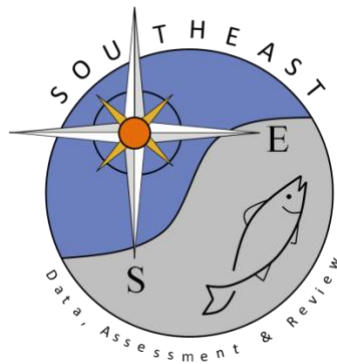# Changes in Red Snapper Diet and Trophic Ecology Following the Deepwater Horizon Oil Spill

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ARTICLE

Changes in Red Snapper Diet and Trophic Ecology Following the Deepwater Horizon Oil Spill

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Abstract

   Red Snapper *Lutjanus campechanus* were sampled at 33 natural and 27 artificial reef sites in the northern Gulf of Mexico prior to (2009–2010) and after (2010–2011) to examine potential diet and trophic shifts following the Deepwater Horizon (DWH) oil spill. We dissected 708 stomachs for gut content analysis and processed 65 muscle tissue samples for stable isotope ratio-mass spectrometry analysis of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$. Forty-eight percent of stomachs contained identifiable prey, which we grouped into seven categories: fish, decapods, cephalopods, stomatopods, gastropods, zooplankton, and other invertebrates. Based on these categories, Red Snapper diet was significantly different following the DWH oil spill, and was differentially affected by fish size. The interaction between habitat (natural versus artificial reefs) and DWH oil spill effects was also significant. Significant differences in diet among Red Snapper size-classes were due to low trophic position prey, such as pelagic zooplankton, being more abundant in the diet of larger (>500 mm) Red Snapper, while decapods and fish constituted a higher proportion of the diet of smaller individuals. Red Snapper consumed higher amounts of decapods at artificial (21.9% by mass) versus natural (14.8%) reef sites, but the habitat effect on diet was not significant. The habitat $\times$ DWH timing interaction was driven by a decrease in zooplankton consumed at both habitat types, increased benthic prey at natural reefs, and increased fish consumption at artificial reefs in post-DWH oil spill samples. Stable isotope data indicated a postspill increase in Red Snapper trophic position (^{15}N enrichment) and an increase in benthic versus pelagic prey (^{34}S depletion), both consistent with observed dietary shifts. Overall, results indicate shifts in Red Snapper diet and trophic position occurred following the DWH oil spill, thus the relative abundance of prey resources likely changed.

The Deepwater Horizon (DWH) oil spill was a catastrophic event for the Gulf of Mexico ecosystem resulting in a total volume discharged of approximately 780,000 m^3 between April 22 and July 15, 2010 (McNutt et al. 2012). Persistence of oil compounds in the water column (Allan et al. 2012; Reddy et al. 2012; Sammarco et al. 2013), impacts to plankton communities (Ortmann et al. 2012; Almeda et al. 2013), and flocculent particulate organic matter that transferred oil compounds to the benthos (Passow et al. 2012; Mason et al.

2014) have been well documented. Direct oiling and toxicological effects of the DWH oil spill on higher taxa, including fishes, sea turtles, birds, and marine mammals, also have been reported (Whitehead et al. 2012; Barron 2012; Schwacke et al. 2013; Murawski et al. 2014). However, little information exists to infer food web effects at higher trophic levels.

We examined changes in the diet and trophic position of Red Snapper *Lutjanus campechanus* following the DWH oil spill, which was only possible due to baseline data from a

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study that actually began 18 months prior to the spill but with very different objectives than to examine oil spill impacts. The original study was focused on examining differences in reef fish ecology on natural versus artificial reefs in the northern Gulf of Mexico. Understanding the relationship between artificial reefs and associated fish communities has important implications for whether artificial reefs are more likely to enhance reef fish production or merely aggregate fish, thus making them more vulnerable to fishing mortality (Bohnsack 1989; Lindberg 1997; Perkol-Finkel et al. 2006). Few fisheries issues in the northern Gulf are as controversial as the ecological versus fishery function of artificial reefs (Cowan et al. 2011), and this debate has mostly centered on Red Snapper.

Red Snapper was an ideal model species given their ecological and economic importance in the region, as well as their abundance on both artificial and natural reefs (Dance et al. 2011; Patterson et al. 2014). Previous studies have been conducted on Red Snapper feeding ecology, but nearly all of the research on this topic has been focused on their ecology on artificial reefs with little to no comparison to fish occupying natural reefs (e.g., Szedlmayer and Shipp 1994; McCawley and Cowan 2007; Dance et al. 2011). Others have clearly demonstrated that comparisons between artificial and natural habitats are critical for assessing the effects of artificial reefs on reef fish ecology (e.g., Carr and Hixon 1997; Perkol-Finkel et al. 2006). Therefore, the original focus of this study was to examine the feeding ecology of Red Snapper at artificial versus natural reefs in the northern Gulf. Analysis of potential habitat effects also required explicitly accounting for the effect of ontogeny given previous reports of ontogenetic shifts in Red Snapper feeding ecology (Ouzts and Szedlmayer 2003; McCawley and Cowan 2007; Wells et al. 2008).

In spring 2010, the occurrence of the DWH oil spill became an unplanned factor in this study. Food web impacts have been reported following previous large-scale spills (Teal and Howarth 1984; Jackson et al. 1989; Moreno et al. 2013), although chronic ecological impacts may not be apparent for

many years following such events (Peterson et al. 2003). Environmental effects of the DWH oil spill have been reported across a variety of habitats and taxa, but effects of the spill on fishes have mostly been restricted to inshore or coastal species (e.g., Fodrie and Heck 2011; Whitehead et al. 2012; Pilcher et al. 2014). Our study occurred over a broad area (about 8,000 km^2) of the northcentral Gulf of Mexico continental shelf. The Red Snapper samples collected there prior to the DWH oil spill provided a unique opportunity to examine the effects of the spill on their diet and trophic ecology. This is significant, not only due to the ecological and economic importance of Red Snapper, but also because relatively few baseline data sets exist to examine the impacts of the DWH oil spill on upper trophic level taxa in the northern Gulf.

METHODS

Red Snapper were sampled between June of 2009 and August of 2011 from 33 natural and 27 artificial reefs south of Dauphin Island, Alabama, to southeast of Destin, Florida (Figure 1). Sampling was conducted onboard chartered fishing boats (home ports of Orange Beach, Alabama, and Pensacola and Destin, Florida) and also onboard the state of Florida's RV *Bellows*. Hook-and-line fishing was performed with two-hook rigs composed of 9/0, 12/0, or 15/0 Mustad circle hooks on 60-lb fluorocarbon leaders. Bait was kept uniform and consisted of cut squid, *Loligo* spp. or Mackerel Scad *Decapterus macarellus*, which allowed for easy identification and segregation from food during diet analysis.

Upon capture, Red Snapper fork length (FL) and total length (TL) were measured (mm) and sex was determined by examination of gonads. A sample ($\geq$50 g) of white muscle tissue was removed above the pectoral fin of each fish and placed in a sealed plastic bag on ice for transport to the laboratory, then stored in an ultralow freezer at $-80°$C until processed. Fish stomachs were also removed at sea and immediately fixed in 10% buffered formalin. A two-factor ANOVA was
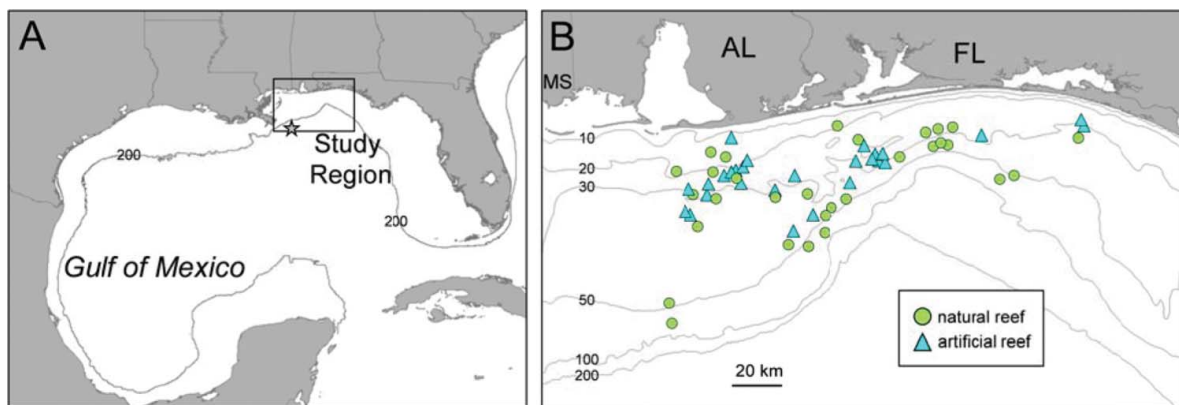

FIGURE 1. (A) Location of the study area in the northern Gulf of Mexico, showing the location of the Macondo wellhead (star), and (B) the natural (green circles [$n = 33$]) and artificial (blue triangles [$n = 27$]) reef sites where Red Snapper were sampled before and after the Deepwater Horizon oil spill; MS = Mississippi, AL = Alabama, FL = Florida. Isobath depths in m.

computed to test for significant differences in Red Snapper total length between habitat types and pre-DWH versus post-DWH. A priori, the experiment-wise error rate (α) was set to 0.05 for all statistical analyses.

Diet analysis.—Red Snapper stomachs were fixed in 10% formalin for at least 48 h and then were transferred to 70% isopropyl alcohol for preservation. Diet composition analysis was performed by identifying stomach contents to the lowest taxonomic level possible with the aid of a dissecting microscope for all stomach samples that had prey items present. Prey items were sorted by taxon and then dried for 48 h at 60°C to obtain dry mass.

Prey were sorted into one of seven categories for statistical analysis of diet: fish, decapods, cephalopods, stomatopods, gastropods, zooplankton, and other invertebrates. Mean percent dry mass was computed as the arithmetic mean among samples within a given factor, the factors being size-class (<400, 400–500, >500 mm), habitat type (natural versus artificial reefs), and DWH oil spill timing (before versus after April 22, 2010). A three-factor permutational multivariate ANOVA (PERMANOVA) was computed with the Primer statistical package (version 6; Anderson et al. 2008) to test for differences in Red Snapper diet by percent dry mass among size-classes, between habitat types, and pre versus post spill. Diet data were square-root-transformed, and a dummy variable with value = 1 was added to each sample to stabilize dispersion in the data prior to computing the Bray–Curtis similarity measure between each pair of samples (Clarke 2006). The PERMANOVA model then was computed in Primer with 10,000 permutations. Type-III sums of squares were utilized to determine significance.

Stable isotope analysis.—Stable isotope analysis was performed on a randomly selected subset of Red Snapper white muscle samples. Muscle tissue was dried at 60°C for at least 24 h, ground with a mechanical tissue grinder, and then pulverized into a fine powder with a glass or agate mortar and pestle. Between 0.2 and 0.5 g of pulverized dried tissue were placed in sterile plastic centrifuge tubes and shipped to a contract laboratory to perform analysis of $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ with a Europa Scientific GSL/Geo 20-20 stable isotope ratio–mass spectrometer. The isotopic ratio of a sample relative to the ratio in an international standard is reported in the standard delta notation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$, where $X = {}^{15}N$, ${}^{13}C$, or ${}^{34}S$ and $R = {}^{15}N : {}^{14}N$, ${}^{13}C : {}^{12}C$, or ${}^{34}S : {}^{32}S$. Standards included nitrogen in air ($\delta^{15}N_{Air}$), Pee Dee Belemnite ($\delta^{13}C_{V-PBD}$), and Canyon Diablo Troilite ($\delta^{34}S_{V-CDT}$). International Atomic Energy Agency standard reference materials were run periodically as check samples to assess machine performance for each stable isotope ratio analyzed. Analytical precision was estimated from duplicate analysis of 20 randomly selected samples.

Trophic level was estimated for each Red Snapper sample following Post (2002): trophic level = $1 + (\delta^{15}N_{fish} - \delta^{15}N_{prod})/\Delta_n$, where $\delta^{15}N_{fish}$ is the $\delta^{15}N$ of a given Red Snapper muscle sample, $\delta^{15}N_{prod}$ is the mean $\delta^{15}N_{prod}$ of primary producers in the system, and Δ_n is trophic fractionation per trophic level. Estimating mean $\delta^{15}N_{prod}$ of primary producers can be problematic if there is a diversity of primary producers present in the system (e.g., phytoplankton, benthic algae, seagrasses, marsh grasses) or if there is considerable temporal variability in $\delta^{15}N$. While seagrass and marsh habitats were present in the study region, they were not present on the shelf or within 30 km of the study reefs. Therefore, the predominant primary producers in the system are phytoplankton and benthic microalgae. There was no significant difference in mean $\delta^{15}N$ between phytoplankton and benthic microalgae samples (n = 33) collected in the northern Gulf shelf prior to the DWH oil spill (two-sample t-test, $P = 0.305$; W. Patterson, unreported data), which is similar to the pattern reported for $\delta^{15}N$ by Radabaugh et al. (2013) for the west Florida shelf, despite considerable variability in $\delta^{13}C$ between phytoplankton and benthic algae. Given the lack of difference in $\delta^{15}N$ among pre-DWH oil spill phytoplankton and benthic microalgae samples, the overall mean $\delta^{15}N$ of 5.82 (SE = 0.13) among combined sample types served as our estimate of $\delta^{15}N_{prod}$. Trophic fractionation (Δ_n) was assumed to equal 3.0‰, which is the mean measured for fishes feeding on high-protein diets (McCutchan et al. 2003; Vanderklift and Ponsard 2003; Rooker et al. 2006).

Values of $\delta^{13}C$ were corrected for percent lipid with the regression equation reported by Post et al. (2007) for aquatic animals: CF = $-3.32 + (0.99 \times C{:}N)$, where CF is the correction factor applied to $\delta^{13}C$ to account for percent lipid and C:N is a proxy for percent lipid. Hereafter, $\delta^{13}C$ always indicates lipid-corrected $\delta^{13}C$. To examine basal sources of C and S, the $\delta^{13}C$ and $\delta^{34}S$ values at the base of the food web were estimated following Post (2002):

$$\delta X_{base} = \delta X_{fish} - [(\text{trophic level} - 1) \times \Delta_x],$$

where δX_{base} = estimated $\delta^{13}C$ or $\delta^{34}S$ of the C or S source, respectively, at the base of the food web, $\delta X_{fish} = \delta^{13}C$ or $\delta^{34}S$ of a given Red Snapper sample, trophic level = estimated trophic level of a given Red Snapper sample derived from $\delta^{15}N$, and Δ_X = trophic fractionation (increase) in $\delta^{13}C$ or $\delta^{34}S$ per trophic level. A value of 1.5‰ was assumed for Δ_C, which is the mean reported by Sweeting et al. (2007) for fish muscle tissue. A value of 0.5‰ was assumed for Δ_S, which is the mean reported by McCutchan et al. (2003).

Linear regressions were computed between Red Snapper $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ and total length to test for ontogenetic effects on those variables. Two-factor ANOVA models were computed to test the effects of habitat type and DWH oil spill timing on total length, estimated trophic level, $\delta^{13}C_{base}$, and $\delta^{34}S_{base}$.

RESULTS

Study reefs ranged in depth from 17 to 92 m. Red Snapper ranged from 238 to 890 mm TL, the means not differing (ANOVA) between habitat types ($F_{1,\,706} = 0.30$; $P = 0.586$) or between pre and post samples ($F_{1,\,706} = 2.45$; $P = 0.118$).

Stomach Content Analysis

A total of 708 Red Snapper stomachs were sampled. Of those, 20.5% ($n = 145$) were empty, 31.7% ($n = 220$) had only chyme present (i.e., no prey items could be identified), and 48.3% ($n = 343$) had identifiable prey items present. However, among the stomach samples with identifiable prey present, approximately 50% by dry mass (mean percent dry mass = 45–52% among factor levels) of their stomach contents had already been reduced to chyme, thus were unidentifiable. Among the identifiable prey items, 85 unique prey taxa were identified and then sorted into the seven prey categories (Table 1). Statistical analysis of Red Snapper diet was based on percent dry mass of these identifiable prey. Results of the PERMANOVA computed for Red Snapper diet were that size-class and DWH oil spill timing significantly affected diet, but habitat type did not (Table 2; Figure 2). However, the interaction between DWH oil spill timing and habitat type was significant.

Three of the seven prey categories constituted >80% of Red Snapper diet by dry mass. Overall, fish prey constituted nearly half (43.2%; Figure 2) of Red Snapper diet, but most (>90%) fish prey could not be identified even to family. Fish remains that could not be identified to order or below were classified as unknown fish. The smallest (<400 mm) Red Snapper size-class contained the highest percentage of fish prey (58.7%), while fish constituted 26.5% of Red Snapper diet in the 400–500 mm size-class, and 28.0% of the diet of Red Snapper >500 mm. Identified fish prey of Red Snapper sampled on natural reef sites consisted principally of nonreef benthic taxa, such as lizardfishes (Family Synodontidae), searobins, Red Porgy, and Southern Hake, while stomach samples of fish from artificial reefs contained a combination of nonreef benthic and pelagic fishes, such as harvestfish *Peprilus* sp. and herrings (Clupeidae). Reef fish taxa identified in Red Snapper stomach samples were rare and consisted of grunts (Haemulidae) and triggerfish (Balistidae).

Overall, zooplankton accounted for 22.6% of Red Snapper prey by dry mass and included 22 unique taxa. Zooplankton made up 14.1% of total prey mass within the <400 mm size-class, 25.3% for fish 400–500 mm, and 27.4% for individuals >500 mm. Although there was no significant difference in the amount of zooplankton consumed between natural reefs (22.6%) and artificial reefs (22.7%), there was a difference in zooplankton taxa consumed. On natural reefs, small pelagic gastropods within order Thecosomata constituted 52.8% of zooplankton prey, but they made a much smaller (5.5%) contribution to Red Snapper diet on artificial reefs. The greatest contributor to zooplankton prey on artificial reefs was the pelagic amphipod *Phrosina*

semiluna, which constituted 84% of zooplankton prey on artificial reefs but only 11% on natural reefs.

Decapods contributed 17.6% of total prey mass, with 22 taxa identified among the diet samples. Decapod prey items tended to be more numerous in the stomachs of smaller Red Snapper but constituted a larger percentage of the diet of larger fish due to the consumption of larger decapods, such as box crabs and Florida lady crabs (Table 1). No difference in decapod diversity was observed in Red Snapper diets between habitat types, but Red Snapper did consume slightly higher amounts of decapods at artificial (21.9%) versus natural (14.8%) reefs.

Overall, cephalopods, stomatopods, gastropods, and other invertebrates combined made up less than 20% of Red Snapper diet by dry mass. The cephalopod category was composed of squid *Loligo* sp., and octopuses (Order Octopoda). Stomatopods (adult mantis shrimp) made up 4.7% of Red Snapper diet, stomatopod consumption on natural reefs being approximately 133% of that on artificial reefs. Benthic gastropods totaled <1% of total diet mass, and other invertebrates consisted of worms, echinoderms, isopods, sponges, barnacles, tunicates, and prey that could not be classified below Order Malacostraca. Other invertebrates constituted a fairly constant but low percentage (approximately 9%) of Red Snapper diet among all size-classes but were more predominant in stomach samples from natural reefs (Table 1; Figure 2).

The significant interaction between DWH oil spill and habitat type effects on Red Snapper diet precludes interpretation of the significant DWH oil spill main effect independently. Fish contribution to diet at artificial reefs more than doubled post-DWH; however, there was no change at natural reefs, and decapod consumption increased by 58.3% at natural reefs but declined by 19.8% at artificial reefs (Table 1; Figure 2). Red Snapper captured at both habitat types had lower zooplankton contribution to their diets after the spill, zooplankton contribution to Red Snapper diets decreasing 55.7% on natural and 64.7% on artificial reefs following the spill. Pteropods, mysid shrimp, and the hyperiid amphipod *Phorina semiluna* were the predominant zooplankton prey at natural reefs prior to the DWH oil spill but were entirely absent from post-DWH diet samples. Mysid shrimp and *Phorina semiluna* were the most abundant zooplankters in pre-DWH Red Snapper diet samples at artificial versus natural reefs, but were also entirely absent from Red Snapper diets at artificial reef sites after the DWH oil spill. Among the minor prey categories, the most substantial change following the DWH oil spill was the appearance of stomatopods in natural reef samples where they had been absent prior to the spill.

Stable Isotope Analysis

Red Snapper white muscle samples included tissue from 32 individuals sampled between June and November 2009 (pre-DWH), as well as 34 fish sampled between March and August

TABLE 1. Mean percent diet by dry mass computed from identifiable prey items within stomachs of 343 Red Snapper sampled at natural and artificial reefs in the northern Gulf of Mexico.

Group	Taxon	Natural reefs		Artificial reefs	
		Pre-DWH	Post-DWH	Pre-DWH	Post-DWH
Fish	Anguilliformes	0.00	0.49	0.77	0.00
	Balistidae	0.22	0.00	0.00	0.00
	Searobins *Bellator* spp.	0.00	0.66	0.00	0.00
	Clupeidae	0.00	0.00	0.00	1.15
	Atlantic Croaker *Micropogonias undulatus*	0.00	0.66	0.00	0.00
	Gulf Butterfish *Peprilus burti*	0.00	0.00	1.58	0.00
	Harvestfish *Peprilus* sp.	0.00	2.15	0.00	0.00
	Pleuronectiformes	0.00	0.00	0.00	1.15
	Red Porgy *Stenotomus caprinus*	0.00	1.73	0.00	0.00
	Synodontidae	0.00	0.95	0.00	0.18
	Unknown Fish	43.24	36.37	22.31	51.02
	Southern Hake *Urophycis floridana*	0.00	0.66	0.00	0.00
	Total Fish	43.46	43.65	24.65	52.50
Decapods	*Albunea* sp.	0.00	0.23	0.00	0.82
	Brachyura	0.00	3.95	0.26	0.97
	Yellow box crab *Calappa sulcata*	0.00	0.00	2.08	0.00
	Calappidae	0.00	0.66	0.00	0.00
	Caridea	0.00	0.66	0.00	0.00
	Decapoda	7.02	2.86	6.02	9.51
	Hippoidea	0.00	0.00	0.00	0.77
	White elbow crab *Leiolambrus nitidus*	0.00	0.00	0.00	1.15
	Fivespine purse crab *Myropsis quinguespinosa*	0.07	0.00	0.00	0.00
	Ogyrides sp.	0.01	0.00	0.00	0.00
	Florida lady crab *Ovalipes floridanus*	0.00	0.66	0.00	1.56
	Paguroidea	0.00	0.00	0.00	0.03
	Bladetooth elbow crab *Parthenope granulata*	1.27	0.00	2.08	0.00
	Penaeidae	1.01	3.59	2.74	1.15
	Brown shrimp *Penaeus aztecus*	0.00	0.04	0.00	0.00
	Portunidae	0.25	0.97	4.40	0.01
	Redhair swimming crab *Portunus gibbesii*	0.00	0.00	3.90	0.00
	Sargassum swimming crab *Portunus sayi*	0.00	0.29	0.00	0.00
	Longspine swimming crab *Portunus spinicarpus*	0.00	1.32	0.00	3.01
	Blotched swimming crab *Portunus spinimanus*	0.78	0.00	0.00	0.00
	Gulf frog crab *Raninoides louisianensis*	0.00	0.00	2.02	0.00
	Brown rock crab *Sicyonia brevirostris*	0.00	1.25	1.58	1.15
	Total Decapods	10.41	16.48	25.10	20.14
Cephaolopods	Cephalopoda	0.04	0.33	0.15	0.00
	Loligo sp.	0.00	2.23	0.21	1.73
	Octopoda	0.00	0.68	0.00	0.00
	Total Cephalopods	0.04	3.23	0.36	1.73
Stomatopods	Manits shrimp *Squilla* sp.	0.00	1.99	0.00	0.36
	Squillidae	0.00	0.00	0.10	1.15
	Stomatopoda	0.00	5.17	5.07	1.65
	Total Stomatopods	0.00	7.16	5.18	3.16
Gastropods	Gastropoda	0.10	0.57	0.00	1.21
	Total Gastropods	0.10	0.57	0.00	1.21

TABLE 1.   Continued.

Group	Taxon	Natural reefs		Artificial reefs	
		Pre-DWH	Post-DWH	Pre-DWH	Post-DWH
Other Inverts	*Aegathoa oculata*	0.00	0.02	0.00	0.00
	Ascidiacea	0.16	0.00	0.00	0.00
	Asellota	0.00	0.00	0.06	0.00
	Cirripedia	0.02	0.00	0.00	0.01
	Crustacea	1.62	0.00	3.77	0.00
	Echinodermata	0.00	0.49	0.00	0.09
	Invertebrata	4.31	0.69	1.92	0.88
	Isopoda	0.00	0.11	0.00	0.01
	Malacostraca	0.00	10.30	0.00	2.30
	Polychaeta	0.00	0.27	0.00	0.00
	Porifera	0.00	0.00	0.00	3.11
	Sessilia	0.02	0.00	0.00	0.00
	Sphaeroma quadridentata	1.68	0.00	0.07	0.00
	Tunicata	0.06	0.00	0.00	0.26
	Worm Tubes	0.00	0.00	0.00	0.89
	Total Other Inverts	7.85	11.89	5.82	7.55
Zooplankton	Amphipoda	0.02	0.68	1.05	0.70
	Aoridae	0.00	0.00	2.08	0.00
	Asteroidea larvae	0.00	0.00	0.06	0.00
	Brachyura megalopa	0.00	2.42	0.00	0.33
	Branchiopoda	19.39	0.00	0.21	0.00
	Carinarioidea	0.00	5.17	0.00	4.59
	Cladocera	1.68	2.42	2.08	0.22
	Decapod megalopa	0.00	0.02	0.00	0.33
	Decapod zoea	0.00	1.45	0.00	0.23
	Haemulidae larvae	0.01	0.00	0.00	0.00
	Hyperiidae	0.66	3.53	2.08	3.46
	Lophogastrida	0.00	0.01	0.00	0.00
	Mysidacea	0.00	0.00	4.12	0.00
	Mysidae	2.49	0.00	2.00	0.00
	Mysidopsis sp.	0.00	0.00	1.06	0.00
	Phronima sp.	0.00	0.00	2.32	0.00
	Phrosina semiluna	1.65	0.00	11.10	0.00
	Phyllosoma	0.00	0.13	0.00	0.03
	Scyllaridae larvae	0.00	0.00	2.08	0.00
	Sergestidae	0.00	0.81	0.00	0.00
	Squilla larvae	0.00	0.40	0.00	0.00
	Thecosomata	12.24	0.01	8.41	3.82
	Unknown Zooplankton	0.00	0.00	0.23	0.00
	Total Zooplankton	38.13	17.03	38.88	13.71

2011 (post-DWH). There was a significant linear relationship between $\delta^{15}N$ and total length (GLM procedure [SAS, Cary, North Carolina], $P = 0.035$), but regressions for $\delta^{13}C$ (GLM, $P = 0.981$) and $\delta^{34}S$ (GLM, $P = 0.130$) were not significant (Figure 3). Total length of fish sampled for stable isotope analysis was significantly different between pre-DWH (mean = 452 mm, SE = 17.8) and post-DWH (mean = 529 mm, SE = 29.7) samples (Table 3). Therefore, $\delta^{15}N$ data were length-detrended by subtracting the slope of the total length versus $\delta^{15}N$ regression times a given sample's total length from the sample's $\delta^{15}N$ value, and then trophic level was estimated as indicated above. The DWH oil spill timing effect

TABLE 2. Permutational multivariate ANOVA model testing the effect of fish size-class (< 400, 400–500, and >500 mm TL), habitat type (natural versus artificial reefs), and the timing of the Deepwater Horizon (DWH) oil spill (pre versus post) on Red Snapper diet.

Source	df	Type-III sums of squares	Mean square	Pseudo-F	P-value
Size	2	15,567	7,783	2.39	0.021
Habitat	1	5,503	5,503	1.69	0.150
DWH	1	21,225	21,225	6.52	0.001
Size × DWH	2	13,989	6,995	2.15	0.053
Size × habitat	2	9,454	4,727	1.45	0.193
DWH × habitat	1	8,903	8,903	2.73	0.049
Size × habitat × DWH	2	11,177	5,589	1.72	0.108
Residual	331	1,080,000	3,256		
Total	342	1,170,000			

was significant for Red Snapper trophic position, but there was no difference between habitat types; the interaction between habitat and DWH oil spill timing also was not significant (Table 3; Figure 4).

Variables $\delta^{13}C_{base}$ and $\delta^{34}S_{base}$ required a $\log_e$ transformation to meet the parametric assumption of normality (Table 3). The decrease in $\delta^{13}C_{base}$ following the DWH oil spill was statistically significant, and the DWH oil spill timing effect was
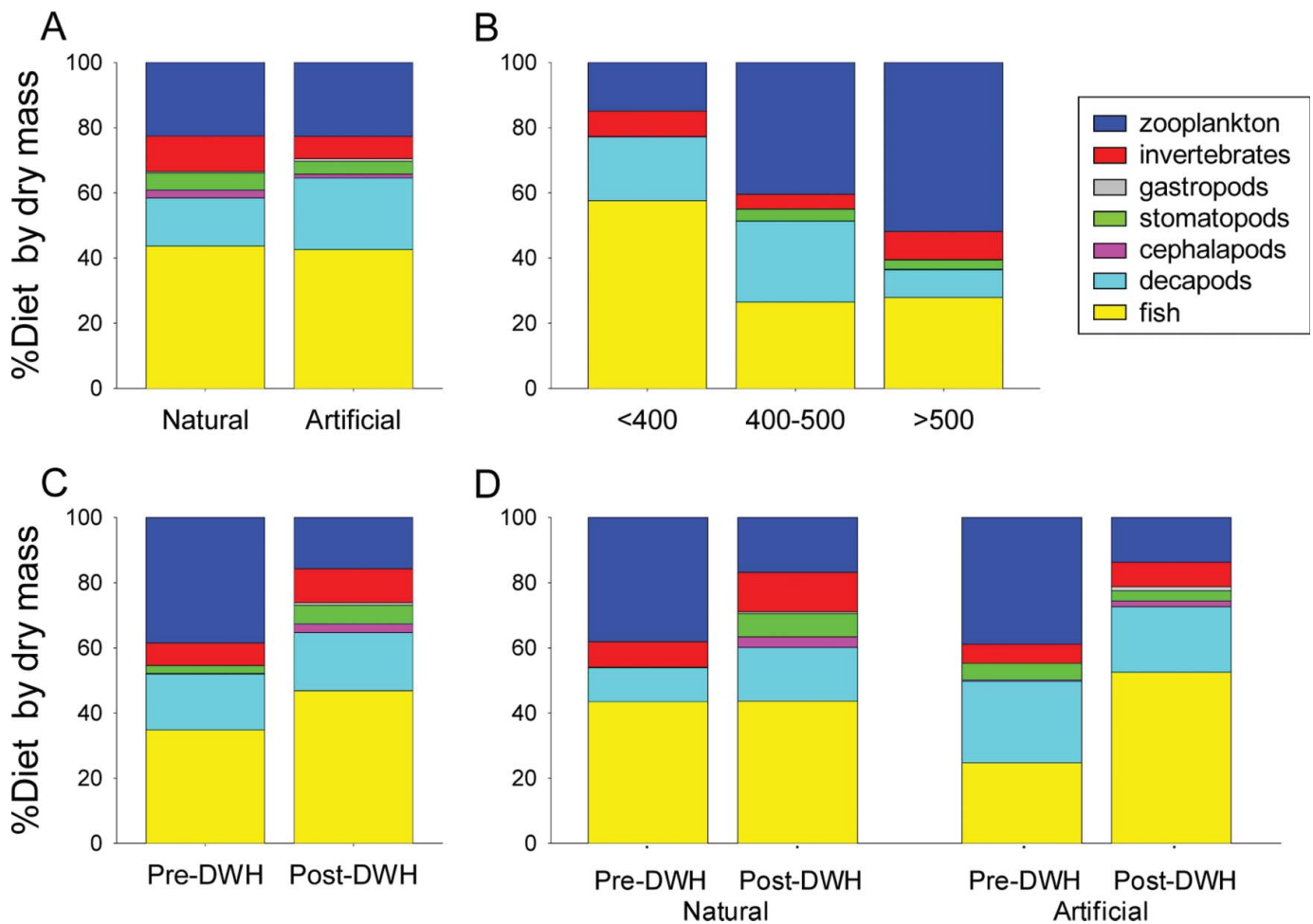

FIGURE 2. Mean percent Red Snapper diet by dry mass estimated among seven prey categories observed among stomach samples. Panels demonstrate the effect of **(A)** habitat (natural versus artificial reefs), **(B)** size-class (total length in mm), **(C)** the timing of the Deepwater Horizon (DWH) oil spill, and **(D)** the interaction between habitat type and DWH timing on Red Snapper diet among samples collected in the northern Gulf of Mexico from June 2009 through August 2011.
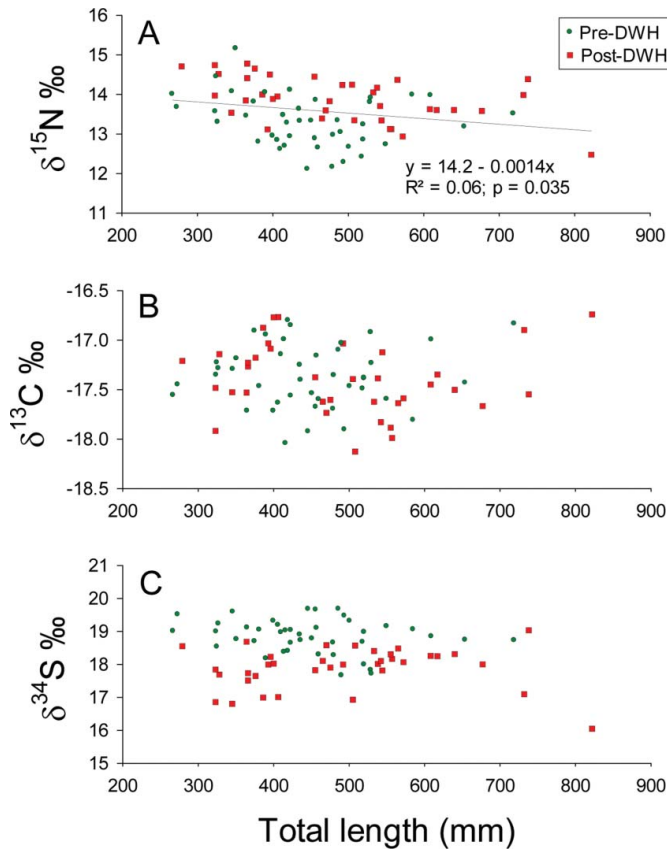
FIGURE 3. Scatterplots of white muscle (A) $\delta^{15}N$, (B) lipid-corrected $\delta^{13}C$, and (C) $\delta^{34}S$ versus total length for pre-Deepwater Horizon (DWH) and post-DWH oil spill Red Snapper samples. Regression fit to $\delta^{15}N$ data in panel A was significant but weak, and regressions for lipid-corrected $\delta^{13}C$ and $\delta^{34}S$ were nonsignificant.

also significant $\delta^{34}S_{base}$, both decreasing the year after spill (Table 3; Figure 4). Consistent with the lack of significant diet differences between natural and artificial reefs, none of the stable isotope variables displayed a significant habitat effect (Table 3).

DISCUSSION

Overall, data from this study demonstrate adult Red Snapper to be generalist mesopredators with broad diets. They are opportunistic foragers that consume prey along a size spectrum ranging from zooplankton to fish. However, nothing in their morphology would suggest they are able to strain or even pick zooplankton from the water column. Instead, they likely forage on swarms of plankton, such as pteropods or hyperiid amphipods (Fenwick 1978; Sanvicente-Añorve et al. 2013), when available. The phenomenon of Red Snapper subsidizing their diet with zooplankton was described previously by Ouzts and Szedlmayer (2003) and McCawley and Cowan (2007) for fish sampled at artificial reefs off Alabama in the northern Gulf of Mexico. McCawley and Cowan (2007) demonstrated

that plankton consumption increased for larger Red Snapper, as is reported here, and that zooplankton consumption was highest in spring. They concluded that zooplankton consumption was probably either a response to artificial reefs being spaced too closely—thus, Red Snapper had to rely on unexpected prey resources to meet basal bioenergetics demands—or that adults subsidized their diet with zooplankton to facilitate maximum reproductive output during their protracted April to September spawning season (Jackson et al. 2007).

We found different zooplankton taxa were predominant in pre-DWH Red Snapper stomachs sampled at natural versus artificial reefs, but zooplankton percent diet by mass was nearly identical between habitat types. Therefore, it seems unlikely that artificial reef spacing explains zooplankton consumption, especially given the fact that Red Snapper density is an order of magnitude higher on artificial versus natural reefs in the system (Patterson et al. 2014). Instead, the presence of zooplankton highlights the extreme diversity of Red Snapper diet and the opportunism they display while foraging. It should also be noted that several zooplankton taxa identified in diet samples were relatively soft-bodied compared with decapods or fishes. Therefore, it is likely that zooplankton prey experienced higher digestion and evacuation rates than other prey types, thus may have constituted an even higher percentage of the Red Snapper diet than the overall 22.6% by mass observed among pre-DWH oil spill samples.

Habitat was not a significant factor with respect to Red Snapper diet or trophic position, and few reef-dependent taxa were present in Red Snapper stomach samples, regardless of habitat type. Densities of larger (>250 mm TL) reef fishes, including Red Snapper, on artificial reefs are typically 150–200% greater than their densities on natural reefs in the northern Gulf (Dance et al. 2011; Patterson et al. 2014), which may lead to greater competition for resources and decreased food web complexity (Bohnsack and Sutherland 1985). However, among our seven broad prey categories, only subtle differences in Red Snapper diet contribution were observed between habitat types, and those differences were probably related to local abundance rather than prey selectivity. The lack of reef-associated prey in Red Snapper stomachs indicates a reliance on nonreef foraging habitat (Bradley and Bryan 1975; Ouzts and Szedlmayer 2003; McCawley and Cowan 2007), regardless of whether fish were associated with natural or artificial reefs.

Many reef fishes, including snappers, have been shown to forage away from reef structure, thus translocate energy and nutrients horizontally back to reefs (Appledoorn et al. 2009; Luo et al. 2009; Berkström et al. 2012). Data presented here and by others suggest Red Snapper also translocate energy and nutrients from surrounding open substrates back to reefs, whether natural or artificial. Lack of habitat-specific differences in Red Snapper diet may at first seem to indicate no foraging advantage conveyed by artificial reef habitat. However, based on foraging distances (typically <100 m) estimated via

TABLE 3. ANOVA models testing for effects of habitat type (natural versus artificial reefs) and Deepwater Horizon (DWH) timing (pre versus post) on Red Snapper stable isotopes or stable isotope-derived variables.

Source	df	Type-III sum of squares	Mean square	Pseudo-F	P-value
Total length					
Habitat	1	46,920	46,920	3.36	0.072
DWH	1	67,654	67,654	4.84	0.031
Habitat × DWH	1	8,792	8,792	0.63	0.431
Residual	62	866,056	13,969		
Trophic level					
Habitat	1	0.045	0.045	1.46	0.232
DWH	1	0.287	0.287	9.25	0.003
Habitat × DWH	1	0.023	0.023	0.39	0.392
Residual	62	1.925	0.031		
$\mathbf{Log}_e(-\delta^{13}C_{base})$					
Habitat	1	8.82×10^{-5}	8.82×10^{-5}	0.28	0.597
DWH	1	2.75×10^{-3}	2.75×10^{-3}	8.80	0.004
Habitat × DWH	1	2.01×10^{-4}	2.01×10^{-4}	0.65	0.425
Residual	62	1.93×10^{-2}	3.12×10^{-4}		
$\mathbf{Log}_e(\delta^{34}S_{base})$					
Habitat	1	3.90×10^{-3}	3.90×10^{-3}	3.07	0.085
DWH	1	2.02×10^{-2}	2.02×10^{-2}	15.90	<0.001
Habitat × DWH	1	1.67×10^{-3}	1.67×10^{-3}	1.31	0.257
Residual	62	7.89×10^{-2}	1.27×10^{-3}		

acoustic telemetry data (Westmeyer et al. 2007; Topping and Szedlmayer 2011), deployment of artificial reefs appears to enable Red Snapper to exploit foraging habitats on the shelf they otherwise would be unlikely to visit, especially given that natural reef habitat in the northcentral Gulf of Mexico is concentrated in deeper (>40 m) waters than where the bulk of artificial reef zones are located (Parker et al. 1983; Schroeder et al. 1988; Patterson et al. 2014).

We observed ontogenetic shifts in Red Snapper diet and trophic position, but the decline in their estimated trophic level with increasing size was not expected a priori. Others have reported shifts to higher trophic position and to greater piscivory during development (Bradley and Bryan 1975; Wells et al. 2008). However, those studies described feeding and trophic shifts from settlement and early life, when a clear shift from planktonic to benthic feeding was observed. Here, we report a similar pattern among subadult and adult Red Snapper as that reported by McCawley and Cowan (2007) in which zooplankton constituted a substantial (>20%) percentage of the diet of larger, reproductively mature fish. Higher trophic-level prey, such as decapods and fish, were predominant in the diet of smaller (<400 mm TL) Red Snapper but became less predominant for larger individuals. Although decapod contribution to diet decreased as Red Snapper length increased, the mass of individual prey was notably greater in the diet of larger fish.

Analysis of $\delta^{15}N$ corroborated a decrease in Red Snapper trophic position with increasing size, which also indicates the presence of lower trophic-level prey in the diet of larger individuals was not ephemeral, given that turnover time of fish white muscle tissue is typically weeks to months (Buchheister and Latour 2010; Nelson et al. 2010). While $\delta^{15}N$ values and trophic level estimates derived from them confirm trends observed in diet data, $\delta^{13}C$ and $\delta^{34}S$ data provide information about Red Snapper trophic ecology that may not be apparent in diet data alone. For example, northern Gulf phytoplankton typically has a $\delta^{13}C$ signature of approximately −22‰ and a $\delta^{34}S$ signature of approximately 18‰, whereas benthic micro-algae has a $\delta^{13}C$ signature of approximately −18‰ and a $\delta^{34}S$ signature of approximately10‰ (Moncrieff and Sullivan 2001; Fry 2006; Rooker et al. 2006). Therefore, estimates of $\delta^{13}C_{base}$ and $\delta^{34}S_{base}$ provide information with respect to the relative contribution of pelagic versus benthic production to Red Snapper biomass, and the lack of a significant relationship between $\delta^{13}C$ or $\delta^{34}S$ and length indicates neither the source of C nor S was related to fish size. The lack of a habitat effect on $\delta^{13}C_{base}$ and $\delta^{34}S_{base}$ indicates the relative contribution of pelagic versus benthic production was not significantly different between natural and artificial reefs, which further indicates that Red Snapper trophic ecology does not differ between these habitat types.

The factor that had the greatest impact on Red Snapper diet and trophic level was DWH oil spill timing. Pre-DWH diet
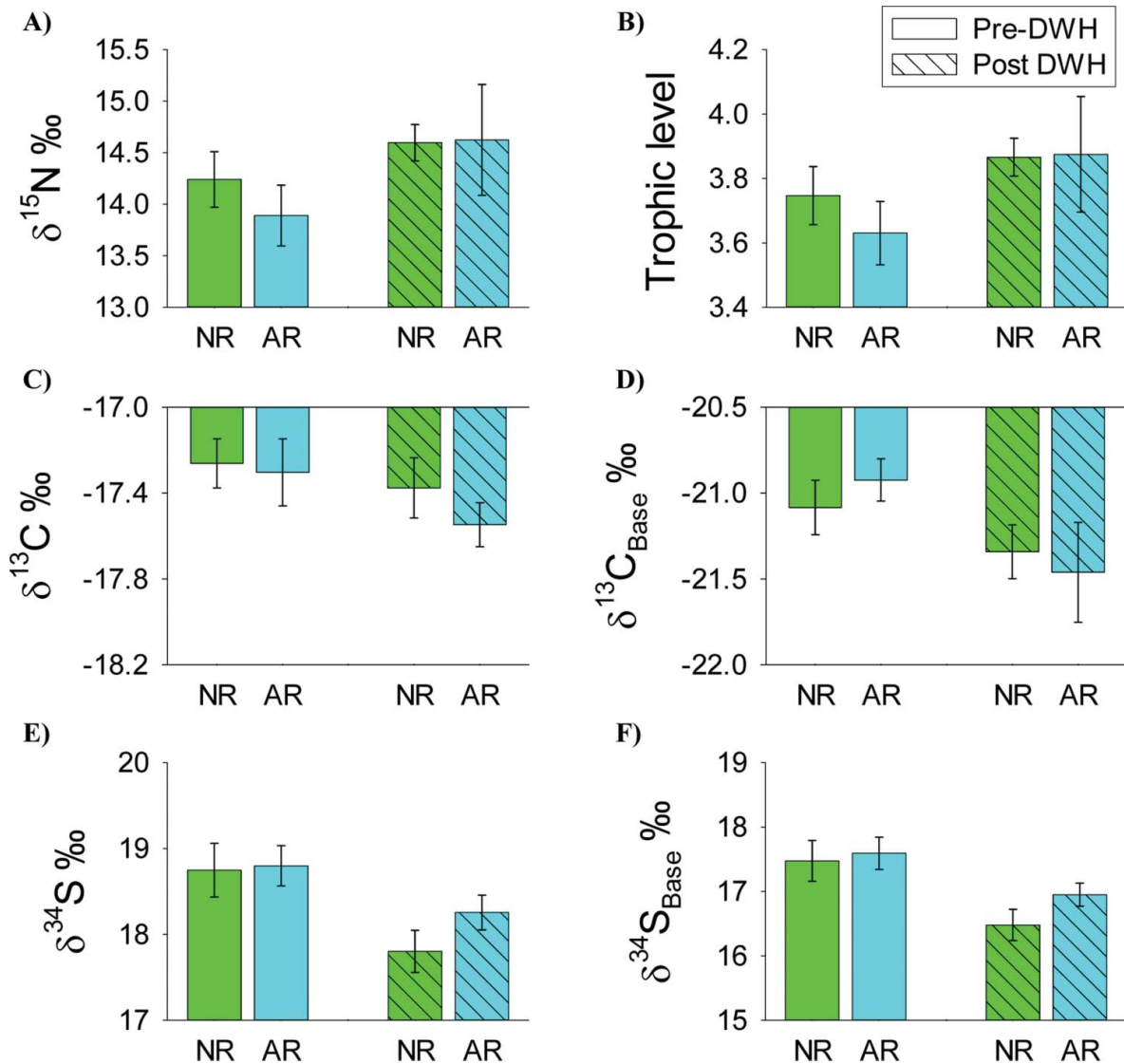
FIGURE 4.   Mean (± 95% CI) habitat (NR = natural reef; AR = artificial reef) and Deepwater Horizon (DWH) oil spill timing-specific values for Red Snapper (A) white muscle δ^{15}N, (B) estimated trophic level, (C) lipid-corrected white muscle δ^{13}C, (D) estimated δ^{13}C at the base of the food web, (E) white muscle δ^{34}S, and (F) estimated δ^{34}S at the base of the food web for fish sampled between June 2009 and August 2011 in the northern Gulf of Mexico.

composition estimates presented here are consistent with earlier estimates reported by Ouzts and Szedlmayer (2003) and McCawley and Cowan (2007) (e.g., fish and crustaceans forming large percentages of Red Snapper diet, but zooplankton also contributing 15–20% of diet by mass), thus providing support that our pre-DWH diet data are generally representative of Red Snapper diet. Following the DWH oil spill, zooplankton consumption decreased markedly at both natural and artificial reefs, which was replaced with higher trophic level prey: decapods, cephalopods, and stomatopods at natural reefs and predominantly fish at artificial reefs. These shifts clearly were persistent for weeks to months as higher post-DWH δ^{15}N values and lower δ^{34}S values in Red Snapper muscle samples indicated a shift to higher trophic level and more benthic prey

resources (i.e., pelagic zooplankton prey replaced by benthic decapods and fishes). Toxicological, immunological, and genetic effects on plankton communities were documented after the spill (Ortmann et al. 2012; Paul et al. 2013), and a decline in zooplankton consumption is consistent with high plankton mortality and a resultant blizzard of marine snow observed in the months following the spill (Passow et al. 2012). Not only did oil toxicity impact northern Gulf plankton communities following the spill, but the release of millions of gallons of Corexit dispersant likely magnified the toxic effects of the spill on plankton (Middaugh and Whiting 1995; Ortmann et al. 2012; Paul et al. 2013). Therefore, while increased higher trophic level prey following the DWH oil spill might suggest greater abundance of those taxa, a more

plausible scenario is that zooplankton were less abundant in the months following the spill which resulted in much lower zooplankton consumption.

The one variable that appears inconsistent with DWH oil spill-related trends observed in diet and other stable isotope data is $\delta^{13}C$, specifically estimates of $\delta^{13}C_{base}$. Phytoplankton are depleted in ^{13}C relative to benthic algae (Moncrieff and Sullivan 2001; Fry 2006); thus, lower $\delta^{13}C_{base}$ values a year after the DWH oil spill should imply greater, not lower, plankton contribution to Red Snapper muscle C. However, hydrocarbons released during the DWH oil spill constitute another source of organic carbon on the shelf, and they were even more depleted in ^{13}C than phytoplankton (Chanton et al. 2012; Cherrier et al. 2013). Results from $\delta^{13}C$ mixing models computed by Cherrier et al. (2013) for northern Gulf particulate organic carbon (POC) sampled in summer 2011 and 2012 indicated 28–43% of POC was derived from fossil CH_4. Due to the sequestration of hydrocarbons beneath the seabed for millions of years, oil hydrocarbons are dead with respect to ^{14}C activity (Chanton et al. 2012). Therefore, extremely low POC $\Delta^{14}C$ values (e.g., less than $-600‰$) provide even stronger evidence that hydrocarbons from the DWH spill entered the food web (Cherrier et al. 2013). The fact that Red Snapper $\delta^{13}C_{base}$ estimates were significantly lower following the spill when other evidence suggests higher values would be expected may suggest that oil carbon reached higher levels of the food web, and did so as early as the year following the spill.

Red Snapper samples collected in 2009-2010 prior to the DWH oil spill provide a unique opportunity to examine potential impacts of the spill on their diet and trophic position, as well as future examination of ecosystem resiliency. These relatively large generalist mesopredators may be an ideal species to examine for such impacts because they have such a broad diet, ranging from zooplankton to fish, thus can easily shift to foraging on locally abundant prey taxa. The corroboration of shifts observed in diet data with trophic shifts inferred from muscle stable isotope ratios provides clear evidence of DWH oil spill impacts to Red Snapper feeding ecology, and likely the northern Gulf food web in general. Where pre-DWH muscle samples or stable isotope data exist, stable isotope analysis also can be employed to examine DWH oil spill effects for other northern Gulf reef fishes for which pre-DWH oil spill diet data are unlikely to be as extensive as they are for Red Snapper.

ACKNOWLEDGMENTS

REFERENCES

Allan, S. E., B. W. Smith, and K. A. Anderson. 2012. Impact of the Deepwater Horizon oil spill on bioavailable polycyclic aromatic hydrocarbons in Gulf of Mexico coastal waters. Environmental Science and Technology 46:2033–2039.

Almeda, R., Z. Wambaugh, Z. Wang, C. Hyatt, Z. Liu, and E. J. Buskey. 2013. Interactions between zooplankton and crude oil: toxic effects and bioaccumulation of polycyclic aromatic hydrocarbons. PLoS (Public Library of Science) ONE [online serial] 8(6):e67212.

Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth, UK.

Appeldoorn, R. S., A. Aguilar-Perera, B. L. K. Bouwmeester, G. D. Dennis, R. L. Hill, W. Merten, C. W. Recksiek, and S. J. Williams. 2009. Movement of fishes (grunts: Haemulidae) across the coral reef seascape: a review of scales, patterns and processes. Caribbean Journal of Science 45:304–316.

Barron, M. G. 2012. Ecological impacts of the Deepwater Horizon oil spill: implications for immunotoxicity. Toxicological Pathology 40:315–320.

Berkström, C., M. Gullström, R. Lindborg, A. W. Mwandya, S. A. S. Yahya, N. Kautsky, and M. Nyström. 2012. Exploring knowns and unknowns in tropical seascape connectivity with insights from East African coral reefs. Estuarine Coastal and Shelf Science 107:1–21.

Bohnsack, J. A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bulletin of Marine Science 44:631–645.

Bohnsack, J. A., and D. L. Sutherland. 1985. Artificial reef research: a review with recommendations for future priorities. Bulletin of Marine Science 37:11–39.

Bradley, E., and C. E. Bryan. 1975. Life history and fishery of the Red Snapper (Lutjanus campechanus) in the northwestern Gulf of Mexico: 1970–1974. Proceedings of the Gulf and Caribbean Fisheries Institute 27:77–106.

Buchheister, A., and R. J. Latour. 2010. Turnover and fractionation of carbon and nitrogen stable isotopes in tissues of a migratory coastal predator, Summer Flounder (Paralichthys dentatus). Canadian Journal of Fisheries and Aquatic Sciences 67:445–461.

Carr, M. H., and M. A. Hixon. 1997. Artificial reefs: the importance of comparisons with natural reefs. Fisheries 22(4):28–33.

Chanton, J. P., J. Cherrier, R. M. Wilson, J. Sarkodee-Adoo, S. Bosman, A. Mickle, and W. M. Graham. 2012. Radiocarbon evidence that carbon from the Deepwater Horizon spill entered the planktonic food web of the Gulf of Mexico. Environmental Research Letters [online serial] 7:045303.

Cherrier, J., J. Sarkoodee-Adoo, T. P. Guilderson, and J. P. Chanton. 2013. Fossil carbon in particulate organic matter in the Gulf of Mexico following the Deepwater Horizon event. Environmental and Science Technical Letters 2014:108–112.

Clarke, K. R., P. J. Somerfield, and M. G. Chapman. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. Journal of Experimental Marine Biology and Ecology 330:55–80.

Cowan, J. H. Jr., C. B. Grimes, W. F. Patterson III, C. J. Walters, A. C. Jones, W. J. Lindberg, D. J. Sheehy, W. E. Pine III, J. E. Powers, M. D. Campbell, K. C. Lindeman, S. L. Diamond, R. Hilborn, H. T. Gibson, and K. A. Rose. 2011. Red Snapper management in the Gulf of Mexico: science- or faith-based? Reviews in Fish Biology and Fisheries 21:187–204.

Dance, M. A., W. F. Patterson III, and D. T. Addis. 2011. Fish community and trophic structure at artificial reef sites in the northeastern Gulf of Mexico. Bulletin of Marine Science 87:301–324.

Fenwick, G. D. 1978. Plankton swarms and their predators at the Snares Islands. New Zealand Journal of Marine Freshwater Research 12:223–224.

Fodrie, F. J., and K. L. Heck Jr. 2011. Response of coastal fishes to the Gulf of Mexico oil disaster. PLoS (Public Library of Science) ONE [online serial] 6(7):e21609.

Fry, B. 2006. Stable isotope ecology. Springer, New York.

Jackson, J. B. C., J. D. Cubit, B. D. Keller, V. Batista, K. Burns, H. M. Caffey, R. L. Caldwall, S. D. Garrity, C. D. Getter, C. Gonzalez, H. M. Guzman, K. W. Kaufmann, A. H. Knap, S. C. Levings, M. J. Marshall, R. Steger, R. C. Thompson, and E. Weil. 1989. Ecological effects of a major oil spill on Panamanian coastal marine communities. Science 243:37–44.

Jackson, M. W., J. H. Cowan Jr., and D. H. Nieland. 2007. Demographic differences in northern Gulf of Mexico Red Snapper reproductive maturation: implications for the unit stock hypothesis. Pages 217–228 in W. F. Patterson III, J. H. Cowan Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red Snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Lindberg, W. J. 1997. Can science solve the attraction versus production debate? Fisheries 22(4):10–13.

Luo, J., J. E. Serafy, S. Sponaugle, P. B. Teare, and D. Kieckbusch. 2009. Movement of Gray Snapper, Lutjanus griseus, among subtropical seagrass, mangrove, and coral reef habitats. Marine Ecological Progress Series 380:255–269.

Mason, O. U., N. M. Scott, A. Gonzalez, A. Robbins-Pianka, J. Bælum, J. Kimbrel, N. J. Bouskill, E. Prestat, S. Borglin, D. C. Joyner, J. L. Fortney, D. Jurelevicius, W. T. Stringfellow, L. Alvarez-Cohen, T. C. Hazen, R. Knight, J. A. Gilbert, and J. K Jansson. 2014. Metagenomics reveals sediment microbial community response to Deepwater Horizon oil spill. ISME Journal 8:1464–1475.

McCawley, J., and J. H. Cowan Jr. 2007. Seasonal and size specific diet and prey demand of Red Snapper on Alabama artificial reefs: implications for management. Pages 77–104 in W. F. Patterson III, J. H. Cowan Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red Snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

McCutchan, J. H. Jr., W. M. Lewis Jr., C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390.

McNutt, M. K., R. Camilli, T. J. Crone, G. D. Guthrie, P. A. Hsieh, T. B. Ryerson, O. Savas, and F. Shaffer. 2012. Review of flow rate estimates of the Deepwater Horizon oil spill. Proceedings of the National Academy of Sciences of the USA 109:20260–20267.

Middaugh, D. P., and D. D. Whiting. 1995. Responses of embryonic and larval silversides, Menidia beryllina, to no. 2 fuel oil and oil dispersants in seawater. Archives of Environmental Contamination and Toxicology 29:535–539.

Moncrieff, C. A., and M. J. Sullivan. 2001. Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotopes. Marine Ecological Progress Series 215:93–106.

Moreno, R., L. Jover, C. Diez, F. Sardà, and C. Sanpera. 2013. Ten years after the Prestige oil spill: seabird trophic ecology as indicator of long-term effects on the coastal marine ecosystem. PLoS (Public Library of Science) ONE [online serial] 8(10):e77360.

Murawski, S. A., W. T. Hogarth, E. B. Peebles, and L. Barbeiri. 2014. Prevalence of fish diseases in the Gulf of Mexico post Deepwater Horizon. Transactions of the American Fisheries Society 143:1084–1097.

Nelson, J., J. Chanton, F. Coleman, and C. Koenig. 2010. Patterns of stable carbon isotope turnover in Gag Mycteroperca microlepis, an economically important marine piscivore determined with a non-lethal surgical biopsy procedure. Environmental Biology of Fishes 90:243–252.

Ortmann, A. C., J. Anders, N. Shelton, L. Gong, A. G. Moss, and R. H. Condon. 2012. Dispersed oil disrupts microbial pathways in pelagic food webs. PLoS (Public Library of Science) ONE [online serial] 7(7):e42548.

Ouzts, A. C., and S. T. Szedlmayer. 2003. Diel feeding patterns of Red Snapper on artificial reefs in the north-central Gulf of Mexico. Transaction of the American Fisheries Society 132:1186–1193.

Parker, R. O. Jr., D. R. Colby, and T. D. Willis. 1983. Estimated amount of reef habitat on a portion of the U.S. South Atlantic and Gulf of Mexico continental shelf. Bulletin of Marine Science 33:935–940.

Paul, J. H., D. Hollander, P. Coble, K. L. Daly, S. Murasko, D. English, J. Basso, J. Delaney, L. McDaniel, and C. W. Kovach. 2013. Toxicity and mutagenicity of Gulf of Mexico waters during and after the Deepwater Horizon oil spill. Environmental Science and Technology 4:9651–9659.

Passow, U., K. Ziervogel, V. Asper, and A. Diercks. 2012. Marine snow formation in the aftermath of the Deepwater Horizon oil spill in the Gulf of Mexico. Environmental Research Letters [online serial] 7:035301.

Patterson, W. F. III, J. H. Tarnecki, D. T. Addis, and L. R. Barbieri. 2014. Reef fish community structure at natural versus artificial reefs in the northern Gulf of Mexico. Proceedings of the Gulf Caribbean Fisheries Institute 66:4–8.

Perkol-Finkel, S., N. Shashar, and Y. Benayahu. 2006. Can artificial reefs mimic natural reef communities? The roles of structural features and age. Marine Environmental Research 61:121–135.

Peterson, C. H., S. D. Rice, J. W. Short, D. Esler, J. L. Bodkin, B. E. Ballachey, and D. B Irons. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. Science 302:2082–2086.

Pilcher, W., S. Miles, S. Tang, G. Mayer, and A. Whitehead. 2014. Genomic and genotoxic responses to controlled weathered-oil exposures confirm and extend field studies on impacts of the Deepwater Horizon oil spill on native killifish. PLoS (Public Library of Science) ONE [online serial] 9:e106351.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189.

Radabaugh, K. R., D. J. Hollander, and E. B. Peebles. 2013. Seasonal δ^{13}C and δ^{15}N isoscapes of fish populations along a continental shelf trophic gradient. Continental Shelf Research 68:112–122.

Reddy, C. M., J. S. Arey, J. S. Seewald, S. P. Sylva, K. L. Lemkau, R. K. Nelson, C. A. Carmichael, C. P. McIntyre, J. Fenwick, G. T. Ventura, B. A. S. Van Moody, and R. Camilli. 2012. Composition and fate of gas and oil released to the water column during the Deepwater Horizon oil spill. Proceedings of the National Academy of Sciences of the USA 50:20229–20234.

Rooker, J. R., J. P. Turner, and S. A. Holt. 2006. Trophic ecology of Sargassum-associated fishes in the Gulf of Mexico determined from stable isotopes and fatty acids. Marine Ecology Progress Series 313:249–259.

Sammarco, P. W., S. R. Kolian, R. A. F. Warby, J. L. Bouldin, W. A. Subra, and S. A. Porter. 2013. Distribution and concentrations of petroleum hydrocarbons associated with the BP/Deepwater Horizon oil spill, Gulf of Mexico. Marine Pollution Bulletin 73:129–143.

Sanvicente-Añorve, L., E. Lemus-Santana, C. Flores-Coto, and M. Alatorre-Mendieta. 2013. Vertical segregation of holoplanktonic molluscs in the epipelagic layer, southern Gulf of Mexico. Helgoland Marine Research 67:397–405.

Schroeder, W. W., A. W. Schultz, and J. J. Dindo. 1988. Inner-shelf hardbottom areas, northeastern Gulf of Mexico. Gulf Coast Association of Geological Societies Transactions 38:535–541.

Schwacke, L. H., C. R. Smith, F. I. Townsend, R. S. Wells, L. B. Hart, B. C. Balmer, T. K. Collier, S. DeGuise, M. M. Fry, L. J. Guillette Jr., S. V. Lamb, S. M. Lane, W. E. McFree, N. J. Place, M. C. Tumlin, G. M. Ylitalo, E. S. Zolman, and T. K. Rowles. 2013. Health of common bottlenose dolphins (Tursiops truncatus) in Barataria Bay, Louisiana, following the Deepwater Horizon oil spill. Environmental Science and Technology 48:93–103.

Sweeting, C. J., J. T. Barry, N. V. C. Polunin, and S. Jennings. 2007. Effects of body size and environment on diet-tissue δ^{13}C fractionation in fishes. Journal of Experimental Marine Biology and Ecology 352:165–176.

Szedlmayer, S. T., and R. L. Shipp. 1994. Movement and growth of Red Snapper, Lutjanus campechanus, from an artificial reef area in the northeastern Gulf of Mexico. Bulletin of Marine Science 55:887–896.

Teal, J. M., and R. W. Howarth. 1984. Oil spill studies: a review of ecological impacts. Environmental Management 8:27–43.

Topping, D. T., and S. T. Szedlmayer. 2011. Home range and movement patterns of Red Snapper (*Lutjanus campechanus*) on artificial reefs. Fisheries Research 112:77–84.

Vanderklift, M. A., and S. Ponsard. 2003. Sources of variation in consumer-diet delta N-15 enrichment: a meta-analysis. Oecologia 136: 169–182.

Wells, D. R. J., J. H. Cowan Jr., and B. Fry B. 2008. Feeding ecology of Red Snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Marine Ecology Progress Series 61:213–225.

Westmeyer, M. P., C. A. Wilson, and D. L. Nieland. 2007. Fidelity of Red Snapper to petroleum platforms in the northern Gulf of Mexico. Pages 105–122 *in* W. F. Patterson III, J. H. Cowan Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red Snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Whitehead, A., B. Dubansky, C. Bodinier, T. I. Garcia, S. Miles, C. Pilley, V. Raghunathan, J. L. Roach, N. Walker, R. B. Walter, C. D. Rice, and F. Galvez. 2012. Genomic and physiological footprint of the Deepwater Horizon oil spill on resident marsh fishes. Proceedings of the National Academy of Sciences of the USA 109:20298–20302.