Seaside Sparrows reveal contrasting food web responses to large-scale stressors in coastal Louisiana saltmarshes

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Abstract. Large-scale ecosystem disturbances can alter the flow of energy through food webs, but such processes are not well defined for Gulf of Mexico saltmarsh ecosystems vulnerable to multiple interacting stressors. The 2010 Deepwater Horizon (DWH) oil spill significantly affected the composition of terrestrial saltmarsh communities in Louisiana, and thus had the potential to alter energy pathways through terrestrial and aquatic food webs, with direct consequences for higher trophic-level species restricted to these habitats. The Seaside Sparrow (Ammodramus maritimus) is endemic to saltmarshes and relies completely on the habitat and resources they provide; thus, the sparrows can serve as indicators of ecological change in response to disturbances. We analyzed food web pathways for birds residing in oiled and unoiled saltmarshes for the four years following the oil spill by quantifying the bulk carbon and nitrogen stable isotopes and fatty acid profiles of liver tissues, in addition to primary producers (e.g., marsh grasses) and invertebrate consumers representing the major energy resources in these systems. The stable isotope values of primary producers and most invertebrate consumers did not differ between oiled and unoiled sites, suggesting that the energy pathways within the food web were stable in spite of observed declines in these populations following the spill. The tracer profiles of the Seaside Sparrows confirmed that there was a nominal effect of oil on resource use or trophic position (TP). However, we detected significant interannual variation in resource use by these birds; the sparrows occupied a lower TP and exhibited greater assimilation of resources derived from benthic–aquatic relative to terrestrial pathways in 2013 compared to other years. This distinction is likely attributable to the effects of Hurricane Isaac in 2012, whose significant storm surge extensively inundated the saltmarsh landscape. Despite widespread concern for the saltmarsh ecosystem after the DWH event, the significant effects noted at the population level translated into only subtle differences to the flow of energy through this food web. These results demonstrate varying responses to different degrees of landscape-level disturbance, such as oil and hurricanes, and establish the need to better understand food web dynamics in these saltmarsh ecosystems.

Key words: Ammodramus maritimus; arthropods; Deepwater Horizon oil spill; fatty acids; hurricane; stable isotopes.

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INTRODUCTION

Modifications in community composition and species abundance can alter interaction patterns within food webs (Paine 1980, Polis and Strong 1996, Thebault and Loreau 2003, Petchey et al. 2008). The food web patterns emerging from a species’ feeding choices give rise to structural complexity, ecosystem stability, and diverse functioning (Rooney and McCann 2012). Changes in resource availability and environmental conditions, as well as disturbance, can lead to changes in trophic interactions (Rooney et al. 2006) in accordance with optimal foraging theory (Schoener 1971), which predicts increased trophic generalism with decreases in food availability or food quality. The extent to which disturbances mediate predator-prey interactions within food webs can lead to individual- and population-level effects through diminished growth, survival, and/or reproductive successes that manifest in subsequent generations. Along the Pacific northwest coast of North America, for example, a shift in the foraging ecology of the Glaucous-winged Gull (Larus glaucescens) from a marine- to terrestrial-based diet was attributable to declining populations of its preferred fish prey resulting from harvesting activities (Blight et al. 2015). Crucially, these changes to gull diets were correlated with the declining egg volume and reproductive potential in their populations (Blight 2011).

Both natural and anthropogenic activities threaten coastal ecosystems and the critical services they provide. The stresses to saltmarsh ecosystems, in particular, include physiological (e.g., salinity, drought conditions), physical (e.g., subsidence, storm surge), and biotic challenges (e.g., competition, predation), all of which can act singularly or synergistically to affect habitat and energy availability to consumers in these ecosystems (Doyle et al. 2010, Stouffer et al. 2013). Oil spills, in particular, pose a heightened threat to ecosystem health because they can be unpredictable in space and time (Silliman et al. 2012). The 2010 Deepwater Horizon (DWH) spill oiled nearly 1800 km of the Gulf of Mexico (GOM) coastline (Michel et al. 2013): It was a large spatial disturbance with the potential to dramatically alter coastal saltmarsh community structure and functioning. The oiling across the GOM shoreline was heterogeneous, with some shorelines experiencing little or no oiling, while others were heavily oiled (Michel et al. 2013). Oiled Spartina alterniflora saltmarshes experienced strong effects, including heavy mortalities that denuded and eroded coastlines (Lin and Mendelsohn 2012, Silliman et al. 2012, McClenachan et al. 2013, Turner et al. 2016). These changes directly and indirectly affected the physical structure of the saltmarsh, and contributed to subsequent declines in the abundance of invertebrate taxa, including insects, spiders, snails, and crabs (McCall and Pennings 2012, Husseneder et al. 2016). There was, however, considerable variability in the sensitivity to oil by saltmarsh taxa. The densities of some terrestrial arthropods, for example, were reported to have recovered one year following initial oiling (McCall and Pennings 2012) at some locations, but not at others (Bam 2015, Husseneder et al. 2016). Densities and size-structure of marsh periwinkle (Littoraria irrorata) populations were still suppressed one year after the initial oiling, with recovery projected to take several years (Zengel et al. 2016a); the recovery of fiddler crabs (Uca spp.) and several other benthic meiofaunal species was still ongoing four years following the initial oiling (Fleeger et al. 2015, 2017, Zengel et al. 2016b). Notably, these saltmarsh-associated taxa play key ecological roles in supporting terrestrial and aquatic food webs, linking production resources to higher trophic levels (Pennings et al. 2014, McCann et al. 2017). Such noted responses of the foundational and lower trophic-level invertebrate taxa to the DWH spill have a capacity to destabilize or re-organize saltmarsh food webs by altering the amount and pathways of energy flow, with direct consequences for higher trophic-level consumers exploiting the affected habitats (McCann et al. 2017).

The Seaside Sparrow (Ammodramus maritimus) is an abundant year-round resident in GOM coastal saltmarshes (Post and Greenlaw 1994, 2006) that feeds on terrestrial and aquatic invertebrates associated with S. alterniflora marshes (Post 1974, Post and Greenlaw 2006). As conspicuous upper trophic-level species, the Seaside Sparrow may serve as an indicator of ecological changes in these ecosystems. In Louisiana, Seaside Sparrows continued to occupy oiled marsh habitat after the spill (Stouffer et al. 2013), confirming their dependence on the habitat and...
resources provided by these ecosystems, despite noted alterations to invertebrate populations after the oil spill. The results from studies evaluating these populations suggest sensitivity to oil from the DWH spill, and also a concern for individual-level growth and fitness that could result in population-level effects in these birds (Bergeon Burns et al. 2014, Bonisoli-Alquati et al. 2016).

Our understanding of the consequences of large-scale ecosystem disturbances in saltmarsh food webs, including the DWH oil spill, benefits from quantitative approaches that can track contemporary changes in a species’ diet through time. To predict effects of a shifting prey base, empirical tools used to accurately characterize dietary trends should allow quantification of changes at several trophic levels and multiple nutrient sources (marine, freshwater, and terrestrial). Bulk stable isotopes (SI) and fatty acid (FA) profiles are commonly used to quantify food webs and characterize trophic relationships (Hebert et al. 2006) because these tracers can integrate both temporal and spatial consumer habitat and dietary resource use. Specifically, bulk carbon isotope content is used to identify production sources (and thus habitat use), and bulk nitrogen isotope content indicates trophic positioning and overall food web structuring (Peterson and Fry 1987). Fatty acids are key nutritional components required for normal growth, development, and reproduction, and their biosynthesis largely occurs in primary producers (Parrish et al. 2000). The FA composition of producers differs—aquatic producers contain higher total omega-3 (Σn-3) FA content, whereas terrestrial producers contain a higher total omega-6 (Σn-6) FA content—and their ratio is useful to specify reliance on aquatic vs. terrestrial resources (Kousoroplis et al. 2008, Hixson et al. 2015).

We used SI values of carbon (δ13C) and nitrogen (δ15N), and FA profiles of taxa from a saltmarsh food web studied over several years to determine (1) which production pathways support the saltmarsh community and (2) the response of Seaside Sparrows to changes in habitat and prey populations within the context of environmental change, that is, the DWH oil spill. Given the well-described responses by invertebrate populations to oil, we hypothesized that (1) the terrestrial food web is simplified in oiled marshes relative to unoiled marshes and (2) Seaside Sparrows using oiled marshes consume different prey compared to conspecifics in unoiled marshes. We expected both results to be attenuated with time following the DWH oil spill.

**Materials and Methods**

**Study area**

An estimated 45% of wetlands oiled by the DWH oil spill were located in coastal Louisiana saltmarsh (60% of all habitats; Michel et al. 2013). The heaviest oiling was most widespread in the low tidal range, *Spartina alterniflora*-dominated saltmarsh, of northern Barataria Bay, Plaquemines Parish, Louisiana. In the absence of pre-spill data with respect to Seaside Sparrow resource use in Louisiana saltmarsh, we used a multi-plot design, which allows examination of the magnitude, reproducibility, and variance in individual- and population-level responses to oiling (Skalski 2000). We established replicate study plots on the basis of results from the Shoreline Cleanup Assessment Technique (SCAT) data to compare unaffected areas with areas that experienced moderate-to-heavy oiling. Specifically, in 2011, we selected two plots, one oiled and one unoiled, in the Port Sulphur area of Barataria Bay. In 2012, we added four additional plots, two oiled and two unoiled. Selection of all plots was based on SCAT maps, with oil contamination confirmed through sediment analyses (Michel et al. 2013, Turner et al. 2014a, b). These six plots laid the basis for our experimental design in 2012–2014. Plots were 25 ha (500 m along the marsh edge × 50 m inland). Plots were a minimum of 1 km apart (Fig. 1).

**Ethics statement**

Seaside Sparrows from 2011 were collected under U.S. Fish and Wildlife Service (USFWS) collecting permit MB679782 and Louisiana Department of Wildlife and Fisheries (LDWF) scientific permit LNHP11-062. Birds from 2012 to 2014 were collected under USFWS collecting permits MB095918-0 and MB095918-1; USFWS Federal Bird Banding permit no. 22648; and LDWF scientific collecting permits LNHP-12-023, LNHP-13-059, and LNHP-14-051. This study was carried out in strict accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institutes of
Health. Protocols were approved by the Institutional Animal Care and Use Committee of the LSU AgCenter (IACUC A2012-05).

Sample collection
Seaside Sparrows \((n = 66)\) were collected in August 2011 and in June of 2012–2014 from the locations outlined above (Fig. 1). Seaside Sparrows exhibit site fidelity (Post 1974; S. S. Taylor, S. Woltmann, and P. C. Stouffer, unpublished data); thus, these discrete locations were deemed sufficient to represent plot-level differences. Birds were flushed into a continuous line of four to five, 12-m mist nets oriented perpendicular to the marsh edge (Gordon 2000). Netted individuals were briefly held in cloth bags until euthanized via thoracic compression. All individuals were immediately weighed (g), sampled for liver and other tissues, and sexed (via examination of gonads upon dissection in the field). The tissues were stored in liquid N\(_2\) in the field and then transferred to a \(-80^\circ\text{C}\) freezer in the laboratory.

Fig. 1. Plot locations in the Port Sulphur area of Barataria Bay, Louisiana. Filled circles represent oiled plots, and filled squares represent unoiled plots.
We collected sediment, primary producer, and all invertebrate species in April, May, and June of 2013 and 2014. Live *S. alterniflora, Juncus roemarianus*, and *Distichlis spicata* plants were sampled by clipping them at ground level. Sediment samples were collected as a composite sample of the upper 1–2 cm to serve as a proxy for the microphytobenthos/detrital pathway. Invertebrate species common to the saltmarsh were opportunistically collected by hand and frozen in the field. These included fiddler crabs (Ocypodidae), oval snails (Ellobiidae), periwinkles (Littorinidae), and ribbed mussels (Mytilidae). Terrestrial arthropods were sampled using sweep nets along a linear transect from the edge of the marsh to 20 m inland (20 × 2 × 2 m for a total of 80 m²; Bam 2015). The collected terrestrial arthropods were transferred into 3.7-L plastic zipper bags containing 95% ethanol. Terrestrial arthropods were classed to order and family using taxonomic keys and the morphospecies approach (see Bam 2015 and references therein, including Triplehorn and Johnson 2005, Wimp et al. 2010, Pennings et al. 2011). Dominant terrestrial arthropod taxa collected included orders Heteroptera, Diptera, Orthoptera, Araneae, and Thysanoptera. We selected a subset of the taxa common to the saltmarsh for further isotopic analysis, including planthoppers (Delphacidae), mirid bugs (Miridae), striped flies (Ulidiidae), crickets (Orthoptera), coccinellid beetles (Coccinellidae), spiders (Araneae), damselflies and dragonflies (Odonata), and wasps (Hymenoptera). All species were collected from both the oiled and unoiled plots.

**Tracer analyses**

Seaside Sparrow FA profiles were quantified using a three-step procedure: (1) triplicate extractions of freeze-dried liver tissue in a 2:1 chloroform/methanol solution for gravimetric determination of the total lipid (Folch et al. 1957); (2) derivatization of FA methyl esters (FAME) using sulfuric acid in methanol (1:100 mixture; Morrison and Smith 1964, Christie 1989); and (3) identification and quantification of FAME on an Agilent Technologies 7890N gas chromatograph equipped with a 30-m J and W DB-23 column (0.25 mm I.D; 0.15 μm film thickness), coupled to a flame ionization detector operating at 350°C. Hydrogen was used as carrier gas flowing at 1.25 mL/min for 14 min and ramped to 2.5 mL/min for 5 min. The split/splitless injector was heated to 260°C and run in splitless mode. The oven program was as follows: 60°C for 0.66 min; 22.82°C/min to 165°C with a 1.97-min hold; 4.56°C/min to 174°C and 7.61°C/min to 200°C with a 6-min hold. The FA standards were obtained from Supelco (37 component mix) and NuChek (54 component mix). A known quantity of an internal standard (x-cholestan; Sigma 170 #C-8003) was added to each sample prior to extraction to provide an estimate of extraction efficiency. Seventy-three FAME were identified using Agilent Technologies ChemStation software via retention time and known standard mixtures, and are reported as the percentage of total FA (% TFA). Each FA is described using the shorthand nomenclature of A:Bn-X, where A represents the number of carbon atoms, B represents the number of double bonds, and X represents the position of the double bond closest to the terminal methyl group. In addition to individual FA, we also present results as Σ5FA (saturated FA) to indicate the sum of all FA with zero double bonds, ΣMUFA (monounsaturated FA) to indicate the sum of all FA with one double bond, and ΣPUFA (polyunsaturated FA) to indicate the sum of all FA with ≥2 double bonds. We included Σn-3 PUFA, Σn-6 PUFA, and the Σn-3/Σn-6 ratio to provide semi-quantitative indices of aquatic vs. terrestrial FA sources (Hebert et al. 2008, Paterson et al. 2014, Hixson et al. 2015).

Plant leaves were cleaned of foreign debris and rinsed with distilled water before SI analysis. Ethanol was evaporated from terrestrial arthropod samples in a hood for 48 h. Multiple individuals (2–10) from each arthropod taxon were pooled to obtain an adequate sample mass for the SI analysis. The snails, crabs, and mollusks were dissected and muscle tissue samples processed. Liver tissue samples from Seaside Sparrows that remained following FA extractions were used for SI analysis. Therefore, all bird tissues were lipid-extracted before SI analysis. All tissue samples were dried, ground to a fine powder, and weighed into tin caps (0.5–1.0 mg), and the relative abundance of carbon (13C/12C) and nitrogen (15N/14N) was determined on a Thermo Finnigan DeltaPlus mass spectrometer (Thermo Finnigan,
San Jose, California, USA) coupled with an elemental analyzer (Costech, Valencia, California, USA). Analytical accuracy was 0.06‰, 0.05‰, and 0.06‰ for δ15N data based on National Institute of Standards and Technology (NIST) standards 8573, 8548, and 8549, and 0.09‰ and 0.04‰ for δ13C data based on NIST standards 8542 and 8573, respectively. The analytical precision based on the standard deviation of two standards (NIST 8573, respectively. The analytical precision based on the standard deviation of two standards (NIST bovine liver and fish muscle laboratory standard) for δ15N was 0.15‰ and 0.11‰ and for δ13C 0.09‰ and 0.07‰ respectively.

Data analysis

We used trophic position (TP) to evaluate the trophic structure of the terrestrial saltmarsh food web. When consumers potentially acquire resources from more than one food web, each with a separate set of primary producers or detrital sources (e.g., species that feed on both terrestrial and aquatic food webs), the estimates of TP must account for the potential spatial heterogeneity at the base of the respective food webs. The primary consumers are temporally and spatially less variable in their δ13C than primary producers (Vander Zanden et al. 1998), and are considered useful integrators of this potential variability in the TP estimate. We used the mean δ15N and δ13C values of primary consumers (i.e., assumed to occupy TP = 2) of S. alterniflora (terrestrial: Delphacidae, δ15N = 4.8‰; δ13C = −12.4‰) and of microphytobenthos/detritus (aquatic: Ocyopodiidae, δ15N = 4.7‰; δ13C = −18.1‰) as the isotopic end-members for calculations of TP (Post 2002):

\[
TP = 2 + \left( \frac{\delta^{15}N_{\text{Consumer}} - (\delta^{15}N_{\text{Aquatic}} \times \chi) + \delta^{15}N_{\text{Terrestrial}} \times (1 - \chi)}{\Delta^{15}N} \right)
\]

\[
\chi = \left( \frac{\delta^{13}C_{\text{Consumer}} - \Delta^{13}C - \delta^{13}C_{\text{Aquatic}}}{(\delta^{13}C_{\text{Terrestrial}} - \delta^{13}C_{\text{Aquatic}})} \right)
\]

where Δ15N and Δ13C represent δ15N and δ13C trophic discrimination factors, respectively. The trophic discrimination factors for δ15N were 3.0% for all species, and −0.5‰, and 0.8‰ for δ13C of Seaside Sparrows and invertebrates, respectively (Oelbermann and Scheu 2002, Kempster et al. 2007, Bartrons et al. 2015). The +2 term is added because the TP is being estimated relative to primary consumers rather than to primary producers (Vander Zanden et al. 2000).

All statistical analyses were completed using the R statistical program (version 3.2.4, R Development Core Team 2016). Before all analyses, we evaluated data for normality (probability plots) and homoscedasticity (boxplots). The relationships between treatment (oiled and unoiled) and the year of the SI values for invertebrate taxa were analyzed with a factorial analysis of variance (ANOVA) followed by Tukey's honest significant difference test with Bonferroni-adjusted P-values (α = 0.01) for significant ANOVA results.

We used a principal component analysis [PCA; package vegan in R (Oksanen et al. 2016)] to investigate patterns in Seaside Sparrow FA profiles. The data were obtained for 73 individual FAs, but the analyses were restricted to 13 FAs contributing to ≥1% of the total FA. Together, these 13 FAs accounted for 93% of the total liver FA of Seaside Sparrow. The sum proportions of saturated FA (ΣSFA), mono- (ΣMUFA), and polyunsaturated FA (ΣPUFA), and aquatic (Σn-3)/terrestrial (Σn-6) marker ratios were also included in ordinations. We applied a logit transformation (Warton and Hui 2011) before analysis to stabilize the normality and variance of the proportional data. All FA data were standardized to a mean of zero and unit variance before inclusion in the PCA. Fatty acid variable weights were extracted unscaled (i.e., scaling = 0) from the first two principal components (PC), and the FA loadings on each component were calculated by multiplying the unscaled FA weight by the square root of the eigenvalue for that PC (McGarigal and Cushman 2000). Fatty acids with loadings ≥± 0.750 were considered influential to that component (McGarigal and Cushman 2000).

A linear mixed-effects model analysis was fit using the restricted maximum likelihood (package lme4 in R; Pinheiro et al. 2017) to evaluate the relationships between SI values and FA profiles of the Seaside Sparrows, and the treatment (oiled and unoiled) and year. The models included the treatment and year as fixed effects, and the plot and sex as random effects, because all plots were not sampled annually and both sexes were not sampled at each plot. An examination of the probability plots of residuals from the models relating tracer profiles to the treatment and year indicated
that the models fit adequately. Quantile-quantile plots showed data to be generally described by normally distributed errors. P-values were obtained by likelihood ratio tests followed by pairwise comparisons (package “multcomp” in R; Hothorn et al. 2008) with adjusted P-values when a significant result was observed. The confidence intervals (95%; CI) were calculated to evaluate the effects, with non-overlapping values considered to represent significant differences. Linear regressions were then used to examine the relationship between $\delta^{15}N$ and $\delta^{13}C$, and the ratio of $\Sigma n$ to $\Sigma n$-6, to document any shift between terrestrial and aquatic sources.

**RESULTS**

Stable isotope values of the primary consumers (Delphacidae and Ocypodidae) did not differ among years or between oiled and unoiled plots (Table 1). Factorial ANOVAs indicated that there were significant spatial differences for the $\delta^{15}N$ values of Littorinidae and for the $\delta^{13}C$ values of Littorinidae and Mytilidae (Table 1). Specifically, the $\delta^{15}N$ values of Littorinidae were lower in samples collected from oiled plots, whereas the $\delta^{13}C$ values for Littorinidae and Mytilidae were higher in samples from oiled plots. ANOVA results also indicated that there

<table>
<thead>
<tr>
<th>Order/Family/Species</th>
<th>Year</th>
<th>Oiled</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$n$</td>
<td>$\delta^{13}C$ (‰)</td>
<td>$\delta^{15}N$ (‰)</td>
<td>$n$</td>
<td>$\delta^{13}C$ (‰)</td>
<td>$\delta^{15}N$ (‰)</td>
<td>TP</td>
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<td><em>Spartina alterniflora</em></td>
<td>Combined</td>
<td>3</td>
<td>$-12.8 \pm 0.1$</td>
<td>$3.7 \pm 0.2$</td>
<td>3</td>
<td>$-12.9 \pm 0.2$</td>
<td>$4.1 \pm 0.2$</td>
<td></td>
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<tr>
<td><em>Distichlis spicata</em></td>
<td>Combined</td>
<td>3</td>
<td>$-13.7 \pm 0.1$</td>
<td>$3.9 \pm 0.1$</td>
<td>3</td>
<td>$-13.7 \pm 0.1$</td>
<td>$3.8 \pm 0.1$</td>
<td></td>
</tr>
<tr>
<td><em>Juncus roemerianus</em></td>
<td>Combined</td>
<td>3</td>
<td>$-29.5 \pm 0.6$</td>
<td>$2.5 \pm 0.6$</td>
<td>3</td>
<td>$-28.1 \pm 0.7$</td>
<td>$3.0 \pm 0.4$</td>
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<tr>
<td>Sediment</td>
<td>Combined</td>
<td>3</td>
<td>$-17.9 \pm 2.0$</td>
<td>$1.9 \pm 0.4$</td>
<td>3</td>
<td>$-18.6 \pm 1.5$</td>
<td>$1.6 \pm 0.2$</td>
<td></td>
</tr>
<tr>
<td>Delphacidae (Leaf hopper spp)</td>
<td>2013</td>
<td>11</td>
<td>$-12.4 \pm 0.5$</td>
<td>$5.0 \pm 0.7$</td>
<td>8</td>
<td>$-12.7 \pm 0.4$</td>
<td>$4.9 \pm 0.6$</td>
<td>$2.0 \pm 0.2$</td>
</tr>
<tr>
<td>Miridae (Leaf bug spp)</td>
<td>2013</td>
<td>11</td>
<td>$-12.0 \pm 0.2$</td>
<td>$6.0 \pm 0.6$</td>
<td>8</td>
<td>$-12.2 \pm 0.3$</td>
<td>$6.1 \pm 0.4$</td>
<td>$2.3 \pm 0.2$</td>
</tr>
<tr>
<td>Odonata (Dragon fly spp)</td>
<td>2013</td>
<td>3</td>
<td>$-20.2 \pm 1.0$</td>
<td>$6.6 \pm 0.7$</td>
<td>2</td>
<td>$-17.9, -18.5$</td>
<td>$6.5, 7.4$</td>
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<td>Orthoptera (Cricket spp)</td>
<td>2013</td>
<td>7</td>
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<td>$7.4 \pm 0.7$</td>
<td>1</td>
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<td>Ulidiidae (Striped fly spp)</td>
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<td>6</td>
<td>$-13.6 \pm 0.3$</td>
<td>$7.8 \pm 0.3$</td>
<td>$3.0 \pm 0.2$</td>
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<td>Araneae (Spider spp)</td>
<td>2013</td>
<td>18</td>
<td>$-15.2 \pm 1.0$</td>
<td>$7.9 \pm 0.7$</td>
<td>12</td>
<td>$-15.5 \pm 1.2$</td>
<td>$7.7 \pm 0.8$</td>
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<td>8</td>
<td>$-13.1 \pm 0.4$</td>
<td>$8.2 \pm 0.9$</td>
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<td>$-19.0 \pm 1.6$</td>
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<td>8</td>
<td>$-17.2 \pm 0.1$</td>
<td>$9.7 \pm 0.1$</td>
<td></td>
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<td>Coccinellidae (Beetle spp)</td>
<td>2013</td>
<td>11</td>
<td>$-13.7 \pm 0.6$</td>
<td>$8.5 \pm 1.1$</td>
<td>2</td>
<td>$-13.8, -14.2$</td>
<td>$9.3, 8.9$</td>
<td>$3.4 \pm 0.3$</td>
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<td>Ellobiidae (Marsh snail spp)</td>
<td>2013</td>
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<td>$4.2 \pm 0.9$</td>
<td>3</td>
<td>$-16.0 \pm 1.9$</td>
<td>$4.3 \pm 0.5$</td>
<td>$1.9 \pm 0.2$</td>
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<td>Ocypodidae (Fiddler crab spp)</td>
<td>2013</td>
<td>6</td>
<td>$-17.6 \pm 0.7$</td>
<td>$4.2 \pm 0.9$</td>
<td>7</td>
<td>$-18.1 \pm 0.8$</td>
<td>$5.3 \pm 1.2$</td>
<td>$2.0 \pm 0.3$</td>
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<tr>
<td>Littorinidae (Periwinkle spp)</td>
<td>2013</td>
<td>22</td>
<td>$-13.8 \pm 1.2$</td>
<td>$6.1 \pm 0.8$</td>
<td>22</td>
<td>$-15.6 \pm 1.6$</td>
<td>$6.5 \pm 0.6$</td>
<td>$2.5 \pm 0.2$</td>
</tr>
<tr>
<td>Mytilidae (Ribbed mussel spp)</td>
<td>2013</td>
<td>20</td>
<td>$-23.2 \pm 1.0$</td>
<td>$7.4 \pm 0.3$</td>
<td>18</td>
<td>$-24.3 \pm 0.5$</td>
<td>$7.5 \pm 0.4$</td>
<td>$2.0 \pm 0.2$</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>8</td>
<td>$-24.6 \pm 0.3$</td>
<td>$7.4 \pm 0.7$</td>
<td>9</td>
<td>$-25.0 \pm 0.7$</td>
<td>$7.4 \pm 0.7$</td>
<td></td>
</tr>
</tbody>
</table>

**Notes:** $n$ represents pooled individuals (2–10) to obtain adequate sample. Lowercase and capital letter superscripts indicate significant year and oil status differences for each species, respectively, at $P = 0.01$. TP estimates are combined across year and oil status.

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were significant temporal differences between the 2013 and 2014 samples for the δ15N values of Orthoptera, and between the δ13C values of Uliidiidae and Mytilidae, with opposite patterns being exhibited by the taxa for each isotope (Table 1).

Individual SI values for all Seaside Sparrow liver tissues ranged between −11.4 and −16.7‰ for δ13C and between 8.4 and 11.6‰ for δ15N (Table 2). Birds had similar δ13C (mean ± SD: −13.3 ± 1.1‰ and −13.4 ± 1.4‰) and δ15N (9.7 ± 0.7‰; 9.8 ± 0.7‰) values at oiled and unoiled plots, and we found no statistical difference in the SI values of these individuals (δ13C: χ² = 0.238, P = 0.627; δ15N: χ² = 0.255, P = 0.613; Fig. 2). Seaside Sparrow δ15C values were also not significantly affected by year (χ² = 5.686, P = 0.068; Fig. 2). In contrast, year was a significant factor for Seaside Sparrow δ13N values (χ² = 32.497, P < 0.01), with birds sampled in 2013 having notably lower δ15N values relative to birds sampled in other years by −0.9 ± 0.2‰ (Fig. 2). Moreover, based on TP calculations, birds in 2013 had lower TP (~3.5 ± 0.2) than in other years (~3.8 ± 0.2).

The major FAs detected in Seaside Sparrow liver tissues included 16:0, 18:0, 18:1n-9, 18:2n-6, 20:4n-6, and 22:6n-3 (Table 2). Seaside Sparrows were characterized by high levels of 16:0 and 18:0, with SFA representing approximately 40% of sum FAs. Polyunsaturated FAs were also present in large proportions (~30%), followed by MUFA (~20%; Table 2). Fatty acid compounds, such as 20:4n-6, 20:5n-3, and 22:6n-3, and marker ratios, including Σ3-, Σ3/Σn-6, and ΣPUFA, were strongly positively correlated with the first principal component (PC1; Fig. 3A). In contrast, the 18:1n-9 and ΣMUFA were strongly and negatively correlated with PC1 (Fig. 3A). Fatty acid compounds including 16:1n-7, 18:1n-7, 22:5n-3, and Σn-3/Σn-6 were strongly correlated with the second principal component (PC2) in the positive direction, whereas FA 18:0, Σn-6, and 18:2n-6 were strongly correlated in the negative direction on PC2 (Fig. 3A). The two axes accounted for a combined 72.5% of the total variance.

Table 2. Stable isotope (‰, mean ± 1 SD) and fatty acid proportions (% TFA) for liver tissues of Seaside Sparrows sampled from the Port Sulphur area of Barataria Bay, Louisiana, USA.

<table>
<thead>
<tr>
<th>Tracer</th>
<th>2011</th>
<th>2012</th>
<th>2013</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Oiled</td>
<td>Unoiled</td>
<td>Oiled</td>
<td>Unoiled</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>8</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>δ13C</td>
<td>−13.9 ± 0.7</td>
<td>−12.9 ± 0.7</td>
<td>−12.2 ± 0.6</td>
<td>−13.0 ± 0.9</td>
</tr>
<tr>
<td>δ15N</td>
<td>10.4 ± 0.5</td>
<td>10.6 ± 0.6</td>
<td>10.1 ± 0.6</td>
<td>10.2 ± 0.6</td>
</tr>
<tr>
<td>14:0</td>
<td>0.3 ± 0.1</td>
<td>0.8 ± 0.3</td>
<td>0.6 ± 0.3</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td>16:0</td>
<td>20.9 ± 1.3</td>
<td>25.7 ± 2.7</td>
<td>21.9 ± 2.6</td>
<td>21.6 ± 2.7</td>
</tr>
<tr>
<td>16:1n-7</td>
<td>2.3 ± 0.6</td>
<td>2.2 ± 0.9</td>
<td>4.2 ± 1.5</td>
<td>2.6 ± 1.1</td>
</tr>
<tr>
<td>17:0</td>
<td>0.6 ± 0.2</td>
<td>0.6 ± 0.2</td>
<td>0.6 ± 0.1</td>
<td>0.8 ± 0.1</td>
</tr>
<tr>
<td>18:0</td>
<td>17.9 ± 3.3</td>
<td>18.2 ± 1.8</td>
<td>17.2 ± 2.0</td>
<td>18.6 ± 1.8</td>
</tr>
<tr>
<td>18:n-9</td>
<td>17.2 ± 4.5</td>
<td>15.1 ± 1.5</td>
<td>19.6 ± 2.7</td>
<td>16.1 ± 2.2</td>
</tr>
<tr>
<td>18:n-7</td>
<td>1.8 ± 0.2</td>
<td>1.3 ± 0.3</td>
<td>1.7 ± 0.3</td>
<td>2.1 ± 0.3</td>
</tr>
<tr>
<td>18:2n-6</td>
<td>9.4 ± 0.8</td>
<td>9.7 ± 1.8</td>
<td>8.8 ± 1.3</td>
<td>8.3 ± 2.1</td>
</tr>
<tr>
<td>18:3n-3</td>
<td>0.5 ± 0.4</td>
<td>0.4 ± 0.3</td>
<td>0.7 ± 0.2</td>
<td>0.6 ± 0.5</td>
</tr>
<tr>
<td>20:4n-6</td>
<td>8.3 ± 2.4</td>
<td>8.7 ± 1.7</td>
<td>9.3 ± 1.8</td>
<td>9.5 ± 3.7</td>
</tr>
<tr>
<td>20:5n-3</td>
<td>0.5 ± 0.2</td>
<td>0.8 ± 0.3</td>
<td>0.9 ± 0.3</td>
<td>0.6 ± 0.3</td>
</tr>
<tr>
<td>22:5n-3</td>
<td>0.7 ± 0.3</td>
<td>1.2 ± 0.3</td>
<td>1.2 ± 0.2</td>
<td>1.3 ± 0.5</td>
</tr>
<tr>
<td>22:6n-3</td>
<td>7.6 ± 3.6</td>
<td>6.8 ± 1.2</td>
<td>6.9 ± 2.1</td>
<td>8.2 ± 3.2</td>
</tr>
<tr>
<td>Σn-3</td>
<td>12.1 ± 2.8</td>
<td>11.1 ± 0.9</td>
<td>11.3 ± 1.8</td>
<td>13.9 ± 1.7</td>
</tr>
<tr>
<td>Σn-6</td>
<td>19.2 ± 2.8</td>
<td>19.8 ± 3.1</td>
<td>19.2 ± 2.2</td>
<td>19.2 ± 4.2</td>
</tr>
<tr>
<td>Σn-3/Σn-6</td>
<td>0.6 ± 0.1</td>
<td>0.6 ± 0.1</td>
<td>0.6 ± 0.1</td>
<td>0.8 ± 0.2</td>
</tr>
<tr>
<td>ΣSFA</td>
<td>41.3 ± 2.6</td>
<td>46.8 ± 2.2</td>
<td>41.7 ± 3.7</td>
<td>42.6 ± 4.0</td>
</tr>
<tr>
<td>ΣMUFA</td>
<td>23.3 ± 5.7</td>
<td>20.1 ± 2.6</td>
<td>27.3 ± 3.3</td>
<td>22.8 ± 2.8</td>
</tr>
<tr>
<td>ΣPUFA</td>
<td>31.8 ± 5.3</td>
<td>31.3 ± 2.6</td>
<td>30.8 ± 3.6</td>
<td>33.5 ± 5.2</td>
</tr>
</tbody>
</table>

Notes: SFA, saturated fatty acid; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid. Only 13 (of 73) of the most abundant fatty acids are shown.
The PCA of liver proportional FA data and marker ratios provided clear separation of Seaside Sparrows collected among years (Fig. 3). Birds collected in 2013 scored in the positive direction of both PC1 and PC2, with birds collected in 2011 generally scoring in the negative direction along these same axes (Fig. 3B). Birds sampled in 2011, 2012, and 2014 exhibited a greater degree of overlap of FA profiles relative to birds collected in 2013, which were distinctly separated (Fig. 3B). Year ($\chi^2 = 10.366, P < 0.01$) was a significant predictor of Seaside Sparrow FA profiles on PC1, with pairwise comparisons indicating that 2011 and 2012 were significantly different from 2013 and 2014. Birds sampled in 2013 and 2014 were generally characterized by a higher proportion of 20:5n-3, 22:6n-3, $\Sigma n$-3, and $\Sigma PUFA$ (Fig. 4), suggesting higher contributions of aquatic resources relative to other years. Birds collected in 2013 and 2014 also showed lower amounts of 18:1n-9. Relative to year, neither the treatment ($\chi^2 = 3.363, P = 0.07$) nor the interaction term of year x treatment ($\chi^2 = 5.715, P = 0.06$) was identified as a significant predictor of the FA profiles of Seaside Sparrows on PC1. Treatment ($\chi^2 = 0.088, P = 0.766$) was also not a significant predictor of FA profiles of Seaside Sparrow on PC2. However, year ($\chi^2 = 6.543, P < 0.01$) was a significant predictor, with pairwise comparisons indicating that the FA profiles of 2013 birds were different from all other years (Fig. 3B). Birds collected in 2013 had significantly lower values of terrestrial-derived FA, including 18:2n-6 and $\Sigma n$-6, and higher values of FA considered to represent an increasing importance of benthic-associated habitats, including 16:1n-7 and 18:1n-7, relative to other years (Fig. 5). Liver tissue $\delta^{15}$N values were inversely related to $\Sigma n$-3/$\Sigma n$-6 ratios (Fig. 6A). Relative to other years, birds collected in 2013 had higher ratios at lower $\delta^{15}$N values. Similarly, liver tissue $\delta^{13}$C values were inversely related to $\Sigma n$-3/$\Sigma n$-6 ratios (Fig. 6B), with birds sampled in 2013 having higher ratios at lower $\delta^{13}$C values, though this relationship was weak.

**DISCUSSION**

Gulf of Mexico coastal saltmarsh is among the world’s most productive and valuable ecosystems (Batker et al. 2010); as such, understanding the effects of large-scale disturbances is critical for developing successful strategies aimed at
maintaining these productive habitats. The DWH oil spill directly affected coastal habitats causing, for example, immediate animal mortality and losses of ecosystem services (e.g., Carmichael et al. 2012, Mendelssohn et al. 2012), as well as longer-lasting effects such as persistence of oil-derived compounds (e.g., McClenachan et al. 2013, Turner et al. 2014). Despite widespread concern for coastal saltmarsh in the aftermath of the DWH oil spill, with the exception of the noted effects on marsh vegetation and invertebrate populations, few studies have focused on assessing the consequences to the food web. Our comparison of trophic relationships between terrestrial saltmarsh consumers that experienced different oil exposure indicated that the DWH oil spill resulted in subtle differences in the saltmarsh food web from the perspective of energy transfer from producers to higher trophic levels. In contrast, significant temporal variation in resource use by Seaside Sparrows did not appear to coincide with trophic changes in the broader food web. Characterizing the trophic response of organisms to changes in their environment is important for understanding food web dynamics in these habitats and for predicting future ecological responses to stressors.

We found that saltmarsh consumers, in general, obtained the majority of their energy from C4 plant-based pathways, rather than from either C3 plant or phytoplankton-based pathways, thus confirming that Spartina alterniflora is an important energetic source for the GOM terrestrial saltmarsh food web. Carbon sourced from plants using the C4 photosynthetic process is enriched in 13C (δ13C range: −6‰ to −15‰) relative to carbon sourced from the C3 process (δ13C range: −24‰ to −30‰; Moncreiff and Sullivan 2001, Winemiller et al. 2007). The mirid and delphacid bugs, represent consumers that were most reliant on S. alterniflora (Denno et al. 2002, Wimp et al. 2010). More mobile consumers, such as the Odonata and ocypodid crabs, represented the saltmarsh consumers that were most reliant on aquatically derived energy—most likely via benthic algal and detrital pathways (δ13C range: −18‰ to −20‰, Galván et al. 2008, 2011)—with the potential to transport aquatic-derived energy into the terrestrial landscape. Across all taxa, the saltmarsh consumers obtained greater energetic contributions from benthic algal and detrital pathways than from either phytoplankton or C3 pathways.

The patterns of variation in δ15N values conformed to the expected trophic differentiation among species groups in the terrestrial saltmarsh food web. Generally, families consisting largely of primary consumers, including herbivores (Delphacidae and Miridae) and detritivores (Ocypodidae and Ellobiidae), had low δ15N...
values compared to arthropod groups containing carnivores, specifically Odonata, Coccinellidae, and Araneae. These primary consumers had SI values that did not vary spatially or temporally, suggesting that the energy available at the base of the food web remained stable throughout our study. There were significant temporal and spatial differences in the $\delta^{15}$N values of intermediate consumers. Orthopterans, for example, had higher $\delta^{15}$N values in 2013 compared to in 2014, and the littorinid snails showed higher $\delta^{15}$N values at unoiled sites relative to oiled sites. Notably, the littorinid snails have been designated as highly sensitive to oil and of high food web importance (i.e., serve as prey resource to many species) to the broader saltmarsh food web (McCann et al. 2017). While changes in the $\delta^{15}$N values of these consumers were significant, they did not result in a trophic-level shift, nor were these changes evident in higher trophic-level species, supporting the limited trophic effects of these factors on the flow of energy through this food web. Further, the lack of significant variation in SI values for primary consumers among years and plots suggests that the differences observed in the SI values of the secondary consumers were not a result of changes in available energy, but likely reflect availability of specific prey. Ascertaining the exact response of saltmarsh consumers to the DWH is challenging due to the lack of baseline data prior to the spill, as well as the potential time lag between post-spill die-offs and ecosystem effects (Rabalais and Turner 2016). However, our comparison of saltmarsh consumers on oiled and unoiled plots did show effects from the oil on consumers, albeit to a limited extent, even two years...
after the oil landed. Tracking energy pathways in coastal systems will aid in the interpretation of DWH impact studies and will—perhaps more importantly—contribute to a new understanding of baseline GOM ecosystem functioning, so that future disturbances can be understood more thoroughly than at present.

The absence of significant differences in tracer profiles of Seaside Sparrows from oiled and unoiled saltmarsh is unexpected given the evidence for reduced biomass of invertebrate prey across oiled saltmarshes in Barataria Bay. Contrary to our initial hypothesis that birds inhabiting oiled saltmarsh would consume different prey resources compared to conspecifics inhabiting unoiled marshes, our data suggest similar resource use among treatments. This finding may reflect when this study began (August 2011—nearly one year after oil landfall) when saltmarsh invertebrate consumers showed some recovery in oiled habitats (McCall and Pennings 2012). Even so, a number of studies provide contrasting accounts of the recovery of invertebrate populations following the spill (including Bam 2015, Fleeger et al. 2015, Husseneder et al. 2016, Zengel et al. 2016a, b). The lack of continuous population data for invertebrate saltmarsh taxa from pre-spill years and from the years immediately following (2011–2012) makes definitive conclusions regarding this point limited. Alternatively, it could be argued that the unoiled plots in our study had measurable amounts of petroleum on them or experienced subsequent re-distribution of oil following storm events which could have equivalently affected prey populations at these locations. However, no identifiable Macondo oil was
detected on unoiled plots (Turner et al. 2014b), and while the baseline conditions at these sites were not pristine, the 2010 oiling event raised the average concentration of alkanes and polycyclic aromatic hydrocarbons (PAHs) in the oiled wetland sediments by 604 and 186 times, respectively (Turner et al. 2014b). Moreover, the lack of reported reductions in invertebrate biomass on unoiled plots does not support this explanation. Despite occurring at lower densities on oiled plots (S. Woltman, S. S. Taylor, P. C. Stouffer, unpublished data), birds appear to be using similar resources, and our data do not support a shift in resource use as a consequence of oiling. Moreover, the limited differentiation in SI values of saltmarsh taxa buoy this contention and indicates that despite oiling, birds used resources consistently among sites.

We think that these findings reflect the heterogeneous distribution of oil across the marsh, because some areas experienced little or no oiling, while others were heavily oiled (Michel et al. 2013). Oil from the DWH was deposited most heavily along the seaward edge of marsh and bulk oiling typically spread into the marsh no more than ~10–15 m perpendicular to the edge due in part to the small tidal range (~0.5 m), although oil did extend further into the marsh in some areas (~100 m; Lin and Mendelsohn 2012, Silliman et al. 2012, Michel et al. 2013, Zengel et al. 2015). Oil concentrations measured at 1, 10, and 100 m from the marsh edge did not differ (Turner et al. 2014a), yet invertebrate population estimates generally were quantified in the areas proximate to, and including, the marsh edge (McCall and Pennings 2012, Bam 2015, Fleeger et al. 2015, Husseneder et al. 2016, Zengel et al. 2016a, b). As such, the consideration that Seaside Sparrows foraged on adjacent areas while nesting is a plausible conclusion. Seaside Sparrows have been observed to move fairly large distances (3+ km; Post 1974; Woltmann et al., unpublished data), which is greater than the width of our plots. However, birds occupied and nested in the designated plots after the spill (Stouffer et al. 2013), and telemetry data from radio-tagged individuals in 2012 indicate average (~0.25 ha (Woltmann et al., unpublished data), suggesting that birds, in this case, were relatively confined spatially on the marsh and were not traveling long distances. Moreover, the high metabolic rate of liver results in the rapid turnover of dietary tracers in that tissue, providing short-term dietary information (~one week; Hobson and Clark 1992, Kelly and Scheibling 2012, Vander Zanden et al. 2015). Therefore, the heterogeneous deposition of oil in the marsh relative to the total marsh surface, to a certain degree, may have limited the direct negative effects on these birds and other saltmarsh taxa.

Significant changes to tracer profiles of Seaside Sparrows demonstrate a temporal effect on the resource use by this species across all plots. Specifically, the tracer profiles of birds sampled in 2013 were markedly different from those in birds sampled in all other years. A likely explanation for this response is Hurricane Isaac, a
category-1 storm that made landfall in Plaquemines Parish, Louisiana, in late August of 2012. In contrast to the heterogeneous deposition of oil from the DWH, the storm surge from this landscape-level event inundated Barataria Bay saltmarsh with 1–4 m of water for ~2–3 d. Flooding together with the high winds and heavy rains that accompanied this storm may have killed or forced organisms to seek refuge elsewhere. For example, it was estimated that ~400,000 Seaside Sparrows were displaced (Stouffer et al. 2013). Dry land along the Mississippi River levee was 5–15 km from our study plots and larger areas of dry marsh required movements of 50–100 km (Stouffer et al. 2013), thus limiting the capacity for many species to escape the inundation. The arthropod communities quantified in 2013 and 2014 differed, with significantly lower abundance of species from groups including Odonata, Orthoptera, Pompilidae, Formicidae, and Culicoides reported on our plots in 2013 (Bam 2015). Such hurricane effects decimated arthropod populations on Bahamian islands, specifically spiders and Hymenopteran parasites, and population recovery was not observed for nearly two years after the event (Spiller and Schoener 2007). Notably, tracer profiles of birds sampled in 2011, 2012, and 2014 did not differ, supporting an effect of Hurricane Isaac on these populations that scaled to higher trophic levels. The similarity in tracer profiles between these years could indicate a recovery of prey populations one year after Hurricane Isaac, suggesting a limited timeline for the impacts from this stressor. Yet, this large-scale disturbance, in contrast to the DWH, may have greater implications for the Seaside Sparrow, as a landscape-level reduction in available prey could increase bird competition for shared resources, decreasing foraging time and nest success (Woodrey et al. 2012, Kern and Shriver 2014), warranting further evaluation.

Seaside Sparrows relied predominately on C₄-based production, which is consistent with their habitat preference for S. alterniflora saltmarsh (Rush et al. 2009). However, birds sampled in 2013 exhibited a departure in δ¹³C values toward benthic algae. In addition, significantly lower proportions of terrestrial-derived FA including 18:2n-6 and Σn-6, and higher proportions of aquatic-derived FA, including 20:5n-3 and 22:6n-3, were quantified in their liver tissues. Marine algae, such as benthic diatoms and dinoflagellates, can make 20:5n-3 and 22:6n-3, but terrestrial plants make 18-carbon PUFA (Richoux and Froneman 2008, Kelly and Scheibling 2012), and species associated with aquatic food webs would be expected to have higher proportions of these FAs than terrestrial species (Hebert et al. 2008, Koussoroplis et al. 2008). Indeed, terrestrial insects have low concentrations of 20:5n-3 and 22:6n-3 in their tissues (Uscian and Stanley-Samelson 1994, Howard and Stanley-Samelson 1996). Thus, the marked increase in the proportions of n-3 FA in Seaside Sparrow tissues, and the negative correlation between δ¹³C and Σn-3/Σn-6 ratios, is consistent with reduced incorporation of terrestrial-based production in the diet of birds in 2013. Concomitantly, birds sampled in 2013 relative to other years had higher proportions of 18:1n-7, a FA characteristic of bacteria (Kelly and Scheibling 2012), and of 16:1n-7, a FA characteristic of diatoms (Kelly and Scheibling 2012). Collectively, the shifts in the relative proportions of terrestrial vs. aquatic biomarkers, and the increase in benthic-derived FA in the diet of these birds, support an increased reliance on prey resources derived from a different food web in 2013. The shift between terrestrial and aquatic resources by these birds suggests trophic plasticity, a mechanism that may allow this species to thrive in highly dynamic environments.

The significant temporal variation in resource use by Seaside Sparrows did not appear to coincide with the structural changes in the broader food web, suggesting a systemic change in prey availability. Based on a visual evaluation of the SI values of the saltmarsh food web (Fig. 2), the birds appeared to feed more broadly and on lower trophic-level prey in 2013 compared with all other years. The change in diet in birds sampled in 2013 is reflective of a trophic shift, whereby increased reliance on aquatic resources (e.g., higher Σn-3/Σn-6 ratios) was correlated with lower δ¹⁵N values. This trophic shift is supported by the lower proportions of 18:1n-9—a FA considered to be an indication of carnivory (Dalsgaard et al. 2003, Kelly and Scheibling 2012)—quantified in birds sampled in 2013. The differences in tracer profiles of these birds, coupled with the significant differences between the arthropod communities quantified in 2013 and 2014 (Bam 2015), support the contention that Seaside Sparrows exhibit trophic generalism when
prey populations are compromised. However, additional research is needed to quantify these relationships and to further investigate the relative influences of arthropod community composition and disturbance on foraging behavior of mobile vertebrate consumers in saltmarsh ecosystems. Importantly, the differences in the quality of aquatic- vs. terrestrial-derived resources will be a key avenue for future research to provide further insight into the energetic linkages and how they affect growth, survival, and reproductive potential in this species.

**Conclusions**

Our findings contribute to the maturing understanding of the energy pathways supporting food webs in the coastal saltmarsh landscape, and illustrate the inherent complexity of understanding the effects of potential stressors in these systems. The impetus for this study was to quantify the effects of the DWH oil spill. However, assessments of large-scale disturbances, such as those discussed here, are problematic because measurements of post-disturbance conditions are common, but measurements of pre-disturbance baselines are often rare. The data derived from our comparative approach suggest that there was a subtle effect of oil on energy transfer through the terrestrial saltmarsh food web, but highlight other factors, such as hurricanes, as potentially being more influential on these processes. These findings have greatly informed our awareness of oil impacts, but have also highlighted the knowledge gaps in our understanding of the effects of environmental stressors on these habitats and also on the baseline ecology of these systems (e.g., population sizes, habitat use, foraging strategies; Henkel et al. 2012). We gained a greater understanding of the energy flow and food web structure of GOM saltmarsh communities through characterization of the trophic linkages across differentially stressed habitats. As dynamic processes may be specific to individual marshes, the extrapolation to, and comparisons of, the responses of saltmarsh consumers to disturbance, even on a small geographic scale, should be approached with care (Erwin et al. 2006). Yet, efforts such as these will not only enhance predictions toward expected responses to future environmental conditions, but also strengthen their application as metrics of saltmarsh integrity.

**Acknowledgments**

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