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Trophic Relationships of a Marsh Bird Differ Between Gulf Coast Estuaries

Scott A. Rush · Jill A. Olin · Aaron T. Fisk ·
Mark S. Woodrey · Robert J. Cooper

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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 (δ^{13}C) and nitrogen (δ^{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. This analysis enabled us 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 and ocean-dominated. For the river-associated estuary, δ^{13}C and δ^{15}N of egg yolks, liver, and pectoral muscle tissue samples provided evidence that clapper rails maintained a similar diet during both the winter and the breeding season. A trophic link between C_3 primary productivity and the clapper rail's diet was also indicated as the δ^{13}C of clapper rail egg yolks related negatively with the aerial cover of C_3 macrophytes. Clapper rails from the ocean-dominated estuary had a narrower trophic niche 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. 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 Egg · Fiddler crab · Mixing model · Northern Gulf of Mexico · Stable isotope analysis

Introduction

Evidence collected from the southern USA's tidal marshes suggests that drought, sea level rise, and nutrient loading have already altered many biological interactions in these ecosystems (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 (Dardeu 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) (Day et al. 1993; Moody and Aronson 2007). Because birds are relatively well studied, they have been used to measure ecological conditions and evaluate the impacts of environmental change within tidal estuaries (Shriver 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

R. J. Cooper
D.B. Warnell School of Forestry and Natural Resources,
University of Georgia,
Athens, GA 30602, USA

S. A. Rush (✉) · J. A. Olin · A. T. Fisk
Great Lakes Institute for Environmental Research,
University of Windsor,
Windsor, ON N9B 3P4, Canada
e-mail: srush@uwindsor.ca

M. S. Woodrey
Coastal Research and Extension Center,
Mississippi State University,
Biloxi, MS 39532, USA

M. S. Woodrey
Grand Bay National Estuarine Research Reserve,
Moss Point, MS 39562, USA

trophic position; environmental conditions that affect basal productivity and physiochemical processes can 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), specifically, as bioindicators of contaminant dynamics through food webs (Rodriguez-Navarro et al. 2006; Cumbee et al. 2008). Collectively, these studies assume fiddler crabs (genus *Uca*) are the clapper rail's principle prey item within northern Gulf of Mexico estuaries (Heard 1982a; citations in Eddleman and Conway 1998). However, this inference is based largely on gut content analysis, an appraisal that tends to be biased toward foods that are harder to digest, such as the 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. 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 (Inger and Bearhop 2008). This approach is based on the principle that the ratios of heavier to lighter isotopes, expressed for carbon as δ^{13}C and nitrogen as δ^{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 δ^{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 (δ^{13}C marine −18‰ to −22‰, C_4 plants −6‰ to −19‰). In contrast, carbon sourced from C_3 plants and terrestrial sources are typically more depleted (δ^{13}C of C_3 plants −23‰ to −30‰) (Sullivan and Moncreiff 1990; Créach et al. 1997; Winemiller et al. 2007). For nitrogen, a δ^{15}N enrichment of 2–4% between producers and consumers is typical (Peterson and Howarth 1987; Michener and Schell 1994; Hobson et al. 2002). Thus, a shift in δ^{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). By selecting several tissues with varying replacement rates, researchers can gain insight into the animal's diet and variation in diet 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 (Hobson and Clark 1992a). 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 fill the knowledge gap on clapper rail dietary ecology, we analyzed δ^{13}C and δ^{15}N and used stable isotope mixing models, in clapper rails and potential prey items collected from two tidal marshes in the northern Gulf of Mexico. By analyzing liver, muscle, and egg yolks of clapper rails, we assess temporal aspects of diet and determine the origin of resources used for egg production. Finally, because the two systems we examined varied in hydrologic characteristics (river (Pascagoula) versus marine (Grand Bay) dominated), we assess the influence of this environmental variable on feeding and egg production in clapper rails.

Methods

Study Area

Our study area consisted of two estuarine systems in Jackson County, MS, USA: Pascagoula River Marsh Coastal Preserve (hereafter Pascagoula, 30° 25′ N, 88° 34′ W) and the Grand Bay National Estuarine Research Reserve (hereafter Grand Bay, 30° 20′ N, 88° 24′ W) (Fig. 1). The emergent marsh of the oligohaline and mesohaline Pascagoula is dominated by *Juncus roemerianus*, *Spartina alterniflora*, and *Spartina 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 (Rush et al. 2009).

Sample Collection

Within both estuaries, during Jan to Aug 2006, we collected pectoral muscle, liver, and egg yolk samples from clapper

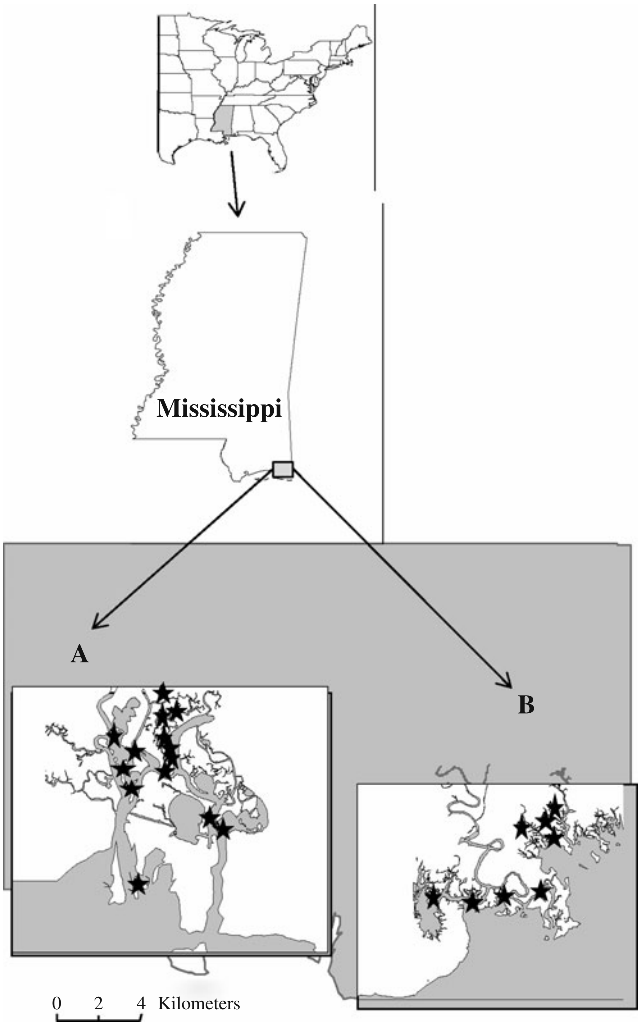

Fig. 1 Map of study locations within Jackson County, MS, USA. *A* shows the river-dominated Pascagoula Marsh Coastal Preserve (Pascagoula), while *B* is the Grand Bay National Estuarine Research Reserve (Grand Bay). *Stars* indicate locations of clapper rail nests

rails (see Table 1 for sample sizes). To obtain samples of pectoral muscle and liver, clapper rails were shot using shotguns and steel shot. Upon collection, all samples were placed on 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 1). Prey items were obtained from within a 50 m radius surrounding each nest location, a distance based on the mean home range of birds within these systems (S. Rush unpublished 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 gastropods (olive nerite *Neretina usnea* and marsh periwinkle *Littorina irrorata*), bivalves (ribbed mussel *Geukensia demissa* and common rangia *Rangia cuneata*; Bishop and Hackney 1987; LaSalle and de la Cruz 1985), tettigoniid grasshoppers (Parsons and de la Cruz 1980), blue crab (*Callinectes sapidus*), and 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, except macrophytes, using a 2:1 ratio of Chloroform/Methanol (Bligh and Dyer 1959).

Stable isotope ratios are expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation: δ^{13}C, δ^{15}N=[R_{sample}/$R_{\mathrm{standard}}-1]\times10^3$, where R^{13}C/^{12}C or ^{15}N/^{14}N. Stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{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). Values of δ^{13}C and δ^{15}N were quantified using three internal lab and NIST standard 8414 (bovine muscle) standards run after every 12 samples. The analytical precision based on the standard deviation of NIST standard 8414 (72 standards analyzed) for δ^{15}N was 0.19‰ and for δ^{13}C was 0.04‰. The analysis of NIST standards (sucrose (NIST 8542) and ammonium sulfate (NIST 8547); n=3 for each) during the analysis of samples generated values that were within 0.01‰ and 0.07‰ of certified values for δ^{15}N and δ^{13}C, respectively. Several metrics were used to explore relationships between diet and habitat. First, using the measurements of δ^{13}C and δ^{15}N obtained from all clapper rail eggs, we measured the total area of convex hull (TA), reflecting the niche breadth of each population (Cornwell et al. 2006). The TA encompasses the smallest convex polygon bounding this sub-set of individuals in the δ^{13}C and δ^{15}N niche space and is a measure of niche width, reflecting variation along both the δ^{13}C and δ^{15}N niche dimensions (Layman et al. 2007). Convex hull areas were calculated using the package *Adehabitat* (Calenge 2006) implemented in the statistical package R (Version 2.7.1: R Development Core Team 2008). Linear relationships (*lm* in R) between the δ^{13}C of clapper rail egg yolks

Table 1 Stable isotope values of clapper rail tissues and prey items collected from two northern Gulf of Mexico tidal marshes (mean ± 95% CI)

Species/tissue	*n*	Pascagoula		*n*	Grand Bay	
		δ^{13}C	δ^{15}N		δ^{13}C	δ^{15}N
Clapper rail						
Egg yolk	28	−21.1 (−23.3 to −19.2)	9.3 (7.7 to 10.9)	8	−18.6 (−20.5 to −16.7)	9.0 (7.5 to 10.4)
Liver	5	−18.8 (−21.1 to −16.6)	7.2 (6.5 to 7.9)	6	−24.8 (−26.8 to −22.8)	10.3 (8.7 to 11.9)
Pectoral muscle	5	−19.4 (−23.5 to −15.4)	8.6 (8.0 to 9.3)	8	−23.3 (−24.4 to −21.6)	9.8 (8.3 to 11.7)
Spartina sp.	18	−13.3 (−13.7 to −13.0)	4.8 (3.6 to 6.1)	3	−13.8 (−14.2 to −13.4)	3.2 (0.7 to 5.7)
Juncus roemerianus	23	−27.3 (−28.0 to −26.7)	4.6 (2.9 to 6.3)	7	−25.3 (−26.3 to −24.3)	2.5 (2.2 to 4.2)
Neretina usnea	22	−20.9 (−21.9 to −19.9)	7.4 (6.9 to 7.9)	0	–	–
Littorina irrorata	8	−20.0 (−21.8 to −18.8)	6.5 (5.9 to 7.1)	8	−15.6 (−17.3 to −13.9)	3.8 (3.4 to 4.3)
Geukensia demissa	2	−27.2 and −24.8	5.8 and 6.6	8	−22.6 (−24.1 to −21.2)	6.7 (5.5 to 7.9)
Rangia cuneata	14	−26.3 (−27.4 to −25.2)	7.2 (6.6 to 7.8)	1	−27.4	6.8
tettigoniid grasshoppers	10	−19.0 (−21.1 to −17.0)	6.4 (5.4 to 7.4)	3	−17.8 (−19.6 to −16.1)	
Callinectes sapidus	3	−22.7 (−27.5 to −18.0)	6.3 (4.8 to 7.8)	3	−15.3 (−17.0 to −13.5)	5.6 (5.4 to 5.8)
Uca longisignalis	14	−20.7 (−21.3 to −20.2)	5.0 (4.6 to 5.4)	8	−21.2 (−23.3 to −19.2)	5.9 (3.9 to 7.9)

n the number of individuals sampled

and the proportion of C$_3$ plants within 50 m of each nest site, within each estuary, 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's rail diet was evaluated using mixing models run in the program MixSIR (Inger and Bearhop 2008), a computational program that can provide estimates of the relative contributions of diet sources to an organism (Moore and Semmens 2008). For all modeled contributions, we assumed the isotopic discrimination factors reported by Hobson (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). 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). Results of the MixSIR models are presented as median and the fifth and ninety-fifth credibility intervals. For all other analyses and unless otherwise specified, parameter estimates are presented as means and 95% confidence intervals.

Results

Values of δ^{13}C showed a continuum from enriched values in C$_4$ grasses (*Spartina* sp.) to depleted values in C$_3$ grasses (*J. roemerianus*, Table 1). In general, δ^{13}C values were depleted in prey species and clapper rail egg yolk from the Pascagoula site compared with Grand Bay. Nitrogen stable isotope values were generally enriched in the Pascagoula system compared with Grand Bay (Table 1). As expected, δ^{15}N was lowest in the primary producers, increased in invertebrates, and were highest in the muscle and liver tissues of the clapper rails (Table 1; Fig. 2). All other prey organisms examined exhibited δ^{13}C values between, and δ^{15}N values greater than, those of the C$_3$ and C$_4$ plants (Fig. 2). The ranges of both δ^{13}C and δ^{15}N were larger among clapper rail egg yolks collected at the Pascagoula than from Grand Bay. The total area of the convex hull (TA) was over three times larger for the Pascagoula (98.84) than Grand Bay (30.96), indicating that clapper rails had a wider trophic niche within the Pascagoula estuary. Mirroring primary production, the δ^{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 ($F_{1,26}=31.4$, $p<0.001$; model slope=−0.10, SE=0.02), although this relationship was not observed in the Grand Bay egg yolks ($F_{1,7}=0.4$, $p=0.55$; model slope=0.17, SE=0.28).

Model estimates of diet composition of the clapper rail egg yolks and pectoral muscle tissues from the Pascagoula identified the gulf fiddler crab comprised the majority of the clapper rail diet (57% to 87%; Table 2). Estimates derived

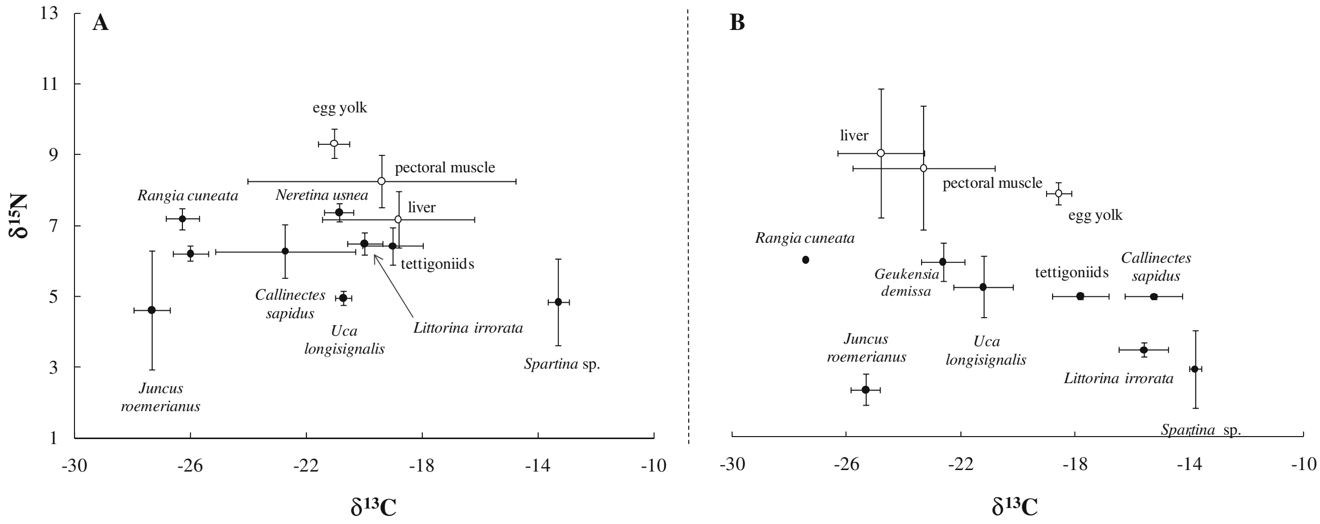

Fig. 2 Values of δ^{13}C and δ^{15}N in clapper rail egg yolks and anticipated diet components in two northern Gulf of Mexico tidal marshes. **a** The Pascagoula and **b** Grand Bay. *Error bars* reflect mean±1 SD. *Open circles* represent clapper rail tissues and *filled circles*, potential prey items. 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

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 2). Models that focused on the isotopic ratios measured in clapper rail liver tissues 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 2).

Discussion

The results of our isotopic analyses provide evidence that the diet of clapper rails differed between estuaries and across time scales. Specifically, by analyzing liver, muscle and egg yolks we were able to assess temporal aspects of diet selection. 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 breeding clapper rails within these estuaries. For the Pascagoula, the river-associated estuary, δ^{13}C and δ^{15}N of egg yolks, liver and pectoral muscle tissue samples, provided evidence that clapper rails maintain a similar diet during both the winter and the breeding season (Table 2). Although egg yolk and pectoral muscle results from Grand Bay 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. These differences between tissues could also be driven by the physiology of the clapper rail. However, because relationships between tissues differed

Table 2 Proportion of prey items contributing to carbon and nitrogen stable isotopes values in different tissues of clapper rails collected from two northern Gulf of Mexico tidal marshes

Estuary	Tissue	*Uca longisignalis*	*Neretina usnea*	*Littorina irrorata*	*Geukensia demissa*	tettigoniid grasshoppers	*Callinectes sapidus*	*Rangia cuneata*
Pascagoula	Yolk	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	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	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	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	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	95 (88–99)	–	0.3 (0.1–0.6)	0.3 (0.1–1.4)	0.2 (0–1)	0.6 (0–1.5)	1.5 (0.3–11)

Estimates obtained using MixSIR (50%; 5–95%)

between estuaries, this explanation seems unlikely. Taken together, δ^{13}C and δ^{15}N 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 (Table 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 site, the δ^{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 clapper rail diet 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 1).

The Pascagoula and Grand Bay estuaries are physiographically distinct systems; some of the characteristics that make these estuaries unique can also provide explanation for variation in the δ^{13}C and δ^{15}N of clapper rail tissues. Within the southeastern USA, 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 (Hackney and de la Cruz 1982). Paralleling seasonal precipitation and tidal differences, greater nutrient loading occurs during Jan 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 (Kaldy et al. 2005). 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 the primary productivity on *S. alterniflora* (Sullivan and Moncreiff 1988). 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 Moncreiff (1990) reported a δ^{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. Although the δ^{13}C of the C_3 plant *J. roemerianus* was depleted in C^{13} and samples collected from the Pascagoula were slightly more depleted than those from Grand Bay (Table 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 macroalgae constituted a greater contribution to the diets of these species (McCallister et al. 2006; Table 1). Evidence indicates that tettigoniid grasshoppers preferentially fed on C_4 plants but also included some C_3 plants in their diets, reflected in a 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), so their δ^{13}C often incorporates signatures of both sources (Currin et al. 1995). However, our δ^{15}N results indicate that the periwinkles' diet may have varied between the Pascagoula and Grand Bay. Increased nitrogen concentrations can positively influence the consumption of *Spartina* by periwinkles. 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 δ^{13}C of blue crabs varied among samples from the Pascagoula, reflecting the habitat heterogeneity within this estuary (Bucci et al. 2007; Table 1). 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). For instance, Sullivan and Moncreiff (1990) noted that the isotopically depleted δ^{13}C of fiddler crabs reflected the dominance of *J. roemerianus* within a Mississippi tidal system.

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). 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 substantial 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 reflect several physiological and chemical processes.

The physiochemical properties experienced within estuarine systems can affect the richness and abundance of estuarine organisms and the ecology of consumers (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 (Moore 1992). 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. Maintenance of heterogeneous energy pathways can act to stabilize food webs and consumer populations (Kreeger and Newell 2000). Communities structured around species-poor food webs may be more vulnerable to habitat change (Jonsson et al. 2006).

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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