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Structural and functional similarity of epibenthic communities on standing and reefed platforms in the northwestern Gulf of Mexico

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ABSTRACT

Fossil fuel extraction in the Gulf of Mexico currently involves the use of approximately 2000 active oil and gas production platforms. These artificial structures provide a number of ecological functions including habitat provision for epibenthic invertebrates and production of food and refuge for a variety of fish species. To mitigate the loss of habitat when active platforms are decommissioned, Rigs-to-Reefs programs maintain existing communities by removing the upper 26 m of platform structure and converting upper and lower portions into artificial reefs. We examined the epibenthic communities of two standing platforms at 5 m and 30 m depths and three reefed platforms at 30 m depths. A combination of stable isotope and community analysis was used to assess the structure and food web functioning of epibenthic communities among these site-types. Reefed platforms (30 m) supported communities with similar food web structure as 5 m and 30 m standing platform communities. However, community composition in standing platform and reefed platform sites at 30 m differed from those of standing platform sites at 5 m depths. Results indicate that, although loss of shallow water habitat associated with platform reefing may diminish some aspects of biodiversity, reefed platforms support similar fundamental ecological functions as standing platforms in the Gulf of Mexico. Thus, the current reefing practice of removal of the upper 26 m of the structure does not substantially influence the functionality of these systems, and the retained structure maintains beneficial habitat for epibenthic communities.

1. Introduction

Artificial reefs have been employed across a variety of coastal and marine habitats for fisheries enhancement, ecological restoration, and recreational purposes (Baine, 2001; Bohnsack and Sutherland, 1985; Buckley and Hueckel, 1985; Seaman, 2007). Fossil fuel extraction in the Gulf of Mexico currently involves the use of ~2100 active oil and gas production platforms (hereafter "platforms"; www.bsee.gov). Platforms and other artificial reef structures provide a number of ecological functions, including support for diverse assemblages of epibenthic invertebrates (Gallaway and Lewbel, 1982; Lewbel et al., 1987; Pickering and Whitmarsh, 1997), increasing secondary biomass production (Cresson et al., 2014), and provision of food and refuge for a variety of fish species (Nelson and Bortone, 1996; Beaver et al., 1997; Rooker et al., 1997; Szedlmayer and Lee, 2004; Ajemian et al., 2015; Streich et al., 2017a). Platforms have been demonstrated to be among the most productive marine fish habitats on earth, primarily due to the high ratio of structural surface area per area of seafloor (Claisse et al., 2014). However, fish production supported by platforms may vary substantially between platform structures and regions (Fowler et al., 2015), and their role in enhancing fisheries remains contentious (Cowan et al., 2011; Gallaway et al., 2009; Macreadie et al., 2011; Shipp and Bortone, 2009).

A large number of platforms in the Gulf of Mexico are reaching the end of their productive lifespans, resulting in a predicted 29% loss of these structures between 1999 and 2023 (Pulsipher et al., 2001) and an associated decrease in complex marine habitat. To mitigate habitat loss, state-run Rigs-to-Reef programs repurpose decommissioned platforms into permitted artificial reefs. Current guidelines generally require reefed platforms to maintain 26 m of clearance depth (without the

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installation and maintenance of navigational aids) to avoid navigational hazards to large vessels. This is accomplished by either: (1) partial platform removal; (2) toppling the structure in place; or, (3) toppling the structure after towing to an approved reefing site (Kaiser and Pulsipher, 2005; Macreadie et al., 2011). As of 2015, 470 platforms in the Gulf of Mexico have been converted to artificial reefs through Rigs-to-Reef programs (www.bsee.gov). The conversion of platforms into artificial reefs results in a structure with lower relief and no physical connection to the upper water column. As decommissioned platforms are increasingly converted into artificial reefs, it is important to evaluate the ecological effects of this physical transformation on platform-associated epibenthic communities and food webs.

Stable isotope analysis can be used in conjunction with standard community analyses (e.g., macrofauna density, biomass, multivariate analysis) as a complementary tool for investigating organic matter flows and trophic structure in marine ecosystems. The isotopic composition of carbon in primary producer tissues is influenced by their photosynthetic pathway and inorganic carbon source, and changes little with trophic transfers. This allows the carbon isotopic composition of consumer tissue to be traced back to its primary producer origins (DeNiro and Epstein, 1978; Peterson and Fry, 1987). The isotopic composition of nitrogen undergoes a predictable step-wise enrichment in ^{15}N with trophic transfers (2–4‰), which allows the evaluation of consumer trophic levels (Post, 2002). Together, the isotopic compositions of carbon (C) and nitrogen (N) can be used to construct a time-integrated biochemical outline of organic matter pathways within food webs. Because of these properties, stable isotopes of C and N have been successfully employed to study trophic structure and ecological functioning artificial reef habitats (Blomberg et al., 2017; Cresson et al., 2014; Daigle et al., 2013; Rezek et al., 2017).

In this study, we compare the structure and food web function of three artificial reef epibenthic communities by platform type and depth to evaluate the effects of current reefing practices using standard community analyses coupled with stable isotope analyses. To this aim, we compare: (1) the structure and functioning of deep (30 m) epibenthic communities from reefed platforms and standing platforms, and (2) the structure and the functioning of deep (30 m) epibenthic communities from reefed platforms and standing platforms with shallow (5 m) standing platforms to determine the effects of removing of the shallowest sections of platforms. To accomplish this, we employ a combination of traditional community analysis approaches (i.e. macrofauna density, biomass, multivariate analysis) with stable isotope-based food web analysis. The results of this study will inform resource manager decision-making related to the effects of reefing practices on platform-associated epibenthic communities and food webs in the Gulf of Mexico.

2. Materials and methods

2.1. Field sampling

Three reefed platforms (RP-A: BA-A-132A, RP-B: MU-A-85B, RP-C: MI-A-7A) and two standing platforms (SP-A: BA-A-133A, SP-B: MU-A-85A) were sampled within a study area located ∼75 km off the Texas coast in the northwestern Gulf of Mexico (Fig. 1), at bottom depths ranging from 60 to 83 m (Table 1). All structures sampled were composed of conventional fixed steel jacket platforms. SCUBA divers sampled the epibenthic community on each structure by scraping ∼20 cm × 20 cm (0.04 m^2) areas with hand tools and collecting all material in fine-mesh (< 1 mm) bags. Standing platforms were sampled at two depths (5 m and 30 m; hereafter SP5 and SP30, respectively) and reefed platforms were sampled at 30 m (near the top of the structure; hereafter RP30). Three replicate samples were taken from each structure at each applicable depth. RP-A, RP-B, RP-C, and both standing platforms were sampled on June 5, July 2, July 14, and October 15, 2014, respectively, in conjunction with cruises for related studies (Streich et al., 2017b). RP-C was also sampled on August 10, 2013 to collect preliminary data that were used in community analyses. Depth profiles of salinity and chlorophyll *a* concentration were measured during separate cruises within the study period (June 11, July 29, September 8, and October 1, 2014) with ∼45 m vertical casts of a Hydrolab® DS5 sonde adjacent to RP-A and RP-C.

Water samples for stable isotope analyses of suspended particulate organic matter (SPOM) were collected at 5 and 30 m depths at each structure using a Van Dorn bottle and sieved through a 250 µm screen to remove large zooplankton and particles. Epibenthic samples for community and stable isotope analyses were collected from separate jackets (legs) on structures. The sampled area was photographed with an Intova® Sport HD II underwater camera along with a scale. These photos were then analyzed with the image analysis software ImageJ® to obtain precise estimates of the area removed for areal macrofauna biomass and density calculations (Schneider et al., 2012). The trapezoid perimeter encompassing removed areas was measured with meter tape and used to calculate sample areas for the 2014 visit of RP-C due to camera loss. Grey triggerfish (*Balistes capriscus*) were opportunistically collected with spears for stable isotope analysis. Water samples were kept on ice and epibenthic community samples were kept in aerated seawater during transport to the laboratory (no longer than 10 h). Macrofauna were euthanized through rapid chilling, following approved Institutional Animal Care and Use Committee of Texas A&M University-Corpus Christi guidelines (IACUC #08-14).

2.2. Sample preparation for stable isotope analyses

Between 500 and 2000 ml of water were filtered through pre-combusted (4 h, 450 °C) Whatman GF/F filters (0.7 µm nominal pore size) for analysis of SPOM (Lebreton et al., 2016). Oyster shell organic matter (OSOM)—a composite of epiphytic microalgae, detritus, bacteria, and other organic material attached to the shell's exterior—was collected by lightly brushing the shell surfaces of the dominant reef building taxa (*Hyotissa mcgintyi*) into artificial seawater. Collected material was sieved through a 250 µm screen to remove large particles and filtered through pre-combusted Whatman GF/F filters. Flora and macrofauna from epibenthic community samples were sorted and subsets of individuals of each taxon (3 or more, if available) were selected. Red algae (Rhodophyta) were separated into three groups: Corallinaceae (articulated coralline algae), red macroalgae (mixed Rhodomelaceae and Gracilariaceae), and filamentous red algae. Among consumer taxa, corals, bivalves, barnacles, and small decapods (less than ∼10 mm length) were kept alive separately in aerated artificial seawater for 24 h to evacuate gut contents and then stored at −20 °C (DeNiro and Epstein, 1978). Other taxa (i.e. large motile macrofauna) were frozen the same day of collection. For starved taxa, calcareous shells were removed, and entire individuals were used for analysis. Muscle tissue was analyzed in large motile macrofauna.

All samples were freeze-dried. Flora and fauna samples were ground into a homogeneous powder with a ball mill (MM 400, Retsch). Samples potentially containing carbonates were acidified. SPOM and OSOM filters were decarbonated by contact with hydrochloric acid (HCl) fumes under light vacuum for 4 h (Lorrain et al., 2003). Tissue samples containing carbonates were decarbonated with 1 mol l^{-1} HCl and dried at 55 °C. δ^{15}N and δ^{13}C measurements were carried out on raw and acidified samples, respectively, to avoid bias on δ^{15}N values due to acidification. Sample powders were precisely (± 1 µg) weighed with a microscale (ME 5, Sartorius) and encapsulated in combustion cups for analysis.

2.3. Stable isotope analyses

Carbon and nitrogen isotopic compositions were determined using an elemental analyzer (ECS 4010, Costech) connected to a continuous flow isotope ratio mass spectrometer (Delta V Plus, Thermo Scientific)

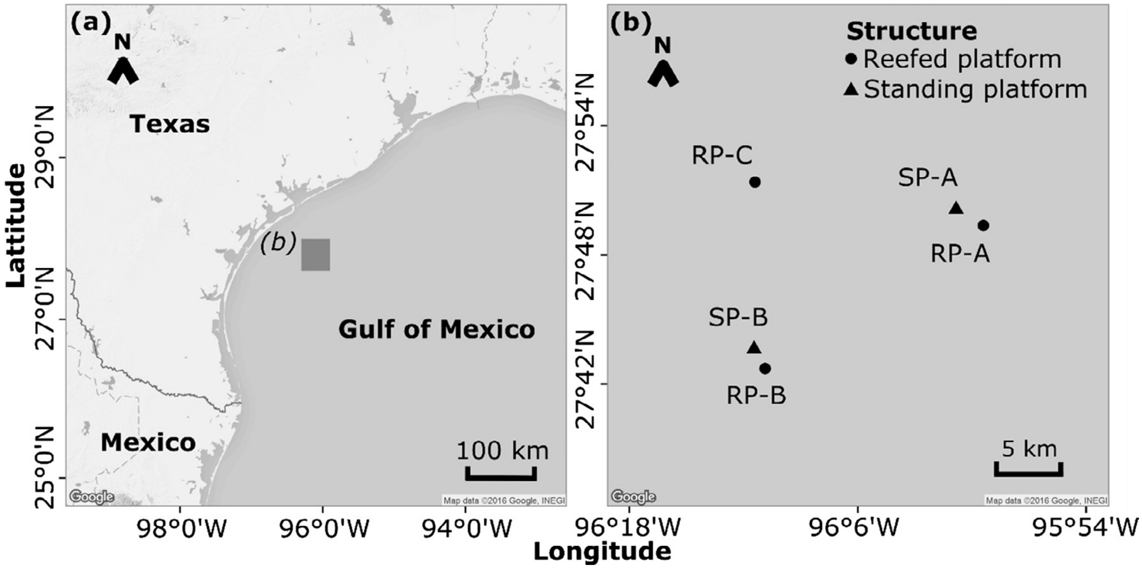

Fig. 1. Location of the sampled standing platforms (a) and reefed platform structures (b).

through a Conflo IV interface (Thermo Scientific) at the Texas A&M University-Corpus Christi Isotope Core Laboratory. Isotopic compositions are given in delta (δ) notation as deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) following the formula: δX (‰) = $[(R_{sample}/R_{standard}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively (Peterson and Fry, 1987). Two-point calibration was performed with L-glutamic acid reference materials (USGS-40 and USGS-41) to normalize preliminary isotopic values to standards (Paul et al., 2007). Methionine standards (Costech) were analyzed after every 12 samples to monitor instrument performance. Analytical precision was ± 0.2‰ for carbon and nitrogen based on repeated measurements of standards.

2.4. Sample preparation for community analysis

Macrofauna were fixed in buffered 10% formalin and then stored in 70% ethanol. Animals were enumerated and identified to the lowest practical taxonomic level. They were then dried for 48 h at 55 °C, weighed (± 0.1 mg), and combusted at 450 °C for 4 h to obtain ash free dry weight (AFDW) biomass. Ahermatypic cup coral density was assessed with polyp counts.

2.5. Data analysis

Differences in sessile and motile macrofauna density and AFDW biomass between site-types (i.e. SP5, SP30, and RP30) were analyzed with mixed effects one-way analysis of variance (ANOVA) tests with individual sites (structures) as a random effect, using the nlme package in R (Pinheiro et al., 2015; R Development Core Team, 2016). ANOVA models were fit using procedures described in Zuur et al. (2009). Residual normality and homoscedasticity assumptions were assessed with Shapiro–Wilk tests and normalized residual vs. fitted value plots, respectively. Models were compared and selected based on corrected Akaike information criterion (AICc) (Hurvich and Tsai, 1989). Post hoc analysis was conducted with Westfall's modification of Tukey's HSD test (Westfall, 1997) using the multcomp R package (Hothorn et al., 2008). Community structure was compared between site-types with non-parametric permutational multivariate analysis of variance (PERMANOVA; permutations = 9999; Anderson, 2001) tests on Hellinger distance matrix (Legendre and Gallagher, 2001) of multivariate community abundance data with the adonis function in the R package vegan (Oksanen et al., 2016). Multiple PERMANOVA comparisons were corrected with Bonferroni *P*-value adjustments. The relationships of multivariate community composition among sites was presented with non-metric multidimensional scaling (nMDS) plots.

The $\delta^{13}C$ and $\delta^{15}N$ values of potential food sources were compared between site-types and each other using Wilcoxon rank-sum tests and Kruskal-Wallis tests. Post-hoc analysis for Kruskal-Wallis tests were conducted with Dunn's tests using the dunn.test R package (Dinno, 2016; Dunn, 1964) with Bonferroni *P*-value corrections for multiple comparisons. To detect community-wide shifts in isotope values, differences in isotope values of co-occurring taxa between site-types were compared with a stratified bootstrap paired test on mean differences (Konietschke and Pauly, 2014). Confidence intervals for the average difference in isotope values of paired co-occurring taxa between sites were generated by bootstrapping isotope values within each consumer species/taxon (4999 resamples) using the boot R package (Canty and Ripley, 2016). Bonferroni adjustments were applied to 95% confidence intervals to obtain family-wise 95% confidence intervals for multiple comparisons. Confidence intervals (95%) for the mean of differences in isotope values of co-occurring taxa between site-types that did not include 0 were considered significantly different.

Table 1
Location and metadata for sampled standing platforms and reefed platforms. For reefed platforms, year constructed (Year con.) indicates year when the original platform was converted, and reefing method indicates if the structure is toppled platform (Topple) or a partially removed platform (Part. Rm.). Information obtained from the Bureau of Safety and Environmental Enforcement (www.bsee.gov) and Texas Parks and Wildlife Department (tpwd.texas.gov) databases.

ID	Structure name	Type	Reefing method	Latitude	Longitude	Year con.	Depth (m)	Relief (m)
RP-A	BA-A-132A	Reefed	Part. Rm.	27°49′22	−95°59′24	1992	61	34
RP-B	MU-A-85B	Reefed	Topple	27°42′43	−96°10′53	2006	83	54
RP-C	MI-A-7A	Reefed	Topple	27°51′23	−96°11′25	2002	60	32
SP-A	BA-A-133A	Platform	–	27°51′16	−96°02′11	1976	61	61
SP-B	MU-A-85A	Platform	–	27°43′37	−96°11′28	1977	79	79

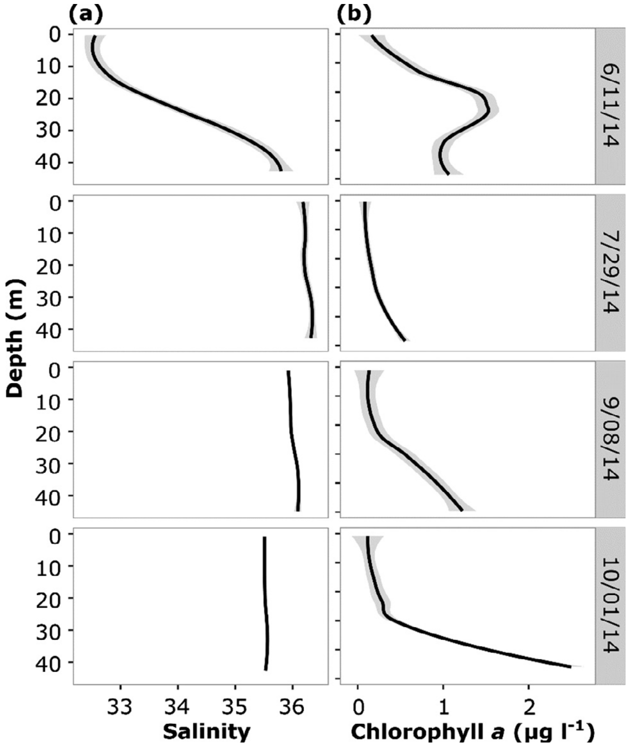

Fig. 2. LOWESS-smoothed depth profiles of salinity and chlorophyll *a* concentration from sonde casts at RP-A and RP-C sites over the course of the survey. Shaded area represents 95% confidence intervals.

Consumer isotopic heterogeneity, a proxy for trophic diversity, was compared between site-types by analyzing variance among consumer mean δ^{13}C and δ^{15}N values with Levene's tests. Levene's test was also used to compare the variance of food source isotope values that were found in all site-types (SPOM, OSOM and Corallinaceae) to validate the assumption that between-site-type differences in consumer isotopic heterogeneity would reflect trophic variation, rather than potential between-site-type differences in the isotopic variance among food sources.

3. Results

3.1. Hydrological conditions

Salinity was relatively low in surface waters during June 2014, with average salinities of 32.6, 32.7, and 34.1 from depths of 0 to 10 m, 10 to 20 m, 20 to 30 m, respectively (Fig. 2a). Average salinity values from all other 10 m intervals during other hydrological sampling periods remained between 35.4 and 36.3 and showed little variation with depth. Chlorophyll *a* concentration in surface waters were the greatest during June 2014, with mean concentrations of 0.22 µg l^{-1} between 0 and 10 m depths, and 1.62 µg l^{-1} between 20 and 30 m depths (Fig. 2b). For comparison, the greatest mean chlorophyll *a* concentration from July through October were 0.13 and 0.34 µg l^{-1} from 0 to 10 m and 20 to 30 m depths, respectively. In July through October, greatest chlorophyll *a* concentration occurred in 40 to 50 m depths, ranging from 0.48 to 2.10 µg l^{-1} (Fig. 2b).

3.2. Community analysis

Forty reef resident macrofauna taxa were identified from collections (Table S1, Table S2). Total macrofauna density (sessile and motile) ranged from 3960 ± 553 to 4584 ± 1199 n m^{-2} and were similar between site-types (ANOVA; F2,17 = 0.4, P = 0.67; Fig. 3a and b).

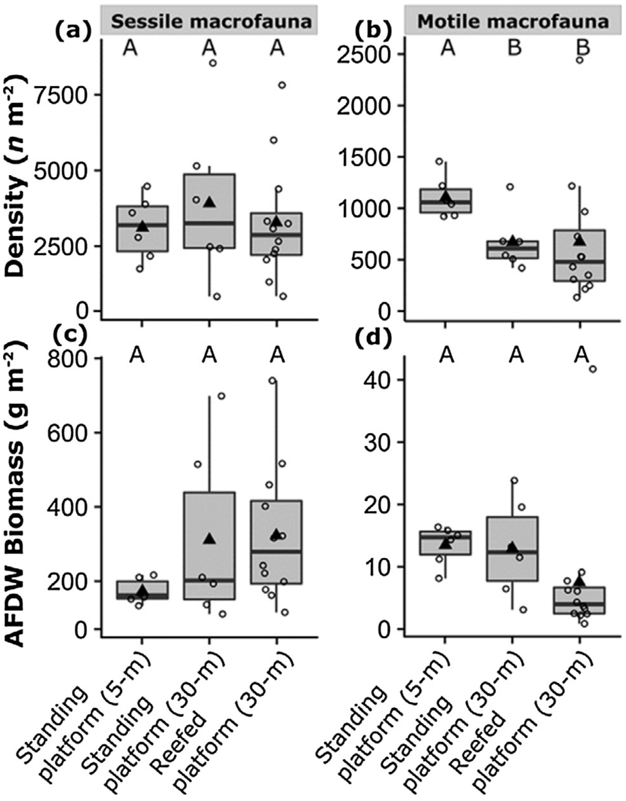

Fig. 3. Density and ash free dry weight biomass of sessile macrofauna (a, c) and motile macrofauna (b, d) from standing platforms at 5 m and 30 m depths, and reefed platforms at 30 m depth. Boxplots indicate median, interquartile range (IQR) and 1.5 • IQR. Raw data are indicated with open circles and means are indicated with triangle points. Tukey groupings obtained from ANOVAs post hoc tests indicated with letters above boxes ($\alpha = 0.05$).

Total macrofauna biomass (sessile and motile) ranged from 186.2 ± 13.0 to 330.4 ± 52.9 g m^{-2} and did not differ between site-types (ANOVA; F2,17 = 0.8, P = 0.46; Fig. 3c and d). Sessile macrofauna densities ranged from 3115 ± 429 to 3912 ± 1106 n m^{-2} and were similar between the three site-types (ANOVA; $F_{2,17} = 0.2$, $P = 0.85$; Fig. 3a). Sessile macrofauna biomass ranged from 172.7 ± 13.9 to 322.9 ± 50.1 g m^{-2} and were similar between site-types (ANOVA; $F_{2,17} = 0.9$, $P = 0.420$; Fig. 3c). Barnacles accounted for < 0.01% of total biomass (0.0042 g AFDW per individual; based on a subsample of 33) and were not included in community biomass analysis. Motile macrofauna density was greater in SP5 sites (1107 ± 83 n m^{-2}) than in SP30 (672 ± 115 n m^{-2}) and RP30 (677 ± 186 n m^{-2}) sites (ANOVA; $F_{2,17} = 6.1$, $P = 0.01$; Fig. 3b). Mean motile macrofauna biomass ranged from 13.4 ± 1.3 to 7.5 ± 3.1 g m^{-2} and did not differ between site-types (ANOVA; $F_{2,17} = 1.5$, $P = 0.25$; Fig. 3d).

Macrofauna community structure in SP5 sites differed from communities in SP30 and RP30 sites (PERMANOVA; SP5 vs. SP30: $t_{1,10} = 4.6$, $P < 0.01$; SP5 vs. RP30: $t_{1,16} = 3.5$, $P < 0.01$) (Fig. 4). Communities on standing and reefed platform sites at 30 m were similar (PERMANOVA; $t_{1,16} = 0.7$, $P = 1.00$). The sessile macrofauna community in SP5 sites were characterized by relatively high densities of tree oysters (*Isognomon* spp.) and relatively low densities of orange cup coral polyps (*T. coccinea*) in comparison to 30 m sites (Fig. 5a, Table S1). Motile macrofauna communities in SP5 sites had higher densities of the brittle star *Ophiactis savignyi* and sipunculid worms in comparison to sites at 30 m (Fig. 5b).

The bivalve *Hyotissa mcgintyi* was the greatest contributor to community biomass in all sites (Fig. 6, Table S1), on average composing 73% of the SP5 (137.4 g m^{-2}), 77% of SP30 (250.8 g m^{-2}), and 57% of

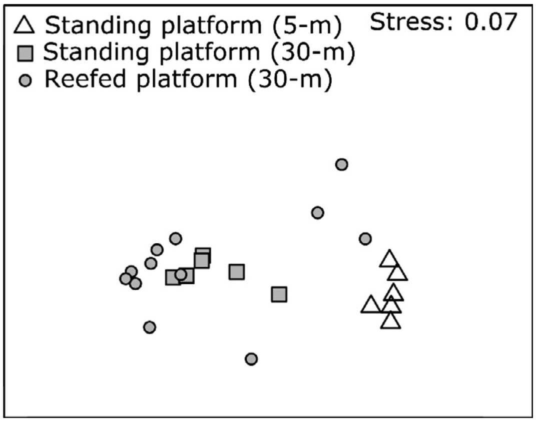

Fig. 4. Non-metric multidimensional scaling plot of Hellinger transformed macrofauna community composition data from standing platforms at 5 m and 30 m depths, and reefed platforms at 30 m depth.

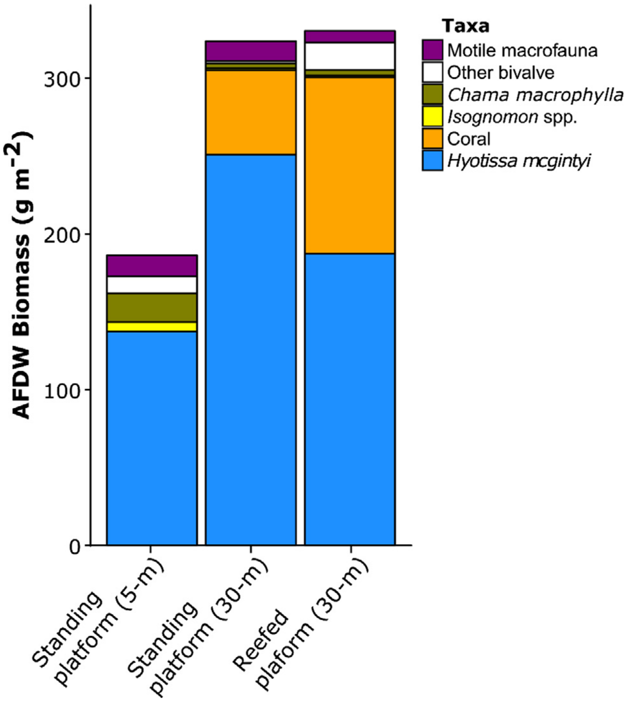

Fig. 6. Mean AFDW biomass of major groups on standing platforms at 5 m and 30 m depths, and reefed platforms at 30 m depth.

the RP30 biomass (187.3 g m^{-2}). Cup corals were the second greatest contributor to biomass at 30 m sites in both standing and reefed platforms; accounting for 16% of the SP30 biomass (54.3 g m^{-2}) and 34% of the RP30 biomass (113.2 g m^{-2}). Corals did not contribute substantially to SP5 biomass (< 1%). The bivalves *Chama macrophylla* and *Isognomon* spp. represented 10% (18.4 g m^{-2}) and 3% (5.9 g m^{-2}) of the SP5 biomass, respectively. These bivalves contributed relatively little to SP30 and RP30 biomass (*C. macrophylla* = 1%; *Isognomon* spp. = < 1%).

3.3. Stable isotope analysis

SPOM δ^{13}C and δ^{15}N values were similar between 5 m and 30 m depths (Wilcoxon tests; δ^{13}C: W = 8, $P = 0.42$; δ^{15}N: W = 11, $P = 0.84$). SPOM (pooled 5 m/30 m) δ^{13}C values (−24.2 ± 0.6‰) did not differ between standing and reefed platform (Wilcoxon test; W = 11, $P = 0.91$), however, δ^{15}N values were lower at standing platforms (5.0 ± 1.1‰) than at reefed platforms (6.0 ± 1.2‰) (Wilcoxon test; W = 24, $P = 0.01$) (Fig. 7). OSOM δ^{13}C values (−21.4 ± 0.9‰) were similar between site-types (Kruskal-Wallis test; $\chi^2 = 5.7$, $P = 0.06$); δ^{15}N values were lower at SP30 (4.0 ± 1.1‰) than at RP30 (6.2 ± 0.4‰) (Kruskal-Wallis test; $\chi^2 = 7.3$, $P = 0.03$).

Corallinaceae were the only macroalgae found at all sites-types (i.e. SP5, SP30, RP30), with δ^{13}C values and δ^{15}N values ranging from −25.9 to −22.4‰ and 3.2 and 6.4‰, respectively. Only one Corallinaceae sample was collected from SP30 sites, so RP30 samples were compared with SP5 samples. Corallinaceae δ^{13}C values were similar between RP30 and SP5 sites (−23.3 ± 1.5‰) (Wilcoxon test; W = 18, $P = 0.73$); δ^{15}N values were lower in SP5 sites (3.8 ± 0.5‰) than RP30 sites (5.4 ± 0.5‰) (Wilcoxon test; W = 42, $P < 0.01$). Other macroalgae were found sporadically. Filamentous red

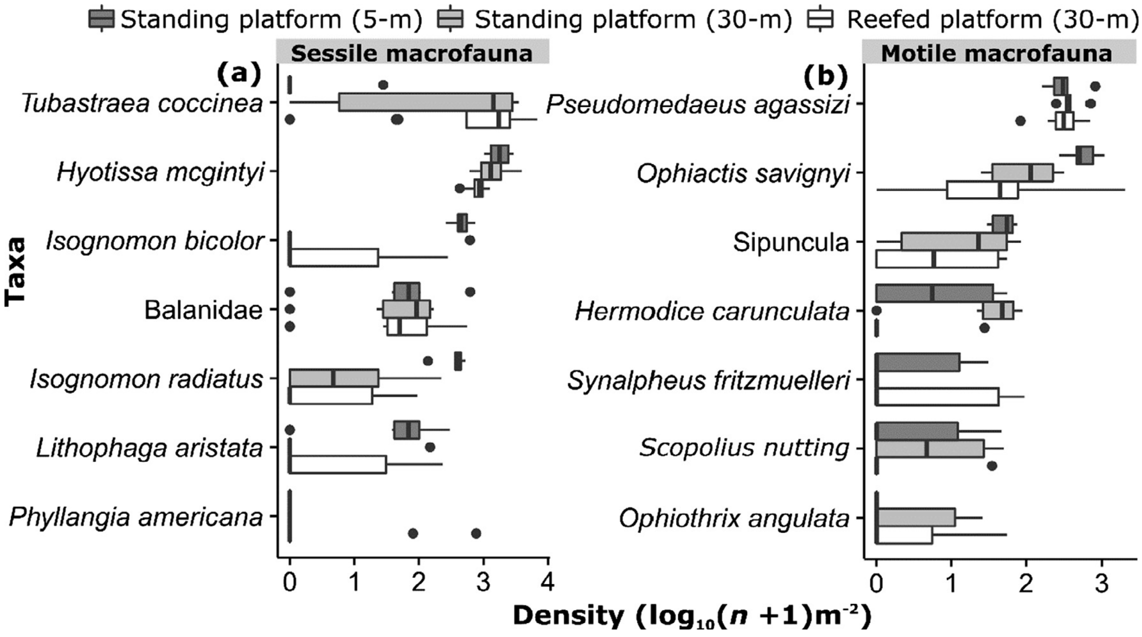

Fig. 5. Densities of the 7 most abundant motile (a) and sessile (b) macrofauna taxa from standing platforms at 5 m and 30 m depths, and from reefed platforms at 30 m depth. Boxplots indicate median, interquartile range (IQR), and 1.5 • IQR. Data outside of 1.5 • IQR are represented with points.

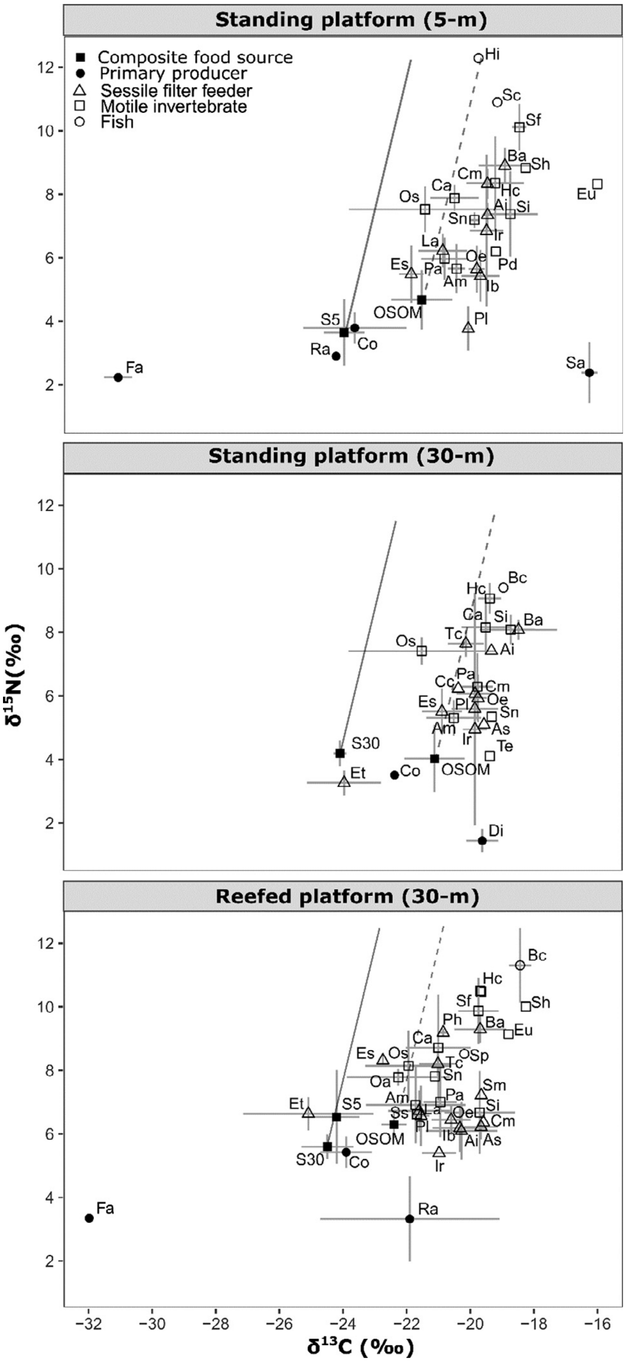

Fig. 7. δ^{13}C and δ^{15}N values (‰, mean ± standard deviation) of primary producers, composite food sources and consumers on standing platforms at 5 m and 30 m depths, and on reefed platforms at 30 m depth. Code list: Ai: *Arca imbricate*; Am: amphipod; As: *Anomia simplex*; Ba: Balanidae; Bc: *Balistes capriscus*; Ca: Capitellidae; Cc: *Chama congregate*; Cm: *Chama macrophylla*; Co: Corallinaceae; Di: *Dictyota* sp.; Es: encrusting sponge; Et: encrusting tunicate; Eu: *Eucidaris tribuloides*; Hc: *Hermodice carunculate*; Hi: *Hypsoblennius invemar*; Hm: *Hyotissa mcgintyi*; Ib: *Isognomon bicolor*; Ir: *Isognomon radiatus*; La: *Lithophaga aristata*; Oa: *Ophiothrix angulate*; Os: *Ophiactis savignyi*; OSOM: Oyster shell organic matter; Pa: *Pseudomedaeus agassizi*; Pd: *Paraliomera dispar*; Ph: *Phyllangia americana*; Pl: Plumulariidae; Ra: red macroalgae; SPOM30: Suspended particulate organic matter (30 m); SPOM5: Suspended particulate organic matter (5 m); Sa: *Sargassum* sp.; Sc: *Scartella cristata*; Sf: *Synalpheus fritzmuelleri*; Sh: *Stramonita haemastoma*; Si: Sipuncula; Sm: *Spondylus americanus*; Sn: *Scopolius nuttingi*; Sp: *Scorpaena plumieri*; Ss: *Stenorhynchus seticornis*; Tc: *Tubastraea coccinea*; Te: *Teleophrys* sp. Lines indicate the influence of OSOM (dashed) and SPOM (solid) based on the relationship between δ^{13}C (0.5‰) and δ^{15}N (2.0‰) trophic fractionation factors.

algae—found on SP5 and RP30 sites—had the lowest δ^{13}C values of all potential food sources (−31.3 ± 0.4‰) and had relatively low δ^{15}N values (2.5 ± 0.5‰) (Fig. 7). δ^{13}C values of red macroalgae (found in SP5 and RP30 sites) ranged from −26.1 to −17.6‰. *Dictyota* sp. (found in RP30 sites) was relatively enriched in ^{13}C (δ^{13}C: −19.7 ± 0.5‰) and had the lowest δ^{15}N values (1.4 ± 0.4‰) of any macroalgae. *Sargassum* sp. had the highest mean δ^{13}C value (−16.3 ± 0.3‰) and was found floating on surface waters around platforms. OSOM was more ^{13}C enriched than Corallinaceae and SPOM, which had similar δ^{13}C values; red macroalgae had highly variable δ^{13}C values and did not differ significantly from these sources (Kruskal-Wallis test; $\chi^2 = 8.5$, $P = 0.01$). SPOM and OSOM δ^{15}N values were greater than those of red macroalgae (Kruskal-Wallis test; $\chi^2 = 11.1$, $P = 0.01$).

Sessile filter feeders had mean δ^{13}C values ranging from −21.9 to −18.9‰ in SP5 sites (9 taxa), from −24.0 to −18.5‰ in SP30 sites (11 taxa), and from −25.1 to −19.6‰ in RP30 sites (14 taxa) (Fig. 7). Motile consumers mean δ^{13}C values ranged from −21.4 to −16.0‰ in SP5 sites (11 taxa), from −21.6 to −18.8‰ in SP30 sites (8 taxa), and −22.3 to −18.3‰ on RP30 sites (13 taxa). Fish had mean δ^{13}C values ranging from −19.8 to −19.2‰ in SP5 sites (2 taxa), of −19.0‰ in SP30 sites (1 taxa), and from −20.2 to −18.5‰ on RP30 sites (2 taxa). Sessile filter feeders mean δ^{15}N values ranged from 3.8 to 8.9‰ in SP5 sites, from 3.2 to 8.1‰ in SP30 sites, and 5.3 to 9.2‰ in RP30 sites. Motile taxa mean δ^{15}N values ranged from 5.7 to 10.1‰ in SP5 sites, from 4.1 to 9.1‰ in SP30 sites, and from 6.6 to 10.4‰ in RP30 sites. Fish δ^{15}N values ranged from 8.5 (*Scorpaena plumieri*, RP30) to 12.3‰ (*Hypsoblennius invemar*, SP5).

δ^{13}C values of co-occurring taxa ($n = 14$) were on average 0.8‰ higher in SP5 sites than in RP30 sites (paired bootstrap comparison; upper, lower 95% CI = −1.1‰, −0.5‰; Fig. 8a) and 1.0‰ higher in SP5 sites than in RP30 sites (paired bootstrap comparison: upper, lower 95% CI = −1.3‰, −0.7‰). δ^{15}N values of co-occurring taxa were on average 0.5‰ lower in SP5 sites than in RP30 sites (Fig. 8b, paired bootstrap comparison: upper, lower 95% CI = 0.8‰, 0.2‰) and 0.7‰ lower in SP30 sites than in RP30 sites (paired bootstrap comparison: upper, lower 95% CI = 1.1‰, 0.3‰). Co-occurring taxa had similar δ^{13}C values and δ^{15}N values between 5 m (SP5) and 30 m (SP30) platforms sites (paired bootstrap comparisons: δ^{13}C: mean = −0.2‰; upper, lower 95% CI = −0.5‰, 0.1‰; δ^{15}N: mean = 0.2‰; upper, lower 95% CI = −0.2‰, 0.6‰).

Variance among co-occurring food source isotope values did not differ between site-types (Levene's tests; δ^{13}C: $F_{2,33} = 0.7$, $P = 0.51$; δ^{15}N: $F_{2,33} = 0.1$, $P = 0.93$). The variance among mean consumer taxa δ^{13}C values were similar between all site-types (Levene's test; $F_{2,65} = 0.7$, $P = 0.52$). The variance among mean consumer taxa δ^{15}N values were also similar between site-types (Levene's test; $F_{2,65} = 0.7$, $P = 0.49$).

4. Discussion

4.1. Community structure differs with depth, but not between structures

The sessile communities on the standing and reefed platforms assessed in this study were dominated by bivalve species that were characteristic of offshore platforms previously surveyed in the Gulf of Mexico. *H. mcgintyi* was the dominant reef building bivalve (by weight and density) on all reefed and standing platform site-types surveyed, followed *C. macerophylla* and *Isognomon* spp. Bivalve community structure on platforms and reefed platforms was comparable to those of offshore platforms near Louisiana (Gallaway et al., 1981; Lewbel et al., 1987), indicating these species are widely distributed on platform-like structures throughout the northwestern Gulf of Mexico. However, the species of dominant reef building bivalve species may vary, with some platform communities reportedly dominated by *C. macrophylla* (Gallaway et al., 1981; Lewbel et al., 1987).

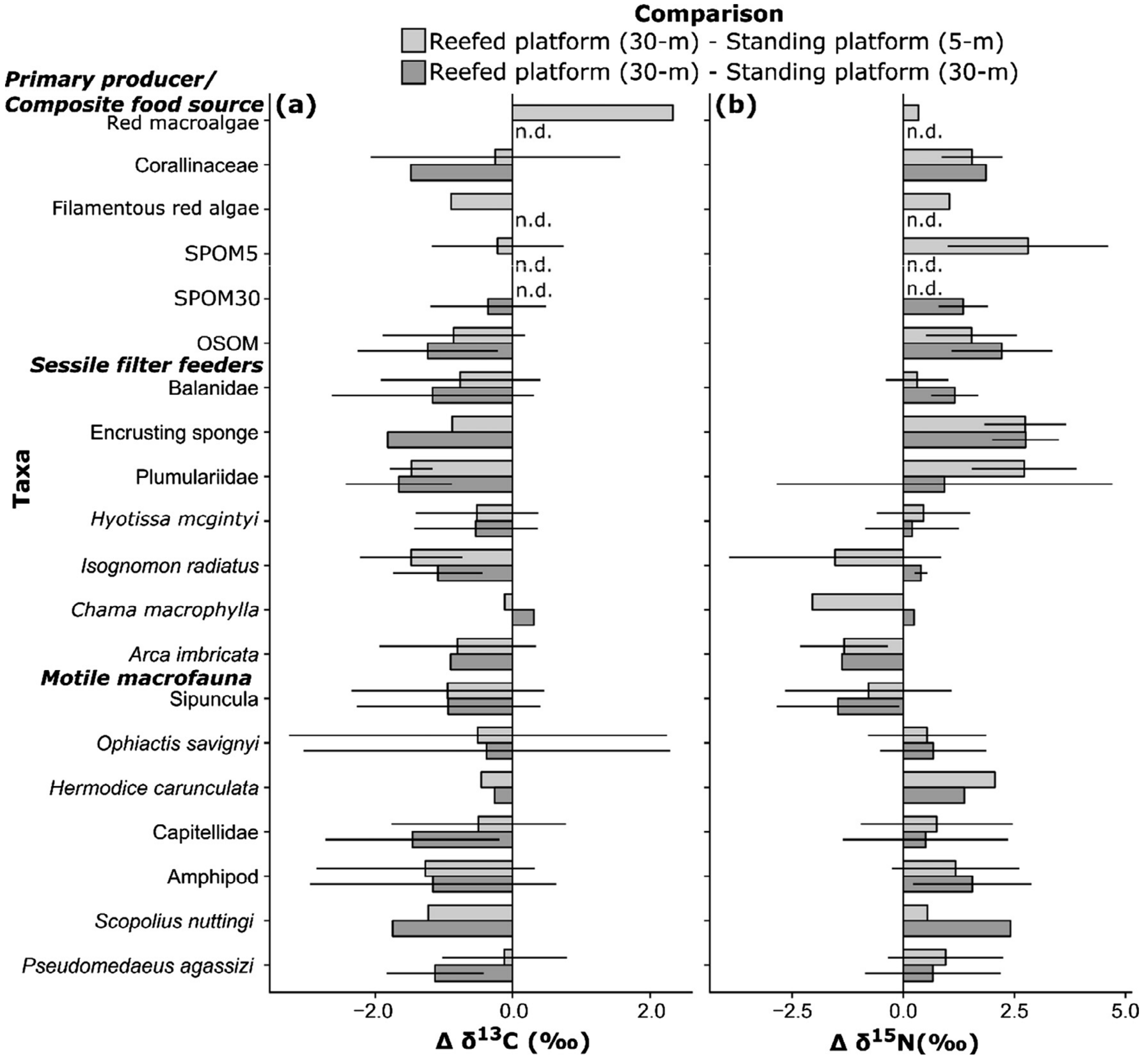

Fig. 8. Differences (Δ) of δ^{13}C (a) and δ^{15}N (b) values (mean ± standard deviation) of primary producers, composite food sources and co-occurring taxa between standing platforms at 5 m depth and reefed platforms (30 m) and between standing platforms at 30 m depth and reefed platforms (30 m). Code list: OSOM: Oyster shell organic matter; SPOM30: Suspended particulate organic matter (30 m); SPOM5: Suspended particulate organic matter (5 m). No data indicated with n.d.

Motile macrofauna assemblages may be relatively similar throughout offshore platforms in the northwestern Gulf of Mexico; nearly all motile macrofauna identified in this survey have been collected on offshore platforms near Louisiana (Gallaway et al., 1981; Lewbel et al., 1987; Daigle et al., 2013). *Pseudomedaeus agassizi*, the rough rubble crab, is a dominant decapod species with densities in the current study (372 n m^{-2}) comparable to previous reports on offshore platforms (up to 496 n m^{-2}, Gallaway et al., 1981; 336 n m^{-2}, Lewbel et al., 1987). Blenny densities in SP5 sites were similar to those reported on other platforms at the same depth (7.9 n m^{-2}, Rauch 2004). A single post-larval spotted scorpionfish (*Scorpaena plumieri,* total length = 14.2 mm) was collected from RP-B, indicating that the complex interstitial space created by sessile macrofauna on offshore structures may provide settlement and nursery habitat for some fisheries species.

These results demonstrate that platforms provide similar deep-water habitat after reefing. However, community variation between 5 m and 30 m sites indicate that current reefing practices result in the loss of unique shallow water communities. Although no significant differences were found between community biomass among site-types, possibly related to high variability, greater average biomass values found in 30 m sites indicate that *T. coccinea* may increase the overall biomass in deep epibenthic communities. Macrofauna community structure in SP5 sites was dissimilar from communities on SP30 and RP30 sites, indicating that depth is a major driver affecting community structure on offshore structures. These observations are consistent with previously documented vertical zonation patterns on offshore platforms. Relatively greater densities of *Isognomon* spp. bivalves and the ophiuroid *O. savignyi* were found in shallower depths by Lewbel et al. (1987) (for 10 m/30 m depths: *Isognomon bicolor:* 128/0 n m^{-2}, *O. savignyi:* 9472/432 n m^{-2}). Relatively greater densities of non-native coral *T. coccinea* were also found in deeper depths by Sammarco et al. (2014) (peak abundance at 35–40 m depths). The similarities between macrofauna community composition, density, and biomass between platforms and reefed platforms at 30 m indicate that comparable communities are able to develop at this depth regardless of physical links to shallow substrate.

4.2. *Food web structure*

Stable isotope data indicated that OSOM was an important food source for epibenthic macrofauna inhabiting these structures. Mean overall macrofauna taxa δ^{13}C values fell within a range from −21.4 to −17.4‰ (except for encrusting tunicates). SPOM δ^{13}C values found in this study (−24.2‰) were relatively low in comparison to macrofauna consumers. Macrofauna δ^{13}C values more closely resembled those of

OSOM (−21.7‰), suggesting that, at the community scale, this resource had a high role in the food web functioning. It is possible that attached benthic microalgae, bacteria, and trapped pelagic detritus contained in OSOM are consumed by suspension feeders after resuspension (Doi et al., 2008; Fukumori et al., 2008) and by motile consumers in these habitats.

The lower abundance of pelagic resources in this region may result in a greater reliance of platform communities on autochthonous epilithic production. These results differ from a stable isotope-based food web study of offshore standing platforms in Louisiana waters conducted by Daigle et al. (2013). Although they found a similar range of macrofauna $\delta^{13}C$ values (−21.5 to −17.6‰), they found higher $\delta^{13}C$ values for SPOM (−20.8 to −19.7‰) and shell-attached microalgae (−18.7 to −15.8‰), indicating SPOM was the most important food source for platform consumers. These divergent results may reflect functional variation associated with regional differences in the availability (i.e. quality/quantity) of pelagic resources between the highly productive, Mississippi River-influenced, Louisiana continental shelf (e.g. chlorophyll *a* concentrations from 5 to 10 $\mu g\, l^{-1}$; Salmerón-García et al. (2011)) and relatively oligotrophic Texas shelf waters in the study area (chlorophyll *a* from 0.13 to 1.62 $\mu g\, l^{-1}$).

Several macroalgae had $\delta^{13}C$ values near or within OSOM $\delta^{13}C$ value range (e.g. red macroalgae: −22.2‰, *Dictyota* sp.: −19.7‰), limiting our ability to rule out the use of these resources. Very low $\delta^{13}C$ values of filamentous red algae (−31.3‰)—typical of macroalgae that are physiologically restricted to the use of CO_2—indicate a minimal contribution to secondary production.

Within-habitat variations among isotope values of sessile suspension feeders may be explained by variation in particle size selection (Cresson et al., 2016; Riisgård and Larsen, 2010) and/or physiological processes (Martínez del Río and Wolf, 2005). Encrusting tunicates had uniquely low $\delta^{13}C$ values in comparison with all other consumers. This may be related to the assimilation of carbon derived from symbiotic cyanobacteria present in this taxon (Schmidt, 2015), or to a unique suspension feeding mechanism. Markedly higher $\delta^{15}N$ values were found in azooxanthellate cup corals (*T. coccinea, P. americana)* and barnacles in comparison to most bivalve filter feeding taxa, indicating greater contributions from heterotrophic prey to their diets. Similar results have been obtained from stable isotope based studies demonstrating higher trophic position of barnacles in comparison to bivalves (Daigle et al., 2013; Rezek et al., 2017; Richoux et al., 2014). These results also support research indicating that some azooxanthellate cup corals rely largely on heterotrophic prey (Goreau et al., 1971; Houlbrèque et al., 2004; Houlbrèque and Ferrier-Pagès, 2009). A large degree of overlap was found between $\delta^{15}N$ values of motile macrofauna and suspension feeding taxa. This is indicative of a motile macrofauna community largely composed of primary consumers, apart from a few ^{15}N enriched secondary consumers (e.g. *S. fritzmuelleri, S. haemastoma,* and blennies).

The slight community-wide shift in consumer isotope values in SP5 and SP30 sites compared to the RP30 sites was most likely related to the shift in isotopic compositions of food sources. The trend in C and N isotope variation between reefed and standing platform consumers was generally reflected in composite food sources—particularly OSOM, which was shown to be an important contributor to these food webs—and primary producers.

The variance in $\delta^{13}C$ and $\delta^{15}N$ values among consumer taxa was homogeneous between all site-types. Similar isotopic variability among consumer taxa indicate that each habitat supported similar trophic diversity; relying on a similar diversity of food resources and supporting food webs with similar trophic levels. This indicates epibenthic communities in SP30 and RP30 site-types relied on similar food sources as the shallower SP5 communities, despite the variation in community composition between these zones. These findings provide evidence that platforms still play a role as a substrate for primary producers and for the trapping of organic matter after they are converted into artificial reefs.

4.3. Function of standing and reefed platform habitats

Standing and reefed platform habitats function as islands of productivity in the relatively unstructured soft bottom habitats typical of the northwestern Gulf of Mexico shelf (Rezak et al., 1985). A platform in 57 m of water can provide 2.2 ha of submerged surface area within a 0.2 ha footprint of ocean floor (MBC, 1987). Based on mean areal macrofauna biomass found in these habitats (293 g AFDW m^{-2}); an offshore platform in the Gulf of Mexico at similar depths could support 6.4 tons of AFDW macrofauna biomass, or 3.2 kg AFDW biomass per m^2 of ocean floor, or 1.3 kg C per m^2 of ocean floor (assuming 40% organic carbon by weight). Although a very rough estimate, this indicates that platform habitats support substantially higher biomass than unstructured benthic shelf habitats in the Gulf of Mexico (0.33–2.01 g C m^{-2}; Escobar-Briones and Soto, 1997). Further research is warranted to quantify the effect of reefing practices on total production supported by platform structures.

Standing and reefed platforms support macrofauna communities that provide a food source for fisheries species such as gray triggerfish (*B. capriscus*), sheepshead (*Archosargus probatocephalus*), rock hind (*Epinephelus adscensionis*), and spadefish (*Chaetodipterus faber*); as well as a variety of non-targeted reef fish (Beaver et al., 1997; Gallaway et al., 1979; Nelson and Bortone, 1996; Vose and Nelson, 1994). Higher growth rates of gray triggerfish (Nelson, 1985) and red snapper (*Lutjanus campechanus*) (Streich et al., 2017b) have been reported on standing and reefed platforms compared to natural reef habitats in the Gulf of Mexico.

Epibenthic communities inhabiting natural hard banks in the northern Gulf of Mexico shelf differ substantially in composition from those on platform-like habitats. Natural hard bank communities have been found to be dominated by cnidarians, sponges and bryozoans (Sammarco et al., 2016; Thompson et al., 1999), in contrast to the bivalve dominated communities characteristic of platform habitats. Much of the natural hard bottom substrate in this region has relatively low relief (> 1 m) and supports relatively low sessile macrofauna abundance due to its exposure to a persistent turbid nepheloid layer that negatively affects many suspension feeding taxa (Rezak et al., 1985). Quantitative comparisons of the biomass supported by natural banks in comparison to platforms and reefed platform structures could yield important insights into the overall influence these artificial habitats have on macrofauna production.

Although our results indicate that platform and reefed platforms support structurally similar communities at equivalent depths (30 m), the distinct compositional characteristics of shallow platform communities are likely to be lost or diminished when standing platforms are converted into artificial reefs. Structures spanning the entire water column are likely to support greater biodiversity than structures with lower relief. This conclusion is consistent with those of a photo-transect based examination of platform and reefed platform epiphytic communities conducted in the same region (Dokken et al., 2000). Compositional dissimilarity in nektonic fish assemblages associated with standing platforms vs. reefed platforms in the Gulf of Mexico have also been documented, with greater abundance of pelagic planktivores (e.g. Bermuda chub, blue runner) reported on standing platforms (Ajemian et al., 2015; Wilson et al., 2003). These fish are generally associated with the upper water column and are less likely to inhabit reefed platforms with relatively low relief. Nevertheless, the current reefing practice of removal of the upper 30 m of the structure does not substantially influence the functionality of these systems, and the habitat value retained creates beneficial habitat for epibenthic communities.

Allowing platforms to remain standing would ameliorate the loss of biodiversity due to the loss of shallow water substrate. However, federal regulations would require a state agency responsible for managing fisheries to assume all liability and costs associated with maintaining standing platforms in perpetuity (Kaiser and Pulsipher, 2005). The high costs associated with maintaining standing platforms as artificial reefs would generally make this approach unfeasible.

Stable isotope data indicate that reefed platforms can be expected to support faunal communities with comparable food web structure to shallow (5 m) and deep (30 m) standing platform habitat. This conclusion has important implications for resource management, as it demonstrates the ability of reefed platforms to retain ecological functions that would otherwise be lost when decommissioned platforms are removed. Although the 26 m clearance guidelines observed in current reefing practices may reduce some aspects of biodiversity associated with platforms, collectively our results indicate that Rigs-to-Reefs programs provide an effective means of preserving the productive epibenthic macrofauna assemblages associated with standing platforms. As offshore platforms in the Gulf of Mexico reach the end of their productive lives at an increasing rate, Rigs-to-Reefs programs may play a critical role in preserving the ecological functions and services associated with these anthropogenic marine habitats.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2018.09.020.

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