species, but many are already facing population declines or reduced habitat availability. For the majority of these species, such as the Clapper Rail (*Rallus longirostris*), ecological information remains limited and hinders predictions relating the impact of habitat loss and alteration on population stability. During three consecutive breeding seasons (2006 to 2008) we estimated annual densities of Clapper Rail adults, salinity levels of tidal waters and lipid concentrations in eggs, a secondary metric of reproduction, to explore trophic interactions at multiple spatial sales in two northern Gulf of Mexico estuaries. We found that that egg lipid concentrations provide a predictive meter of the abundance of adults in subsequent years, and that lipid concentrations may be governed by trophic feedbacks experienced during egg formation and driven by hydrologic conditions. Similarities among populations suggest that these patterns may be influenced by salinity regime, highlighting the interplay between spatial and temporal dynamics within estuarine systems. Our results indicate that within estuaries, drivers of predator-prey dynamics should be viewed as spatially and temporally dynamic. Thus, conservation initiatives developed for tidal marsh-dependent organisms should include consideration of factors at multiple spatio-temporal scales.

KEYWORDS: estuaries, fiddler crab, hydrology, northern Gulf of Mexico, predator-prey, *Rallus longirostris*, salinity, *Uca longisignalis*

INTRODUCTION

Estuaries are productive systems, with dynamic processes structuring the distributions of organisms (Stephens and Bertness 1991, Frederick and Loftus 1993, Callaway and King 1996, Normann and Pennings 1998, Beck et al. 2001, Behum et al. 2005). However, predicting the response of estuarine ecosystems to changing environmental conditions is challenging, as it necessitates understanding the complex interactions among several trophic levels (e.g., primary production, predators and their prey) (Boesch and Turner 1984, Costanza et al. 1990, Day et al. 1993, McFadden et al. 2007, Moody and Aronson 2007).

Historically, consumers have been considered to play a dominant role in shaping trophic structure within estuarine ecosystems (Odum and Smalley 1959, Smalley 1960, Teal 1962, Marples 1966). More recent work, however, has challenged this view and emphasized the importance of consumers and their interaction with other biotic and abiotic factors. Fiddler crabs (Ocypodidae: *Uca*) are common inhabitants of coastal tidal marshes and have adapted to wide ranges of environmental conditions such as temperature, salinity, and relative humidity (Miller and Vernberg 1968, Miller and Maurer 1973, Rabalais and Cameron 1985). One species, *Uca longisignalis*, inhabits tidal marshes of the northern Gulf of Mexico where the salinity of burrow and adjacent waters range from 18 to 34.5‰ (Rabalais 1983). Like most fiddler crabs, *U. longisignalis* has a complex life cycle that spans multiple habitats (Mouton and Felder 1995). In particular, adults live and spawn in brackish estuaries, with spawning beginning in early spring and peaking in mid-summer (Mouton and Felder 1995). Larvae (zoea) hatch, are transported from the estuary during flood tides, and are dispersed into the coastal ocean where development is completed (Tankersley et al. 1995, Christy and Morgan 1998, Godley and Brodie 2007). Developed larvae (late stage zoeae) reinvade estuaries during flood tides and find suitable benthic habitats by settling in response to environmental cues (O'Connor & Epifanio 1985, Christy 1989, O'Connor 1993, Tankersely et al. 1995). On returning to the estuary, postlarvae (megalopae) may experience drastic changes in ambient salinity, especially during rainstorms when the quantity of freshwater runoff entering tidal creeks increases. Young crabs may be more sensitive to changes in ambient salinity than adults, who can dig burrows and have more mature osmoregulatory systems. As an example, Rabalais and Cameron (1985) and Thurman (2003) reported mortality of 50% of adult populations of *U. longisignalis* when salinity fell below 62 Mos. M / kg, or approximately 5‰. In contrast, juvenile *U. longisignalis* often cannot survive salinities < 15‰ (Rabalais1983). Therefore, as for other species, drastic reductions in salinity during megalopae reinvasion may significantly reduce settlement and recruitment (Godley and Brodie 2007).

Fiddler crabs play important roles in estuarine ecosystems. The burrowing activity of fiddler crabs has been shown to have profound effects on estuarine productivity (Montague 1980, Bertness 1985). Here, burrowing effects extend to both marsh substrata and the growth and distributions of emergent macrophytes (Bertness 1985, Gribsholt et al. 2003). In turn, macrophytes can provide refugia from ambient conditions such as heat and dessication, and from predation (Teal 1958, Normann and Pennings 1998). Within estuaries, birds such as the Clapper Rail (*Rallus longirostris*) prey on fiddler crabs (Teal 1958, Crane 1975, Thurman 2003, Eddleman and Conway 1998) and fiddler crab distributions exert bottom-up effects limiting predator distributions (Johnson et al. 1990, Ribeiro et al. 2003, Valiela et al. 2004). For example, low recruitment in fiddler crab populations can reduce nutrient availability to breeding Clapper Rails, and previous research identified a positive relationship between the density of fiddler crab adults and lipid concentrations in the yolks of Clapper Rail eggs (S. Rush unpubl. data).

For birds such as the Clapper Rail, reproduction is a nutrient-demanding process (Carey 1996), and physiological limitation during egg development may have marked effects on productivity and population trends (Monaghan et al. 1998, Nager et al. 2000, Nager et al. 2001, Visser and Lessells 2001). Thus, understanding periodicities in fiddler crab recruitment may ultimately serve to explain variations in estuarine productivity and Clapper Rail populations (Katz 1980, Montague 1980, Bertness 1985).

Many species of marsh birds, including Clapper Rail, are already facing population declines (Eddleman et al. 1988, Erwin et al. 2006). Although predictive models and conservation plans have been developed for most species, these efforts are often hampered by limited understanding of trophic interactions such as predator-prey dynamics (Eddleman and Conway 1998, Greenberg et al. 2006). The present study was initiated to improve understanding of broad-scale relationships associated with Clapper Rail population trends in two estuarine systems of the northern Gulf of Mexico. One primary objective was to examine whether prey population dynamics may influence Clapper Rail populations from the "bottom-up." Specifically, does evidence support a link between precipitation, salinity of estuarine waters, fiddler crab recruitment, Clapper Rail reproduction and the subsequent density of breeding adults? Conceptually, salinity affects the recruitment of *U. longisignalis* in year t which provides prey stock for Clapper Rails breeding in year $t + 1$, and can influence Clapper Rail adult populations in year $t +$

2 (Fig. 8.1). Accordingly, we evaluated associations among salinity profiles in year *t*, concentrations of lipids in Clapper Rail eggs in year *t* + 1, and the density of Clapper Rails in year *t* + 2. These metrics were also compared between estuaries to identify any differences at the landscape scale. Finally, we comment on the possible significance of our findings in relation to habitat alteration, climate change and conservation of marsh birds and estuarine ecosystems.

STUDY AREA AND METHODS

STUDY AREA – Our study area was two estuarine systems in coastal Jackson County, Mississippi, USA: 1) the Pascagoula River Marsh Coastal Preserve (hereafter Pascagoula, 30º 25'N, 88º 34'W) and 2) the Grand Bay National Estuarine Research Reserve (hereafter Grand Bay, 30º 20'N, 88º 24'W) (Fig. 8.2). The approximately 4500 ha of the oligohaline to mesohaline emergent marsh of the Pascagoula was dominated by *Juncus roemerianus*, *Spartina alterniflora*, *S. cynosuroides* and *Sagittaria lancifolia*. The approximately 7000 ha of the polyhaline Grand Bay site was dominated by *J. roemerianus*, with *S. alterniflora* found in narrow fringes along the water interface. Both estuaries experience irregular micro-tides (<1 m: Dardeu et al. 1991), warm vernal climates with mean summer temperature of 27˚ C, and average monthly summer precipitation of 16 cm. By the definition of Cowardin et al. (1979), the Pascagoula is considered truly estuarine, subject to heightened tides and fluctuations in river flow (Eleuterius 1972), while the polyhaline tidal marsh of Grand Bay receives oceanic input and is not directly associated with riverine discharge.

CLAPPER RAIL DENSITY – Following the sampling methodology described in the North American Marshbird Monitoring Protocol (Conway 2008) and Conway and

Droege (2006), we conducted Clapper Rail surveys at 118 locations in Mississippi during 2006, 2007, and 2008. Survey points were all at least 400 m apart and four replicate surveys were conducted at each survey point. Surveys were structured to ensure > 2 weeks between visits. Each year, initial surveys were conducted between 27 Mar and 25 April with the final survey conducted by 9 July, and the mean number of days between replicate surveys was 25. During each survey, the presence of Clapper Rails was recorded only if they were detected (heard or seen) within 200 m of the survey point. All surveys were conducted by one of three surveyors.

For the entire three-year period 2006 to 2008 we estimated the density of Clapper Rails at Grand Bay and the Lower Pascagoula using program DISTANCE (Version 5.0: Thomas et al. 2006). Program DISTANCE models the probability of detection at increasing distances from the observer, which are incorporated into estimates of density (Buckland et al. 2001). We assessed the ability of various combinations of key functions (half-normal and hazard-rate) and adjustment terms (cosine, simple polynomial and hermite polynomial) to model detection curves for Clapper Rails using Akaike's Information Criterion (AIC; Akaike 1973) and goodness-of-fit (GOF) chi-square analysis. We applied a post stratification scheme to model differences in the density of Clapper Rails among years and within each of our two study areas (Buckland et al. 2005). Additionally, we used individual surveyors as model covariates to adjust for detection differences among observers. To improve model fit, we truncated all observations beyond 100 m, and to avoid heaping, we grouped observations into distance intervals (Buckland et al. 2001).

CLAPPER RAIL REPRODUCTION – From April to July in 2006, 2007 and 2008, we searched for active Clapper Rail nests in areas where adults had been heard calling (Adams and Quay 1958), or by walking through suitable nesting habitat. Once a nest was discovered, all eggs were aged using floatation methods outlined in Rush et al. (2007) and a single egg was collected at random.

Prior to chemical analysis, all Clapper Rail eggs were frozen and freeze-dried to remove moisture. Yolks were separated from each egg and lipids were extracted using a 2:1 ratio of Chloroform / Methanol (Bligh and Dyer 1959). Yolk samples were immersed in a volume of solvent three to five times greater than sample volume, mixed for 30 s, and left undisturbed for 24 hrs. The supernatant and solids were poured through glass filter paper (Whatman Ashless Filter Paper, Whatman International Ltd., Kent, UK), and the supernatant was collected. Mass balance equations were used to determine the proportion of lipid relative to each sample.

Egg yolk lipid concentrations were standardized relative to the age of the egg (number of days post- laying) and among nests using random intercepts to accommodate the hierarchical structure of nests within estuaries and among years. Within each estuary, we modeled egg yolk lipid concentration as a function of nest-level predictors plus a random error:

$$Y_{ijk} = \pi_{0jk} + \pi_{pjk}\alpha_{ijk} + e_{0ijk}$$

where Y_{ijk} is the concentration of lipids in an egg collected from nest *i* in estuary *j* and year *k*. Further, π_{0jk} is the intercept for estuary *j* in year *k*, α_{ijk} is a nest characteristic that predicts the effect of egg age on mean yolk lipid concentration, π_{pjk} are the corresponding estuary level characteristics that indicate the direction and strength of the association between each nest characteristic, a_p, and the outcome in estuary *jk*, and $e_{0_{ijk}}$ is a level-1 random effect representing the deviation of lipid concentrations measured in an egg sampled from nest *ijk* from the predicted concentration based on the estuary –level model. These residual nest effects were assumed to be normally distributed with a mean of 0 and a variance σ^2. Variation among estuaries within years was modeled, with each estuary effect, π_{pjk} as:

$$\pi_{pjk} = \beta_{p0k} + \sum_{q=1}^{Q_P} \beta_{pqk} X_{qjk} + r_{pjk}$$

where β_{p0k} is the intercept for year *k* in modeling the estuary effect π_{pjk}, X_{qjk} is an estuary characteristic used as a predictor of the estuary effect π_{pjk}, β_{pqk} is the coefficient representing the direction and strength of the association between estuary characteristic X_{qjk} and π_{pjk}. Lastly, r_{pjk} is a level-2 random effect that represents the deviation of estuary *jk*'s level-1 coefficient, π_{pjk}, from its predicted value based on the estuary-level model. Similarly, each level-3 "outcome" may be predicted by some year-level characteristic.

$$\beta_{pqk} = \gamma_{pq0} + \sum_{s=1}^{S_{pq}} \gamma_{pqs} W_{sk} + u_{pqk}$$

Similar to other levels, γ_{pq0} is the intercept term, W_{sk} is a year characteristic used as a predictor for year effect, γ_{pqs} is the corresponding level-3 coefficient, and u_{pqk} is the level-3 random effect.

This model partitioned the total variability in the outcome Y_{ijk} into three compartments: (level 1) among nests within estuaries, σ^2; and (level 2) among estuaries within years, τ_π; and (level 3) among years, τ_β. This process allowed us to estimate the proportion of variation in egg yolk lipid concentrations within estuaries, among estuaries within years, and among years (Raudenbush and Bryk 2002). Models were estimated with the statistical package R, (version 2.7.1: *lmer*, R Development Core Team 2008) using Laplace approximation and maximum likelihood (Bates and Sarkar 2007).

Model intercepts, reflecting variation in lipid concentrations among years, were assessed using 95% confidence intervals. Estimates were derived with the function *mcmcsamp* in the R package *lme4* (Bates and Sarkar 2007) by first generating a Markov Chain Monte Carlo (MCMC) sample from the posterior distribution of each parameter estimate. We then computed the Bayesian highest posterior density (HPD) 95% confidence intervals of the MCMC sample for each parameter estimate using the function *HPDinterval* in *lme4* (Bates and Sarkar 2007).

SALINITY AND FIDDLER CRAB RECRUITMENT − The severity and duration of salinity alterations can affect the survival, settlement and recruitment of fiddler crabs (Rabalais and Cameron 1985, Thurman 2003, Godley and Brodie 2007). Rabalais (1983) and Thurman (2003) found that *U. longisignalis* megalopae experience reduced survival in salinities < 2.5 mS/cm. Therefore, we assumed an increase in juvenile mortality at this concentration. *U. longisignalis* breed between May and September in northern Gulf Coast estuaries (Mouton and Felder 1995), and recruitment of juveniles may peak in mid to late summer (Mouton and Felder1996). From 1 May – 31 Aug, in 2006, 2007, and 2008, we obtained salinity profiles from monitoring stations located within each estuary (NWIS 2001, NOAA 2004), and we calculated the proportion of days with salinity concentration <2.5 mS/cm. Similarly, mean daily precipitation measurements were obtained from a monitoring station located within the greater watershed of the study area (mean distance from study sites: 5 km: Weather Underground station KMSPASCA3, The Weather Underground 2008).

Data were log-transformed or arc-sine square-root transformed to meet normality assumptions when necessary. Except where indicated, we report the parameter means and 95% confidence intervals.

RESULTS

From 1 May – 31 Aug of 2004 to 2008, precipitation varied considerably among years with periods of precipitation correlating with lower salinities measured within both estuaries (Fig. 8.3). In general, salinity concentrations were considerably lower at the Pascagoula than at Grand Bay, although the Pascagoula experienced a greater proportion of days with salinity concentrations below the LC_{50} of *U. longisignalis* megalope (2.5 mS/cm: Table 8.1); the one exception was 2006 when neither estuary experienced salinities below 2.5 mS/cm. Both estuaries experienced the greatest number of days with salinity concentrations below the LC_{50} of *U. longisignalis* during 2005 (Table 8.1).

Clapper Rail egg yolk lipid concentrations varied considerably more within estuaries and among years than between estuaries (Table 8.2). Variance decomposition revealed that the greatest proportion of variation in egg yolk lipids was within estuaries (60%), a smaller proportion among years (40%), and a negligible proportion (< 0.01%) among estuaries within years. As expected with embryonic development (Carey 1996), the proportion of lipids in Clapper Rail egg yolks decreased relative to the age of the egg (estimate = -0.003, 95% CI: -0.001, -0.004). Mean parameter estimates indicated that within both estuaries, egg yolk lipid concentrations were highest during 2007, lowest during 2006, and mid-range in 2008 (Table 8.2).

The best supported model describing the distribution of adult Clapper Rails indicated that observer and site were important variables to consider in explaining Clapper Rail detection (Table 8.3). Evidence indicated that the density of Clapper Rails differed between years and estuaries (Table 8.4). However, the population at Grand Bay exhibited greater inter-annual variation (Fig. 8.4). Here, the density of Clapper Rails was lowest in 2006 and although, at the Pascagoula, Clapper Rail density was also low in 2006, estimates did not differ between 2006 and 2007. Within both estuaries, Clapper Rail densities were highest during 2008 (Fig. 8.4).

DISCUSSION

Physical forcing, such as salinity change, can structure biological communities and shape ecological interactions within estuaries (Ritter et al. 2005, Lucero et al. 2006, Jyothibabu et al. 2007), effects that can extend across trophic levels, habitat gradients and landscapes (Crain et al. 2004, Posey et al. 2005, Speckman et al. 2005). Although we did not quantify fiddler crab recruitment directly, limitations in prey availability have been shown to manifest in secondary metabolite concentrations in the eggs of predatory birds (Török et al. 2007). Clapper Rails feed predominantly on fiddler crabs, including species such as *U. longisignalis* (Teal 1958, Crane 1975, Thurman 2003, Eddleman and Conway 1998). Reductions in the abundance of this prey resource, via limited recruitment, can translate to lowered nutrient availability for reproduction.

Generally, our results support this model where for the Pascagoula and Grand Bay estuaries, precipitation was linked to the salinity of the estuarine waters. These salinity patterns were reflected in Clapper Rail egg yolk lipid concentrations, where lipids measured in year $t + 1$ reflected the proportion of days with salinity concentrations below 2.5 mS/cm (the LC_{50} of *U. longisignalis* megalope) measured in year *t* (Tables 8.1, 8.2). This relationship appeared strongest for the Pascagoula, where the proportion of days with salinity concentration below the LC_{50} of *U. longisignalis* megalope was highest in 2005 and lowest in 2006. Egg yolk lipid concentrations tracked this relationship, as they were lowest in 2006 and highest in 2007 (Table 8.2). Although Grand Bay also experienced low salinities in 2006, there were no days of low salinities measured in 2006 and 2007 (Table 8.2). Despite these limited salinity differences at Grand Bay, Clapper Rail egg yolk lipid concentrations differed between years and were relatively similar to the Pascagoula (Table 8.3). Within both estuaries, densities of adult Clapper Rails were highest in 2008. At Grand Bay, densities were lowest in 2006, while at the Pascagoula, the density of adult Clapper Rails did not differ between 2006 and 2007 (Fig. 8.4). These results indicate that dynamic relationships link precipitation, salinity, fiddler crabs and Clapper Rails; however, they also suggest that the magnitude of the linked effects may vary by estuary.

Within microtidal estuaries such as the Pascagoula and Grand Bay, dominant physical processes such as mixing are governed by the actions of wind, waves and freshwater inflow (Monbet 1992). Here, the magnitude of freshwater discharged into an estuary is influenced by complex forces and environmental conditions, including the strength and duration of storm events and landscape characteristics (Dyer 1997, Russel and Montagna 2007, Williams et al. 2008). Additionally, the effects of anthropogenic alteration and changes in landscape connectivity, such as tidal flushing, can influence chemical patterns (Levin and Talley 2000, Paerl et al. 2006, Lane et al. 2007), where watershed alteration increases freshwater runoff and salinity patterns across space and time (Blood and Smith 1996). The watershed of the Pascagoula and Grand Bay estuaries has not been extensively developed (S. Rush. unpubl. data), though these two estuaries represent distinct geophysical characteristics. The Pascagoula lies at the mouth of the Pascagoula River and is subject to riverine discharge. Contrasting with marine-dominated estuaries such as Grand Bay, estuaries such as the Pascagoula may experience lower salinities or greater salinity variation over spatial scales (Dyer 1982, Moore 1992). In general, the salinity profile of the Pascagoula followed this expectation with lower salinities measured across the five years of this study (Fig. 8.3). Conversely, following a storm event, the intrusion of freshwater, marked by large quantities of precipitation, preceded a strong dip in the salinity profile (Fig. 8.3). This relationship means that storm events induce similarities in forcing patterns among estuarine systems (Day et al. 1989, Mallin et al. 1993, Kimmerer 2002, Godley and Brodie 2007).

Physical and chemical gradients can influence settlement patterns of consumers such as fiddler crabs (Levinton and Kelaher 2004, Godley and Brodie 2007). In the present study, salinity profiles were obtained from a single location and depth within each estuary and did not account for localized variation. Although salinity measurements illustrated similarities between estuaries, the settlement pattern of fiddler crab megalopae can be influenced by hydroperiod, depth, latitudinal variation in salinity regime and physical habitat characteristics, differences among which often occur at localized spatial scales (Johnson 1985, O’Connor and Epifanio 1985, Epifanio et al. 1988, Little and Epifanio 1991, DeVries et al. 1994, Garrison 1999, Forward et al. 2001, Jones and

Epifanio 2005, Godley and Brodie 2007). Consequently, factors influencing the recruitment of megalopae and their settlement within habitats may not have been apparent. These local differences can also affect the spatial patterning of adults and their predators (Behum et al. 2005). For instance, previous research identified a positive relationship between the density of fiddler crab adults and lipid concentrations in the yolks of Clapper Rail eggs (S. Rush unpubl. data). While not measured in the present study, variation in the density of fiddler crabs may provide an explanation for the considerable variation in Clapper Rail egg yolk lipid concentrations among nests (60%), variation that far exceeded differences among estuaries (<1%). These differences underscore the importance of both spatial and temporal patterns in estuarine ecology (Ellis and Schneider 2008).

Freshwater inflow is essential for delivering nutrients to estuaries and has been linked to increased production at fundamental and higher levels (Odum 2000, Rabalais et al. 2002). Although evidence suggests that the impact of restricting freshwater inflow to estuarine aquatic communities can vary, there are apparent differences among taxa (Dame and Kenney 1986, Drinkwater and Frank 1994, Crain et al. 2004, Gillanders and Kingsford 2002, Montagna et al. 2002). As a positive example Litulo (2006) found that the reproductive output of the fiddler crab *U. chlorophthalms* increased in proportion to rainfall in a given season. Litulo (2006) suggested that this relationship was driven by the delivery of nutrient rich waters to the estuary, which decreased local salinity and promoted conditions conducive to reproduction. Although freshwater inflows may carry long-term benefits for some species, as noted here, reductions can have acute negative impacts on both survival and reproduction (Gillanders and Kingsford 2002, Godly and

Brodie 2007) and may extend non-linearly to higher trophic levels (Bruno and O'Connor 2005, Putland and Iverson 2007).

For birds such as the Clapper Rail, reproduction is a nutrient-demanding process (Carey 1996). Physiological limitations during egg formation and embryonic development may have marked effects on offspring survival and development (Monaghan et al. 1998, Nager et al. 2000, Nager et al. 2001). Past research has demonstrated that the density of fiddler crab burrows correlates positively with lipid concentration in Clapper Rail eggs (S. Rush unpubl. data). In turn, increased lipid concentrations benefit developing embryos and hatched young, through survival and fitness (Williams 1994).

Other factors, such as habitat structure, influence productivity of Clapper Rails. In particular, breeding Clapper Rails select features of available habitat that allow plasticity in nest height, an effort aimed at minimizing nest loss due to flooding and predation (Storey et al. 1988, Gaines et al. 2003). The frequently flooded polyhaline and mesohaline salt marshes of the northern Gulf Coast, such as Grand Bay, are characterized by a relatively low richness of vascular plant species (Eleuterius 1972, Odum 1988, Visser et al. 1998). As a result, the structural diversity of marsh vegetation often decreases relative to the salinity of the system (Odum et al. 1995). Clapper Rails nesting within polyhaline tidal marshes of the northern Gulf Coast, such as Grand Bay, experience increased nest loss as a result of tidal flooding (S. Rush unpubl. data). Therefore, the implication of habitat differences can extend to reproductive success and may explain greater annual variability in the population of Clapper Rails at Grand Bay (Fig. 8.4).

Within many coastal areas, the occurrence of heavy rainfall is predicted to increase due to climatic warming (Diffenbaugh et al. 2005, Trapp et al. 2007). It is therefore important to know the likely impact of heavy rainfall, both now and in the future. As we have shown for the northern Gulf of Mexico, rainfall may influence predator-prey dynamics in estuarine systems. Additionally, within tidal marshes of the southern United States, hydrologic conditions can act in concert with sea-level fluctuations and anthropogenic development altering coastal vegetation and tidal marsh ecosystems (Turner 1997, Brinson and Christian 1999, Greenberg et al. 2006, Lee et al. 2006, Xu and Wu 2006, Field and Mortech 2007). Increased understanding of the drivers of trophic-habitat relationships at localized, landscape and watershed levels will help us to predict the effects of environmental change on biotic communities within estuarine systems. To this end, conservation initiatives developed for tidal marsh-dependent organisms should consider ecological attributes, such as predator-prey dynamics, as spatially and temporally dynamic. The functional estuary and its ecological attributes, including predator-prey dynamics, must be viewed as spatially and temporally dynamic. Attributes of functional estuaries, such as connectivity, must be maintained in order to achieve resilience in the face of climate and other global change.

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TABLE 8.1. Percentage of days with salinity < LC_{50} of larval *Uca longisignalis* during 5 years within two northern Gulf of Mexico estuaries.

Year	Percentage of days with minimum specific conductivity < LC_{50}*	
	Grand Bay	Pascagoula
2004	0	24
2005	13	29
2006	0	0
2007	0	2
2008	7	21

*LC_{50} considered 2.5 mS/cm as given in Rabalais (1983) and Thurman (2003)

TABLE 8.2. Sample size and lipid concentration of yolks of Clapper Rail eggs from two estuarine ecosystems in coastal Mississippi. Lipid concentrations derived from random intercept mixed model.

Year	Number of eggs sampled		Intercept coefficients for egg yolk lipid concentrations (%) (Mean, 95% CI)	
	Grand Bay	Lower Pascagoula	Grand Bay	Lower Pascagoula
2006	8	27	0.69, 0.66 – 0.72	0.67, 0.60 – 0.74
2007	4	12	0.84, 0.79 –0.89	0.86, 0.82 – 0.90
2008	5	5	0.77, 0.72 – 0.82	0.71, 0.64 – 0.78

TABLE 8.3. Model selection for models fitting detection functions to survey data collected from Clapper Rails in coastal Mississippi. Models developed using DISTANCE. For each model K represents the number of parameters and w_i is the model weight or the strength of evidence in favor of a particular model. Covariates used to model detection at the stratum level were observer (Obs) and Site. Null indicates stratum-specific covariates were not included in the model.

Key function	Detection covariates	K	Log-likelihood	AIC	ΔAIC	w_i
Half-normal	Obs + Site	11	-1773.23	3568.45	0.0	0.88
Half-normal	Null	3	-1783.54	3573.07	4.62	0.09
Hazard-rate	Null	3	-1784.68	3575.36	6.91	0.03
Hazard-rate	Obs + Site	17	-1771.77	3577.53	9.08	0.01

TABLE 8.4. Density estimates (using DISTANCE) for Clapper Rails during 3 years and within two estuarine systems in coastal Mississippi.

Model selected	GOF	Location	Year	Density (birds / ha) mean, 95% CI	n	% CV
Half-normal cosine	0.11	Lower Pascagoula	2008	0.90, 0.77 – 1.06	280	11.89
	0.05		2007	0.46, 0.36 – 0.60	225	13.61
	0.10		2006	0.50, 0.41 – 0.62	366	10.99
	0.05	Grand Bay	2008	1.17, 0.94 – 1.44	216	15.16
	0.16		2007	0.52, 0.42 – 0.67	190	13.55
	0.38		2006	0.28, 0.22 – 0.36	153	13.01

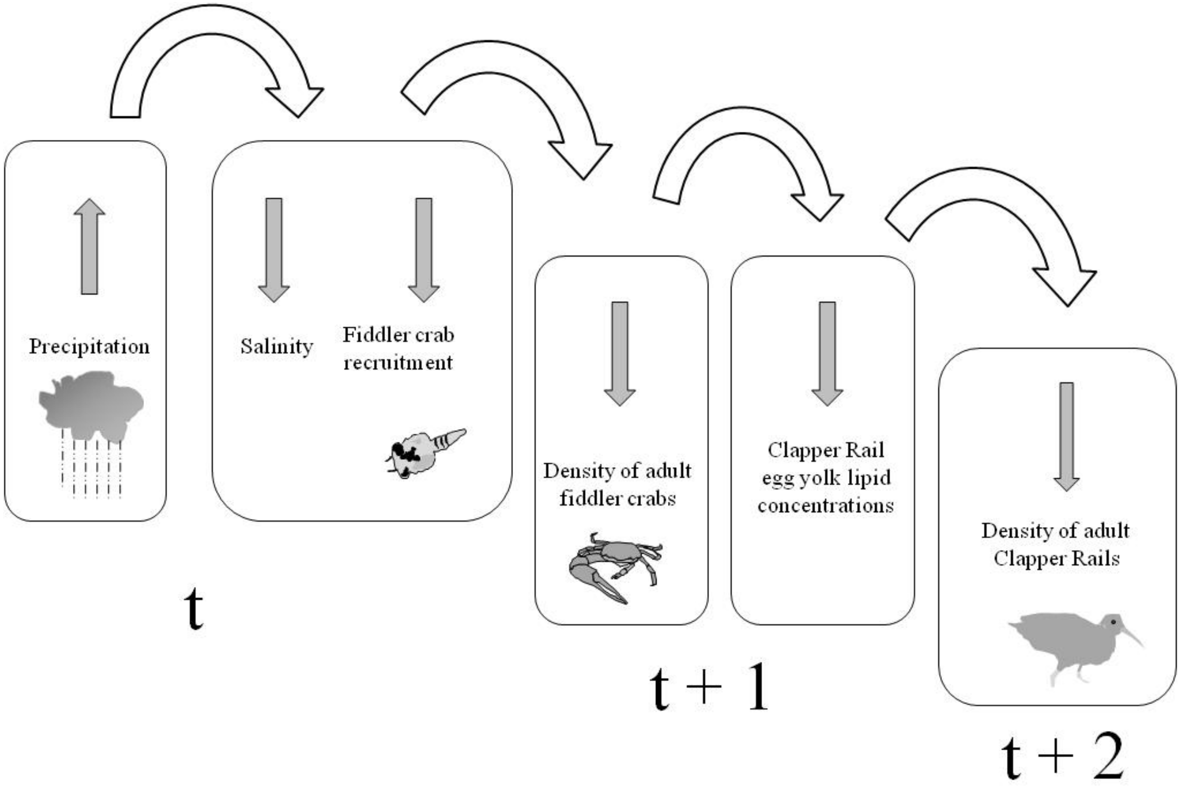

FIGURE 8.1. Conceptual model of relationships between precipitation, salinity, fiddler crabs and Clapper Rails over a three year period. Letters below boxes denote time periods where t represents year 1, t + 1 year two and t + 2 year three. Arrows above individual model components represent hypothetical directional effects initiated with increased precipitation.

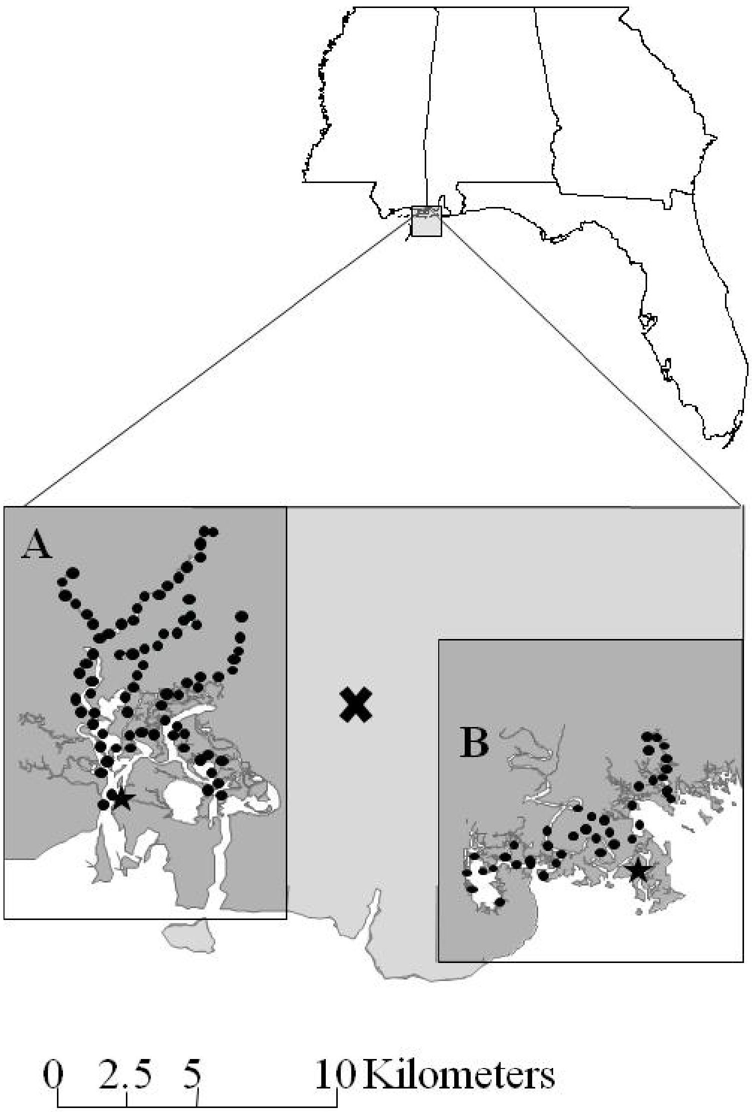

FIGURE 8.2. Study areas within Jackson Count, Mississippi. Panel (A) the Lower Pascagoula River and (B) Grand Bay. For each panel black circles indicate locations where marsh bird surveys were conducted and the black star represents the location of the water quality monitoring station where salinity measurements were recorded. The black X between the panels indicates the location of the weather monitoring station where precipitation was measured.

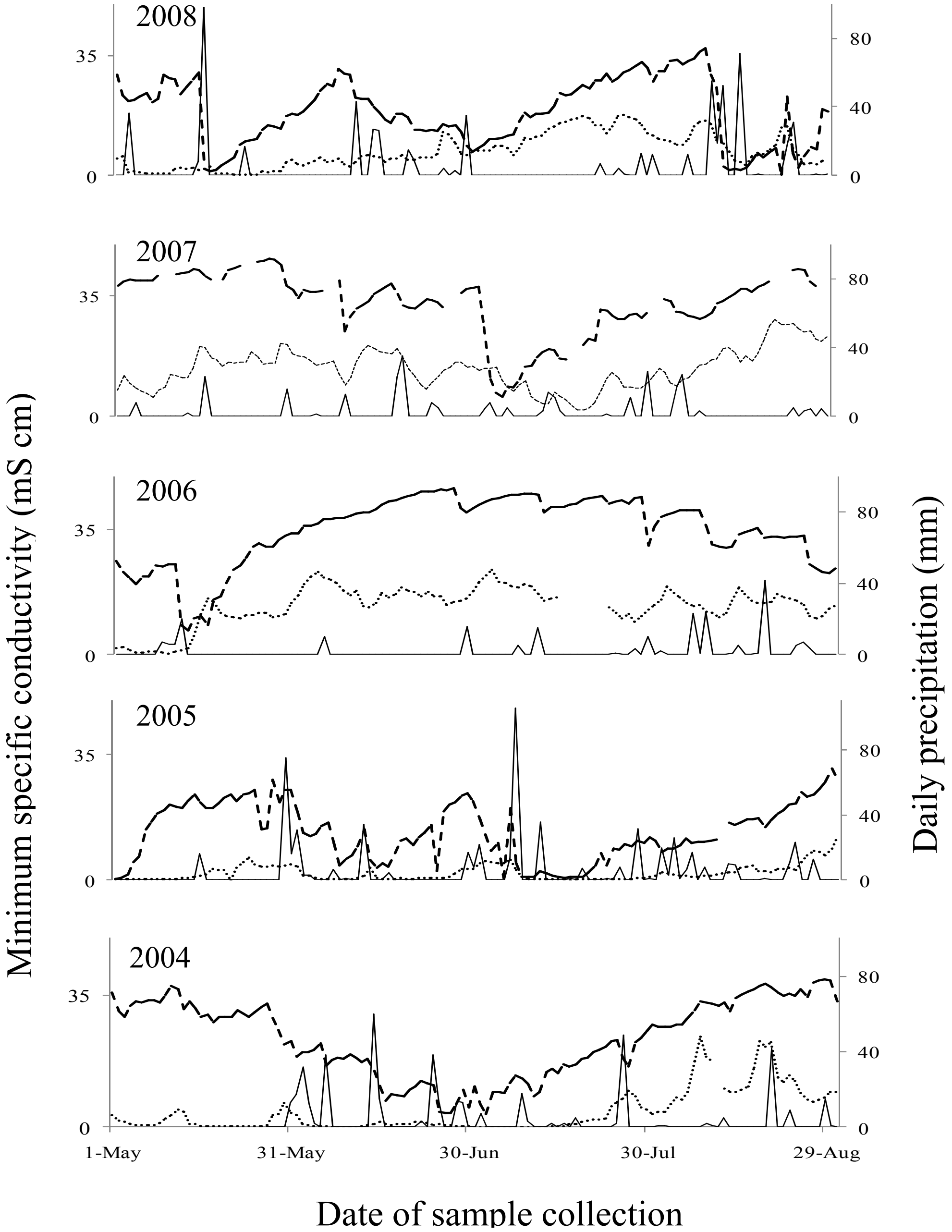

Figure 8.3. Yearly salinity profiles of the Pascagoula and Grand Bay Estuaries relative to precipitation. Light dashed line represents salinity at the Pascagoula while the heavy dashed line represents salinity at Grand Bay. Light solid line indicates precipitation measurements obtained at a monitoring station located between the two estuaries

FIGURE 8.4. Density of Clapper Rails in two northern Gulf of Mexico estuaries. Gray bars represent the Pascagoula while white bars represent Grand Bay. Error bars are 95% confidence intervals.

CHAPTER 9

SUMMARY AND CONCLUSIONS

In the preceding chapters I provided an evaluation of factors that influence the spatial, reproductive and trophic ecology of Clapper Rails within northern Gulf of Mexico tidal marshes. This research provides insight into the forces that shape the distributions of Clapper Rails in both space and time. This type of information is critical to furthering our understanding of the ecology of Clapper Rails, other marsh birds and the tidal marsh ecosystems of the northern Gulf of Mexico.

In Chapter 1 I provided an overview of some of the important characteristics of the tidal marshes of northern Gulf of Mexico, dominant threats to these unique ecosystems, and highlighted some interesting facets of marsh birds and their ecology. Further, I provide limited discourse in how the loss of tidal marsh habitat can affect marsh birds such as the Clapper Rail. In Chapter 2 we applied occupancy models (MacKenzie et al. 2006) to identify current distributions of selected marsh bird species. Based on anticipated habitat alteration we projected changes in the distributions of these marsh birds under several different scenarios. For Least Bittern, Marsh Wren and Common Yellowthroat, species most frequently associated with freshwater to oligohaline tidal marsh, anticipated habitat change such as increased salinity may negatively influence future occupancy. While Seaside Sparrow and Clapper Rails may profit from the effects of increased salinity, the anticipated loss of emergent marsh habitat may negatively but uniquely influence the distribution of each species.

In Chapter 3 we explored Clapper Rail reproductive ecology by examining the interplay between this species' nest success and some of the biotic and abiotic forces that dominate tidal estuaries. The results of this study suggest that Clapper Rails breeding within northern Gulf of Mexico tidal marshes nest in habitat that reduce nest loss to tidal flooding. Although this relationship has been identified elsewhere (Storey et al. 1988, Eddleman and Conway 1998), our research provides evidence that where habitat permits, Clapper Rails exhibit nest height plasticity in response to increased tidal height. The results of this study indicate that habitat limitations borne out through sea-level rise and habitat alteration may limit Clapper Rail nest success.

Although previous studies have quantified Clapper Rail diet (*references in* Eddleman and Conway 1998), inference drawn from these studies may have biased source contributions. Stable isotope analysis has proven to be a powerful tool for the study of avian trophic relationships in coastal ecosystems. In Chapter 4 we applied stable isotope analysis to examine the trophic composition of Clapper Rails in two northern Gulf of Mexico tidal marshes. Our results demonstrated that diet composition and source and niche-width of clapper rails can vary significant across different estuaries and appear to be influence by hydrological conditions, but that egg production is much less variable and tightly linked to fiddler crabs.

The substance of Chapter 5 focused on relationships between the distribution of Clapper Rails, habitat and the dominant food resource, fiddler crabs. Here, we explored movement patterns that endorse the importance of marsh edge habitat to adult Clapper Rails and their young. We also identified an inverse relationship between the density of fiddler crab burrows and Clapper Rail movements. These results support earlier ecological research (McNab 1963, *references in* Newton 1998) where prey density was negatively correlated with a predator’s territory size and movement patterns. This relationship suggested Clapper Rails that nested in areas with higher densities of fiddler crabs experienced energetic benefits; however, direct evidence of these benefits, such as reproductive metrics, were not explored in this chapter.

In Chapter 6 we began to explore facultative and adaptive relationships that structure Clapper Rail reproductive strategies. This chapter provides a complement to Chapter 2 but highlights the interplay between the biotic and abiotic conditions present in tidal estuaries and how these forces influence Clapper Rail reproductive ecology. Clapper Rails lay relatively large clutches (mean = 8.41 eggs, n = 60), and although nitrogen isotope ratios indicate somatic energy resources are mobilized during clutch production, ultimate factors may be more influential in shaping metrics such as clutch size and egg volume. Here, the volume of Clapper Rail eggs increased and clutch size decreased within breeding seasons, supporting an adaptive trade-off between losses in productivity due to tidal flooding and the mortality of recently hatched young. And although these adaptations provide explanations for the observed patterns in Clapper Rail egg volume and clutch size, our results provide evidence that proximate factors also affect the allocation of energy to the developing embryo.

In Chapter 7 we employed occupancy models and expanded on the research presented in Chapter 4. Here, however, results showed a relationship between Clapper Rail occupancy and the density of fiddler crab burrows. By contrasting the distributions of fiddler crab burrows and Clapper Rails between two disparate estuarine systems, we provided additional evidence that the spatial arrangement of fiddler crabs affects Clapper

Rail distributions. Furthermore, for each estuary, chemical tracers provided evidence that linked primary production to the distribution of a primary consumer (the Gulf Marsh Fiddler Crab *Uca longisignalis*) and the concentration of lipids in Clapper Rail egg yolks. For other birds, egg yolk lipid concentrations have been linked to the survival of the young (Carey 1996). The observed variation in the lipid concentrations in Clapper Rail eggs yolks may further link Clapper Rail reproduction to localized habitat and may serve as a marker for future population trends.

Constructs provided in Chapter 8 worked predominantly off of foundations laid in Chapter 7. Rather than focus on localized habitat effects, we explored precipitation and shifting salinity regimes as a potential link that explained patterns in Clapper Rail distributions and reproductive metrics between two unique tidal estuaries. The results we presented in Chapter 8 provide evidence that watershed-level conditions influence Clapper Rail populations through mechanisms of trophic ecology and reproduction.

Recent studies indicate that the habitats and species assemblages of the tidal estuaries of the northern Gulf of Mexico will change considerably over the coming decades (Forbes and Dunton 2006, Day et al. 2008). The potential for divergent ecological effects among species and predator-prey dynamics, such as those illustrated here, should be taken into account in planning for wetland conservation and management. Most importantly, the functional estuary and its dynamic ecological attributes must be maintained in order to achieve resilience in the face of climate and other global change.

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