Mar Biol (2017) 164:92
DOI 10.1007/s00227-017-3122-0

ORIGINAL PAPER

Influence of mesoscale oceanographic features on pelagic food webs in the Gulf of Mexico

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Received: 1 August 2016 / Accepted: 3 March 2017
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Abstract This study examined the influence of mesoscale oceanographic features (anticyclonic; warm core and cyclonic; cold core) on offshore pelagic food webs in the Gulf of Mexico. Mean total biomass (wet weight) of all consumers was significantly higher in samples collected within cyclonic features (mean 3.78 g per 10 min tow) than anticyclonic features (mean 0.51 g per 10 min tow) during each survey date. Using stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), we contrasted the two main primary producers in this ecosystem: phytoplankton (based on particulate organic matter, POM) and *Sargassum* spp. over a 2-year period. In addition, consumers (zooplankton, six invertebrate species, and eight fish species) collected in upper surface waters were analyzed for $\delta^{13}C$ and $\delta^{15}N$. Both producers and ten of the fifteen consumer species had significantly enriched ^{15}N in cyclonic relative to anticyclonic features in year one and each of the six selected 'model taxa' collected during both years showed this same pattern. Model taxa included POM, *Sargassum* spp., zooplankton, glass shrimp (*Leander tenuicornis*), Sargassum crab (*Portunus sayi*), and blackwing flyingfish (*Hirundichthys rondeleti*). $\delta^{13}C$ values were more variable and dependent upon feature and survey date. Contributions for the two primary producers were estimated using a two-source Bayesian mixing model. Results support equal contributions of organic matter from phytoplankton and *Sargassum* spp. to consumers, but estimates were species and feature dependent and nitrogen-fixing *Trichodesmium* was likely important. For example, contribution estimates of *Sargassum*-derived organic matter to zooplankton in anticyclonic features ranged from 68 to 76%, in contrast to cyclonic features that varied from 29 to 83%. This study highlights the differences in $\delta^{13}C$ and $\delta^{15}N$ among producers and consumers collected within mesoscale oceanographic features in the Gulf of Mexico and demonstrates the need to obtain feature-dependent baseline estimates for calculating contribution estimates using stable isotope mixing models.

Keywords Feeding ecology · Pelagic food web · $\delta^{13}C$ · $\delta^{15}N$ · Stable isotopes · Eddies · Loop current

Introduction

Mesoscale oceanographic features including currents, gyres, and eddies are important in regulating the structure and dynamics of marine food webs (Lima et al. 2002). Swift moving western boundary currents produce strong eddy-like features branching off into isolated anticyclonic and cyclonic eddies at scales on the order of hundreds of kilometers in diameter. Anticyclonic eddies (warm core) are generally considered nutrient depleted relative to cyclonic eddies (cold core). Production in anticyclonic

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Responsible Editor: C. Harrod.

Reviewed by Undisclosed experts.

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Published online: 23 March 2017

eddies is commonly supported by regenerated nitrogen while cyclonic eddies have shallower thermoclines and receive new nitrogen from upwelling into the mixed layer (Biggs et al. 1988; Seki et al. 2001). Frontal zones of eddies are often associated with increased microbial, zooplankton, and nekton abundances (Zimmerman and Biggs 1999; Godo et al. 2012; Dorado et al. 2012; Williams et al. 2015) and often support higher productivity than surrounding open water habitat (Biggs et al. 1988). The size and temporal persistence of these mesoscale oceanographic features has the potential to significantly contribute to marine food webs by supporting higher trophic levels and apex predators.

The Gulf of Mexico (GOM) is a productive marginal sea with unique oceanographic conditions that affect community structure and trophic relationships of producers and consumers (Richards et al. 1993; Dorado et al. 2012; Lindo-Atichati et al. 2012). High primary and secondary productivity in nearshore waters of the northern GOM is heavily influenced by nutrient loading from the Mississippi River (Chesney et al. 2000), while productivity in offshore areas is influenced by the Loop Current and associated mesoscale features including anticyclonic and cyclonic eddies (Biggs 1992). In the GOM, mesoscale anticyclonic eddies spin off the Loop Current and drift westward as warm-core convergence features (Vukovich and Crissman 1986), while cyclonic eddies are often formed by frictional interactions with the continental margin creating cold-core divergence features (Hamilton 1992). These eddy features have lifespans ranging from days to a full year moving approximately 2–5 km day^{-1} (Elliott 1982; Forristall et al. 1992; Sturges and Leben 2000). Elevated nitrate and chlorophyll concentrations combined with high zooplankton and nekton biomass are often associated with cyclones or in confluence zones between cyclones and anticyclones (Biggs 1992; Zimmerman and Biggs 1999; Lindo-Atichati et al. 2012), suggesting that these physical features play an important role in structuring marine communities.

Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are useful tracers for examining energy flow and food web structure in aquatic ecosystems. Carbon stable isotopes are used to trace carbon pathways because little fractionation occurs between predator and prey, and different primary producers (energy sources) often have unique δ^{13}C values (Fry and Sherr 1984). Nitrogen stable isotope ratios become enriched with increasing trophic levels and are, therefore, used to infer trophic position (Peterson and Fry 1987). Combining both δ^{13}C and δ^{15}N provides useful information on food webs and has highlighted the importance of both phytoplankton (particulate organic matter, POM) and pelagic *Sargassum* spp. (hereafter *Sargassum*) as important primary producers in the offshore pelagic environment (Rooker et al. 2006; Wells and Rooker 2009). The role of oceanographic features on the distribution and abundance of marine fishes in the GOM has been examined (Bakun 2006; Lindo-Atichati et al. 2012; Rooker et al. 2012), yet little information exists on the role of these mesoscale oceanographic features to food web structure and dynamics in offshore waters.

Objectives of this study were to examine carbon pathways and trophic associations within anticyclonic and cyclonic mesoscale oceanographic features in the northern GOM. We targeted both producers and consumers during summer months over a 2-year period to account for spatial and temporal variability in food web dynamics. Finally, mixing models were used to estimate the contribution of organic matter derived from POM and *Sargassum* to four model consumers representing zooplankton, shrimp, crab, and fish in offshore surface waters of the GOM.

Materials and methods

Field collections

Sampling was conducted in slope waters of the northern GOM during June and July of 2008 and 2009. Producers and consumers were collected within both anticyclonic and cyclonic eddies (Fig. 1). Eddy features were identified during each survey using sea surface height anomaly (SSHA) data with values exceeding 17 cm considered to be associated with the core of the Loop Current or an associated anticyclone (Leben et al. 2002) and negative SSHA (<0 cm) indicative of cyclonic eddies. A total of four surveys (June and July 2008, June and July 2009) occurred with each targeting one to two anticyclone(s) and cyclone(s). A total of five to ten stations were sampled within each of the targeted features per survey during daylight hours only (Fig. 1). Sampling stations were typically located 15 km apart, although some stations were closer (5–10 km apart) to sample within the targeted feature.

POM and *Sargassum* samples were obtained at each station; however, *Sargassum* was not present at all stations sampled. Surface seawater collections of POM were used as a proxy for phytoplankton and samples were obtained by towing a plankton net for 5 min station^{-1} (20 μm mesh size targeting microphytoplankton 20–200 μm) and filtered over 47 mm GF/F filters (precombusted for 4 h at 450 °C) with an effective pore size of 0.7 μm. Zooplankton was collected by towing a 333 μm mesh plankton net for 5 min station^{-1}. Zooplankton (chaetognaths, copepods, and other crustaceans) was isolated using forceps and removed, filters were rinsed with filtered (0.2 μm) seawater three times, and transferred to precombusted GF/F filters following the methods of Dorado et al. (2012). *Sargassum*, fishes,

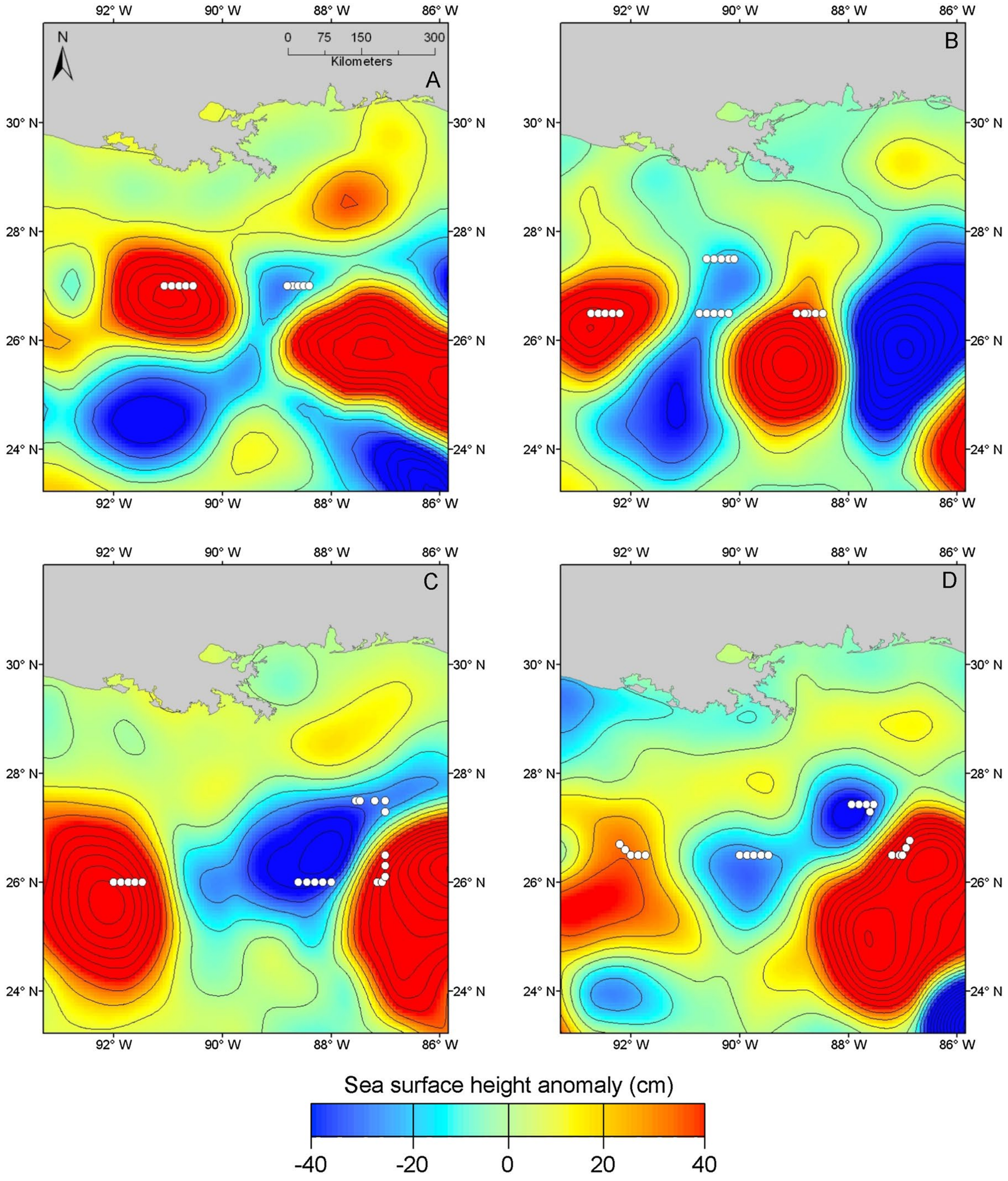

Fig. 1 Map of sampling locations within anticyclonic (warm core) and cyclonic (cold core) features in the Gulf of Mexico. Collection stations (*white dots*) during surveys taken in June 2008 (**a**), July 2008 (**b**), June 2009 (**c**), and July 2009 (**d**)

and invertebrates were captured using two neuston nets towed concurrently at each station (500 µm mesh and 1200 µm mesh) with opening dimensions of 2 m (width) × 1 m (height). Nets were towed at 2.5 knots for 10 min station^{-1}. Total biomass estimates were obtained based on combining all consumer material collected with both nets in wet weight (g).

Environmental parameters were measured at each station including sea surface temperature (SST) (°C), salinity (psu), and dissolved oxygen (DO) (mg L^{-1}) using a Sonde 6920 Environmental Monitoring System (YSI Inc.). Equipment malfunctions prohibited dissolved oxygen measurements during the June 2009 survey along with a sea surface temperature and salinity measurement at one of the stations

(Table 1). Other environmental parameters were extracted from remotely sensed data to match sampling dates and station locations. Sea surface height anomaly (SSHA) (cm) at 0.25° resolution was generated every 7 days from merged satellite altimetry measurements using Jason-1, ENVISAT/ERS, Geosat Follow-On and Topex/Poseidon interlaced (AVISO, http://www.aviso.oceanobs.com) (Teo et al. 2007; Rooker et al. 2012). Sea surface chlorophyll concentrations (mg m^{-3}) with 0.1 degree resolution were downloaded from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) (http://las.pfeg.noaa.gov) with data consisting of 8-day average periods. Depth (m) at each station was extracted from Google Earth using bathymetry data provided by Scripps Institution of Oceanography, National Oceanic and Atmospheric Administration (NOAA), United States Navy, National Geospatial-Intelligence Agency (NGA), and General Bathymetric Chart of the Oceans (GEBCO) resources.

POM, *Sargassum*, zooplankton, six invertebrate species, and eight fish species were collected within each feature during the first year of the study. Invertebrate species collected and analyzed in year one included: bryozoan (*Jellyella tuberculata*), polychaete (*Spirorbis* spp.), sea skater (*Halobates* spp.), Sargassum shrimp (*Latreutes fucorum*), glass shrimp (*Leander tenuicornis*), and Sargassum crab (*Portunus sayi*). Fish species collected and analyzed in year one included: gray triggerfish (*Balistes capriscus*), blue runner (*Caranx crysos*), rainbow runner (*Elagatis bipinnulata*), Sargassum frogfish (*Histrio histrio*), margined flyingfish (*Cypselurus cyanopterus*), blackwing flyingfish (*Hirundichthys rondeleti*), bluntnose flyingfish (*Prognichthys gibbifrons*), and smallwing flyingfish (*Oxyporhamphus micropterus*). In year two, a model species was used from each taxa to examine interannual variability: POM, *Sargassum*, zooplankton, glass shrimp, Sargassum crab, and blackwing flyingfish. Selection of each model species was made before stable isotope analysis and was based upon the numeric availability of each representative taxa.

Stable isotope analysis

All species collected were frozen on dry ice until being moved to a −80 °C freezer. Crabs were measured to the nearest mm carapace width (CW), fishes were measured to the nearest mm total length (TL), and both stomachs and heads were removed to minimize any effect on stable isotope analysis of muscle tissue. Epibiota were removed from *Sargassum* to minimize the influence of other flora and fauna on stable isotope ratios. Plant and fish tissue samples were dried at 60 °C for 24 h and stored in individual cryovials. Lipids were not extracted from fish tissue; however, C:N ratios were low (<4) across the size spectrum of fishes, indicating a low lipid content and little influence of lipids on fish tissue $\delta^{13}C$ values (Post et al. 2007). Isotopic ratios for $\delta^{13}C$ and $\delta^{15}N$ in both producers and consumers were determined at the Institute of Environmental Change and Society (IECS) at the University of Regina, Canada, with a Thermo Finnigan DeltaPlus isotope ratio mass spectrometer coupled to a Costech elemental analyzer (Wissel et al. 2005). Analytical error for both $\delta^{13}C$ and $\delta^{15}N$ was 0.2‰ and internal standards of wheat and bovine liver were used to account for instrument drift. Isotopic ratios are reported relative to Vienna PeeDee belemnite for carbon and atmospheric N_2 for nitrogen.

The potential carbon contribution of POM and *Sargassum* to consumers was estimated with a Bayesian two-source mixing model using Stable Isotope Analysis in R (SIAR) version 4.0 (Parnell et al. 2010). A carbon trophic enrichment factor of 1.0‰ (SD ± 0.3‰) was used (DeNiro

Table 1 Mean environmental parameters (±SE) by mesoscale oceanographic feature sampled in 2008 and 2009

Year	Month	Feature	SSHA (cm)	Chl a (mg/m^3)	SST (°C)	Salinity (psu)	DO (mg/L)	Depth (m)
2008	June	Anticyclone	28	0.07 (0.02)	28.15 (0.03)	36.65 (0.01)	7.11 (0.04)	1695
2008	June	Cyclone	−8	0.13 (0.01)	28.51 (0.05)	36.50 (0.02)	6.89 (0.07)	2540
2008	July	Anticyclone	37	0.11 (0.01)	29.33 (0.09)	36.97 (0.01)	6.33 (0.01)	2095
2008	July	Anticyclone	18	0.26 (0.09)	29.38 (0.01)	36.73 (0.04)	6.20 (0.02)	2588
2008	July	Cyclone	−4	0.10 (0.01)	29.16 (0.07)	35.81 (0.51)	6.15 (0.01)	2794
2008	July	Cyclone	−4	0.24 (0.03)	29.83 (0.09)	33.98 (0.95)	6.70 (0.05)	1194
2009	June	Anticyclone	33	0.06 (0.01)	na	na	na	2374
2009	June	Anticyclone	22	0.03 (0.01)	28.36 (0.20)	36.14 (0.02)	na	3121
2009	June	Cyclone	−11	0.16 (0.01)	27.64 (0.20)	36.24 (0.05)	na	2989
2009	June	Cyclone	−4	0.31 (0.03)	27.06 (0.20)	35.12 (0.30)	na	961
2009	July	Anticyclone	17	0.13 (0.05)	31.24 (0.16)	35.76 (1.04)	5.86 (0.06)	1998
2009	July	Anticyclone	39	0.06 (0.01)	31.16 (0.14)	36.02 (0.18)	5.74 (0.07)	3001
2009	July	Cyclone	−23	0.42 (0.06)	30.92 (0.52)	31.30 (0.97)	5.84 (0.07)	2932
2009	July	Cyclone	−10	0.39 (0.07)	30.68 (0.08)	33.78 (0.57)	5.80 (0.03)	3083

and Epstein 1978; Fry and Sherr 1984). $\delta^{15}N$ enrichment values range from 2.5 to 3.5‰ (SD ± 0.6‰) in aquatic systems (Vander Zanden and Rasmussen 2001; Vanderklift and Ponsard 2003); therefore, a nitrogen enrichment value of 3.0‰ was used per trophic position (Fry and Sherr 1984; Rooker et al. 2006). Underestimation of trophic position and resulting food web compression can occur for top predators (Hussey et al. 2014); however, given the early life stages used in this study an assumption of constant isotopic discrimination likely did not alter the trophic position estimates. In addition, early life stages of model taxa were selected for this study with the intent of comparing groups with relatively similar tissue turnover rates and to minimize movement outside of the feature it was collected. Model inputs for SIAR included no concentration dependence, 500,000 iterations, and 50,000 burnins or number of initial iterations to discard. One goal of this study was to evaluate if differences in contribution estimates of consumers exist relative to mesoscale oceanographic features. Diagnostic matrix plots were used to examine correlation of posterior distributions between the primary producers for each model scenario. Consequently, mixing models were first examined using primary producer data that were feature specific (anticyclone and cyclone) and by survey date. Next, mixing models were developed by combining feature type (anticyclone and cyclone averaged together) by survey date to evaluate the difference in contribution estimates of primary producers based on combined features versus feature-specific baselines.

Data analysis

A *t* test was used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ between organic sources (POM and *Sargassum*). Similarly, *t* tests were used to examine differences in environmental variables (SSHA, chlorophyll, SST, salinity, DO, depth) with respect to feature. Multivariate analysis of covariance (MANCOVA) was used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ among producers and consumers. Dependent variables included both $\delta^{13}C$ and $\delta^{15}N$, consumer size was used as the covariate, and independent factors included survey, feature, and location (inshore > 27°N versus offshore < 27°N, and east < 90°W versus west > 90°W within each survey by feature). Pillai's trace statistic was used to test for significance. Univariate tests for both $\delta^{13}C$ and $\delta^{15}N$ were also performed using analysis of variance (ANOVA) and a posteriori differences among means were analyzed with Tukey's honestly significant difference (HSD) test. No significant location effect within each survey existed for any species ($P > 0.05$); therefore, locations within each survey were combined so the final model included survey and feature as independent factors. Six 'model taxa' collected during both years of the study were analyzed over all four surveys, while the 11 other species were only analyzed during the first two surveys (June, July) of year one (2008). Biomass was evaluated with ANOVA using both survey and feature as independent factors. Normality was evaluated using a Shapiro–Wilk test and the equal variance assumption was assessed by the Spearman rank correlation between the absolute value of the residuals and the observed value of the dependent variable. Statistical significance for all tests was determined at the alpha level of 0.05.

Results

Several environmental parameters were significantly different between anticyclonic and cyclonic features. As expected, mean SSHA measurements were significantly higher in anticyclonic compared to cyclonic features during each survey ($t_{65} = 14.68$, $P < 0.001$) ranging from 17 to 39 cm in anticyclones and −23 to −4 cm in cyclones (Table 1). Chlorophyll concentrations were significantly lower in anticyclone compared to cyclone features during all surveys ($t_{65} = -4.028$, $P < 0.001$), except July of 2008 (Table 1). Salinity was significantly higher within anticyclonic relative to cyclonic features by an average of 0.15–4.72 psu during each survey ($t_{59} = 3.72$, $P < 0.001$), except June of 2009. Mean dissolved oxygen values were similar averaging 6.48 (±0.19) and 6.31 (±0.14) mg/L at sampling stations within anticyclones and cyclones ($t_{51} = 0.81$, $P = 0.424$), respectively. Similarly, mean depths were similar with anticyclonic features averaging 2410 m and cyclonic averaging 2586 m and ($t_{65} = -1.24$, $P = 0.219$).

Mean total biomass was higher in samples collected within cyclonic relative to anticyclonic features during each survey (Fig. 2). A significant feature effect ($F_{1,32} = 15.50$, $P < 0.001$) existed with mean biomass averaging 3.78 (±0.85) and 0.51 g (±0.09) per 10 min surface tow in cyclonic and anticyclonic features, respectively. Mean biomass in cyclones ranged from a low of 2.40 g (±0.45) per 10 min tow in July of 2008 to a high of 6.58 g (±2.91) per 10 min tow in June of 2008. In contrast, mean biomass in anticyclones ranged from 0.37 (±0.15) to 0.69 g (±0.25) per 10 min tow in June 2008 and July 2009, respectively. No significant survey ($F_{3,32} = 1.20$, $P = 0.325$) or interaction effect between feature and survey ($F_{3,32} = 1.41$, $P = 0.259$) existed.

Feature type was the most important factor influencing $\delta^{15}N$ of both producers and consumers with enriched ^{15}N values in many of the taxa collected in cyclonic relative to anticyclonic features. Specifically, both producers and ten of the fifteen consumer species collected in cyclonic features were significantly enriched in ^{15}N relative to those

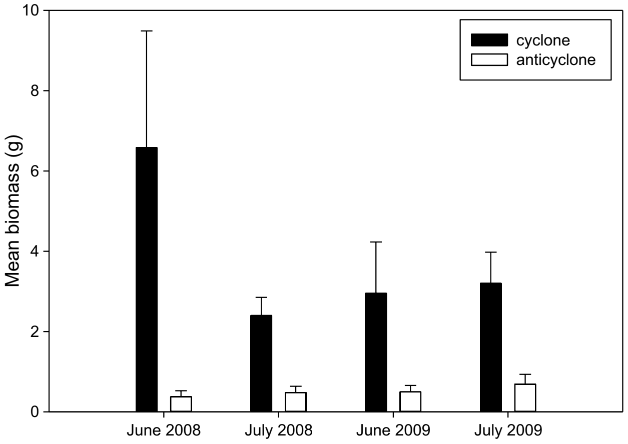

Fig. 2 Mean biomass (g) (±1 SE) values from anticyclonic and cyclonic features during each survey of the 2-year study period

collected in neighboring anticyclonic features in year one ($P \leq 0.05$). These included POM, *Sargassum*, zooplankton, four of the six invertebrates (sea skater, polychaete, glass shrimp, Sargassum crab), and five of the eight fish species (gray triggerfish, margined flyingfish, rainbow runner, blackwing flyingfish, smallwing flyingfish). Each of the six 'model taxa' examined during both years had significantly enriched ^{15}N in cyclonic relative to anticyclonic features (Fig. 3, $P \leq 0.05$). For primary producers, mean δ^{15}N of POM ranged from 2.2 to 3.9‰ in cyclonic features and 0.6 to 2.1‰ in anticyclonic features ($F_{1,54}$=7.43, $P = 0.009$), while mean δ^{15}N of *Sargassum* ranged from 1.0 to 1.4‰ in cyclonic and −1.2 to −0.6‰ in anticyclonic features ($F_{1,52}$ = 48.39, $P < 0.001$). Zooplankton ^{15}N was enriched in samples collected within cyclonic features by an average of 1.7–2.8‰ during each of the four surveys ($F_{1,61} = 21.86$, $P < 0.001$). Glass shrimp ranged from 5.0 to 6.2‰ and 3.8 to 6.1‰ in cyclonic and anticyclonic features, respectively ($F_{1,32} = 5.97$, $P = 0.020$), but was not significantly different during 2008 surveys ($P > 0.05$). Sargassum crabs were significantly enriched in ^{15}N within cyclones relative to anticyclones during July surveys by an average of 5.2‰. ^{15}N of blackwing flyingfish was significantly enriched within cyclones for three of the four surveys by an average of 1.4 to 2.1‰. A significant survey effect was detected for blackwing flyingfish ($F_{3,42} = 5.76$, $P = 0.002$), where enriched ^{15}N occurred in July 2009 relative to both July 2008 and June 2009. For species examined only in year one, only sea skater had a significant survey effect ($F_{1,12} = 20.44$, $P < 0.001$), with enriched ^{15}N in July 2008 over June 2008. No significant interaction or survey effects existed for the other ten species examined ($P > 0.05$).

Patterns in δ^{13}C among producers and consumers were variable between features and across surveys. One producer and five of the fifteen consumer species showed a significant feature effect and had enriched ^{13}C in anticyclonic relative to cyclonic features ($P \leq 0.05$). These species included POM, glass shrimp, Sargassum crab, gray triggerfish, blackwing flyingfish, and smallwing flyingfish. A significant survey effect was found for 11 of the 17 species examined ($P \leq 0.05$). Four of these species (bryozoan, rainbow runner, margined flyingfish, bluntnose flyingfish) were only collected during year one of the study period and all taxa collected in July were significantly enriched in ^{13}C relative to June collections ($P \leq 0.05$). For 'model taxa' collected during both years (Fig. 3); zooplankton, glass shrimp, and blackwing flyingfish were significantly enriched in ^{13}C during July relative to June ($P \leq 0.05$), but did not differ for similar months between years. On average, zooplankton collected in July was enriched by 0.50–2.13‰ relative to zooplankton collected during June surveys within the same feature and year. Similarly, glass shrimp and blackwing flyingfish collected in July were enriched by up to 1.50 and 1.02‰, respectively, when compared to June surveys. A significant survey and feature interaction effect was only detected for POM ($F_{3,56}$=13.73, $P < 0.001$), with enriched ^{13}C in anticyclonic features in July of both years and significantly depleted ^{13}C in anticyclonic features of June 2009.

Percent contribution estimates from the two primary producers were species and feature specific (Fig. 4). Contribution estimates of *Sargassum*-derived organic matter (relative to POM) was higher to zooplankton in anticyclonic features (70% mean contribution), with consistently high contribution estimates ranging from 68 to 76% during each of the surveys. In contrast, contribution estimates of *Sargassum* to zooplankton in cyclonic features widely varied from 29 to 83%. *Sargassum*-derived organic matter was higher to crabs in both anticyclonic (61% mean contribution) and cyclonic features (64% mean contribution). Highest contribution estimates of *Sargassum* to crabs in both features occurred in June of 2009 with mean contributions of 72 and 78% in anticyclonic and cyclonic features, respectively. POM contribution estimates were not substantially higher than *Sargassum* to any of the model species examined; however, mean contribution estimates were 56 and 54% for glass shrimp and blackwing flyingfish in anticyclonic features, respectively. Posterior distributions from matrix plots used to diagnose the performance of mixing models showed negative and high correlations between primary producers (POM and *Sargassum*) suggesting a potential missing primary producer or source (i.e., *Trichodesmium*). In addition, δ^{13}C and δ^{15}N of primary producers of POM and *Sargassum* may not have been large enough to clearly separate from one another.

Organic contribution estimates of POM and *Sargassum* to consumers was largely feature dependent and changed by an average of 10.3% when primary producers

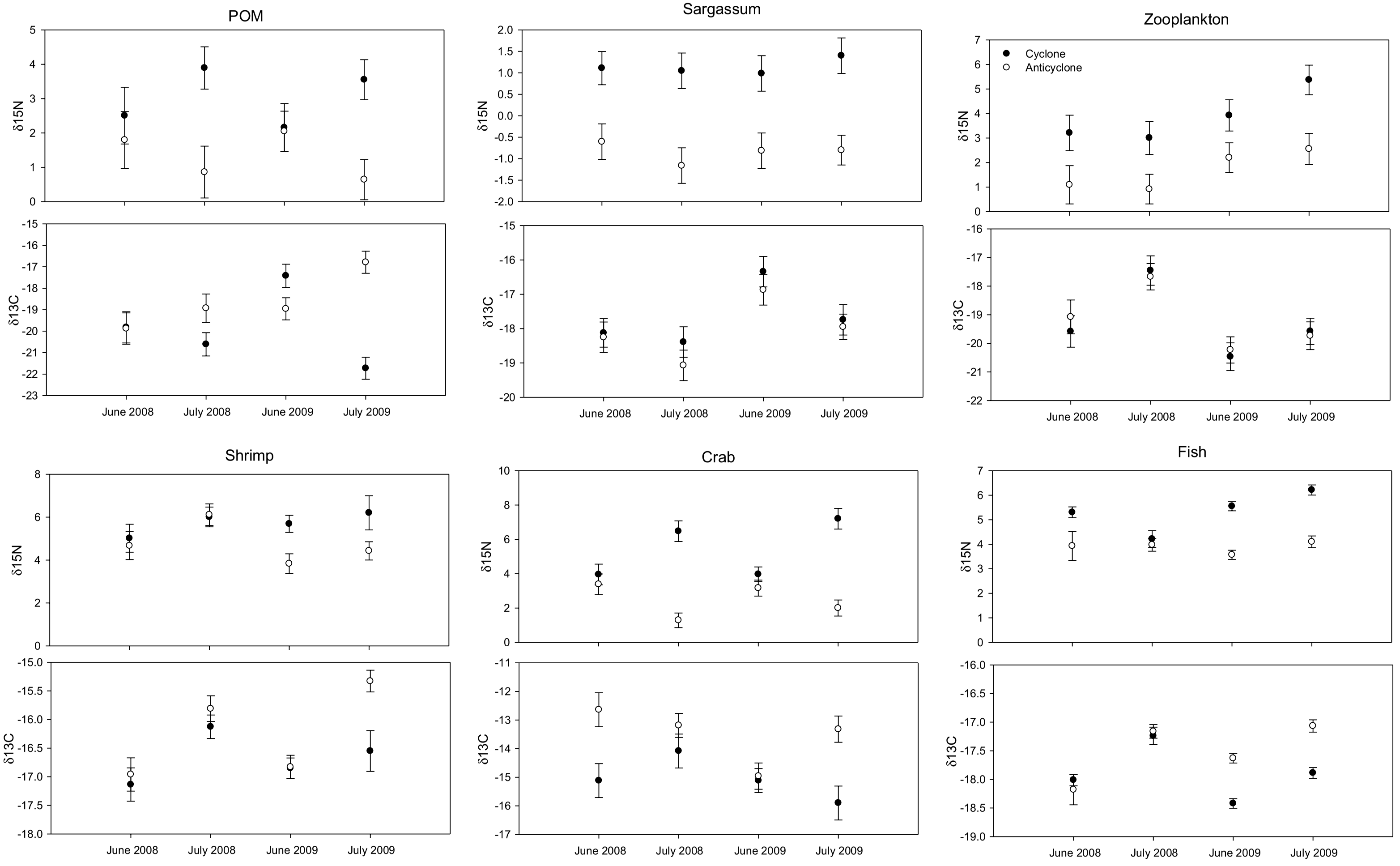

Fig. 3 Mean δ^{13}C and δ^{15}N values (±1 SE) of the six species collected in anticyclonic and cyclonic features during each survey of the 2-year study period. *White* and *black circles* represent mean values from anticyclonic and cyclonic features, respectively. Note differences in *scales* on *y*-axes

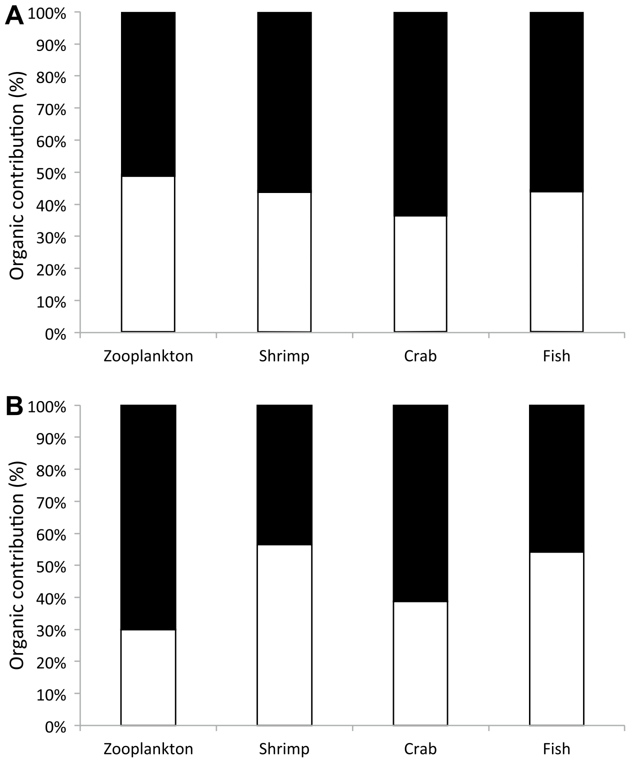

Fig. 4 Organic contribution estimates (%) derived from particulate organic matter (POM, *white*) and *Sargassum* spp. (*black*) to four consumer groups collected in cyclonic (**a**) and anticyclonic (**b**) features

were averaged between anticyclonic and cyclonic features for the mixing models. Largest changes occurred for the blackwing flyingfish as *Sargassum*-derived organic contribution estimates increased by 20% in anticyclones and decreased by 14% in cyclones. Moderate shifts in organic contribution estimates were found for glass shrimp (10–11%), Sargassum crabs (6–11%), and zooplankton (3–7%) when using averaged baseline values of primary producers between cyclonic and anticyclonic features.

Discussion

Environmental conditions encountered in this study confirmed that our sample locations represented anticyclonic and cyclonic features. Cyclonic eddies are divergent features characterized by upwelling within their interiors and, therefore, have identifiable parameters including depressed sea surface heights (i.e., low SSHA), lower salinity, and cooler sea surface temperatures relative to convergent anticyclonic features (Seki et al. 2001; Bakun 2006). The geographic location of anticyclones were initially identified during each survey using the criterion that SSHA exceeding 17 cm be considered part of the Loop Current or an associated anticyclone (Leben et al. 2002). Mean SSHA ranged from 17 to 39 cm at the stations classified as being located within anticyclones, in contrast to mean ranges from −4 to −23 cm at stations considered to be in cyclones. The presence of high salinities (>36 psu) within upper surface waters has also been used to identify anticyclonic features originating from the Loop Current due to excess evaporation over precipitation from its Caribbean source (Morrison et al. 1983; Biggs 1992). Mean surface salinities at stations categorized within anticyclonic features ranged from 36.6 to 36.9 in 2008, and 35.7 to 36.1 in 2009, and were significantly higher than corresponding salinities measured at stations classified to be within cyclonic features. Similar salinities were reported by Williams et al. (2015) when examining both feature types within the GOM.

Differences in $\delta^{13}C$ and $\delta^{15}N$ between primary producers of POM and *Sargassum* were similar to previous studies that have reported depleted ^{13}C and enriched ^{15}N for POM compared to *Sargassum* (Moncrieff and Sullivan 2001; Rooker et al. 2006; Wells and Rooker 2009). $\delta^{13}C$ values of both producers showed consistent trends relative to one another with mean POM ^{13}C in cyclonic and anticyclonic features depleted by 0.6 and 2.3‰ relative to *Sargassum*, respectively. Other studies found POM ^{13}C slightly more enriched relative to *Sargassum* by an average of 3–5‰ (Moncrieff and Sullivan 2001; Rooker et al. 2006). Similarly, mean POM ^{15}N was enriched relative to *Sargassum* in cyclones by 1.9‰ and anticyclones by 2.2‰. Findings by Wells and Rooker (2009) had enriched ^{15}N values of POM relative to *Sargassum* of 2.0‰, closely matching results from this study where samples were collected from the same general region. *Sargassum* can utilize both inorganic and organic forms of nitrogen (Vonk et al. 2008) and, therefore, this producer has the ability to incorporate nitrogen compounds released by blue-green algae of the genus *Trichodesmium*, which has been shown to be enriched in ^{13}C and depleted in ^{15}N relative to other marine phytoplankton (Carpenter et al. 1997; Dorado et al. 2012). The unique $\delta^{13}C$ and $\delta^{15}N$ values of *Trichodesmium* averaged approximately −14 and −1‰, respectively (Dorado et al. 2012), likely contributing to the enriched ^{13}C and depleted ^{15}N values of *Sargassum* relative to POM.

$\delta^{13}C$ and $\delta^{15}N$ values of both producers were largely dependent upon mesoscale oceanographic features. In addition, each of the 'model taxa' consumers followed feature-specific patterns of primary producers with enriched ^{15}N in cyclonic relative to anticyclonic features. Differences in the isotopic baseline (POM and *Sargassum*) are likely driving this trend suggesting the source and subsequent trophic transfer of nitrogen varies between features. Waite et al. (2007) found similar trends of POM and associated consumers, enriched ^{15}N and depleted ^{13}C, in cyclonic relative to anticyclonic features associated with the Leeuwin Current off western Australia and attributed this to higher vertical fluxes of nitrates into the cyclonic feature. Enriched ^{13}C and depleted ^{15}N in anticyclonic relative to cyclonic features are consistent with Dorado et al. (2012) who suggested the importance of diazotrophy by *Trichodesmium*. Dorado et al. (2012) showed mean POM δ^{13}C values of −22.2 and −17.0‰ in neritic and oceanic waters, respectively, and δ^{15}N values of 4.2‰ and 0.5‰ in these same two environments. POM δ^{13}C values reported here nearly matched those of Dorado et al. (2012) with mean values ranging from −21.7 to −17.4‰ in cyclonic features and −19.9 to −16.8‰ in anticyclonic features. POM δ^{15}N values ranged from 2.2 to 3.9‰ and 0.6 to 2.1‰ in cyclonic and anticyclonic features, respectively. No significant inshore versus offshore location effects were found, which were used as a proxy for neritic and oceanic waters; however, a similar processes of nitrogen fixation (diazotrophy) by *Trichodesmium* is most likely occurring.

Anticyclonic oceanographic features in the GOM have been shown to be depleted in nitrate (<0.3 µg L^{-1}) relative to cyclonic features (>10 µg L^{-1}) (Biggs et al. 1988; Biggs 1992) with the assumption that the anticyclonic features are supported by regenerated nitrogen versus cyclonic features with shallower nitraclines introducing new nitrogen into the mixed layer or euphotic zone. This evidence suggests that there are differences in nitrogen cycling between cyclonic and anticyclonic features and that nitrogen derived from diazotrophy may occur within anticyclonic features supporting previous research that N_2 fixation (primarily by *Trichodesmium*) is important in the GOM (Mulholland et al. 2006; Holl et al. 2007; Dorado et al. 2012). Documentation of diazotrophic nitrogen into coastal and oceanic pelagic food webs is an increasing trend that warrants further consideration as a potential link in food web studies (Woodland et al. 2013). An assumption with our approach was to attempt to choose organisms with relatively similar tissue turnover rates and minimize movement into and out of the features so the organism's isotopic values were reflective of the feature by which it was collected within. Given that only the early life stages of model consumer taxa (glass shrimp, size range: 4–8 mm total length, Sargassum crab, size range: 5–13 mm carapace length, blackwing flyingfish size range: 7–23 mm total length), along with zooplankton, were chosen for this study its likely that tissue turnover times were several days and movement was minimal.

Organic contribution estimates to the consumers examined suggests both POM and *Sargassum* are important sources of organic matter and are feature dependent. The approximate equal contribution of both primary producers to larval and juvenile stages of fishes and invertebrates (defined as trophic level < 2.0) has been reported in the same general study region (Rooker et al. 2006; Wells and Rooker 2009). Overall contribution rates of POM and *Sargassum* averaged 44 and 56% among the four model consumers, respectively; however, it is unlikely that this fraction of organic matter is derived directly from *Sargassum*. Rooker et al. (2006) suggested high levels of polyphenols from *Sargassum* (used as a chemical defense against grazers) could be incorporated into higher trophic levels, while it is also probable enriched *Trichodesmium* (mean δ^{13}C of −14‰) is being incorporated into the food web. Mixing model diagnostics demonstrated that a potential primary producer may be missing, thus contribution estimates of the two primary producers of POM and *Sargassum* may be different if other potential sources such as *Trichodesmium* had been collected and included. Mixing model results also support the importance of obtaining primary producers and consumers from the same feature. For example, *Sargassum*-derived organic estimates in anticyclones ranged from a low of 28% for blackwing flyingfish to a high of 83% for zooplankton, but when using averaged baseline values of primary producers over the same survey date independent of feature type, contribution estimates increased by as much as 20% for blackwing flyingfish.

Increased biomass at higher trophic levels has been well documented within upwelling features such as cyclonic eddies (Bakun 2006; Muhling et al. 2007; Godo et al. 2012). Upwelling within many cyclonic features stimulates production at lower trophic levels by supplying nutrients to phytoplankton (Denman and Gargett 1983; McGillicuddy et al. 1999), which is then transferred up the food web. In Hawaiian waters, 3- to 15-fold increases in nitrate and nitrite levels were observed in surface waters of cyclonic features relative to areas outside these features consequently leading to increases in primary and new secondary production (Seki et al. 2001). In this study, average biomass in cyclones was over seven times that within anticyclones, which is consistent with production estimates within these mesoscale oceanographic features. However, total biomass was recorded and our calculations between features may differ if trophic level proportions were directly compared. Biggs (1992) described anticyclones in the northern GOM as oligotrophic with depleted nitrates in the upper 100 m, chlorophyll standing stocks <20 mg m^{-2}, primary productivity <0.4 mg C m^{-3} h^{-1} and zooplankton biomass 4–6 mL 100 m^{-3}. In contrast, outside the anticyclonic features higher nitrates were measured in surface waters, chlorophyll standing stocks nearly doubled (35 mg m^{-2}) and primary production was 1.5–2 times higher. Greater standing stocks of zooplankton and micronekton in GOM cyclonic relative to anticyclonic features were also found using acoustic measurements in the GOM (Zimmerman and Biggs 1999), supporting our findings that production occurring within cyclonic features may be important in supporting the pelagic food web.

In summary, mesoscale oceanographic features such as cyclones and anticyclones appear to play an important role in the pelagic food web of the GOM. The size of these features combined with their temporal persistence (months to years) highlights the importance of primary and secondary production to serve as food stocks for higher trophic levels. However, mixing models based on stable isotope data need to incorporate the demonstrated differences in the base of the food web (i.e., POM, *Sargassum*) that may be dependent upon feature type. These differences in the base of the food web may be manifested up the food chain, therefore, necessitating feature-dependent collections for meaningful stable isotope data of higher trophic levels. Given the measured differences in primary producers and the need to utilize feature-dependent mixing models, it may be possible to use stable isotopes of δ^{13}C and δ^{15}N as tracers to retrospectively determine the amount of time consumers spend in different mesoscale oceanographic features.

Acknowledgements Special thanks to staff and students at Texas A&M University at Galveston and the crew of the Lady Bride. In particular, A. Schultze, L. Wetmore, and S. Dorado for assistance in the field and laboratory. We also appreciate the valuable suggestions and feedback from the handling associate editor and two anonymous reviewers that improved the manuscript.

Compliance with ethical standards

This project was funded by the McDaniel Charitable Foundation. The authors declare that they have no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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