Marine Pollution Bulletin 94 (2015) 241–250

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

# $\delta^{13}C$ and $\delta^{15}N$ in deep-living fishes and shrimps after the Deepwater Horizon oil spill, Gulf of Mexico

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ARTICLE INFO

*Article history:*
Available online 14 March 2015

*Keywords:*
Mesopelagic fauna
Stable isotopes
Deepwater Horizon
Gulf of Mexico
Oil spill

ABSTRACT

The blowout of the Deepwater Horizon (DWH) drill-rig produced a surface oil layer, dispersed micro-droplets throughout the water column, and sub-surface plumes. We measured stable carbon and nitrogen isotopes in mesopelagic fishes and shrimps in the vicinity of DWH collected prior to, six weeks after, and one year after the oil spill (2007, 2010 and 2011). In 2010, the year of the oil spill, a small but significant depletion of $\delta^{13}C$ was found in two mesopelagic fishes (*Gonostoma elongatum* and *Chauliodus sloani*) and one shrimp (*Systellaspis debilis*); a significant $\delta^{15}N$ enrichment was identified in the same shrimp and in three fish species (*G. elongatum*, *Ceratoscopelus warmingii*, and *Lepidophanes guentheri*). The $\delta^{15}N$ change did not suggest a change of trophic level, but did indicate a change in diet. The data suggest that carbon from the Deepwater Horizon oil spill was incorporated into the mesopelagic food web of the Gulf of Mexico.



## 1. Introduction

The explosion of the Deepwater Horizon (DWH) drilling rig resulted in the largest offshore oil spill in U.S. history, releasing more than 4.5 million barrels of oil into the Gulf of Mexico (GOM) in only 86 days (McNutt et al., 2011). The spill occurred under a unique set of circumstances as the broken well-head was deep (>1.1 km below the sea surface), chemical dispersants were released at depth, and several sub-surface plumes of oil were detected (Kujawinski et al., 2011; Reddy et al., 2011; Socolofsky et al., 2011), some of which persisted for months without substantial biodegradation (Camilli et al., 2010). The effects of the spill have been difficult to model (Valentine et al., 2012), but isotopic carbon depletion has been documented in two plankton size classes (Graham et al., 2010) and exposure to hydrocarbon-like chemicals has been documented in marsh fishes (Whitehead et al., 2011). Those results suggested the incorporation of near-surface oil-spill carbon into the coastal food web. However, incorporation of hydrocarbons into the intermediate trophic levels comprising the mesopelagic fauna of the GOM has yet to be addressed.

Mesopelagic fauna include a diverse suite of fish and crustacean species, the majority of which reside at depths below 600 m during the day and perform a migration into the upper 250 m at night (Gartner, 1991; Hopkins and Sutton, 1998; Hopkins et al., 1994; Lancraft et al., 1988). The diel vertical migration of GOM mesopelagic species greatly increased the probability of encounters with subsurface oil plumes, which may have acted as a "hydrocarbon curtain" interfering with their normal diel movement patterns. Additionally, since most of the mesopelagic community is zooplanktivorous and feeds in the upper 200 m at night (Hopkins et al., 1994; Hopkins and Sutton, 1998; Lancraft et al., 1988), consumption of prey rich in depleted carbon from the dispersed oil incorporated into their zooplankton prey would potentially shift their isotopic signature. Midwater fishes such as myctophids, or lanternfishes, contribute significantly to the vertical transport of organic matter from the epipelagic zone (upper 200 m) to the mesopelagic zone (generally between 200 and 1000 m) (Brodeur and Yamamura, 2005; Hidaka et al., 2001) and moreover, are important prey items for larger pelagic species such as the tunas and billfishes.

Movement of oil-spill carbon through the food web can be monitored using stable isotopes. Stable carbon and nitrogen isotope analysis provides the ability to identify carbon sources supporting heterotrophic activity and elemental cycling in an ecosystem (Kelley et al., 1998). Depleted isotope values are indicators that

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http://dx.doi.org/10.1016/j.marpolbul.2015.02.002
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carbon from sources such as dispersed oil and methane have entered the food chain via prokaryotic consumers and the microbial loop (Graham et al., 2010).

Stable N isotope ratios are frequently used as indicators of trophic position (McClelland and Montoya, 2002). The C/N ratio provides an additional method of discriminating the source of organic material (Mackie et al., 2005). For example, marine phytoplankton and zooplankton have atomic C/N ratios ranging between 4 and 10. Conversely, terrestrial vascular plants and their derivatives have atomic C/N ratios generally higher than 15 (Vreca and Muri, 2006; Rumolo et al., 2011). Additionally, the C/N ratio closely tracks changes in organism lipid content. Lipids are composed mainly of carbon, and most lipid classes do not contain nitrogen (Barnes et al., 2007). Thus, an increase in tissue total lipid concentrations correlates with increases in C/N ratios (Barnes et al., 2007). All else being equal, individuals in better condition (higher lipid content) could be expected to exhibit higher C/N ratios (Schmidt et al., 2006; Sweeting et al., 2006).

In this study we examined the isotopic signature of key mesopelagic fish and shrimp species collected offshore in the GOM prior to, six weeks after, and one year after the oil spill. We specifically examined isotopic signatures changes that could be attributed to the oil spill. The $\delta^{13}C$ signature of the weathered and fresh oil was $-27.23 \pm 0.03$ and $-27.34 \pm 0.34$, respectively, in early June (Graham et al., 2010). We examined shifts in stable carbon and nitrogen isotopes as indicators of food web modifications during the oil spill. Quantification of environmental impacts are often challenging because in most cases there are no available data prior to the major event that help identify the baseline characteristics of the environment and its biotic communities. Here we present a comparison of carbon and nitrogen stable isotopic signatures of mesopelagic fish and shrimps prior to, during and after the oil spill (2007, 2010 and 2011). This is the first study to suggest that oil-derived carbon, likely from DWH, entered the intermediate trophic levels of the offshore pelagic community. The results also indicated that the movement of oil into the food web is complex and not uniform to all mesopelagic species.

## 2. Methodology

### 2.1. Sampling

Specimens were collected in August 2007, September 2010 and September 2011. The DWH spill lasted from 20 April until 15 July 2010. Our 2010 sampling took place approximately six weeks after the well was capped. Sampling procedures in 2007 and 2010/2011 varied slightly (see below); however, they were highly consistent in that both sampling protocols occupied the upper 1000 m of the water column and that most sampling occurred at night. Time of day was divided into four categories: day (0730–1830 h), night (2030–0530 h), dawn (0530–0730 h, 1 h on either side of average sunrise), and dusk (1830–2030 h, 1 h on either side of average sunset).

*2007:* As part of a larger study (Ross et al., 2010), sampling was conducted during 24-h operations at two sites from 20–28 August 2007 [note: the whole study was 9–29 Aug but these 2 stations were sampled 20–28 Aug] (Fig. 1). The two sites were located at the following coordinates: 29°10.20′N, 88° 0.21′W and 27°38.18′N, 88°21.01'W, approximately 63 km northeast and 117 km south, respectively, of the DWH wellhead. A total of 85 trawls (17 day, 45 night, 31 dawn, and 11 dusk) were done using a $2 \times 2$ m Tucker trawl (1.59 mm mesh, 505 μm cod end bucket) with a plankton net (0.5 m diameter, 335 μm mesh) attached inside the Tucker trawl mouth to simultaneously sample the smaller components of the midwater fauna. A Sea-Bird SBE39 temperature-depth recorder (TDR) was attached to the upper frame bar to record time, depth, and temperature during tows. Upon reaching the designated depth, the trawl fished for approximately 30 min at a ground speed of 2 knots (3.7 km/hr) and then closed using a double trip mechanism. The mean depth for each Tucker trawl tow was calculated by averaging all depths recorded by the TDR from the start to the end of each tow. See Ross et al. (2010) for further details of 2007 sampling.

*2010–2011:* Sampling was conducted during two research cruises: 5–11 September 2010 and 11–17 September 2011. Sampling sites were located in the vicinity of 28°38.19′ N, 87°52.11′ W, approximately 55.5 km east and southeast of the DWH wellhead (Fig. 1). A total of 15 trawls (3 day, 8 night, 2 dawn, and 2 dusk) were done using either a 4 $m^2$ MOCNESS or a 9 $m^2$ Tucker trawl (both with 3 mm mesh in the main body of the net and 1000 μ in the trailing meter nets and in the cod-end buckets).

### 2.2. Hydrography

The methods used to measure hydrography during the 2007 research cruise have been previously described (Ross et al., 2010). In the 2010 and 2011 cruises, a Sea-Bird SBE 25 CTD was used to record profiles of temperature (°C) and salinity in the upper 1000 m of the water column. CTD casts were made in the morning and evening in the same areas where specimens were collected. A total of 6 casts were conducted at the two sites in 2007 (see Ross et al. (2010) for details); seven casts were done in 2010 and nine casts in 2011.

### 2.3. Handling of specimens collected

The most common species representing different ecotypes (e.g., vertically migrating zooplanktivore, decapod specialist, piscivore) were used for statistical comparisons in the stable isotope analysis. For statistical comparisons, a species had to be collected in at least two of the three sampling years. This was done to increase the number of statistical comparisons and be able to identify possible oil spill effects.

In all cruises, specimens were removed from the catch immediately after the net reached the deck. Specimens were sorted, identified to the lowest possible taxonomic level (usually species), weighed, and measured to the nearest millimeter standard length (SL) (fishes) or total length (TL) (shrimp). In cases in which standard length was not available, length–weight regressions generated using previously collected data (Torres and Donnelly, unpublished data; Sutton, unpublished data) were used to calculate standard length. The 2007 catches were subsampled to remove tissue for stable isotope analysis of dominant and representative fauna. In 2007, the majority of samples were dried to a constant weight in an oven at 50–60 °C prior to chemical analysis. The rest of the 2007 samples and all of the 2010–2011 samples were frozen at −80 °C. Species identification was made prior to tissue collection.

White muscle tissue was used due to its low isotopic variability relative to other tissues (Pinnegar and Polunin, 1999). Epaxial muscle tissue of fish was removed from behind the head, and muscle tissue of shrimp was removed from the caudal region of the abdomen. Minimal contamination from other tissue types occurred as the scales and photophores were removed from specimens. All collected isotope samples were frozen (−80 °C) and freeze-dried prior to analysis, except as noted above for 2007.

### 2.4. Analysis of stable isotopes

Tissue samples of fish and shrimp were analyzed for bulk carbon and nitrogen (C, N, C:N), and stable isotope ratios ($\delta^{13}C$,

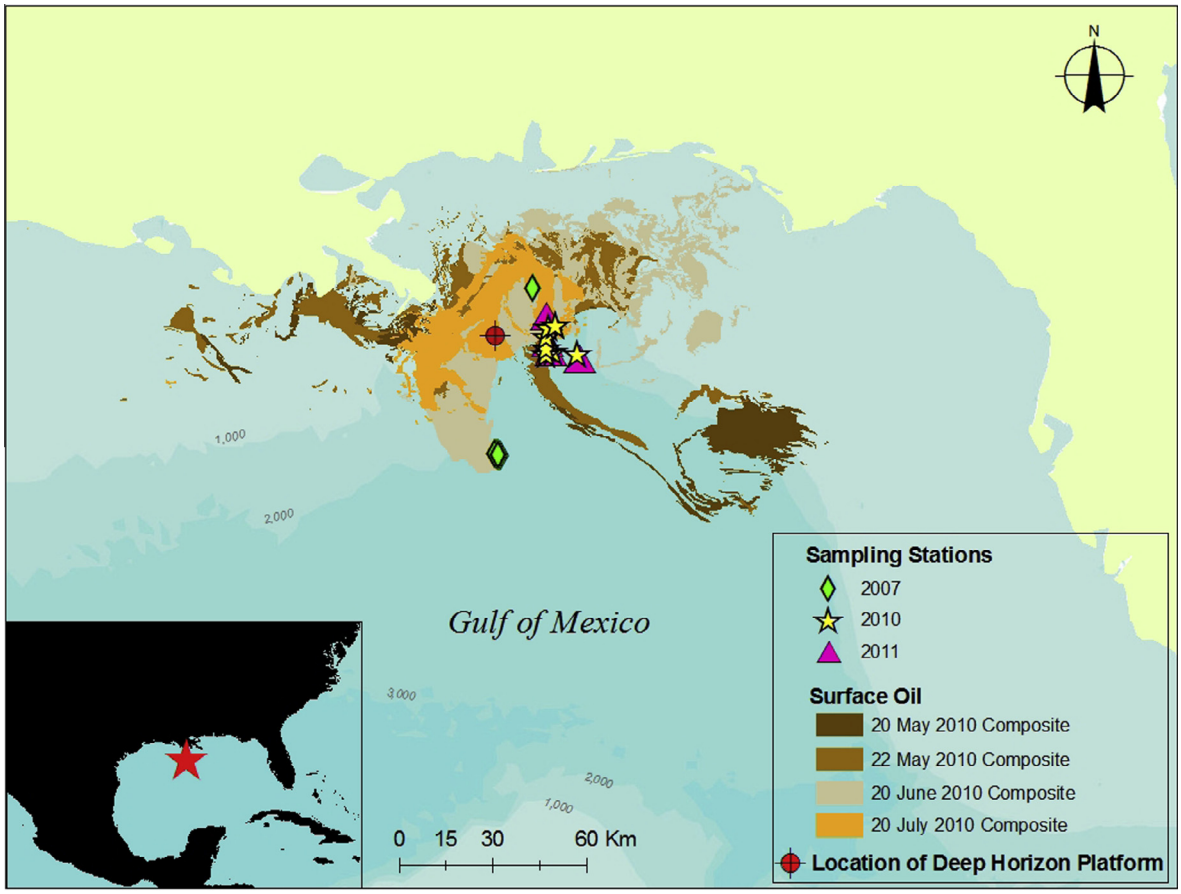


**Fig. 1.** Study area sampling locations in the vicinity of the Deepwater Horizon (DWH) in the Gulf of Mexico. Samples were collected in 2007, 2010, and 2011 in an area ranging from approximately 55.5 km to 117 km from the DWH. Hydrocarbon data are available to the public by the U.S. National Oceanic and Atmospheric Administration (NOAA; http://gomex.erma.noaa.gov/erma.html#x=88.25810&y=27.03211&z=6&layers).

$\delta^{15}$N). Each sample (200–800 μg) was weighed on a Mettler-Toledo precision micro-balance, encapsulated in tin foil and loaded into a Costech Technologies Zero-Blank Autosampler prior to combustion at 1050 °C in a Carlo-Erba NA2500 Series-II Elemental Analyzer (EA) coupled in continuous-flow mode to a Finnigan Delta Plus XL isotope ratio mass spectrometer (IRMS) at the University of South Florida College of Marine Science. Stable isotopic compositions are expressed in per mil (‰) using delta notation: e.g. $\delta^{15}N = (R_{sample}/R_{standard}) - 1] \times 1000$; where $R = 15\ N/14\ N$. C:N measurements were calibrated and $\delta^{15}$N and $\delta^{13}$C measurements were normalized to the AT-Air and VPDB scales, respectively, using NIST 8573 and NIST 8574 L-glutamic acid Standard Reference Materials. Analytical precision, estimated by replicate measurements of a lab working standard (NIST 1577b Bovine Liver SRM, $n = 32$), is ±0.17‰ $\delta^{15}$N, 0.10‰ $\delta^{13}$C, and ±0.33 C/N.

Data were examined to determine if lipids could have significantly impacted the stable isotope results. A large portion of samples with C/N > 4 are likely affected by the presence of lipids (Post, 2002). However, the results (Table 1) showed that lipids did not significantly impact the isotope ratios; therefore, no lipid extraction or acidification methods were necessary.

### 2.5. Hydrocarbons in water

To assess potential exposure to hydrocarbons by mesopelagic fishes, we used hydrocarbon data available to the public from the U.S. National Oceanic and Atmospheric Administration (NOAA) as part of their Natural Resource Damage Assessment for the GOM (http://www.gulfspillrestoration.noaa.gov). NOAA performed hydrocarbon analyses using standard U.S. Environmental Protection Agency (EPA) methods for sample preparation and cleanup (Methods 3500 and 3600). The EPA analytical methods used were 8270 (alkylated polycyclic aromatic hydrocarbons), 8260 (paraffins, isoparaffins, aromatics, naphthalenes and olefins), and 8015 (saturated hydrocarbons). We used NOAA data results and calculated total hydrocarbons (the sum of individual volatile, aromatic, paraffin and saturated hydrocarbons) to examine the presence of oil over the four months before fish and shrimp samples were collected (May–August 2010) in an area of approximately 16,000 km$^2$, which included all the collection sites. Data were pooled together over 100 m depth intervals to examine total hydrocarbons in the water column.

### 2.6. Statistical analysis

Analysis of covariance (ANCOVA) was used to compare isotopic values of fishes and shrimp. Standard length was used as a covariate to control for variations in the isotopic values due to fish or shrimp size. A post hoc Tukey test was used to determine differences between years. In some cases, standard lengths were not available. In those cases, either 1) regression equations were used to convert mass to standard length (Burghart, 2006; Lancraft et al., 1988; Torres and Donnelly, unpublished data; Sutton, unpublished data) and an ANCOVA was performed, or 2) if mass information was also not available, a basic analysis of variance was used. If samples were collected in two years only, a *t*-test was used for

**Table 1**
Stable isotope values (mean ± standard error) for 13 species of mesopelagic fish and shrimp collected in the vicinity of the Deepwater Horizon in 2007, 2010 and 2011.

| Family/Species | 2007 | | | | 2010 | | | | 2011 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | $\delta^{13}C$ | $\delta^{15}N$ | C/N | N | $\delta^{13}C$ | $\delta^{15}N$ | C/N | N | $\delta^{13}C$ | $\delta^{15}N$ | C/N |
| Myctophidae | | | | | | | | | | | | |
| *Ceratoscopelus warmingii* | | | | | 8 | −19.39 ± 0.14 | 8.68 ± 0.36 | 4.09 ± 0.10 | 15 | −19.48 ± 0.09 | 7.66 ± 0.21 | 4.03 ± 0.09 |
| *Diaphus dumerilii* | 17 | −19.65 ± 0.17 | 8.61 ± 0.31 | 4.12 ± 0.05 | 18 | −19.34 ± 0.12 | 9.23 ± 0.39 | 4.21 ± 0.10 | | | | |
| *Lampanyctus alatus* | 4 | −19.34 ± 0.19 | 7.81 ± 0.57 | 4.11 ± 0.06 | 4 | −19.42 ± 0.24 | 8.67 ± 0.40 | 3.99 ± 0.06 | 9 | −19.61 ± 0.11 | 8.22 ± 0.07 | 3.95 ± 0.15 |
| *Lepidophanes guentheri* | 17 | −18.76 ± 0.11 | 6.63 ± 0.40 | 4.01 ± 0.06 | 5 | −18.99 ± 0.25 | 8.28 ± 0.67 | 4.06 ± 0.11 | 7 | −19.20 ± 0.05 | 8.08 ± 0.25 | 3.73 ± 0.08 |
| Gonostomatidae | | | | | | | | | | | | |
| *Gonostoma elongatum* | 22 | −18.97 ± 0.09 | 8.14 ± 0.21 | 3.98 ± 0.07 | 30 | −19.24 ± 0.08 | 9.08 ± 0.105 | 4.03 ± 0.64 | 10 | −19.19 ± 0.14 | 8.82 ± 0.21 | 3.97 ± 0.17 |
| *Argyropelecus aculeatus* | 11 | −18.67 ± 0.13 | 8.50 ± 0.166 | 3.83 ± 0.08 | | | | | 11 | −18.80 ± 0.06 | 8.91 ± 0.23 | 3.87 ± 0.05 |
| *Argyropelecus hemigymnus* | 6 | −18.73 ± 0.09 | 7.93 ± 0.46 | 3.82 ± 0.11 | 4 | −18.44 ± 0.18 | 9.61 ± 0.48 | 4.04 ± 0.12 | 4 | −18.77 ± 0.89 | 8.68 ± 0.24 | 3.76 ± 0.07 |
| Stomiidae | | | | | | | | | | | | |
| *Eustomias* sp. | | | | | 1 | −18.60 | 5.41 | 4.03 | 3 | −18.89 ± 0.57 | 7.43 ± 0.66 | 3.82 ± 0.12 |
| Chauliodontidae | | | | | | | | | | | | |
| *Chauliodus sloani* | 7 | −18.45 ± 0.14 | 8.66 ± 0.39 | 3.79 ± 0.06 | 2 | −19.23 ± 0.00 | 7.31 ± 0.62 | 3.79 ± 0.13 | 9 | −18.89 ± 0.07 | 8.94 ± 0.10 | 3.65 ± 0.06 |
| Penaeoidae | | | | | | | | | | | | |
| *Gennadas* sp. | | | | | 12 | −18.54 ± 0.09 | 7.16 ± 0.15 | 3.52 ± 0.32 | 10 | −18.47 ± 0.11 | 7.23 ± 0.41 | 3.54 ± 0.04 |
| *Gennadas valens* | 5 | −18.52 ± 0.17 | 6.96 ± 0.38 | 3.84 ± 0.17 | | | | | | | | |
| Caridea | | | | | | | | | | | | |
| *Acanthephyra purpurea* | | | | | 12 | −18.40 ± 0.10 | 7.92 ± 0.17 | 3.98 ± 0.06 | 10 | −18.39 ± 0.12 | 7.59 ± 0.17 | 3.64 ± 0.06 |
| *Acanthephyra* sp. | 1 | −18.12 | 8 | 3.58 | | | | | | | | |
| *Oplophorus gracilirostris* | 4 | −18.25 ± 0.09 | 7.71 ± 0.16 | 3.82 ± 0.06 | 5 | −18.76 ± 0.13 | 8.15 ± 0.31 | 3.79 ± 0.08 | 8 | −18.55 ± 0.13 | 8.15 ± 0.28 | 3.65 ± 0.09 |
| *Systellaspis debilis* | 5 | −18.79 ± 0.42 | 5.99 ± 0.19 | 4.02 ± 0.21 | 12 | −17.92 ± 0.14 | 7.11 ± 0.22 | 3.66 ± 0.04 | 6 | −18.19 ± 0.09 | 7.22 ± 0.13 | 3.57 ± 0.07 |
| Total | 99 | | | | 113 | | | | 102 | | | |

the analysis. All data were analyzed for normality and homogeneity of variance using the Kolmogorov–Smirnov and Spearman rank tests. Data that failed normality or equal variance tests were analyzed with ANOVA on the Ranks and the post hoc Dunn's test. A *p*-value equal to or less than 0.05 was the cut-off for statistical significance.

An ANCOVA was used to elucidate whether the $\delta^{13}C$ depletion was due to the presence of oil in the water column or to the assimilation and incorporation of oil-derived C by resident fauna (Graham et al., 2010). The prediction was that any subdermal oil intrusion into muscle tissues of the fishes or shrimps due to exposure to oil-contaminated water would yield anomalously high C/N values (Graham et al., 2010). Thus, we compared the regression plots of the relationship between $\delta^{13}C$ and C/N for a given species among years using an ANCOVA. For significant overall model differences, post-hoc multiple comparisons were performed using the Bonferroni adjustment (Huitema, 2011).

Isotope data were reported as mean ±1 standard error. Statistical analysis was performed using SPSS 20.0 and Statistica 10 (StatSoft Inc.).

## 3. Results

### 3.1. Hydrography

Representative temperature and salinity data acquired in eight CTD casts done during the 2010 and 2011 research cruises are shown in Fig. 2. Overall, temperature varied between 5.22 °C and 9.01 °C at depths between 500 m and 1000 m; very little variation occurred between 1000 m and 1500 m (temperature range 5.22–5.44 °C). Salinity also varied little within and between cruises, remaining between 35.0 and 35.7 at depths ranging from 500 m to 1500 m. The overall observed patterns were similar to the ones reported in the area in previous years (Ross et al., 2010). The dominant physical and biological features of the GOM have been summarized in other papers (Burghart, 2006; Camilli et al., 2010; Ross et al., 2010).

### 3.2. Stable isotopes and hydrocarbons

Stable isotope analysis was done on 314 tissue samples corresponding to nine species of fish (four families) and six species of shrimp (one family; Table 1). However, statistical comparisons were only possible on seven species of fish and two species of shrimp. Of those, two species of fish and one species of shrimp showed no significant change in $\delta^{13}C$ among years (Table 2). Additionally, three species of fish and one species of shrimp showed no significant changes in $\delta^{15}N$ among years (Table 2).

Two high-level mesopelagic fish predators exhibited differences in stable isotope signatures before and after the oil spill. In 2010, the year of the oil spill, the bristlemouth fish *Gonostoma elongatum* showed a significant depletion in $\delta^{13}C$ and a significant enrichment in $\delta^{15}N$ (Table 2). In the case of $\delta^{13}C$, no significant differences were found between 2010 and 2011, although in 2011 the average values showed less depletion in $\delta^{13}C$ and less enrichment in $\delta^{15}N$ (Table 1). The isotopic values were significantly different from each other between 2007 and 2011. The dragonfish *Chauliodus sloani* also showed a significant depletion in $\delta^{13}C$ in 2011 in comparison to 2007 (Table 2). No statistical comparisons were possible with

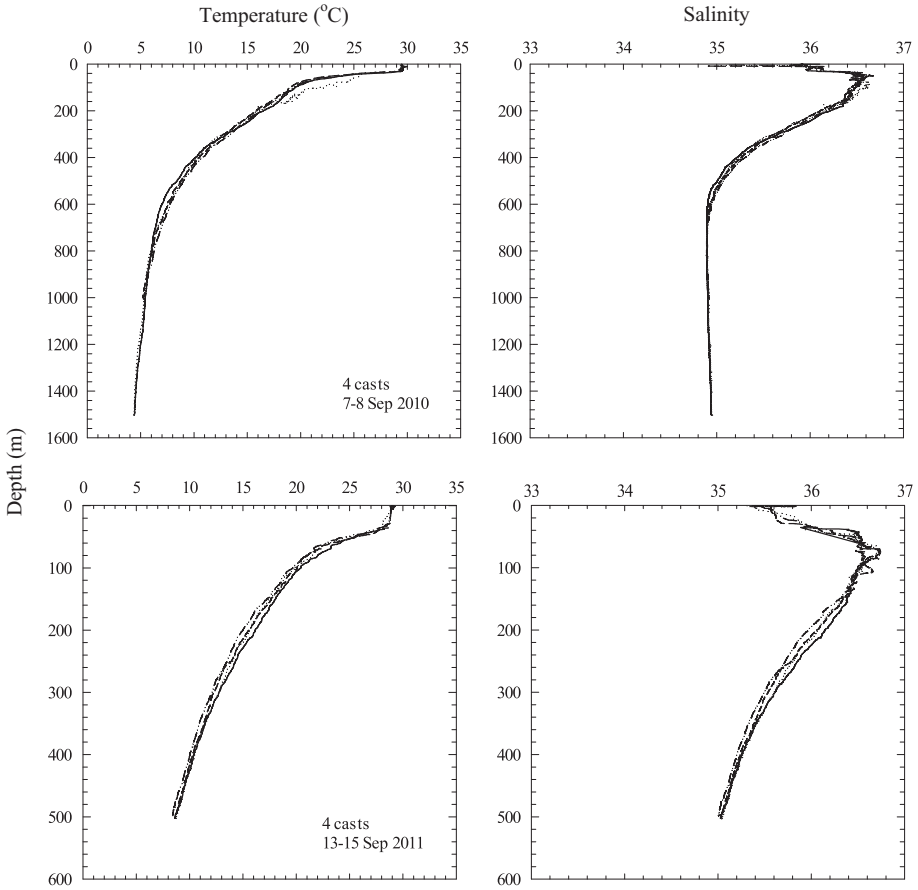


**Fig. 2.** CTD (Sea-Bird SBE 25) casts collected in the vicinity of the Deepwater Horizon, Gulf of Mexico, illustrating water temperature and salinity profiles.

**Table 2**
Summary of statistical results of temporal comparisons of bulk carbon stable isotope ($\delta^{13}C$) and bulk nitrogen stable isotope ($\delta^{15}N$) of fish and shrimp collected in the vicinity the Deepwater Horizon in 2007, 2010, and 2010. Numerical values of *t*-test (*t*), analysis of covariance/variance (F), and ANOVA on the Ranks (H) are included. Degrees of freedom (df) are shown inside parenthesis. Asterisk denotes a significant difference.

| | Years compared | | | $\delta^{13}C$ | | | | $\delta^{15}N$ | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 2007 | 2010 | 2011 | t/F/H (df) | *p* | Pairwise comparisons | *p* | t/F/H (df) | *p* | Pairwise comparisons | *p* |
| Fish | | | | | | | | | | | |
| *Argyropelecus hemigymnus* | ● | ● | ● | 0.66 (2,10) | 0.54 | | | 1.44 (2,10) | 0.28 | | |
| *Ceratoscopelus warmingii* | | ● | ● | 0.59 (21) | 0.56 | | | 2.64 (21) | 0.01* | | |
| *Chauliodus sloani* | ● | | ● | −3.10 (1,12) | 0.02* | | | −7.93 (1,12) | 0.76 | | |
| *Diaphus dumerilii* | ● | ● | | −1.48 (1,29) | 0.32 | | | −1.22 (1,29) | 0.11 | | |
| *Gonostoma elongatum* | ● | ● | ● | 6.43 (2,53) | 0.003* | 2007–2010 | 0.05* | 3.95 (2,53) | 0.02* | 2007–2010 | <0.01* |
| | | | | | | 2007–2011 | 0.36 | | | | |
| | | | | | | 2010–2011 | 0.90 | | | | |
| | | | | | | | | | | 2007–2011 | 0.08 |
| | | | | | | | | | | 2010–2011 | 0.74 |
| *Lampanyctus alatus* | ● | ● | ● | 1.38 (2,12) | 0.30 | | | 1.69 (2,13) | 0.18 | | |
| *Lepidophanes guentheri* | ● | ● | ● | 2.79 (2,25) | 0.07 | | | 6.57 (2,26) | 0.005* | 2007–2010 | 0.01* |
| | | | | | | | | | | 2007–2011 | 0.05* |
| | | | | | | | | | | 2010–2011 | 0.76 |
| Shrimp | | | | | | | | | | | |
| *Oplophorus gracilirostris* | ● | ● | ● | 2.93 (2,14) | 0.09 | | | 0.62 (2,14) | 0.55 | | |
| *Systellaspis debilis* | ● | ● | ● | 4.46 (2,20) | 0.02* | 2007–2010 | 0.02* | 6.88 (2,20) | 0.005* | 2007–2010 | <0.01* |
| | | | | | | 2007–2011 | 0.05* | | | 2007–2011 | 0.01* |
| | | | | | | 2010–2011 | 0.21 | | | 2010–2011 | 0.94 |

2010 due to the small number of samples collected that year ($n = 2$).

Changes in $\delta^{15}N$ were significantly different not only in *G. elongatum,* noted above, but also in the lanternfishes *Lepidophanes guentheri* and *Ceratoscopelus warmingii* (Table 2). The caridean shrimp *Systellaspis debilis* showed a different stable isotopic pattern than the one observed in the fishes. In those three species, $\delta^{15}N$ was enriched in 2010, slightly decreasing in 2011 (Table 1). *S. debilis* was significantly enriched in $\delta^{13}C$ in 2010 and 2011 in comparison to 2007 (Table 2); however, in 2011, the $\delta^{13}C$ was slightly less enriched, and the values appear to be dropping to the level observed in 2007 (Table 1). $\delta^{15}N$ was significantly enriched in 2010 and 2011 but no significant relationship between $\delta^{13}C$ and C:N was found ($F(2, 19) = 3.07$, $p = 0.07$).

## 4. Discussion

The $\delta^{13}C$ value of pure DWH oil (−27) is significantly more depleted than that observed in the pelagic specimens examined here ($\delta^{13}C$ range −18 to −21; a difference of about 30%). The only possible mechanism for introduction of oil-derived carbon is either through ingestion of contaminated prey (cf. Graham et al., 2010) or in the case of fishes, accidental ingestion into the gut as part of the drinking required for osmoregulation. The structure of the gut and the mechanics of water absorption make it unlikely that oil derived carbon would do anything but pass through the gut, making ingestion of contaminated prey the most likely route for oil-based carbon to be incorporated into the protein of the fish's muscle. Likewise, in the case of Crustacea, ingestion of contaminated prey is the only realistic path. The questions that remained unanswered were the number of contaminated prey items that would be required to cause significant excursions in the $\delta^{13}C$ of the fish muscle with only a 30% initial difference, the strength of the carbon signal of carbon ingested by the prey, how efficiently the prey express that signal, and how long the fishes and crustaceans were exposed to that signal.

As noted previously, the 2010 depletion in $\delta^{13}C$ in the muscle tissues of *Gonostoma* and *Chauliodus* is most likely due to oil-derived C transferred through the ingestion of contaminated prey. Isotope turnover rates, i.e. how quickly the isotopic signature in a body changes following a dietary change in fish muscle varies from 18 to 100 days (Buchheister and Latour, 2010; McIntyre and Flecker, 2006; Weidel et al., 2011). This is well within the time frame of our sample collection, which happened 52 days after the wellhead was capped. Additionally, the significant depletion of $\delta^{13}C$ in two of the fish species a year after the oil spill occurred suggests that the light carbon entered and was retained in the food web. Other studies demonstrated that subsurface oil carbon was incorporated into the plankton food web and they suggested that the application of chemical dispersants accelerated microbial consumption of oil components (Graham et al., 2010). Those studies also generated strong evidence for oil carbon being present in species at least two trophic levels beyond prokaryotic consumers (Graham et al., 2010). The significant changes in $\delta^{13}C$ reported in our study were small ones at the isotopic level but the biological implications are unknown. Small changes could be due to a variety of reasons including differences in turnover rates according to age of the specimens (Matthews and Mazumder, 2008) and strength of the original signal of carbon ingested by the prey (more below).

Trophic shifts between years, as indicated by changes in $\delta^{15}N$, were observed in three species of fishes (*G. elongatum, L. guentheri* and *C. wamingii*). Generally, an increase in $\delta^{15}N$ by +3‰ suggests a step up in trophic level (Peterson and Fry, 1987), and this level of change was observed in some specimens of *L. guentheri*. Changes in trophic level may have been influenced by a scarcity of common prey items that forced fishes to change their diet. The diet of *L. guentheri* normally consists of about 50% copepods, with other food items being euphausiids, ostracods and fish (Hopkins and Gartner, 1992; Kinzer and Schulz, 1985; McClain-Counts, 2010; Peterson and Fry, 1987). Changes in $\delta^{15}N$ could also be related to the location of the study sites. Freshwater input from the Mississippi River, about 100 km from the collection sites, could have affected the isotope values of mesopelagic fish as has been reported for migratory species such as the king mackerel (*Scomberomorus cavalla*) in the GOM (Roelke and Cifuentes, 1997). Indeed, the plume of the Mississippi River was found to substantially influence the near surface transport of oil in 2010 (Kourafalou and Androulidakis, 2013). However, if the Mississippi River caused the temporally observed changes in isotope signatures, its effects would have been apparent in more species of fishes; yet, this was not the case. Therefore, diet composition was the most likely cause for enriched $\delta^{15}N$ in specimens of *L. guentheri*.

The diets of the fishes collected during our study are variable in terms of their preferred prey species; however, over 60% of the biomass consumed by myctophids and gonostomatids in the Gulf is made up of crustaceans (Hopkins et al., 1994) and the majority of midwater fishes are considered to be intermediate trophic level species in the zooplanktivore guild. Other isotope data have indicated that midwater fishes have a zooplanktivorous diet and that they occupy roughly one trophic level above zooplankton taxa (McClain-Counts, 2010; Rau et al., 1991). Diet analyses show that *G. elongatum* feeds primarily on the copepod *Pleuromamma* spp. with ostracods contributing substantially to the diet in early juvenile stages and euphausiids becoming more important in the larger sizes (Hopkins et al., 1996; Lancraft et al., 1988; McClain-Counts, 2010). As a result, during different times in its life, the species may occupy two different trophic guilds despite consuming similar taxa (McClain-Counts, 2010). On the other hand, *C. sloani* is specialized for a predatory oceanic existence, and its diet consists primarily of large decapods and fishes (Hopkins and Sutton, 1998; McClain-Counts, 2010), and thus, it has been classified in the piscivory guild. *C. sloani* has asynchronous migrations and it appears that only hungry individuals migrate to the epipelagic zone (Sutton and Hopkins, 1996).

The ingestion of carbon-depleted prey occurred either because the vertical distribution of mesopelagic fishes and their prey overlapped with regions of hydrocarbon concentration in the water column (Fig. 3), because fishes ingested contaminated prey, or because contaminated food prey moved to the fishes. In contrast to the animals that exhibited carbon-depletion, those fishes and shrimps that showed no changes in isotope signature had not ingested contaminated prey or did not ingest enough over a long enough period of time for the signal to show up in muscle tissues. The vertical migration of the study species and the relative movement of currents at daytime and night-time depths create a considerable shear both between species and between individuals of a species on a daily basis. Thus, the parcel of water used by individuals of a species for hunting varies considerably from night to night. The patchy nature of the oil plumes coupled with the vertical movement of the study species made encounters with contaminated prey episodic by nature. The finding that differences were observed at all is indicative of the pervasiveness and persistence of the subsurface plumes.

According to the hydrocarbon data from NOAA, there were two plumes of oil. The first one was below the water surface and ranged up to 600 m in depth. This depth stratum is in the middle of the vertical range of most of the GOM mesopelagic fauna. For instance, *G. elongatum* exhibits a strong diel migration in which individuals aggregate at depths ranging between 425–725 m during daytime, and at night, they migrate to the surface (25–325 m) (Fig. 3) (McClain-Counts, 2010; Ross et al., 2010). *C. sloani* exhibits an asynchronous diel vertical migration pattern and individuals are found between 450 and 750 m during day, and at either 100–200 or 500–600 m at night (Ross et al., 2010; Sutton and Hopkins,

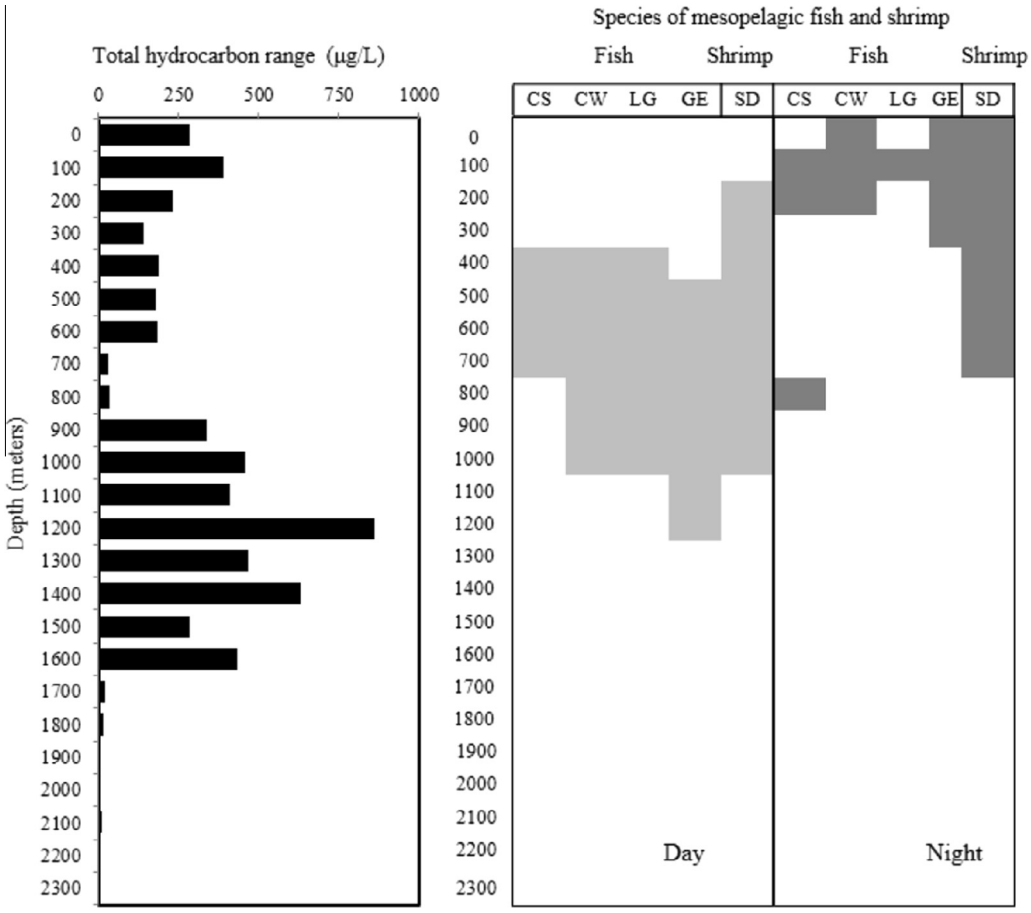


**Fig. 3.** Total hydrocarbon concentrations (µg/L) and diel vertical distribution of four species of mesopelagic fish and one species of shrimp collected in the vicinity of the Deepwater Horizon. The figure represents the distribution range of a given species and its presence/absence only. Fishes: CS: *Chauliodus sloani*, CW: *Ceratoscopelus warmingii*, LG = *Lepidophanes guentheri*, and GE = *Gonostoma elongatum*. Shrimp: SD = *Systellaspis debilis* (Felder and Camp, 2009; Gartner et al., 1987; Hopkins et al., 1989; Kinzer and Schulz, 1985; Lancraft et al., 1988). Hydrocarbon values correspond to the period of time from May to August 2010 in an area of approximately 16,000 km$^2$ around the sampling sites. Total hydrocarbon data are available to the public by the U.S. National Oceanic and Atmospheric Administration (NOAA; http://gomex.erma.noaa.gov/erma.html#x=88.25810&y=27.03211&z=6&layers).

1996) (Fig. 3). The overlapping distribution of hydrocarbons and specimens further supports a likely exposure of individuals to elevated concentrations of hydrocarbons before the collection date in early September 2010.

The vertical migration of fishes could also contribute to the vertical transport of depleted carbon. Under normal conditions, the vertical migrations of both zooplankton and micronekton contribute to the active flux of organic matter. They ingest organic material in the euphotic zone through nocturnal feeding, and release part of the assimilated material below the euphotic zone during the day as respiratory carbon and fecal matter (Hidaka et al., 2001). In addition, myctophid fecal matter has been suggested as a potential source of essential amino acids for deep-sea organisms (Hidaka et al., 2001). Myctophid fecal material could thus play a role as a downward transporter of the depleted oil carbon that was available in the upper 600 m of the water column.

All the mesopelagic fishes showing a significant change in their stable isotope composition are dominant species of the mesopelagic fauna, important predators and prey in the open waters of the GOM. For example, *G. elongatum* is not only highly abundant in the GOM (McEachran and Fechhelm, 1998), it is a dominant stomiiform species in the northern and equatorial Atlantic (Lancraft et al., 1988). *L. guentheri* is one of the top five non-*Cyclothone* spp. reported in the GOM (Hopkins and Lancraft, 1984; Ross et al., 2010).

The mesopelagic community of the GOM is one of the best described in the global ocean, but data are scanty with respect to animal growth rate and longevity. The best known are the myctophids, who have a life expectancy of one to two years depending on the species (Gartner et al., 1987), reproducing at the end of their lives. Likewise, the gonostomatid, *Gonostoma*, lives for about a year (Lancraft et al., 1988). No data exist on the decapods to our knowledge, but, based on years of sampling, it is believed that they also have a life expectancy of a year or less. Thus, individuals sampled in 2007 would have expired prior to the oil spill and an unknown fraction of the assemblage sampled in 2010 would have expired prior to 2011 as well. The main point of the 2007 data was to have a baseline pre-spill isotope signature for comparison with the individuals captured in 2010 and 2011. The baseline signature was presumed to have a variability typical of intermediate trophic level species, such that isotope signatures taken on the same species in different years at the same location would fall within the same 95% confidence limits unless subjected to environmental insult. No data are available addressing isotope signature variability over multiple years in the GOM mesopelagic fauna (or mesopelagic fauna anywhere to our knowledge) to allow us to support or refute this assumption. The 2007 data provided the best baseline for comparison.

Shrimp seem to respond differently than fish to oil exposure, although it is important to note that only one species of shrimp showed significant temporal changes. It is possible that some shrimp show little change in $\delta^{13}C$ when exposed to oil because they can metabolize petroleum hydrocarbons rapidly (Cox and Anderson, 1973). Yet, other crustaceans have shown chronic effects when exposed to fuel oil in laboratory settings (Stacey and Marcotte, 1987). In our study, *S. debilis* was significantly enriched in both $\delta^{13}C$ and $\delta^{15}N$ in the year of the oil spill and after. The $\delta^{15}N$ results strongly suggest a change in diet in *S. debilis* during and after the oil spill, but other than an ingestion of prey with a heavier isotope signature, the $\delta^{13}C$ results are harder to explain. *S. debilis* is the most abundant species of caridean shrimp in the region (Hopkins et al., 1989) and they play an important role in trophic-dynamics at the intermediate levels of the food web (Hopkins et al., 1994).*S. debilis* has a mixed diet of crustaceans, fishes, euphausiids, and chaetognaths (Hopkins and Sutton, 1998). They support upper trophic levels in the ecosystem by acting as food for midwater fishes, commercially important epipelagic fishes, and cephalopods (Hopkins et al., 1994). They are also strong vertical migrators, being found in the upper 300 m at night and below 500 m during the day (Hopkins et al., 1989). Thus, the implication is that prey switching occurred in *S. debilis*, resulting in a shift in its isotope signature. It may be the result of a favorable prey item (or several) that dropped in abundance due to oil-spill influence forcing the species to shift its diet.

It is important to recognize that a negative change in isotopic signature after the oil spill does not definitely rule out exposure. The Gulf of Mexico is a dynamic system. The most prominent circulatory feature in the eastern GOM is the loop current, which exhibits a varying northward penetration, sometimes influencing the study area, but most often turning east well south of it. There is little question that the loop current is a vehicle for transport of mesopelagic species into the Gulf from the Caribbean, and into the Sargasso Sea from the Gulf. The dominant myctophids in the GOM and the Sargasso Sea overlap considerably (Gartner et al., 1989). The complexity of the Gulf circulation, including eddy shedding from the loop current front, meanders, and considerable variability in its northward penetration mean that a steady state "conveyor belt" is unlikely.

All the species reported on in the present study are considered residents of the GOM in that they can be consistently captured, and usually in similar relative numbers, from year to year. The most reasonable assumption for the composition of GOM mesopelagic fauna, particularly in the northeastern Gulf at the time of the study, is a blend of residents with a small, variable component of recently transported fauna. The present study suggests that the mesopelagic community in the northeastern GOM was exposed to DWH oil at sublethal levels. The full extent of exposure and any large-scale lethal events with initial exposure are temporally out of reach. Monitoring for persistence of anomalous isotope signatures as well as for changes in community structure will tell the long-term story of the effects of the DWH oil spill on the pelagic biota.

## 5. Conclusions

Our data showing carbon isotope depletion in some of the mesopelagic fishes and shrimp support the findings of other studies indicating that depleted carbon was transferred into the food web of the GOM (Graham et al., 2010). Those studies showed effects on mesozooplankton (Graham et al., 2010) and coastal fishes (Whitehead et al., 2011), but this is the first study to demonstrate its effects in the intermediate trophic levels of the deep-water GOM. The vertical distribution of the study organisms overlapped with areas in which hydrocarbons were present and the transfer of depleted carbon probably occurred through trophic transfers. The affected species are some of the most abundant taxa of mesopelagic organisms in the region.

The open ocean community of the GOM in the vicinity of the DWH was episodically exposed to sub-surface plumes of oil over the four months of the spill itself and to any oil plumes that persisted in the Gulf after the well-head was capped. Mesopelagic fishes are not only prey for apex predators such as tuna and dolphin, they are also vertical vectors for oil-spill carbon because of their migratory habits. The finding that significant changes were observed in the stable isotope signature of several species of fishes indicating either incorporation of oil-spill carbon or changes in diet, suggest that the oil spill had begun to influence the character of the midwater community. In addition, the isotope data showed that sub-lethal effects were present, even though we were unable to collect sufficient data to speak to pre- and post-spill distribution and abundance. The open ocean has a diverse

pelagic community replete with commercially important apex predators such as bluefin tuna that spend much of their lives in the water a long way from shore. Oil spill effects can be obvious in those species that are easily observed e.g. in the air-breathing megafauna like seabirds, turtles, and dolphins. In contrast, the mesopelagic community is virtually invisible to anyone without a net, yet they feed many of the species we are familiar with. A catastrophic die-off in the mesopelagic fishes and shrimps of the open ocean would have reverberations up and down the trophic pyramid.

## Acknowledgments

This research was supported by a RAPID grant for oil spill research from the National Science Foundation to J.J. Torres and D. Hollander (OCE-1047693). We would like to thank C. Ames, S. Artebane, Heather Broadbent, Scott Burghart, Tara Casazza, Dante Fenolio, Lara Henry, Ralph Kitzmiller, Charles Kovach, Liane Marshman, Eloy Martinez, Erica Ombres, Ernst Peebles, A. Quattrini, A. Roa-Varon, Benjamin Ross, and the crews of the R/V *Weatherbird II* and R/V *Cape Hatteras* for laboratory, field, and logistical support. The 2010 and 2011 cruises aboard the R/V *Weatherbird II* were funded by support from the USF Office of Sponsored Research and the Florida Institute of Oceanography, largely resulting from the efforts of William Hogarth, Director of FIO. The 2007 fieldwork was supported by the Department of the Interior U.S. Geological Survey under Cooperative Agreement No. 05HQAG0009, subagreement 05099HS004 (to S.W. Ross, lead PI). Isabel Romero and Kathleen Watson were partially funded by C-image. Kerri Scolardi prepared the figure of the study area and David Jones provided helpful statistical advice.

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