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Change and Recovery of Coastal Mesozooplankton Community Structure During the Deepwater Horizon Oil Spill

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Corrigendum: Change and recovery of coastal mesozooplankton community structure during the Deepwater Horizon oil spill (2014 *Environ. Res. Lett.* 9 124003)

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In the original article, the reported values for river discharge in supplement 1 were incorrect. An error was found in our conversion from $ft^3\ s^{-1}$ to $m^3\ s^{-1}$. Correct values are provided in the revised table; the error did not change our overall findings, interpretations or conclusions.

Supplementary material 1:
Historical (2004 to 2009) monthly range (min–max) of environmental values compared to values observed during the oil spill year (2010). See table 2 for variables units and resolution.

	MAY		JUNE		JULY		AUGUST	
Variables	Historical	Oil spill	Historical	Oil spill	Historical	Oil spill	Historical	Oil spill
NAO	(−1.73–1.68)	−1.49	(−1.39–0.84)	−0.82	(−2.15–1.13)	−0.42	(−1.73–0.37)	−1.22
SOI	(−1.30–1.70)	1.50	(−1.40–1.00)	0.60	(−1.00–0.50)	3.00	(−1.70–1.70)	3.00
Wind speed	(3.74–5.41)	4.07	(2.70–3.40)	3.01	(2.22–3.44)	3.90	(2.24–3.71)	3.84
u-wind	(−2.99–1.12)	−1.54	(−1.13–1.94)	−1.00	(−1.01–1.18)	−0.97	(−1.15–0.70)	−0.37
v-wind	(−0.03–2.50)	1.51	(−0.09–2.01)	1.70	(0.41–1.83)	0.99	(−0.82–1.19)	0.61
Atmospheric pressure	(1013.67–1018.25)	1015.39	(1012.70–1017.03)	1015.94	(1014.9–1017.35)	1016.69	(1012.26–1016.69)	1013.63
Water temperature	(24.80–25.99)	26.40	(28.63–29.58)	30.18	(29.30–30.20)	30.53	(28.79–31.30)	30.74
River discharge	(252.85–3009.72)	2009.85	(210.82–2113.59)	802.13	(255.13–2709.25)	404.56	(201.22–1068.32)	321.96

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Change and recovery of coastal mesozooplankton community structure during the Deepwater Horizon oil spill

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Abstract

The response of mesozooplankton community structure to the Deepwater Horizon oil spill in the northern Gulf of Mexico was investigated using data from a long-term plankton survey off the coast of Alabama (USA). Environmental conditions observed in the study area during the oil spill (2010) were compared to historical observations (2005–2009), to support the contention that variations observed in zooplankton assemblage structure may be attributed to the oil spill, as opposed to natural climatic or environmental variations. Zooplankton assemblage structure observed during the oil spill period (May–August) in 2010 was then compared to historical observations from the same period (2005–2009). Significant variations were detected in assemblage structure in May and June 2010, but these changes were no longer significant by July 2010. The density of ostracods, cladocerans and echinoderm larvae were responsible for most of the differences observed, but patterns differed depending on taxa and months. Many taxa had higher densities during the oil spill year, including calanoid and cyclopoid copepods, ostracods, bivalve larvae and cladocerans, among others. Although this result is somewhat surprising, it is possible that increased microbial activity related to the infusion of oil carbon may have stimulated secondary production through microbial-zooplankton trophic linkages. Overall, results suggest that, although changes in zooplankton community composition were observed during the oil spill, variations were weak and recovery was rapid.

S Online supplementary data available from stacks.iop.org/ERL/9/124003/mmedia

Keywords: assemblage structure, planktonic communities, shallow pelagic ecosystems, hydrocarbon pollution

Introduction

On 22 April 2010, an explosion occurred on the Deepwater Horizon (DWH), a deep-water oil drilling platform off the coast of Louisiana (northern Gulf of Mexico), and thereafter released an estimated 780 000 m^3 of crude oil into the marine environment over a period of 85 days [1]. Approximately 25% of the released oil was either immediately recovered or burned at sea, while the remaining 75% was left to degrade in the marine environment, either naturally or enhanced by chemical dispersants [2]. Unlike accidental surface spills where most volatile components of the oil evaporate into the atmosphere, the release of oil at 1.5 km depth resulted in an extended submerged period, which allowed water-soluble portions to dissolve in the surrounding water column [3]. Over 1.7 million gallons of chemical dispersant were applied

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at the surface and at depth to emulsify the oil into small droplets and enhance bacterial degradation [4]. However, the widespread use of dispersants also increased exposure pathways of oil and dispersant to pelagic organisms, with yet largely unknown ecological consequences [5, 6].

The few studies that have addressed the impacts of the DWH oil spill on mesozooplankton suggested oil and dispersant impacted planktonic assemblages in the northern Gulf of Mexico. For example, Graham *et al* (2010) [7] and Chanton *et al* (2012) [8] used stable carbon isotope ($\delta^{13}C$) and radiocarbon ($\delta^{14}C$) tracers, respectively, to detect the introduction of oil from the DWH spill into the planktonic food web, presumably via microbial-zooplankton trophic linkages. Further, Almeda *et al* (2013) [6] reported increased mortality in field-collected mesozooplankton with increasing oil concentrations in mesocosm experiments, and that treatments with dispersant (either alone or with oil) resulted in the highest mortality. They also documented bioaccumulation of some polyaromatic hydrocarbons in mesozooplankton, which suggests these organisms may serve as a conduit for oil compounds to move up the food chain, as they are a major food source in pelagic environments. While these studies highlight pathways of exposure for mesozooplankton, no studies to date have examined the realized impact on mesozooplankton abundances and assemblage structure in the field [9].

Mesozooplankton provide a crucial link between primary producers and consumers within planktonic food webs. Many species (e.g., calanoid and cyclopoid copepods and nauplii) are the primary prey for larval fishes [10], and thus their availability and abundance have important fish recruitment implications. As such, information on zooplankton response to the DWH oil spill is critical for the estimation of the oil spill impacts on coastal open water ecosystems in the northern Gulf of Mexico [5]. The goal of this study is to examine variations in mesozooplankton community structure in response to the DWH oil spill, based on data from a unique, long-term plankton survey conducted within the impact region. Specifically, we (1) resolved potential changes in mesozooplankton assemblage structure during and shortly after the oil spill, as compared to historic, pre-spill data; and (2) quantified taxon-specific changes in abundance in response to the DWH event.

Material and methods

Field collections

All plankton samples were collected at two sites, stations T20 and T35, located approximately 20 km and 30 km south of Dauphin Island, respectively, as part of the Fisheries Oceanography of Coastal Alabama (FOCAL) plankton survey [11] (figure 1). Stations T20 and T35 were impacted by pulses of oil during the DWH spill, and were the same stations sampled by Graham *et al* (2010) [7]. Plankton samples were collected monthly during daytime hours using a Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS; Open Seas Instrumentation, Musquodoboit Harbor, Nova Scotia) with a 0.25 m^2 mouth opening. Full details on the BIONESS sampling protocols are provided in Hernandez *et al* (2011) [11] and Carassou *et al* (2012) [12]. In short, the BIONESS was fished obliquely from the surface to the bottom with a 0.202 mm mesh net, and then towed up the water column to collect depth-discrete samples using 0.333 mm mesh nets. For this study, only oblique samples that integrated the entire water column (approximately 1–18 m and 1–33 m depth at stations T20 and T35, respectively) using a 0.202 mm mesh net were used for analysis. Upon retrieval, net contents were rinsed, filtered on a 0.149 mm sieve, and preserved in a 5% borate-buffered formalin-seawater solution for 48 h, before being transferred to 70% ethanol in the laboratory. A total of 50 oblique plankton samples were collected before the oil spill (hereafter grouped as ‘historic samples’) between May and August 2005–2009 at station T20, and between May and August 2007–2009 at station T35 (table 1). The frequency of sampling was increased at T20 and T35 from monthly to twice-monthly during the oil spill (between May and August 2010), to detect possible changes in planktonic communities, resulting in a total of 38 samples collected during or shortly after the oil spill (table 1).

Zooplankton processing

Each sample was split twice using a Folsom plankton splitter, generating four aliquots, from which one was randomly selected for zooplankton processing. The contents of the quarter aliquots were poured into a graduated beaker and mixed for one minute with an aquarium air bubbler. After mixing, smaller plankton aliquots were removed using a Stempel pipette (1, 2, 5 or 10 ml). Suitable aliquot volumes were achieved when counts of at least 200 copepods and 200 non-copepod organisms were reached. Zooplankton were classified into one of 24 taxonomic groups and counted under a stereomicroscope.

Environmental data

A suite of climatic indices and environmental variables were compared between 2007–2009, pre-spill seasons, and 2010, oil spill season, to explore the possibility that variations in mesozooplankton assemblage structure may have varied in response to natural environmental and climatic sources of variations. Descriptions of data sources and processing are detailed in Carassou *et al* (2011) [13]. A total of eight environmental variables were gathered from the National Oceanic and Atmospheric Administration (NOAA) National Weather Service Climate Prediction Center [14], NOAA National Data Buoy Center (stations 42 007 and DPIA1 [15]), and the United States Geological Survey (USGS) websites [16, 17]. These variables described both large-scale climatic conditions (i.e., North Atlantic Oscillation and Southern Oscillation Indices) and local weather and water column factors (i.e., wind conditions, atmospheric pressure, river discharge, water temperature and salinity) (table 2). Large-scale climatic data were provided at monthly intervals. Other data on local weather and water column conditions were

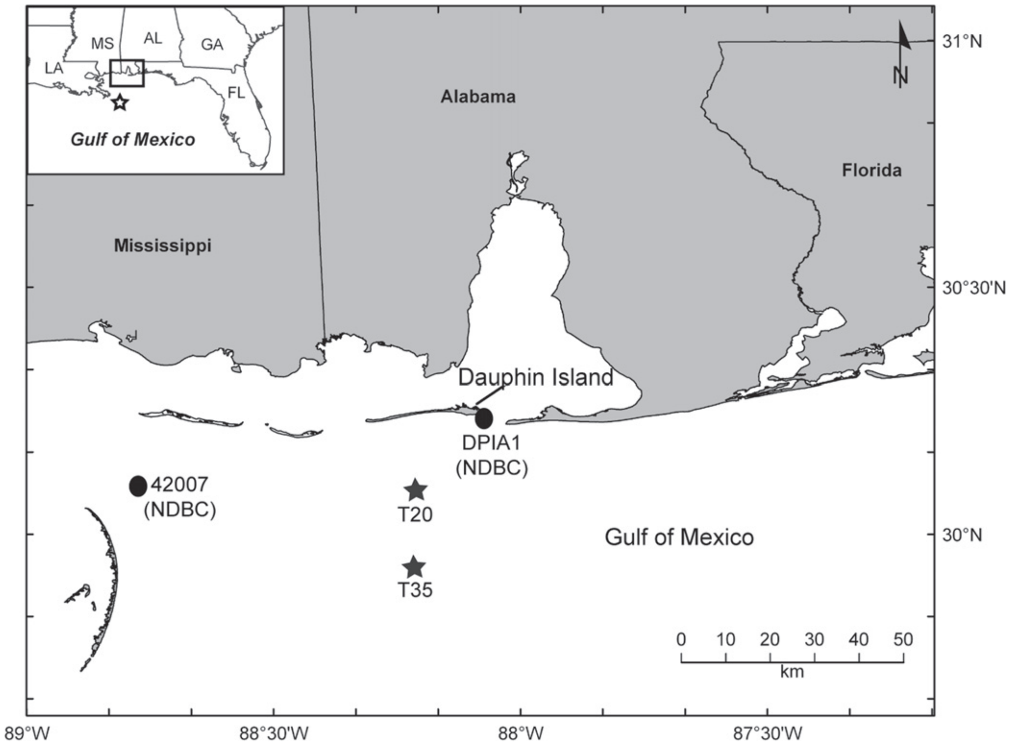

Figure 1. Sites of zooplankton sampling (stars) and environmental measurements (filled circles) in Alabama coastal waters. The extent of oil pollution in the study area during different months in 2010 is given in Graham *et al* (2010) [7]. The white star in the top-left insert indicates the approximate location of the DWH site.

Table 1. Number of oblique plankton samples (0.202 mm mesh) collected from May to August in 2010 (oil spill year) and during previous years (historic data) at sites T20 and T35 on the Alabama shelf. Locations for study sites are depicted in figure 1.

	T20		T35	
Months	2005–2009	2010	2007–2009	2010
May	9	4	5	3
June	7	10	5	4
July	7	5	5	4
August	7	4	5	4
Total	30	23	20	15

collected at hourly intervals. Daily river discharge data were collected from two USGS gaging stations in the Alabama River (Claiborne Lock and Dam [16]) and in the Tombigbee River (Coffeeville Lock and Dam [17]). Their sum was used as total freshwater discharge into Mobile Bay [18]. All environmental data were expressed as monthly averages for analyses.

Data analysis

Environmental conditions during the DWH oil spill period were compared with seasonal historic (pre-spill) conditions using normed Principal Component Analysis (correlation PCA [19]), in which historic data were used as the main observations, and data from the oil spill year as supplementary observations. This allowed for a visual assessment of environmental conditions during the DWH oil spill relative to the range of natural variability that historically characterized

Table 2. Climatic and environmental factors examined, with their respective units and sources. Measurement stations are depicted in figure 1.

Source	Variables	Unit
NOAA National Weather Service	El Niño Southern Oscillation Index (SOI)	—
Climate Prediction Center [14]	North Atlantic Oscillation index (NAO)	—
NOAA National Data Buoy Center	Water temperature	°C
Stations 42 007 and DPIA1 [15]	Wind speed (amplitude)	$m\ s^{-1}$
	Along-shore wind (u-wind)	$m\ s^{-1}$
	Cross-shore wind (v-wind)	$m\ s^{-1}$
	Atmospheric pressure	bar
USGS National Water Information	River discharge	$m^3\ s^{-1}$
System, Claiborne and Coffeeville	—	—
Lock and Dams [16, 17]	—	—

the area during this period of the year. Convex hulls were used to group observations by months, and the relative position of group centroids was used to assess if and how oil spill season conditions differed from historical conditions.

Zooplankton abundance data were standardized with the volume of water filtered, providing estimates of zooplankton density (number.m^{-3}) for each taxon in each sample. Density data were $\log(x+1)$ transformed before analysis to reduce the weight of dominant taxa relative to rare ones [20]. Zooplankton assemblage structure observed during the DWH oil spill at each sampling site was then compared with seasonal historical assemblage structure using Correspondence Analyses (CA [19]), in which historical data were used as the main observations, and data from the oil spill year as supplementary observations. This allowed for a visual assessment of zooplankton assemblage structure observed at the two study sites during the DWH oil spill relative to the range of natural variability which characterized these assemblages at this period of the year. Convex hulls were used to group observations by months, and the relative position of group centroids was used to explore if and how zooplankton assemblages differed during the oil spill as compared to historical observations.

Analyses of Similarity (ANOSIM) were used to statistically test for differences in the relative composition of zooplankton assemblages between historical and oil spill years by month and location. Values of R statistics were used to assess the strength of these differences, on a scale of 0 (indistinguishable) to 1 [21]. Analyses of Contribution to the Dissimilarity (SIMPER) were used to identify the taxa responsible for differences in assemblage composition. Variations in the mean density of those taxa, and of major zooplankton larval fish prey, i.e., calanoid and cyclopoid copepods, between historical and oil spill months were then individually tested through Mann–Whitney non-parametric tests [20].

Results

Environmental conditions

Approximately 54% of the variability in environmental conditions during May, June, July and August 2004–2009 was explained by the two first components of the PCA (figure 2). Historical observations from May were generally characterized by strong winds, high river discharge, low water temperature and weak along-shore winds. Conversely, along-shore winds were dominant, sea water was warm, and river discharge and wind speed were low in August (figure 2). June and July were characterized by intermediate conditions. Observations from 2010 (during DWH) fell within the range of historical values, as monthly centroids positioned within the convex hulls formed by historical values each month, with the exception of July (figure 2). In July 2010, values for SOI, wind speed and water temperature were indeed slightly higher than usual (supplementary material 1). However, the difference appeared minor with regards to the large variability characterizing historical values (figure 2; supplementary material 1). Overall, regional environmental conditions during the oil spill year were very similar to those in previous years.

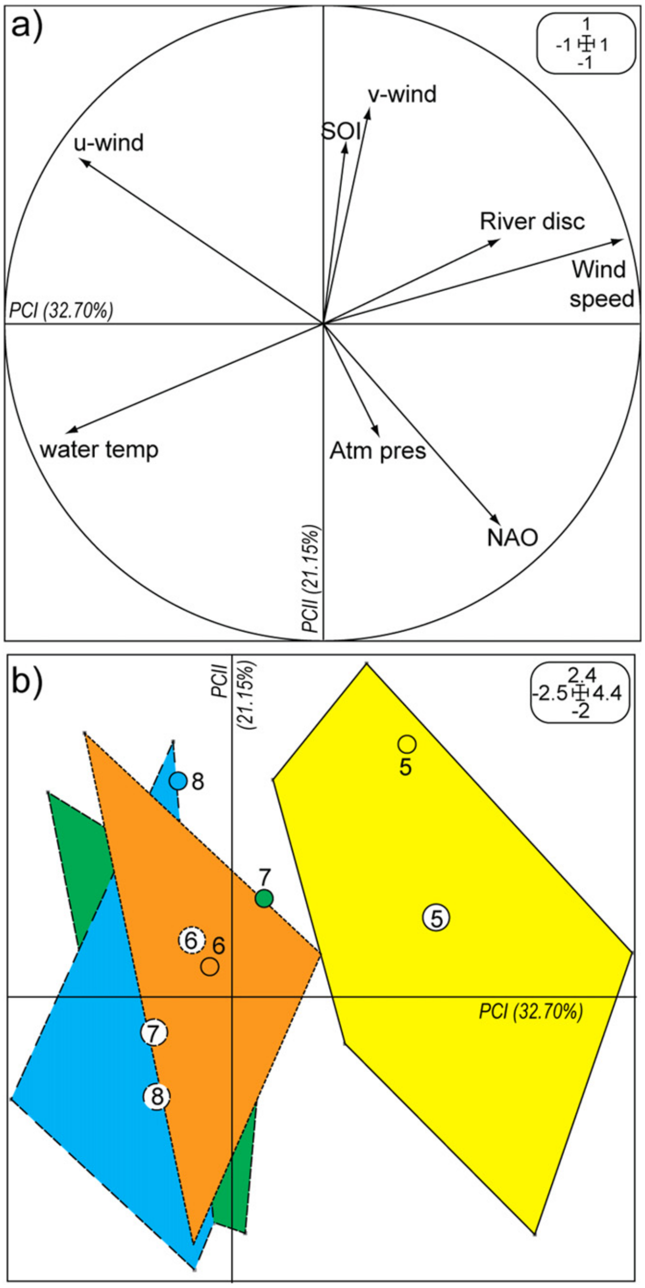

Figure 2. Principal component analysis (PCA) on climatic and environmental factors, with (a) correlations between variables, and (b) projection of monthly samples on the two first principal components (PCI-PCII), with historical data (2004–2009) used as main observations, and data collected during and shortly after the oil spill (2010) overlaid as supplementary observations. Monthly centroids are as follows: 5 = May, 6 = June, 7 = July, 8 = August, color-filled circles: oil spill year (2010), open (white) circles: historical data (2004–2009). Convex hulls show monthly variability characterizing historical samples, with black line contour and yellow shape = May, dotted line contour and orange shape = June, regular dashed line contour and green shape = July, irregular dashed line contour and blue shape = August. Scales are given in top-right rounded boxes. Variables are described in table 2.

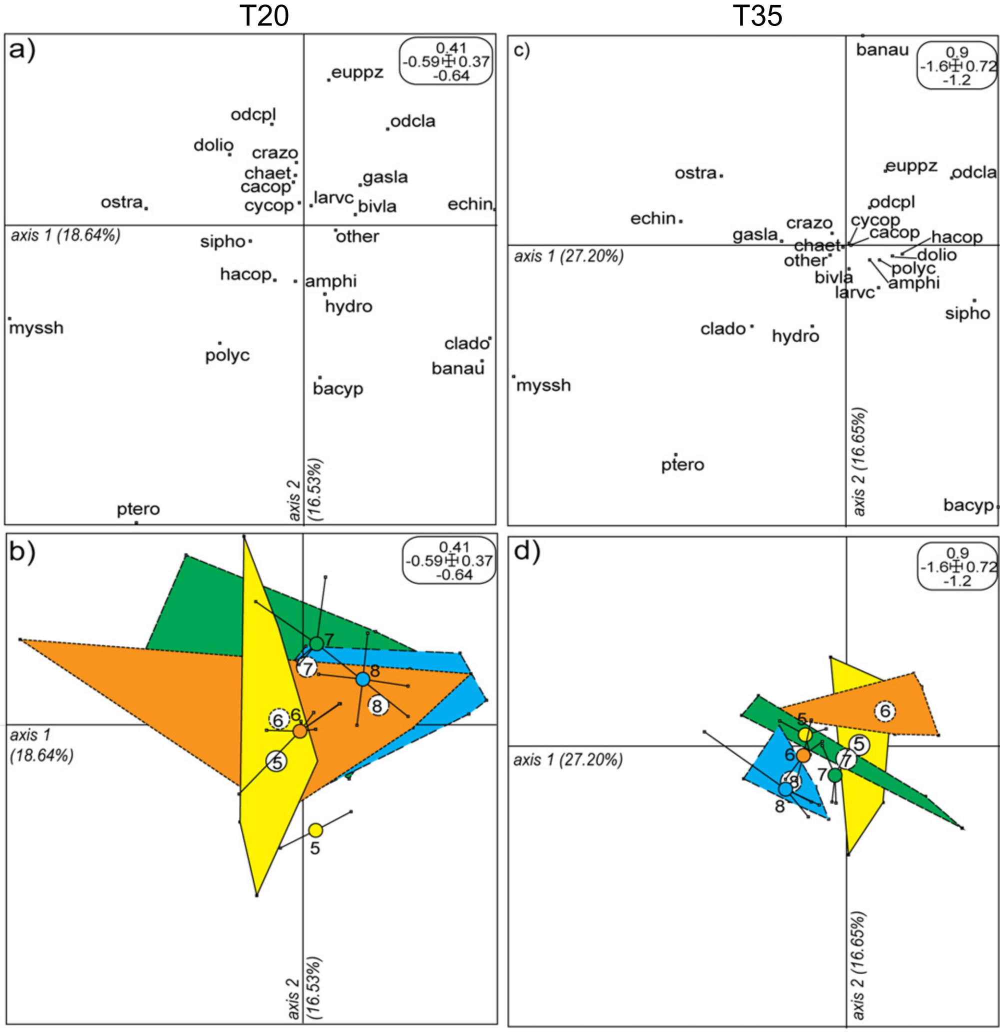

Figure 3. Correspondence Analysis (CA) on log(x + 1) transformed zooplankton densities observed at site T20 (a) and (b) and T35 (c) and (d), with historical data (2004–2009) used as main observations, and data collected during and shortly after the oil spill (2010) overlaid as supplementary observations. Top panels (a and c) are projections of variables (zooplankton taxa) on the two first axes of the CA. Bottom panels (b and d) are projections of observations (samples) on the same factorial plane. Months centroids are as follows: 5 = May, 6 = June, 7 = July, 8 = August, color-filled circles: oil spill year (2010), open (white) circles: historical data (2004–2009). Convex hulls show monthly variability characterizing historical samples, with black line contour and yellow shape = May, dotted line contour and orange shape = June, regular dashed line contour and green shape = July, irregular dashed line contour and blue shape = August. Scales are given in top-right rounded boxes. Taxa codes are given in supplementary material 2.

Zooplankton assemblages

Among the 24 taxa identified in zooplankton samples, calanoid and cyclopoid copepods, chaetognaths, cladocerans, doliolids, and ostracods were consistently the most abundant (supplementary material 2). The two first axes of the Correspondence Analysis explained approximately 35% and 44% of the variance in zooplankton assemblage composition at sites T20 and T35, respectively (figure 3).

At site T20, polychaetes and barnacle cyprids were more abundant in May, whereas euphausiid protozoea and decapod larvae were more abundant in July and August (figures 3(a) and (b)). The centroid for May 2010 fell outside of the convex hulls formed by historical data (figures 3(a) and (b)), suggesting a significant difference in assemblage composition. Conversely, centroids for June, July and August 2010 fell within convex hulls formed by historical samples, indicating little if no variation in assemblage composition during the oil spill year for these months.

At site T35, barnacle nauplii, euphausiid protozoea and decapod larvae were abundant in May and June, while mysid shrimps and pteropods were abundant in August (figures 3(c) and (d)). Centroids for May, June and July 2010 fell outside of the convex hulls formed by historic data, suggesting a probable change in assemblage composition during the oil spill. Conversely, the centroid for August 2010 fell within the convex hulls formed by historic values (figures 3(c) and (d)).

ANOSIM confirmed significant, albeit weak, variations in mesozooplankton assemblage composition during the oil spill years as compared to historic years. Mesozooplankton assemblages were different during the oil spill at both sites when all months were combined together ($R < 0.2$; table 3).

Table 3. Analyses of similarity (ANOSIM) comparing the composition of zooplankton assemblages observed from May to August between 2010 (oil spill year) and previous years (historical data) at stations T20 and T35 in the Alabama inner shelf. Corresponding number of observations are reported in table 1. When significant differences were detected ($P < 0.05$), the list of taxa contributing to at least 5% of the dissimilarity (SIMPER), are listed. Taxa codes are given in supplementary material 2.

	T20				T35			
	ANOSIM		SIMPER		ANOSIM		SIMPER	
Months	*R*	*P*	Taxa	Contrib (%)	*R*	*P*	Taxa	Contrib (%)
All combined	0.120	0.006	ostra	6.95	0.085	0.033	ostra	6.84
			clado	5.81			clado	6.42
			echin	5.50			echin	6.12
			polyc	5.43			dolio	5.85
			euppz	5.34			odcla	5.67
			hydro	5.05			hacop	5.08
			myssh	5.04				
May	0.410	0.015	ostra	6.80	0.600	0.036	dolio	10.22
			polyc	6.39			clado	9.54
			bacyp	5.56			echin	7.64
			ptero	5.47			myssh	7.56
			euppz	5.23			banau	6.43
			myssh	5.20			chaet	5.95
			amphi	5.10			larvc	5.72
			siphon	5.08				
			gasla	5.04				
June	0.318	0.002	ostra	7.76	0.688	0.008	ostra	11.47
			euppz	6.55			echin	7.86
			clado	6.25			odcla	6.83
			bivla	6.01			euppz	5.61
			odcla	5.97			bivla	5.37
			echin	5.74				
			banau	5.30				
			polyc	5.02				
July	0.150	0.117	—	—	0.194	0.135	—	—
August	0.222	0.094	—	—	0.225	0.127	—	—

Assemblages significantly diverged from historic values in May and June 2010 at both sites, but were not different in July and August (table 3). Differences in May and June 2010 were stronger at site T35 than at site T20, with the strongest difference detected at site T35 in June 2010 (table 3).

Taxa responsible for differences observed between oil spill and historical samples varied depending on sites and months. When all months were combined together, ostracods, cladocerans and echinoderms contributed the most to differences between historic and oil spill samples at both sites. When months were analyzed separately, barnacle nauplii, bivalve larvae, cladocerans, doliolids, echinoderms, euphausiid protozoea, mysid shrimps, ostracods, larval decapods and polychaetes often contributed to more than 5% of differences between oil spill and historic samples (table 3).

Significant differences in mesozooplankton densities were observed between the historic (pre-spill) period and the oil spill year, though patterns were highly variable both within and among taxa and stations. When the whole study period was considered, significant differences between historical and oil spill values were observed for barnacle nauplii, euphausiid protozoa, ostracods, polychaetes, calanoid and cyclopoid copepods at station T20, and for mysid shrimps and cyclopoid copepods at station T35 (table 4; figures 4 and 5).

When months were considered separately, most significant differences in densities of individual taxa were observed in June (table 4; figures 4 and 5), and in most instances, taxon densities were significantly higher during the oil spill year than in previous years (e.g., euphausiid protzoea, mysid shrimps, calanoid and cyclopoid copepods at station T20, and bivalve larvae, cladocerans, ostracods, calanoid and cyclopoid copepods at station T35). Mesozooplankton found in lower densities during the oil spill year included barnacle nauplii (June) and ostracods (May, June) at station T20, and bivalve larvae (August), doliolids (May), and other larval decapods (June) at station T35. No significant differences were found during any month for bivalve larvae and cladocerans at station T20, and barnacle nauplii and polychaetes at station T35.

Discussion

One of the major challenges in assessing DWH impacts on the northern Gulf of Mexico ecosystem is teasing apart variability in response to the oil spill and dispersant

Table 4. Mann–Whitney non-parametric tests of differences in mean densities between historical and oil spill observations for the ten taxa contributing the most to variations in the relative composition of zooplankton assemblages, and for dominant copepod groups (see figure 3 and table 3 for assemblage analysis). Monthly mean densities for the ten taxa and for calanoid and cyclopoid copepods are plotted in figures 4 and 5, respectively, and global means are given in supplementary material 2. When significant differences are detected ($P < 0.05$, in bold), the direction of change relative to historic conditions (2005–2009) is indicated by arrows.

Taxa	Month	T20			T35		
		W statistic	*P*		*W* statistic	*P*	
Barnacle nauplii	May–August	470.0	0.018	↓	146.0	0.893	
	May	18.0	1.000		1.0	0.072	
	June	58.0	0.014	↓	9.0	0.898	
	July	25.0	0.225		14.0	0.240	
	August	13.0	0.921		NA	NA	
Bivalve larvae	May–August	309.0	0.529		120.0	0.324	
	May	8.0	0.142		4.0	0.371	
	June	43.0	0.221		0.0	0.020	↑
	July	6.0	0.074		7.5	0.623	
	August	11.0	0.637		19.0	0.034	↓
Cladocerans	May–August	259.0	0.125		166.0	0.602	
	May	12.0	0.394		13.5	0.081	
	June	24.0	0.304		1.0	0.037	↑
	July	14.0	0.626		12.0	0.712	
	August	14.0	1.000		15.0	0.270	
Doliolids	May–August	284.0	0.278		198.0	0.112	
	May	24.0	0.395		15.0	0.032	↓
	June	35.0	1.000		14.0	0.389	
	July	10.0	0.256		11.0	0.903	
	August	2.0	0.030	↑	8.5	0.806	
Echinoderms	May–August	249.0	0.085		111.0	0.192	
	May	6.0	0.075		3.0	0.204	
	June	15.0	0.056	↑	2.0	0.062	
	July	15.0	0.741		12.0	0.709	
	August	21.0	0.218		12.0	0.713	
Euphausiid protozoea	May–August	181.0	0.003	↑	135.0	0.628	
	May	10.0	0.243		5.0	0.551	
	June	12.0	0.027	↑	11.5	0.806	
	July	10.0	0.256		13.0	0.540	
	August	12.5	0.850		4.0	0.171	
Mysid shrimps	May–August	258.0	0.109		74.5	0.001	↑
	May	19.0	0.931		0.0	0.017	↑
	June	6.0	0.005	↑	5.0	0.131	
	July	17.0	1.000		7.5	0.371	
	August	14.5	1.000		6.0	0.308	
Ostracods	May–August	546.0	<0.001	↓	95.5	0.071	
	May	34.0	0.017	↓	10.0	0.551	
	June	64.0	0.005	↓	0.0	0.019	↑
	July	18.0	1.000		7.0	0.539	
	August	20.5	0.216		11.0	0.903	

Table 4. (Continued.)

Taxa	Month	T20 U statistic	T20 P		T35 U statistic	T35 P	
Other decapods, larvae	May–August	299.0	0.413		145.0	0.880	
	May	22.0	0.583		6.0	0.766	
	June	28.5	0.555		20.0	0.020	↓
	July	23.0	0.417		0.0	0.018	↑
	August	1.0	0.018	↑	15.0	0.262	
Polychaetes	May–August	176.0	<0.001	↑	124.0	0.394	
	May	0.0	0.007	↑	9.0	0.766	
	June	21.0	0.184		12.0	0.713	
	July	4.0	0.035	↑	5.0	0.262	
	August	7.0	0.218		10.0	1.000	
Calanoid copepods	May–August	175.0	0.002	↑	131.0	0.538	
	May	10.0	0.246		9.0	0.766	
	June	18.0	0.107		2.0	0.066	
	July	6.0	0.074		16.0	0.178	
	August	1.0	0.018	↑	0.0	0.020	↑
Cyclopoid copepods	May–August	119.0	<0.001	↑	51.0	0.001	↑
	May	0.0	0.007	↑	0.0	0.037	↑
	June	0.0	<0.001	↑	0.0	0.020	↑
	July	9.0	0.194		2.0	0.066	
	August	9.0	0.395		8.0	0.713	

application from natural environmental ‘noise’. Mesozooplankton assemblage composition and abundance are often highly variable, largely a result of spatial and temporal variability in oceanographic conditions [22]. At seasonal scales, temperature, salinity and nutrient availability often drive primary and secondary production, thus factors such as freshwater discharge can play a significant role in structuring communities [23, 24]. Decadal patterns have also been observed, in particular related to warming trends that have impacted zooplankton distributions and phenology [25, 26]. These factors, as well as other anthropogenic factors already present in the Gulf of Mexico prior to the oil spill (e.g., seasonal hypoxia, algal blooms) need to be considered when weighing potential impacts.

Due to the highly variable nature of our sampling region, we cannot absolutely link observed changes in zooplankton assemblage structure with the DWH oil spill. However, our characterization of the Alabama shelf environment suggests that the May–August 2010 period was typical for the region. When environmental differences were observed between historic and oil spill periods (e.g., temperature and wind speed in July), the magnitudes of these differences were slight (supplementary material 1). Further, most of the significant differences in monthly assemblage structure were observed at our T35 station (figure 3), which is the furthest offshore, nearest to the DWH site, and experienced the greatest oil coverage [7]. Although there may be other community-structuring factors not examined in our analyses (e.g., abundance of zooplanktivores), we posit that our observed variations in zooplankton community composition were in response to the DWH oil spill, having eliminated many other probable factors.

The combination of analytical methods used in this study revealed some significant variations in zooplankton assemblage composition during the DWH oil spill on the Alabama shelf, particularly in May and June 2010, the period when the oil pollution was the most severe on the Alabama shelf [7]. A variety of taxa contributed in explaining these variations, with different patterns depending on taxa, sites and months. Overall, responses were taxon-specific, with no consistent pattern. Most changes observed within zooplankton assemblage structure were either weak in strength, or did not last more than a few months, with assemblages returning to the structure observed before the spill as soon as July 2010. These findings are consistent with previous studies which emphasized a low response of planktonic communities to other oil spills including the ‘Prestige’ spill in the Bay of Biscay [27], the ‘Sea Empress’ oil spill in the Irish Sea [28] or the ‘Tsesis’ spill in the Baltic Sea [29]. Further, these results are not surprising given the known patchy distribution of zooplankton assemblages, which increases natural variability associated with zooplankton abundance data, especially on relatively short, seasonal scales [30]. Overall, however, our analyses identified significant changes in zooplankton community composition that may be attributed to the DWH oil spill, as well as the taxa which responded most to the oil spill, and provided a preliminary estimation of the period of direct incidence of pollution on the structure of zooplankton communities in the region.

Although the depth-integrated structure of the assemblages did not change much, there may have been significant variations in vertical structure. There is evidence to suggest that zooplankton can detect and possibly avoid areas with high concentrations of hydrocarbons [5, 31]. Much of the oil in our sampling region was observed at the surface [32, 33],

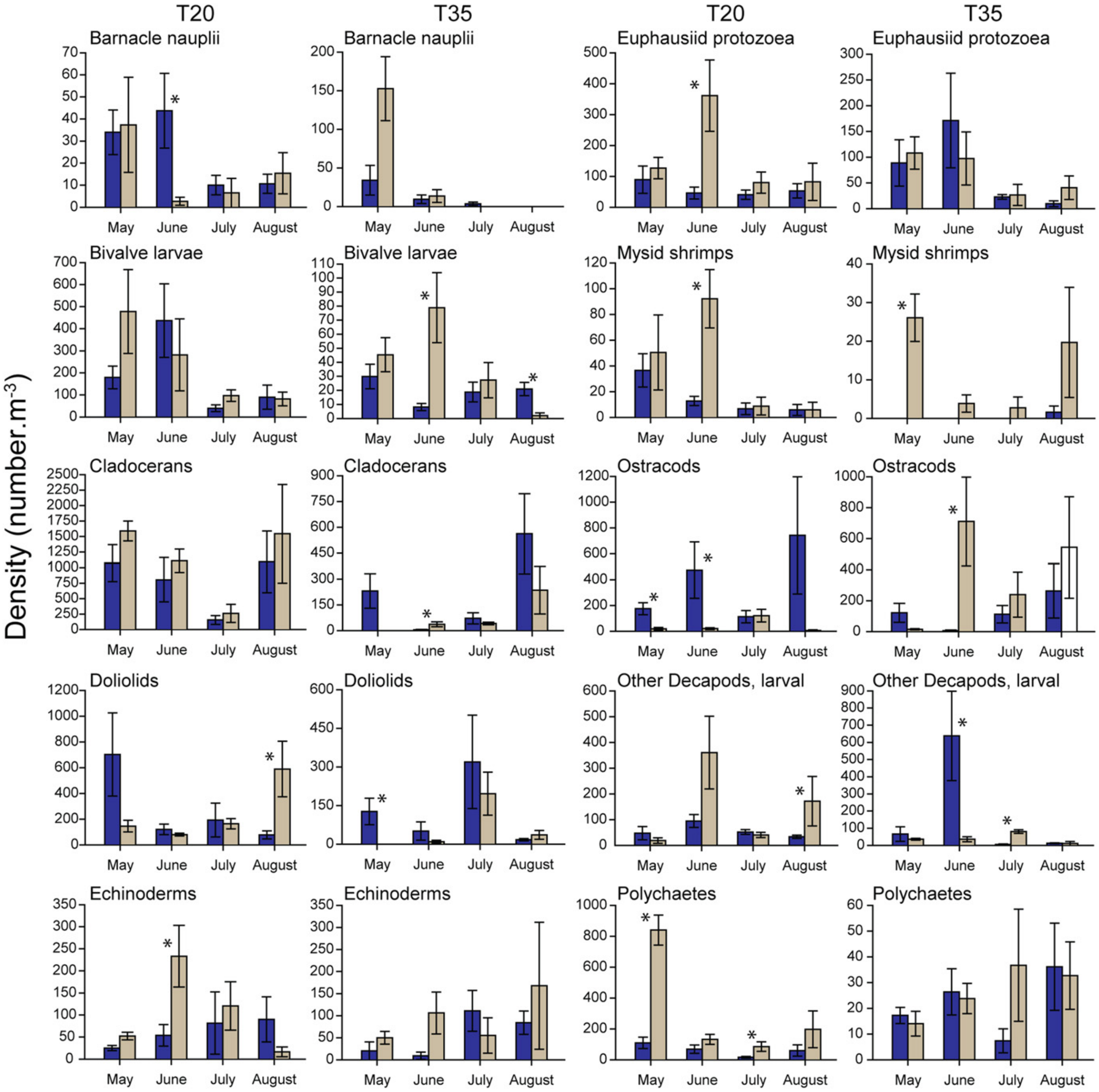

Figure 4. Monthly mean densities of ten taxa shown to contribute at least 5% of variations in zooplankton assemblage structure between historical (2004–2009) and oil spill (2010) samples in two sites from coastal Alabama. Blue bars represent historical values while gray bars are values observed during the oil spill season. Error bars are standard errors. Results of taxa-specific tests are given in table 4. Asterisks indicate significant differences. Study sites are depicted in figure 1.

thus zooplankton may have migrated to deeper waters in response. Further, bottom hypoxic conditions were observed during the spill, presumably a result of bacterial breakdown of oil [34]. Previous observations from the Gulf of Mexico 'dead zone' suggest mesozooplankton also migrate to avoid hypoxic waters [35]. Therefore, if zooplankton were faced with the combined effect of surface hydrocarbons and bottom hypoxia, this may have effectively compressed the organisms into the middle water column. The present study is based on oblique tows, and thus cannot address these hypotheses; however, depth-discrete samples from the FOCAL survey are being processed to examine zooplankton vertical behaviors during the oil spill.

Our study suggests that many zooplankton taxa were present in significantly higher abundances during the oil spill period relative to historic observations, a result that contradicts expectations of higher mortalities based on laboratory responses to contamination [6] and field surveys in the wake of other oil spills, such as the 1979 Ixtoc-1 oil spill in the southern Gulf of Mexico [36]. One possible explanation is

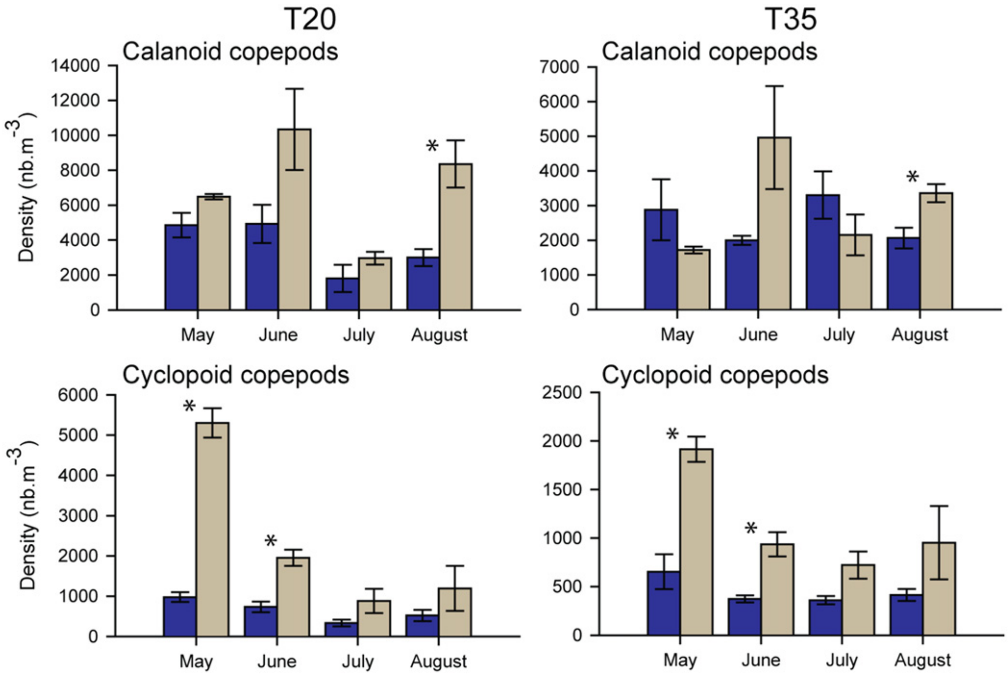

Figure 5. Monthly mean densities of major larval fish prey, i.e., calanoid (top) and cyclopoid (bottom) copepods between historical (2004–2009) and oil spill (2010) samples in two sites from coastal Alabama. Blue bars represent historical values while gray bars are values observed during the oil spill season. Error bars are standard errors. Results of taxa-specific tests are given in table 4. Asterisks indicate significant differences. Study sites are depicted in figure 1.

that the zooplankton population increased in response to elevated primary productivity (i.e., bottom-up control). Satellite measurements after the spill provided evidence for elevated chlorophyll-a concentrations in the northeastern Gulf of Mexico [37]. However, this anomaly occurred only in August 2010, and was centered further offshore and to the east of our sampling region. Further, chlorophyll data collected during the oil spill at our two sampling locations (T20 and T35) varied little from June through July, and did not show evidence of bloom conditions [7], which suggests this hypothesis is not a likely explanation for increased abundances for some taxa.

A second possible explanation for increased zooplankton abundances in the wake of the DWH oil spill is that management actions in response to the spill may have impacted the food web (including zooplankton abundances) via top-down control processes. At the peak of the DWH oil spill, approximately 229 270 km^2 of US federal waters in the Gulf of Mexico were closed to recreational and commercial harvesting [38]. This unprecedented release of fishing pressure could have resulted in cascading indirect effects [39]. For example, large piscivores released from fishing mortality likely increased in abundance (and size), and subsequently exerted greater predation pressure on smaller, zooplanktivorous fishes, thus releasing zooplankton populations. Estimates of DWH impacts on adult fish abundances are lacking particularly for shelf and offshore species, therefore the relative importance of bottom-up and top-down controls in food webs after the oil spill remain unknown.

A third possible explanation is that the higher abundances of some zooplankton may be attributed to an increase in the abundance and activity of oil-degrading bacteria in response to oil pollution in the water column [40], which presumably enhanced microbial-zooplankton trophic linkages, and therefore contributed in stimulating secondary production, as suggested by Graham *et al* (2010) [7] and Chanton *et al* (2012) [8]. However, other zooplankton taxa had lower densities during the oil spill period. These contrasting responses might be attributable to multiple causes that are difficult to disentangle, such as species-specific resistance to oil pollution, predation rates, and competitive advantages in feeding [41].

Our field-based observations of zooplankton further highlight the disconnect between expectations based on organismal responses to the DWH oil spill versus natural populations [42]. For example, numerous exposure studies on small coastal fishes (primarily *Fundulus grandis*) suggest negative impacts on an individual level [43, 44, 45], however field observations from coastal habitats suggest fish population abundances were stable, or in some instances greater, after the oil spill [42, 46]. There is also evidence to suggest that commercially important shrimp species (*Farfantepeneus aztecus* and *Litopeneus setiferus*) from impacted areas increased in abundance after the spill, and mean size of shrimp was unchanged, even though previous lab studies suggest decapods are negatively impacted by contaminants present in oil [47]. Compensatory processes and complex interactions in marine ecosystems may lessen the overall impact of large disturbances at a population level [42], however as in the case of Pacific herring following the Exxon Valdez spill, latent effects may exist within populations, therefore continued biological monitoring in northern Gulf of Mexico ecosystem is advisable.

Conclusion

Our results indicate a significant but short-term impact of DWH oil spill on the structure of zooplankton assemblages in our study region. Although the recovery in assemblage structure to historic conditions was relatively rapid, such a change may have significant consequences on other components of shallow pelagic ecosystems. The feeding success of fish larval stages is indeed a crucial determinant of fish recruitment success and therefore fish year-class strength [48, 49]. Variability in the types and abundances of mesozooplankton prey, combined with taxon-specific feeding preferences, may have created short-term, 'match-mismatch' dynamics in the planktonic food web. While many of the mesozooplankton taxa were significantly more abundant during the oil spill period than in previous years, further work is needed to determine larval fish diet preferences with regards to these changes in mesozooplankton abundance and community structure, as well as subsequent larval fish growth and condition. Also, our analysis to date does not include information on the size-spectra of zooplankton, which may be more telling than abundances with regards to their availability to larval fish predators. These and other indirect effects of detected changes in the planktonic community structure need to be investigated in further detail before final conclusions can be drawn about the long-term effect of the DWH incident on fisheries production in the northern Gulf of Mexico.

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