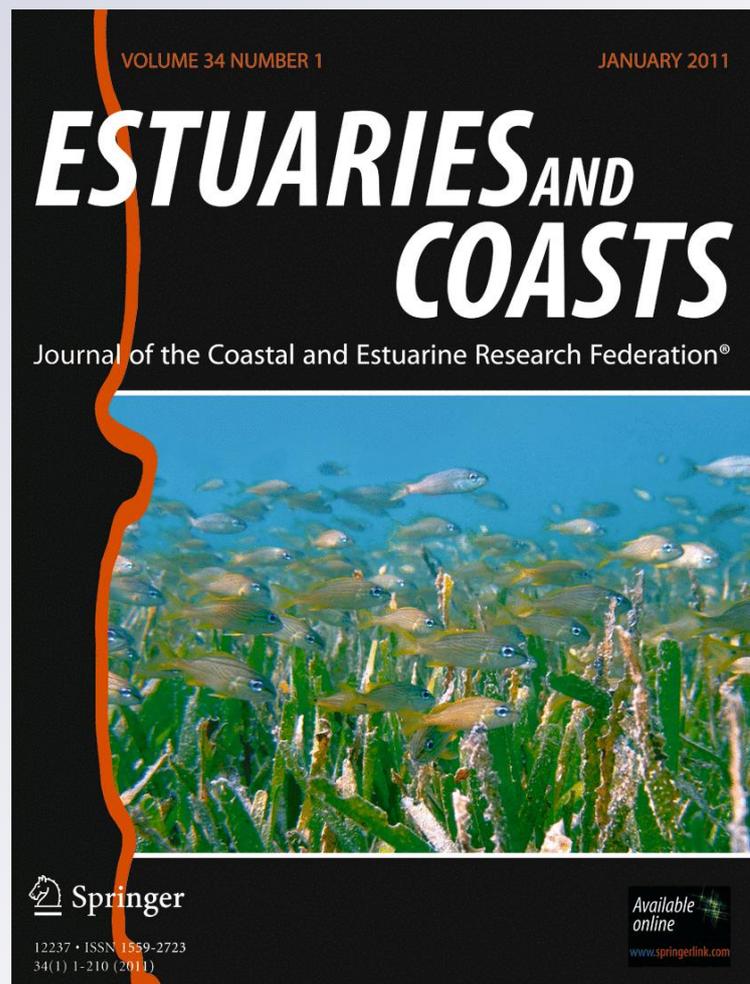


Evaluating Ecological Equivalence of Created Marshes: Comparing Structural Indicators with Stable Isotope Indicators of Blue Crab Trophic Support

Estuaries and Coasts
Journal of the Coastal and
Estuarine Research Federation

ISSN 1559-2723
Volume 34
Number 1

Estuaries and Coasts (2010)
34:172-184
DOI 10.1007/s12237-010-9297-
y



Your article is protected by copyright and all rights are held exclusively by U.S. Government. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

Evaluating Ecological Equivalence of Created Marshes: Comparing Structural Indicators with Stable Isotope Indicators of Blue Crab Trophic Support

Chris Llewellyn · Megan La Peyre

Received: 11 September 2009 / Revised: 22 March 2010 / Accepted: 2 April 2010 / Published online: 7 May 2010
© U.S. Government 2010

Abstract This study sought to examine ecological equivalence of created marshes of different ages using traditional structural measures of equivalence, and tested a relatively novel approach using stable isotopes as a measure of functional equivalence. We compared soil properties, vegetation, nekton communities, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of blue crab muscle and hepatopancreas tissue and primary producers at created (5–24 years old) and paired reference marshes in SW Louisiana. Paired contrasts indicated that created and reference marshes supported equivalent plant and nekton communities, but differed in soil characteristics. Stable isotope indicators examining blue crab food web support found that the older marshes (8 years+) were characterized by comparable trophic diversity and breadth compared to their reference marshes. Interpretation of results for the youngest site was confounded by the fact that the paired reference, which represented the desired end goal of restoration, contained a greater diversity of basal resources. Stable isotope techniques may give coastal managers an additional tool to assess functional equivalency of created marshes, as measured by trophic support, but may be limited to comparisons of marshes with similar vegetative communities and basal resources, or require the development of robust standardization techniques.

Keywords Blue crab · Louisiana · Ecological equivalence · Dredged marsh · Restoration · Stable isotopes

Introduction

Identifying appropriate metrics for measuring success of ecosystem restoration is critical. In many restoration cases, structural measures of ecosystem restoration are often selected as they are most easily measured and understood (Moy and Levin 1991). When the goal of ecosystem restoration is to create ecologically equivalent systems however, it is not clear that equivalent structural characteristics will beget functional or ecological equivalency, as is often assumed (Palmer et al. 1997). For example, studies in various ecosystems have found that many patterns related to functional ecosystem characteristics such as productivity or nutrient cycling are broadly independent of the structure of the ecosystem (Naeem et al. 1994; Lockwood and Pimm 1994; McCay et al. 2003).

For coastal marshes, where concern for fisheries support is high, structural indicators of nekton abundance, density, and biomass are often used to assess equivalency despite recent work, suggesting that they may not be accurate indicators of ecosystem fisheries support or equivalence due to the highly mobile nature of the nekton that use the marshes (Callaway et al. 2001; La Peyre et al. 2007). More meaningful measures of habitat value for fisheries have been suggested, such as measures of community ecology and trophic support (Moy and Levin 1991; Minello and Rozas 2002; McCay et al. 2003); the difficulty remains in identifying accurate and easily accessible indicators of these functions.

Recently, stable isotope techniques have been suggested as a possible tool for development of indicators of

M. La Peyre (✉)
U.S.G.S., Louisiana Fish and Wildlife Cooperative Research Unit,
School of Renewable Natural Resources,
Louisiana State University AgCenter,
Baton Rouge, LA 70803, USA
e-mail: mlapey@lsu.edu

C. Llewellyn
School of Renewable Natural Resources,
Louisiana State University AgCenter,
Baton Rouge, LA 70803, USA

ecological change and for assessing functional equivalence of habitats for organisms as they can be used to trace the food web support to consumers, thus providing an assessment of the functional aspects of the marsh (i.e., trophic or food web support) (Weinstein et al. 2000; Wozniak et al. 2006; Layman et al. 2007a, b; Fry et al. 2008). Consumers acquire an isotopic signal from their diet. These isotope signals are derived from the various trophic pathways of their food items that have been integrated over time and are habitat specific (Schmidt et al. 2007). Specifically, consumer $\delta^{13}\text{C}$ isotope values have been used to determine the base of the food web, because $\delta^{13}\text{C}$ fractionates very little between trophic steps (DeNiro and Epstein 1978; Peterson and Fry 1987). In contrast, $\delta^{15}\text{N}$ isotope values can be used to assess an organism's trophic position in a food web relative to the base of that food web due to well documented $\delta^{15}\text{N}$ fractionation rates in various tissues (DeNiro and Epstein 1981; Peterson and Fry 1987; Post 2002). Furthermore, different metrics derived using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of consumers have been suggested as a means to assess an organism's position within a food web (Peterson and Fry 1987; Post 2002), dietary niche width (Layman et al. 2007a, b), and the value of the food resources within that habitat (Fantle et al. 1999). Comparisons of these measures of the food web through the use of stable isotopes may provide a snapshot approach that could be used to assess functional differences in food web development or trophic equivalency between created and restored sites.

As an estuarine-dependent and ubiquitous species dependent on coastal marshes, the blue crab (*Callinectes sapidus* Rathbun, 1896), presents a good test organism as a means to compare functional equivalency of marshes as defined by provision of equivalent trophic (food web) support. The blue crab is a generalist and opportunistic feeder (Perry and McIlwain 1986) and uses marsh habitats throughout much of its benthic life (Wilson et al. 1990; McClintock et al. 1993). While crabs move large distances over their life cycle, they have relatively small ranges (male 108 m²; immature female 157 m², female mature 1,052 m²) when in the marsh (Wrona 2004). We explored the feasibility of using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements to compare food web support of blue crabs in restored and reference marsh sites as a potential measure of functional equivalence. Critical to the interpretation of these isotope results, we conducted a laboratory study which examined turnover rates of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in blue crab muscle and hepatopancreas tissues.

The overall goal of this project was to compare and examine different measures of ecological equivalence in coastal Louisiana marshes. We examined commonly used metrics to assess structural equivalence (nekton abundance and density, sediment, and vegetation characteristics) and explored the use of indicators based on stable isotope

analysis to examine food web support for blue crabs as a measure of functional equivalence in created marshes. We selected four marshes created with the same source dredge material, but at different time periods. As created marshes are expected to more closely approximate their reference counterparts over time, we hypothesized that the oldest created marshes included in the study would be more similar to the reference marshes, as compared to the younger created marshes. We further hypothesized that the analysis of stable isotopes as a measure of blue crab trophic support would provide further details as to the equivalency of the created and reference marshes in comparison to results from the structural measures.

Methods

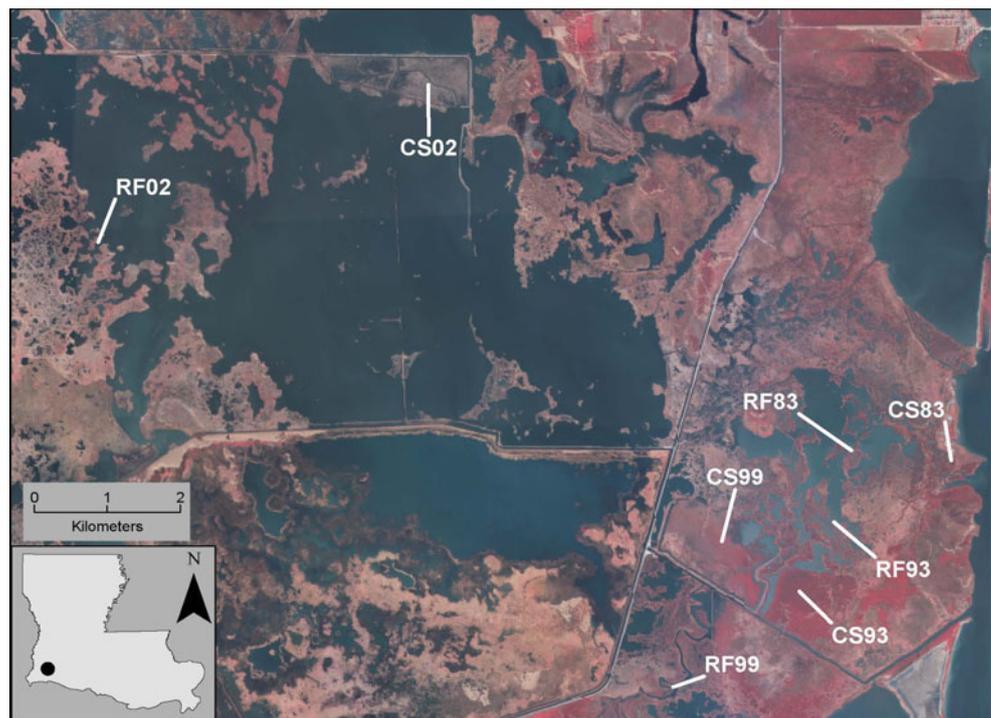
Field Study

Study Site

The study was conducted at created and reference marshes located in Sabine National Wildlife Refuge (NWR) in southwest, Louisiana (Fig. 1). The Sabine NWR encompasses approximately 50,000 ha of fresh, intermediate, and brackish marshes located between the eastern shore of Sabine Lake and the western shore of Lake Calcasieu. Study sites were located in the brackish areas on the eastern portion of the refuge in the Hog Island area adjacent to the Lake Calcasieu ship channel and ranged from 40 to 240 ha in size. Tidal range is negligible in this area and water levels in the marsh are controlled more by meteorological forces than by tidal forces, typical of the northern Gulf of Mexico (Chabreck 1989).

Four marshes created in different years (1983, 1993, 1999, and 2002) using the same source dredge material from the Lake Calcasieu Ship Channel were selected for this study. In all cases, the marshes were created by pumping a sediment slurry of dredge material into containment levees. However, there were slight variations in three aspects of the construction and design of the created marshes. (1) Marshes created in 1983, 1993, and 1999 were all allowed to revegetate naturally, while the 2002 created marsh was planted with *Spartina alterniflora* along its border. (2) The 2002 created marsh was designed with trenasses, which are man-made bayous, created around the perimeter and bisecting the interior in a zig-zag pattern, while the 1999 site was built with a trenasse along the perimeter between the marsh and containment levee, and the other two sites did not have trenasses of any kind built in. (3) There were differences in the creation and maintenance of containment levees; the 2002-created marsh had a discontinuous containment levee designed to allow

Fig. 1 Location of study area in southwest Louisiana USA on the Sabine National Wildlife Refuge. The *CS* prefix refers to created marshes, and the *RF* prefix refers to reference marshes. The last two numbers refer to the year the marsh was created (i.e., 02 2002, 99 1999, 93 1993, 83 1983)



fish passage and increase hydrologic connectivity with adjacent marshes. In contrast, the older created marshes were all created with continuous containment levees, but most have been removed over the last 10 years. All marshes were dominated by *S. alterniflora*, with the paired 1983 sites also having significant *Juncus roemerianus* in the interior marsh; the 2002 marsh was also unique with the presence of submerged aquatic vegetation, *Ruppia maritima*, at all adjacent reference marshes. Thus, the study sites differed in age, and in some extent in design, as marsh-creation techniques and designs have progressed over the 20-year time period. However, it was hypothesized that age would override other factors in the development of marsh vegetative and nekton communities.

Each created marsh was paired with a nearby reference marsh to minimize variation in salinity, water temperature, and other environmental conditions (i.e., precipitation and flooding). Reference sites selected were within 5 km of their paired created site and selected to have similar hydrology and salinity conditions. These reference sites were selected such that they represented the desired target characteristics for each created site. Samples were taken in spring (May and June) and fall (October) 2007 at three random sites per study marsh for all variables (8 study marshes \times 3 sites/marsh \times 3 samples \times 2 sample dates = 144 samples).

Structural Indicator Samples

At each sampling site, water quality and nekton were collected within 1 m of the vegetation–water edge, on the

water side, while sediment and vegetation samples were collected within 1 m of the vegetated edge, on the vegetation side of the vegetation–water interface. Water temperature ($^{\circ}\text{C}$), salinity, and dissolved oxygen (mg L^{-1}) were measured at each site using a YSI Model 556 water quality monitor.

Sediment samples were collected using a 5-cm diameter, 10-cm deep core in the spring and fall. Cores were immediately placed in plastic bags on ice and transported to the laboratory at Louisiana State University AgCenter for processing. In the laboratory, wet weight and length of the cores were recorded. Cores were then dried to a constant weight at 55°C and weighed. To determine percent organic matter, samples were ground and homogenized, and triplicate subsamples were placed in a muffle furnace and burned at 450°C for 4 h in order to burn off all organic matter. Samples were then weighed, and percent organic matter was calculated. Mean percent organic matter of all subsamples per core was used for statistical analysis.

Emergent vegetation was sampled in triplicate at each marsh using a 0.25-m^2 quadrat. Percent cover by species was visually estimated for each sample. Vegetation in quadrats was then clipped at the soil level, placed in plastic bags, and returned to the laboratory for processing. All clipped vegetation was sorted by species, dried at 55°C to a constant weight, and then weighed to the nearest 0.01 g dry weight to determine biomass (g dry wt m^{-2}).

Nekton was collected using a 1-m^2 (3 mm mesh diameter) throw trap similar to that described by Gossman

(2005). The trap was cleared using a 1-m wide bar seine (3 mm mesh diameter) and was considered free of nekton when five consecutive sweeps were made without any nekton being caught in the nets (Duffy 1997). All nekton were placed in marked bags on ice until return to the lab, where they were frozen. All organisms were identified to the lowest practical taxon and total length (mm) and wet weight (nearest 0.001 g) recorded for each individual.

Isotope Samples

Blue crabs and primary producers were collected from each study site for isotope analyses. Blue crabs were collected using either standard baited crab traps or were dip netted using bait on a string. The traps were not left out longer than 12 h to prevent crabs from cannibalizing each other inside the traps. The bait in the traps was placed in mesh bags (1 mm) and wrapped in fine metal mesh (5 mm) to prevent blue crabs from ingesting the bait. Three crabs were collected for stable isotope analysis at each sample site. Only crabs between 90 and 150 mm carapace width were kept and were placed on ice until return to the lab for stable isotope analysis. Samples from the three crabs per site were pooled together for analysis, resulting in $N=3$ samples for each sample period, for each marsh (8 marshes \times 3 sample sites \times 3 sample periods \times 2 tissue types=144 samples). The use of composite samples of individuals has been found to reduce errors around stable isotope averages while reducing the number of isotope samples required, and has been suggested for monitoring programs when the goal is to detect significant temporal or spatial changes (Fry et al. 2008). Primary producers were collected at each sample site, including several stems of the dominant C3 (*Iva frutescens*, *Juncus romerianus*, and *Schoenoplectus robustus*) and C4 (*S. alterniflora*, *S. patens*, and *Distichlis spicata*) plants, in addition to any submerged aquatic vegetation, benthic macroalgae, and detritus found. All primary producers were placed on ice until return to the lab and frozen.

Tissue Turnover Rate Laboratory Study

During the summer of 2007, a laboratory experiment was conducted to determine the stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) turnover rate of blue crab hepatopancreas and muscle tissue. Forty-one crabs were collected from Hog Island Gully, Sabine National Wildlife Refuge. The crabs were kept in coolers surrounded by wet burlap. Upon return to the lab, crabs were placed into individual containers held in a re-circulating system holding 1,000 L of artificial seawater (Hawaiian Marine Imports). Water in each system was filtered through 10- and 1- μm filters, constantly aerated, and recirculated at a rate of four times per hour (except during feeding). Food was withheld for 2 days prior to initiation of

experiment to allow for complete evacuation of gut contents. Water temperature was maintained at 18°C, and salinity was maintained at 25 throughout the experiment. Water quality (pH, NO_2 , NH_3) was monitored weekly.

Crabs were sampled on days 0, 2, 7, 10, and 20. On day 0, five crabs were randomly collected for isotope analysis. Remaining crabs ($N=36$) were randomly assigned to one of three feeding treatments ($N=12$ crabs/treatment). Feeding treatments consisted of unique diets of either: (1) thin-ribbed mussel (*Geukensia demissa*), (2) detritus, or (3) smallmouth buffalo (*Ictiobus bubalus*). The first two diets represent commonly found food items in our study area with different isotope signatures, while the third diet item represents a food item with a distinctly different signature from what the crabs would have been eating in the field. Crabs were fed ad libitum for 30 min, once a day, for the remainder of the experiment. During feeding, water bypassed each container. Any uneaten food was removed from containers after 30 min. Wet weight (g) and carapace width (mm) were recorded for all crabs remaining on all sample days. Following measurements, three crabs from each of the three treatments were randomly selected and placed in labeled mesh bags on ice until return to the lab for isotope analysis. Triplicate samples of each diet item used were also collected for isotope analysis at the initiation of the experiment.

Isotope Analysis

In preparation for isotope analysis, all tissues were rinsed with distilled water and dried at 55°C to a constant weight. Crabs were first rinsed with distilled water to remove ectoparasites and sediment before wet weight (g) and carapace width (mm) were recorded. Hepatopancreas tissue and muscle tissue from one claw were collected from each crab. After drying, hepatopancreas tissue samples were placed in separate scintillation vials. Lipids in the hepatopancreas tissue were extracted in two separate 24-h decantations with hexane at room temperature following Fry et al. (2003). Once residual hexane had evaporated from hepatopancreas samples, the vials were placed back into the drying oven at 55°C to a constant weight. Once samples were dry, they were ground with a mortar and pestle or Wig-L-Bug into a fine powder. Blue crab tissue samples of 1 ± 0.2 mg and plant tissue samples of 2–3 mg were weighed for stable isotope analysis. All samples were analyzed by the University of California Stable Isotope Facility for dual isotope natural abundance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. A second set of detritus samples were also analyzed for $\delta^{15}\text{N}$ natural abundance (5–6 mg) using a PDZ Europa ANCA-GSL elemental analyzer interfaced with to a PDZ Europa 20-20 isotope ratio mass spectrometer (Secron Ltd., Cheshire, UK).

Data Analysis

For all analyses, a significance level of $\alpha=0.05$ was used. Data were tested for normality and homogeneity of variance (Proc UNIVARIATE, SAS 9.1). Unless otherwise stated, results are presented as mean \pm standard error. Soil organic matter, nekton density, and nekton biomass were log-transformed ($\log(x+1)$) to meet assumptions of normality and homogeneity of variance.

Structural Indicator Data

Pearson correlation analysis (Proc CORR, SAS 9.1) was performed on all habitat and nekton variables. Soil bulk density and soil organic matter were correlated (Pearson coefficient = -0.83473 ; $p \leq 0.0001$), soil bulk density was excluded from further statistical tests. Similarly, nekton density and nekton biomass were correlated (Pearson coefficient = 0.8354 ; $p < 0.0001$), and nekton biomass was excluded from further statistical tests. For nekton analyses, rare species (those that contribute $<5\%$ total abundance) were removed from analyses because rare species contribute little to the explanative value of the analyses (Gauch 1982).

Multivariate analysis of variance (Proc GLM, SAS 9.1) was used to test whether environmental and nekton variables (water temperature, salinity, dissolved oxygen, soil organic matter, aboveground biomass, percent cover, and nekton density), compared simultaneously, differed significantly among marshes and seasons. When present, significant interactions (i.e., marsh by season) were further tested using LSMeans. When only main effects were significant, a one-factor ANOVA was run by season, and a priori contrasts of paired created and reference marshes were run when marsh was significant.

Isotope Field Comparisons

Stable isotope data were analyzed by tissue type using a two-factor analysis of variance (Proc MIXED; SAS 9.1.3) to determine if there were differences in mean values of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for crab tissues (muscle and hepatopancreas) and primary producers (dominant C3, C4, SAV, benthic macroalgae, and detritus) by marsh and season. When present, significant interactions (i.e., marsh by season) were further tested using LSMeans. When only main effects were significant, a one-factor ANOVA was run by season, and a priori contrasts of paired created and reference marshes were run when marsh was significant.

Blue crab trophic position at each marsh was estimated using a simplified model from Post (2002):

$$\text{TP} = 1 + (\delta^{15}\text{N}_{\text{blue crab}} - \delta^{15}\text{N}_{\text{base}}) / \text{TEF}$$

TP is trophic position, $\delta^{15}\text{N}_{\text{blue crab}}$ is the mean blue crab $\delta^{15}\text{N}$ value at marsh x , $\delta^{15}\text{N}_{\text{base}}$ is the mean $\delta^{15}\text{N}$ for the base of the food web at marsh x , and TEF represents the trophic enrichment factor per trophic level. To estimate trophic position of blue crabs collected at the Aransas National Wildlife Refuge, Hoeninghaus and Davis (2007) used a TEF of $+2.5\%$ based on meta-analysis of $\delta^{15}\text{N}$ fractionation by Vanderklift and Ponsard (2003). Based on comparisons of blue crab and primary producer $\delta^{13}\text{C}$ values, it was decided that detritus served as the primary basal resource at our marshes.

Blue crab dietary niche breadth and trophic diversity at each marsh were calculated following Layman et al. (2007a, b). Blue crab $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values were plotted together for each marsh and pooled across seasons. To measure niche breadth, the total area (TA) of the minimum convex hull polygon that contained all points was calculated using a VBA script that created a minimum convex polygon around the data in ESRI ArcMap 9.2. TA is a measure of overall dietary niche space occupied and can serve as an indicator of the extent of trophic diversity for a species at a site (Layman et al. 2007b). The centroid, or mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, at each marsh was then plotted, and the Euclidean distance from the centroid to each point was determined using Hawth's Tools in ArcMap 9.2 (Hawth's Analysis Tools for ArcGIS, www.spataleecology.com/htools). The mean distance to the centroid (CD) can provide a measure of the average degree of trophic diversity for a particular species or food web (Layman et al. 2007a, b). TA values were compared between paired created and reference marshes, but statistical analysis were not performed because only one TA value for each marsh was available. Mean CD was analyzed using a one-way ANOVA by marsh with a priori contrasts between paired marshes when significant ANOVAs were found.

Taking all five lines of isotope evidence together (trophic position, total niche breath (TA), and trophic diversity (CD) for muscle and hepatopancreas tissues), we ran a Wilcoxon's signed rank test by paired sites to test the hypothesis that the median difference between paired created and reference sites did not differ from zero (i.e., there was no difference in trophic indicators).

Tissue Turnover Laboratory Study

One-way analysis of variance (SAS, PROC GLM; factor: day) using a priori contrasts was used to test if there were significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes over time, by food item, and by tissue type (muscle and hepatopancreas).

Crabs that were fed the smallmouth buffalo (*I. bubalus*) diet during the laboratory study were used to calculate the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope half-life in the hepatopancreas and muscle tissue as smallmouth buffalo isotope values differed

the greatest compared to the initial blue crab values. Simple linear regression was used to analyze growth of crabs, which was measured as the relative growth rate (final weight/initial weight) and reported as a ratio. Isotope turnover rates can be attributed to organismal growth, tissue replacement, or a combination of the two. Over the course of this laboratory experiment, no significant growth was observed for blue crabs so isotope turnover associated with only tissue replacement was calculated. Hesslein et al. (1993) used the following equation to calculate the metabolic coefficient for each isotope for tissue replacement alone:

$$\ln(1 - (\delta_x - \delta_{\text{initial}})/(\delta_{\text{final}} - \delta_{\text{initial}}))$$

δ_x represents the blue crab isotope value at time interval x , δ_{initial} represents the initial blue crab isotope value before the change in diet, and δ_{final} represents the blue crab isotope value at equilibrium with the new diet. Based on the data, it appears that the feeding experiment was not conducted long enough for the blue crab tissue isotopes to reach equilibrium with the new diet. For the purpose of this calculation, the new diet (smallmouth buffalo) isotope values were chosen to be the blue crab equilibrium values, or δ_{final} . A simple linear regression (SLR, Proc REG) was used to determine the effect of time on the calculated metabolic coefficient. The slope of the line of regression was then used to calculate the isotope half-life using the following equation:

$$\ln(0.5)/(\text{slope of line of regression})$$

These equations were used to calculate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope half-life in the hepatopancreas and muscle tissue.

Results

Structural Indicators

Created and reference marshes had similar structural characteristics except for soil organic matter and salinity (Table 1). All created marshes had significantly lower ($p \leq 0.0138$) soil organic matter when compared to their paired reference marshes. Salinity differed significantly by marsh with created and reference 2002 marshes having significantly lower salinity as compared to the remaining pairs of marshes in both spring and fall, although the created and reference 2002 marshes did not differ from one another ($p < 0.01$).

Nekton density and biomass did not differ between marshes (Table 2). In the spring, 253 organisms, representing 14 species, were collected using the throw trap. Catch was composed of 64% crustaceans and 36% fishes. After rare species were removed, 239 organisms, representing four species, were used in the analysis. Total nekton biomass was

152.12 g. In the fall, 217 organisms, representing 17 species, were collected using the throw trap. Catch was composed of 39% crustaceans and 61% fishes. After rare species were removed, 197 organisms, representing seven species, were used in the analysis. Total nekton biomass was 181.47 g.

Isotope Field Comparisons

Blue crab hepatopancreas and muscle tissue $\delta^{15}\text{N}$ values differed by individual marsh (hepatopancreas: $p = 0.0033$; muscle: $p < 0.0001$) and by season (hepatopancreas: $p = 0.007$; muscle: $p < 0.0001$) (Fig. 2). In most cases, blue crab $\delta^{15}\text{N}$ values were more enriched at created versus reference sites. In the spring, $\delta^{15}\text{N}$ values at marshes created in 2002 and 1999 were more enriched for both tissues (hepatopancreas and muscle), as compared to their reference marshes. In the fall, hepatopancreas $\delta^{15}\text{N}$ values from the marsh created in 2002 were significantly more enriched (7.00 ± 1.29) than its reference (4.62 ± 0.43). Muscle $\delta^{15}\text{N}$ values for the marsh created in 1983 were significantly more enriched than its reference in the fall ($p < 0.05$).

Blue crab hepatopancreas tissue $\delta^{13}\text{C}$ values were found to have a significant marsh by season interaction ($p = 0.0249$) (Fig. 2). LSMeans indicated that this interaction was due to significant differences between the 2002 reference site and all other marshes examined. In contrast, blue crab muscle tissue $\delta^{13}\text{C}$ values differed significantly between individual marshes ($p < 0.0001$) and seasons ($p = 0.0384$). A priori contrasts found that in the spring, the mean blue crab muscle $\delta^{13}\text{C}$ value at the marsh created in 2002 (-17.3 ± 0.28) was significantly more enriched than at its paired reference (-19.36 ± 0.61 ; $p = 0.0006$).

For primary producers, only $\delta^{15}\text{N}$ values differed significantly by marsh ($p < 0.0001$) and season ($p = 0.0009$). A priori contrasts showed that this difference was due to $\delta^{15}\text{N}$ of primary producers at the marsh created in 2002 being significantly higher than $\delta^{15}\text{N}$ of primary producers at its reference site ($p < 0.0001$). Comparison of mean $\delta^{13}\text{C}$ values of blue crabs to mean $\delta^{13}\text{C}$ values from various primary producers within each marsh indicates that the crabs collected in this study are primarily in a detritus-based food web with the exception of the reference for the 2002 site, which appears to be in an algal/detritus-based food web (Fig. 3). Using detritus as the contributing primary producer, little difference was found between blue crab trophic position and marsh (Table 3).

Blue crab total dietary niche breadth (TA) was smaller at created marshes compared to their paired reference marshes in most instances for both the hepatopancreas and muscle tissue (Fig. 4; Table 4). There was no significant marsh effect for mean centroid distance (CD) in the hepatopancreas ($p = 0.0989$) or muscle ($p = 0.1155$) tissue (Table 4). Wilcoxon's signed rank test indicated a

Table 1 Environmental and habitat variables (mean±SE) by marsh

Variable	Paired marsh comparisons							
	2002		1999		1993		1983	
	Created	Reference	Created	Reference	Created	Reference	Created ^a	Reference ^b
Spring								
Temp (°C)	27.42±0.5	31.3±0.3	31.8±0.9	32.0±0.2	28.9±0.6	31.9±0.8	29.0±0.2	30.7
Salinity	19.1±0.2	15.7±0.6	24.0±0.4	20.0±0.3	21.0±0.0	21.4±0.2	20.4±0.1	20.2
DO (mg L ⁻¹)	1.9±0.3	2.7±0.1	4.5±0.3	5.1±0.6	4.9±0.3	5.0±0.2	3.5±0.2	3.8
Soil org. matter (%)	7.7±0.9	28.3±1.6	6.3±0.3	16.3±1.6	7.8±0.7	22.3±3.0	5.9±0.3	23.1
Veg. cover (%)	76.7±12.0	80.0±15.9	65.0±15.0	76.7±14.5	50.0±5.8	90.0±5.0	60.0±0.2	90
Aboveground biomass (g m ⁻² dry weight)	585.0±162.4	506.0±53.5	546.5±150.2	461.5±44.6	370.5±165.9	361.8±79.0	90.9±0.4	65.8
Fall								
Temp (°C)	26.1±0.5	24.6±1.6	20.6±0.3	26.5±0.1	26.3±0.1	24.8±0.5	22.2±0.3	–
Salinity	8.5±0.4	8.5±0.4	17.1±0.1	16.0±0.0	15.8±0.2	16.2±0.44	17.2±0.1	–
DO (mg L ⁻¹)	1.5±0.0	2.7±1.1	2.7±0.1	3.0±0.1	1.2±0.5	2.4±0.3	4.6±0.2	–
Secchi (cm)	42.3±2.9	36.5±2.5	20.3±0.9	26.0±3.1	19.0±0.0	26.0±3.1	32.3±5.9	–
Soil org. matter (%)	8.8±1.2	28.1±4.4	6.2±0.1	19.7±2.3	7.1±0.5	24.8±6.0	5.8±0.7	–
Vegetative cover	75.0±12.6	97.5±2.5	61.3±21.4	73.3±12.0	43.3±8.8	36.7±14.5	48.3±7.3	–
Aboveground biomass (g m ⁻² dry weight)	345.1±98.6	607.2±347.9	443.1±221.2	631.0±211.4	593.8±180.5	202.7±69.2	405.1±117.7	–

Variables that differed significantly between created and reference marshes are identified in italics. $N=44$

^a The 1983 reference site was only sampled at one location in the spring due to difficulties accessing the site

^b The 1983 reference was not sampled in fall; due to the proximity of the 1993 reference, values from this sample were used for the 1983 created marsh comparison

difference only for the 2002 created marsh and its reference ($p=0.06$).

Tissue Turnover Laboratory Study

Crabs fed a diet of detritus showed no significant change in isotope ratios during the study. Crabs fed a diet of *G. demissa* only showed a significant change from days 0 to 20 for $\delta^{13}\text{C}$ hepatopancreas values. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of *Geukensia* and detritus items closely matched the initial crab isotope ratios. However, for crabs fed smallmouth buffalo, there was a significant difference in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values between days 0 and 20 in the muscle ($\delta^{15}\text{N}$, $p=0.0002$; $\delta^{13}\text{C}$, $p=0.0158$) and hepatopancreas ($\delta^{15}\text{N}$, $p<0.0001$; $\delta^{13}\text{C}$, $p<0.0001$) tissues (Fig. 5). For all feeding treatments, there was no significant growth of blue crabs.

In the hepatopancreas tissue, the $\delta^{13}\text{C}$ isotope half-life is approximately 10 days ($y=-0.0756x-0.2634$, $r^2=0.7839$; 9.75 days), and the $\delta^{15}\text{N}$ isotope half-life is approximately 10 days ($y=-0.0722x-0.2294$, $r^2=0.9133$; 9.60 days) (Fig. 6). In the muscle tissue, the $\delta^{13}\text{C}$ isotope half-life is approximately 39 days ($y=-0.0179x-0.1219$, $r^2=0.7056$; 38.72 days), and the $\delta^{15}\text{N}$ isotope half-life is approximately 22 days ($y=-0.0316x-0.0802$, $r^2=0.8804$; 21.94 days).

Discussion

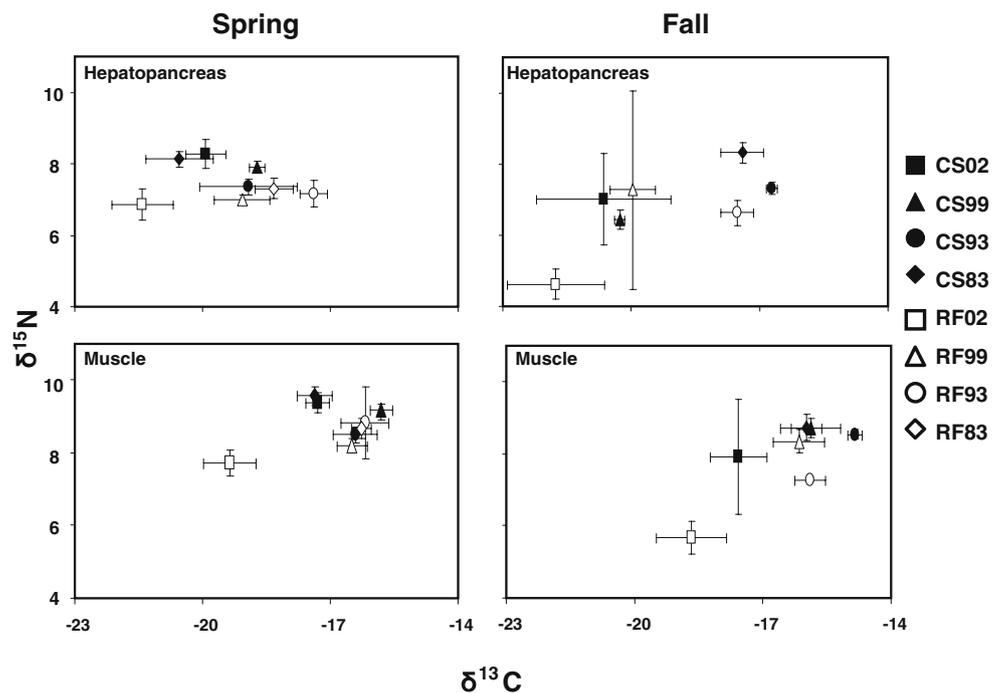
Created marshes were found to be structurally equivalent for nekton abundance and emergent vegetation in comparison to

Table 2 Mean nekton density and biomass (±SE) for each marsh

Marshes	Mean density (nekton m ⁻²)		Mean biomass (g m ⁻²)	
	Spring	Fall	Spring	Fall
2002				
Created	6.3 (±3.0)	16.3 (±14.8)	1.9 (±0.5)	2.6 (±1.6)
Reference	11.0 (±10.5)	13.3 (±6.7)	6.2 (±6.9)	2.8 (±1.8)
1999				
Created	1.7 (±0.9)	10.3 (±8.3)	1.3 (±0.9)	1.4 (±0.7)
Reference	7.1 (±1.8)	3.3 (±0.3)	7.1 (±5.3)	1.9 (±1.1)
1993				
Created	34.3 (±13.3)	6.7 (±5.7)	21.7 (±7.7)	2.5 (±2.2)
Reference	16.0 (±14.1)	1.3 (±0.9)	4.0 (±2.1)	1.8 (±1.8)
1983				
Created	0	13.0 (±4.0)	0	4.5 (±1.0)
Reference	8.0 (±0)	–	5.4 (±0)	–

All data reported are after rare species were removed from analysis

Fig. 2 Mean blue crab $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from each marsh for the muscle and hepatopancreas tissue. Filled symbols represent created marshes, and open symbols represent reference marshes. The CS prefix refers to created marshes, and the RF prefix refers to reference marshes. The last two numbers refer to the year the marsh was created (i.e., 02 2002, 99 1999, 93 1993, 83 1983)



their paired reference marshes; however, stable isotope evidence indicated some differences in functional equivalence in terms of trophic support, between created and reference sites. Stable isotope derived indicators for the three older sites (8, 14, and 24 years old) tended to indicate that trophic support and diversity were similar between the paired sites indicating some level of functional equivalency between the sites. In contrast, the stable isotope analyses indicated that the youngest created site (created in 2002; 5 years old) did not match its reference in terms of blue crab trophic support; however, these results need to be interpreted with caution as the 2002 reference site had greater diversity of basal resources. While this greater basal diversity (i.e., SAV) represents the

desired goals for the 2002 created site, it also highlights a challenge in applying the use of some stable isotope indicators when created marshes are expected to depend on natural recruitment of their basal community. The development of standardization techniques or stable isotope reference norms based on different marsh types/communities may be necessary for this type of approach to be used more widely.

For structural indicators, the only difference found was that all created sites had significantly lower percent organic matter as compared to their reference sites. Differences in soil bulk density and percent organic matter can be a concern in marsh creation as they have been linked to differences in plant productivity and benthic infaunal

Fig. 3 Comparison of blue crab and primary producer isotope values from paired created and reference marshes. The letter in the top left corner of each graph represents the paired comparison (a) CS02 versus RF02; (b) CS99 versus RF99; (c) CS93 versus RF93; (d) CS83 versus RF83. Created marshes are represented with filled symbols, and reference marshes are represented with empty symbols. Circles represent blue crab hepatopancreas tissue isotope mean values. Squares represent blue crab muscle tissue isotope mean values. Diamonds represent primary producers, and each primary producer is labeled by type

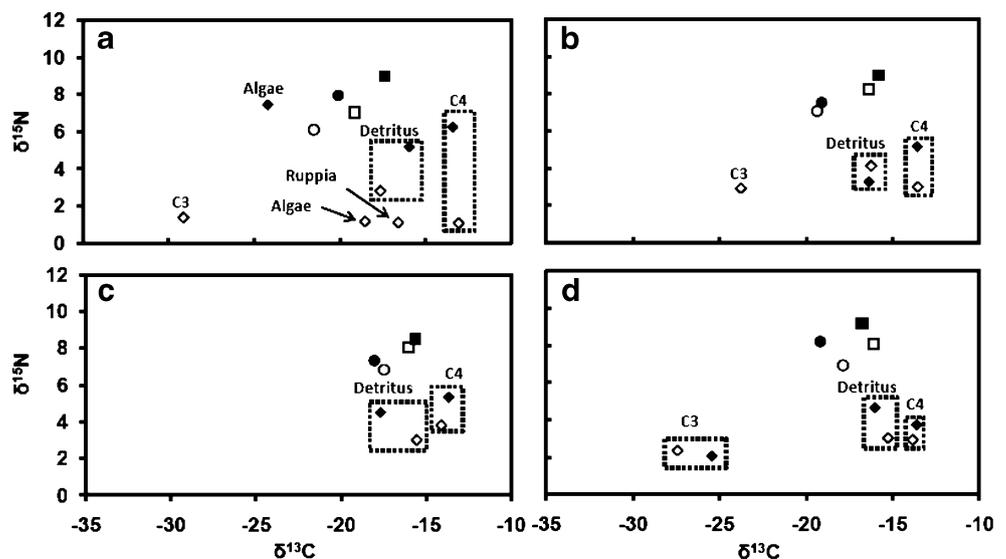


Table 3 Mean blue crab $\delta^{15}\text{N}$, mean primary producer $\delta^{15}\text{N}$, and estimated trophic position of blue crabs from each marsh

Marsh	Crab $\delta^{15}\text{N}$	Base $\delta^{15}\text{N}$	Trophic position (TP)
2002			
Created	7.96 (± 0.44)	5.18 (± 0.62)	2.11 (± 0.76)
Reference	6.11 (± 0.48)	2.80 (± 0.24)	2.32 (± 0.54)
1999			
Created	7.54 (± 0.59)	3.27 (± 0.66)	2.71 (± 0.89)
Reference	7.08 (± 0.17)	4.13 (± 0.80)	2.18 (± 0.82)
1993			
Created	7.33 (± 0.13)	4.49 (± 0.65)	2.14 (± 0.66)
Reference	6.83 (± 0.26)	3.01 (± 0.55)	2.53 (± 0.61)
1983			
Created	8.21 (± 0.16)	4.64 (± 1.01)	2.43 (± 1.02)
Reference	6.93 (± 0.25)	3.03 (± 0.38)	2.56 (± 0.45)

The $\delta^{15}\text{N}$ value for the blue crabs for each marsh comes from the mean $\delta^{15}\text{N}$ found in the hepatopancreas tissue. The mean primary producer $\delta^{15}\text{N}$ (Base $\delta^{15}\text{N}$) is from detritus samples collected at that marsh. Trophic position is calculated as: $\text{TP} = 1 + (\delta^{15}\text{N}_{\text{blue crab}} - \delta^{15}\text{N}_{\text{base}}) / \text{TEF}$. A constant fractionation rate of +2.5‰ is assumed based on meta-analysis by Vanderklift and Ponsard (2003). All results are reported as mean (\pm SE)

communities (Moy and Levin 1991; Sacco et al. 1994; Levin et al. 1996), which can affect the diets of nekton (Moy and Levin 1991). The findings of similar percent organic matter among all four created sites, regardless of age, is in contrast to the conclusions of other long-term studies that 25 years post marsh creation, percent organic matter was still increasing towards that of reference marshes (Lindau and Hossner 1981; Craft et al. 1999), as well as an earlier study which examined the same 1983, 1993, and 1999 created marshes, finding that percent organic matter and site age were highly correlated exponentially with age (Edwards and Proffitt 2003). These soil properties may have been affected by a significant stochastic event. Interestingly, Edwards and Proffitt (2003) noted that one sample from a marsh area had experienced marsh dieback 2 years earlier and had significantly higher percent organic matter than their other marsh samples. This sample was excluded from their analyses as they hypothesized that the high organic matter was a result of the dieback. They suggest that localized disturbance events may play a significant role in increasing soil organic matter in created marshes. It is possible that our soil properties were affected by a significant stochastic event, such as Hurricane Rita, which passed through the area in 2005, which overrode any marsh age effects. Recent hurricanes were responsible for the deposition of significant amounts of inorganic sediments on coastal marshes in Louisiana (Turner et al. 2006).

Consumer $\delta^{13}\text{C}$ isotope values are useful in determining the use of basal resources within food webs, because these

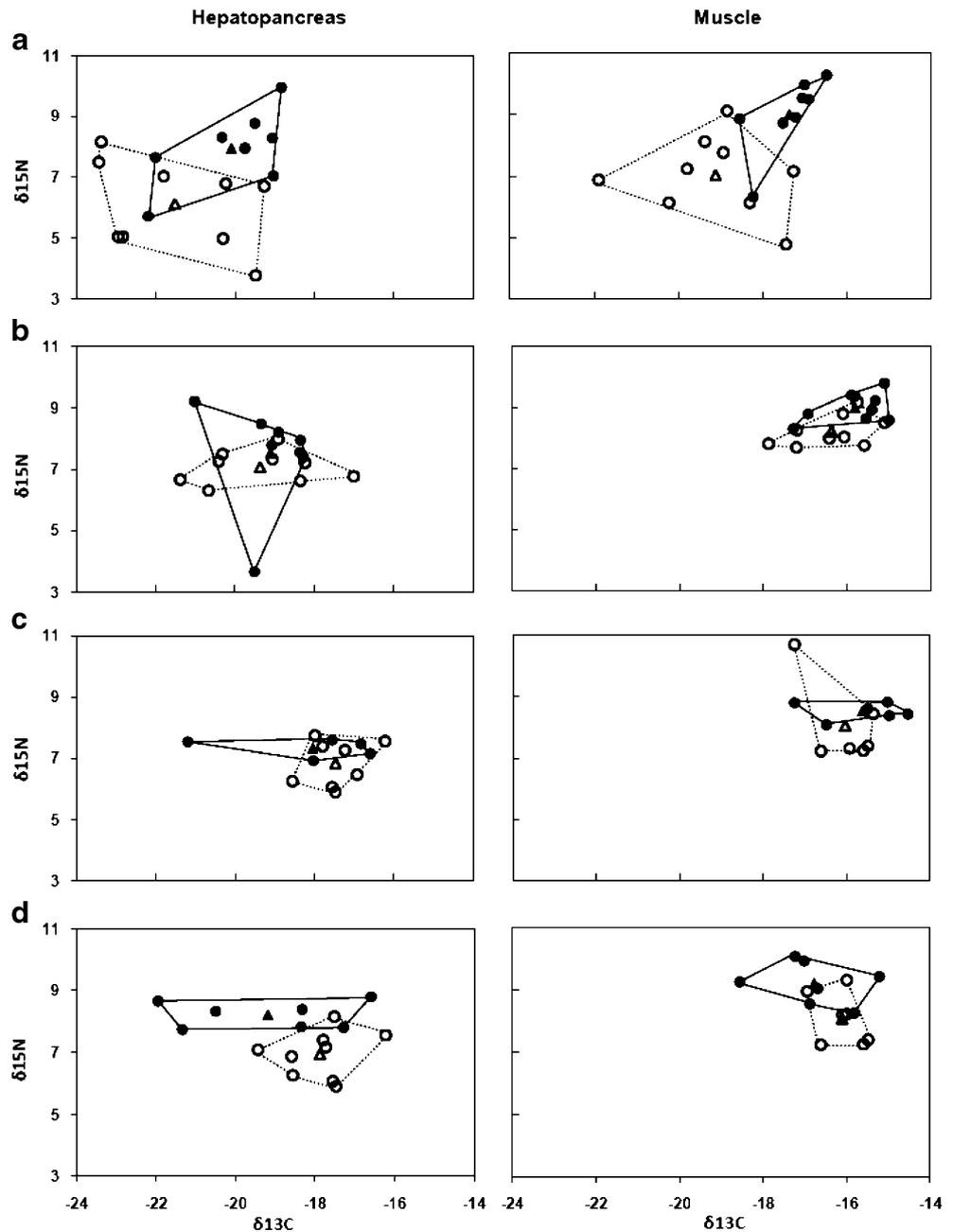
isotopes seldom fractionate across trophic steps. The data from this study indicated that created and reference marshes appeared to have similar basal resources at seven of the eight sites. Similar to findings by Hoetinghaus and Davis (2007), blue crabs in our size class (90–150 mm) were found to rely on detritus-based food webs. Specifically, the created marshes in this study provided equivalent basal primary producer trophic support to blue crabs in *S. alterniflora*-dominated systems where the crabs relied heavily on a detritus-based food web, but this trophic support differed in the more diverse primary producer 2002 reference site where other basal resources such as benthic macroalgae and *R. maritima* were present

Consumer $\delta^{15}\text{N}$ isotope values can be used to estimate an organism's trophic position within a food web because the $\delta^{15}\text{N}$ isotope fractionates approximately 2.5–3.4‰ at each trophic step causing incremental enrichments in consumer $\delta^{15}\text{N}$ values (Peterson and Fry 1987; Vanderklift and Ponsard 2003). Based upon tissue-specific blue crab isotopic analysis, blue crabs in created marshes were found to have more enriched $\delta^{15}\text{N}$ values as compared to their reference counterparts. However, examining only blue crab $\delta^{15}\text{N}$ is somewhat misleading without further analysis of food web resources. This $\delta^{15}\text{N}$ enrichment found in crabs from the created marshes appears to be caused by enriched $\delta^{15}\text{N}$ values of the primary producers in the created marshes compared to the reference marshes. When blue crab trophic position is calculated following Post (2002), the blue crabs from created marshes actually occupy a lower trophic position even though they have a more enriched $\delta^{15}\text{N}$ value than crabs collected from reference marshes.

Two other indicators, trophic niche breadth and dietary diversity analysis, are relatively novel techniques that have been suggested as a way to quantitatively evaluate the complexity of food webs using stable isotope data (Layman et al. 2007a, b). Recent discussions of this approach however indicate that it may only be valuable when isotope ratios from basal resources are equal or standardized (Hoetinghaus and Zeug 2008; Layman and Post 2008). In this study, the 1999, 1993, and 1983 marsh comparisons met this requirement, and in all three of these paired marshes, there were no significant differences in the trophic niche breadth or dietary diversity. These data for the three older sites coupled with a lab study, which demonstrated relatively rapid turnover of the blue crab hepatopancreas tissues (~10 days), suggest that the use of stable isotopes for assessment of marsh equivalence could be a useful tool that provides insight into the development of trophic support in created marshes and may guide managers in identifying suitable time frames for achieving functionally similar and resilient marsh systems.

In contrast to the findings for the older three sites, the 2002 reference marsh had a greater trophic niche breadth and

Fig. 4 Total area of each paired created and reference marsh for hepatopancreas and muscle tissue ($N=9$ for each tissue and marsh). Filled symbols and black lines represent created marshes. Open symbols and gray lines represent reference marshes. Triangles represent the centroid, mean $\delta^{13}\text{C}$ and mean $\delta^{15}\text{N}$, for each marsh. (a) CS02/RF02, (b) CS99/RF99, (c) CS93/RF93, (d) CS83/RF83



dietary diversity than its created counterpart; however, these data need to be interpreted with caution due to the greater diversity of basal resources of submerged aquatic vegetation (*R. maritima*) and dense mats of benthic macroalgae at the 2002 reference site. In order to achieve functional equivalence of created marshes in estuarine environments with greater basal diversity, it may take more active restoration of a greater diversity of primary producers or more time for the diversity of species to recruit. Furthermore, the difficulty in interpreting the results suggest that the use of stable isotopes for comparisons of trophic support may require general reference norms based on equal basal resources or that standardization techniques be developed.

Summary

Both structural and functional evidence were used to examine ecological equivalence at marshes created over a broad temporal range (5–24 years old). In space-for-time approaches, the question of whether any site-based differences detected aligned with patterns of marsh age is relevant. Although there were other differences between sites in terms of location, salinity, and creation techniques, we hypothesized that age would override these other factors. However, with the exception of the soil data, indicating lasting differences between all paired created and reference sites, few differences were found. One fact that

Table 4 Total niche breadth, measured by total area, and trophic diversity, measured by mean centroid distance (CD) by blue crab tissue type for each marsh

Marsh	Hepatopancreas		Muscle	
	Total area	Mean (CD)	Total area	Mean (CD)
2002				
Created	7.35	1.45 (±0.34)	2.91	1.05 (±0.30)
Reference	11.59	2.02 (±0.23)	10.24	1.64 (±0.27)
1999				
Created	7.04	1.36 (±0.44)	1.70	0.76 (±0.15)
Reference	3.92	1.30 (±0.20)	2.13	0.88 (±0.14)
1993				
Created	1.73	1.36 (±0.49)	1.28	0.87 (±0.20)
Reference	2.60	0.90 (±0.11)	3.22	1.21 (±0.34)
1983				
Created	4.49	1.82 (±0.30)	3.29	1.04 (±0.21)
Reference	3.94	1.01 (±0.16)	2.06	0.80 (±0.17)

All results are reported as mean (±SE)

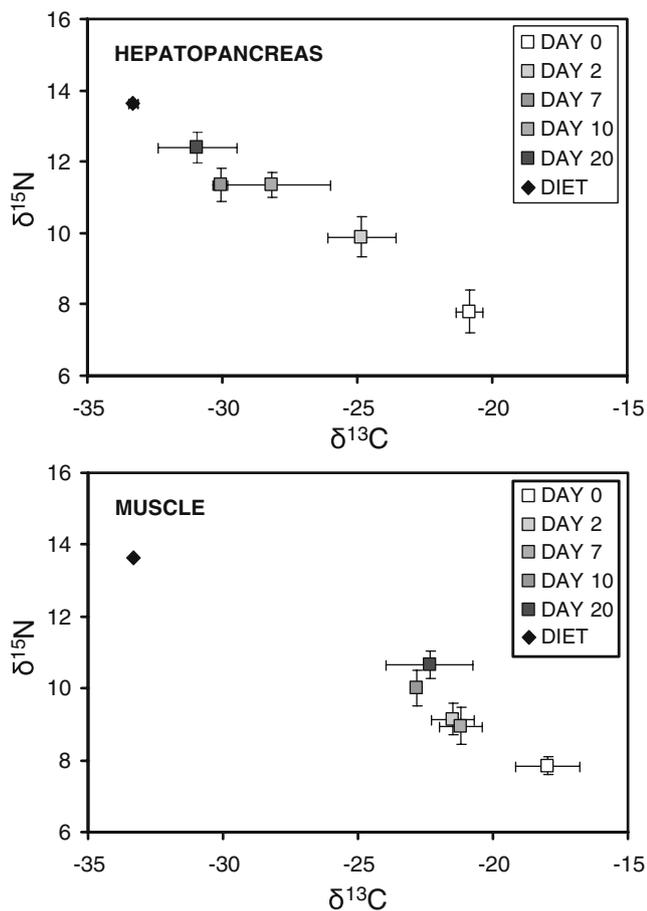


Fig. 5 Mean blue crab isotope values by sample period during the feeding experiment from the smallmouth buffalo diet treatment. Results are presented as mean blue crab value from sample period

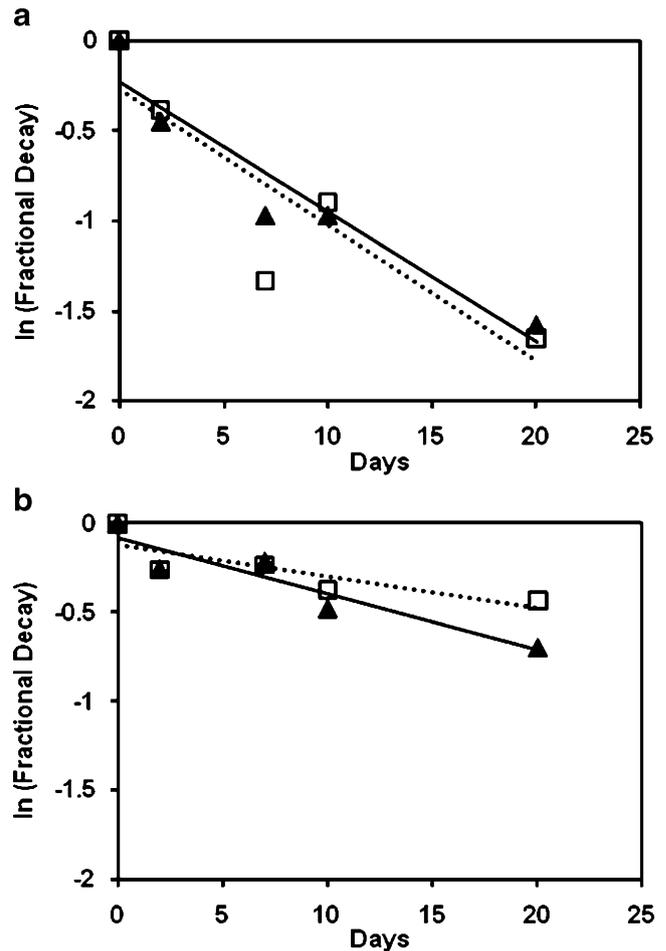


Fig. 6 Regression analysis of blue crab $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope metabolic coefficients from the hepatopancreas (a) and muscle (b) tissue. The slope from these regression lines were used to calculate the turnover rate of each isotope in the muscle and hepatopancreas tissues. Filled triangles represent $\delta^{15}\text{N}$ metabolic coefficient values, and open squares represent $\delta^{13}\text{C}$ metabolic coefficient values

should be noted is that significant improvements have been made in the field of wetland creation over this 24-year time period in which the marshes were created as is evidenced by the differences in marsh creation, noted in the site descriptions. These improvements, which may have overridden age effects, include emphasis on the importance of achieving proper site elevation, building tidal creeks into the created marsh design, placement of the dredge pipes, and the removal of containment levees.

In terms of trophic support to blue crabs, it appears that created marshes may be functionally equivalent to their reference counterparts in a relatively short time period. Comparison of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values overall indicate that the blue crabs at the youngest created marsh (5 years) possess the lowest relative trophic position compared to all other marshes in addition to possessing lower trophic diversity and trophic niche breadth compared to its reference marsh. However, these data need to be

interpreted with caution as the youngest site's reference contained a greater diversity of basal resources compared to all other sites. While quantitative measures of trophic support may serve as important indicators of functional equivalence (Layman et al. 2007b), this approach requires similar basal support between sites. The development of reference levels of trophic support, trophic diversity, and niche breadth based on different marsh types, locations, and basal resources may provide a more standardized and more widely applicable approach for the use of isotope indicators, particularly when basal resources may differ between sites. Further exploration of stable isotope techniques may give coastal managers an important tool to assess functional equivalency of marshes that provides added insight over structural indicators.

Acknowledgments This project could not have been completed without the help of Whitney Gayle, Bryan Gossman, Katie Llewellyn, Bryan Piazza, and Mason Piehler who worked tirelessly in the lab and field. Raw data for this work are available in the electronic thesis by C. Llewellyn (<http://etd.lsu.edu/docs/available/etd-10282008-094243/unrestricted/llewellynthesis.pdf>). Thanks to Dr. Jerome La Peyre for use of the wetlab space. Dr. Brian Fry provided invaluable insight and help with the stable isotope analyses and extremely helpful comments on various versions of this manuscript. Dr. Ken Brown provided valuable comments that improved the manuscript. Dr. Heather Haas provided significant comments that greatly improved the manuscript. This project was funded by the Louisiana Department of Wildlife and Fisheries. Mention of trade names does not imply endorsement from the U.S. government.

References

- Callaway, J.C., J.S. Desmond, G. Sullivan, G.D. Williams, and J.B. Zedler. 2001. Assessing the progress of restored wetlands: Hydrology, soil, plants and animals. In *Handbook for restoring tidal wetlands*, 1st ed, ed. J.B. Zedler, 271–335. Boca Raton: CRC.
- Chabreck, R.H., (1989) Creation, restoration and enhancement of marshes of the northcentral Gulf coast. In Kusler J.A. and Kentula M.E. (eds.) *Wetland Creation and Restoration: The Status of the Science*. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, OR, USA. 127–144, EPA 600/3-89/038a.
- Craft, C., J. Reader, J.N. Sacco, and S.W. Broome. 1999. Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecological Applications* 9(4): 1405–1419.
- DeNiro, M.J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochemica et Cosmochimica Acta* 42: 495–506.
- DeNiro, M.J., and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochemica et Cosmochimica Acta* 45: 341–351.
- Duffy, K.C. 1997. Macrofaunal community structure in the introduced and native submerged macrophyte beds of Lake Pontchartrain estuary. Ph.D. dissertation. Louisiana State University, Baton Rouge, Louisiana, USA.
- Edwards, K.R., and C.E. Proffitt. 2003. Comparison of wetland structural characteristics between created and natural salt marshes in southwest Louisiana, USA. *Wetlands* 23: 344–356.
- Fantle, M.S., A.I. Dittel, S.M. Schwalm, C.E. Epifanio, and M.L. Fogel. 1999. A food web analysis of juvenile blue crab, *Callinectes sapidus*, using stable isotopes in whole animals and individual amino acids. *Oecologia* 120: 416–426.
- Fry, B., D.M. Baltz, M.C. Benfield, J.W. Fleeger, A. Grace, H.L. Haas, and Z.J. Quiñones-Rivera. 2003. Stable isotope indicators of movement and residency for brown shrimp (*Farfantepenaeus aztecus*) in coastal Louisiana marshscapes. *Estuaries* 26(1): 82–97.
- Fry, B., M. Cieri, J. Hughes, C. Tobias, L.A. Deegan, and B. Peterson. 2008. Stable isotope monitoring of benthic-planktonic coupling using salt-marsh fish. *Marine Ecology Progress Series* 369: 193–204.
- Gauch Jr., H.G. 1982. *Multivariate analysis in community ecology*, 298. New York: Cambridge University Press.
- Gossman, B.P. 2005. Use of terraced marsh habitats by estuarine nekton in southwestern Louisiana. M.S. thesis. Louisiana State University, Baton Rouge, Louisiana, USA.
- Hesslein, R.H., K.A. Hallard, and P. Ramlal. 1993. Replacement of sulphur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a shift in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2071–2076.
- Hoeinghaus, D.J., and S.E. Davis. 2007. Size-based trophic shifts of saltmarsh dwelling blue crabs elucidated by dual stable C and N isotope analyses. *Marine Ecology Progress Series* 334: 199–204.
- Hoeinghaus, D.J., and S.C. Zeug. 2008. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 89: 2353–2357.
- La Peyre, M.K., B. Gossman, and J.A. Nyman. 2007. Assessing functional equivalency of nekton habitat in enhanced habitats: Comparison of terraced and unterraced marsh ponds. *Estuaries and Coasts* 30: 526–536.
- Layman, C.A., D.A. Arrington, C.G. Montaña, and D.M. Post. 2007a. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88(1): 42–48.
- Layman, C.A., J.P. Quattrochi, C.M. Peyer, and J.E. Allgier. 2007b. Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecological Letters* 10: 937–944.
- Layman, C.A., and D.M. Post. 2008. Can stable isotopes provide for community-wide measures of trophic structure? Reply. *Ecology* 89: 2358–2359.
- Levin, L.A., D. Talley, and G. Thayer. 1996. Succession of macrobenthos in a created salt marsh. *Marine Ecology Progress Series* 141: 67–82.
- Lindau, C.W., and L.R. Hossner. 1981. Substrate characterization of an experimental marsh and three natural marshes. *Soil Science Society of America Journal* 45: 1171–1176.
- Lockwood, J.L., and S.L. Pimm. 1994. Species: Would any of them be missed? *Current Biology* 4: 455–457.
- McCay, D.P.F., C.H. Peterson, J.T. DeAlteris, and J. Cantena. 2003. Restoration that targets function as opposed to structure: Replacing lost bivalve production and filtration. *Marine Ecology Progress Series* 264: 197–212.
- McClintock, J.B., K.R. Marion, J. Dindo, P.W. Hsueh, and R.A. Angus. 1993. Population studies of blue crabs in soft bottom, unvegetated habitats of a subestuary in the northern Gulf of Mexico. *Journal of Crustacean Biology* 13(3): 551–563.
- Minello, T.J., and L.P. Rozas. 2002. Nekton in gulf coast wetlands: Fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12(2): 441–455.
- Moy, L.D., and L.A. Levin. 1991. Are *Spartina* marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. *Estuaries* 14: 1–16.
- Naeem, S., L.J. Thompson, S.P. Lawler, J.H. Lawton, and R.M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734–737.

- Palmer, M.A., R.F. Ambrose, and N.L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* 5: 291–300.
- Perry, H.M., and T.D. McIlwain. 1986. *Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico)–blue crab*. Washington: United States Fish and Wildlife Service. Biology Report 82 (11.55).
- Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293–320.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83(3): 703–718.
- Sacco, J.N., E.D. Seneca, and T. Wentworth. 1994. Infaunal community development of artificially established salt marshes in North Carolina. *Estuaries* 17: 489–500.
- Schmidt, S.N., J.D. Olden, C.T. Solomon, and M.J. Vander Zanden. 2007. Quantitative approaches to the analysis of stable isotope food web data. *Ecology* 88(11): 2793–2802.
- Turner, R.E., J.J. Baustian, E.M. Swenson, and J.S. Spicer. 2006. Wetland sedimentation from Hurricanes Katrina and Rita. *Science* 314: 449–452.
- Vanderklift, M.A., and S. Ponsard. 2003. Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: A meta-analysis. *Oecologia* 136 (2): 169–182.
- Weinstein, M.P., S.Y. Litvin, K.L. Bosley, C.M. Fuller, and S.C. Wainright. 2000. The role of tidal salt marsh as an energy source for marine transient and resident finfishes: A stable isotope approach. *Transactions of the American Fisheries Society* 129: 797–810.
- Wilson, K.A., K.W. Able, and K.L. Heck. 1990. Habitat use by juvenile blue crabs: A comparison among habitats in southern New Jersey. *Bulletin of Marine Science* 46(1): 105–114.
- Wozniak, A.S., C.T. Roman, S.C. Wainright, R.A. McKinney, and M. J. James-Pirri. 2006. Monitoring food web changes in tide-restored salt marshes: A carbon stable isotope approach. *Estuaries and Coasts* 29: 568–578.
- Wrona, A.B. 2004. Determining movement patterns and habitat use of blue crabs (*Callinectes sapidus* Rathbun) in a Georgia saltmarsh estuary with the use of ultrasonic telemetry and a geographic information system (GIS). Ph.D. dissertation. University of Georgia, Athens, Georgia, USA.