1 Phytoplankton and the Macondo oil spill: A comparison of the 2010
2 phytoplankton assemblage to baseline conditions on the Louisiana Shelf.

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4 M.L. Parsons ^{a,*}

5 W. Morrison ^b

6 N.N. Rabalais ^b

7 R.E. Turner ^c

8 K.N. Tyre ^a

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10 ^a – Coastal Watershed Institute, Florida Gulf Coast University, 10501 FGCU Blvd South, Fort
11 Myers, FL 33965, United States

12 ^b – Louisiana Universities Marine Consortium, Chauvin, LA 70344, United States

13 ^c – Department of Oceanography and Coastal Sciences, Louisiana State University, Baton
14 Rouge, LA 70803, United States

15
16 * Corresponding author

17 Email address: mparsons@fgcu.edu (M.L. Parsons)

ABSTRACT

The Macondo oil spill was likely the largest oil spill to ever occur in United States territorial waters. We report herein our findings comparing the available baseline phytoplankton data from coastal waters west of the Mississippi River, and samples collected monthly from the same sampling stations, during and after the oil spill (May – October, 2010). Our results indicate that overall, the phytoplankton abundance was 85% lower in 2010 versus the baseline, and that the species composition of the phytoplankton community moved towards diatoms and cyanobacteria and away from ciliates and phytoflagellates. The results of this study reaffirm the view that phytoplankton responses will vary by the seasonal timing of the oil spill and the specific composition of the spilled oil. The trophic impacts of the purported lower abundance of phytoplankton in 2010 coupled with the observed assemblage shift remain unknown.

Keywords: Deepwater Horizon; Gulf of Mexico; phytoplankton; protozoans

Capsule: Phytoplankton biomass was 85% lower in 2010 versus baseline. The phytoplankton community moved towards diatoms and cyanobacteria and away from ciliates and phytoflagellates. Trophic impacts remain unknown.

1. Introduction

One unfortunate consequence of the extraction, transport, and refining of crude oil is the risk of accidental spillage into the environment and, in particular, into marine environments. Significant oceanic oil spills first began during World War I, with the commencement of transoceanic oil transport and the wartime targeting of commercial shipping (Albers, 1995). A large number of these oil spills adversely affected marine birds (Bourne, 1968). Compared to World War II, however, the spills in World War I pale in comparison. Michel et al. (2005) estimated that more than 75% of the 8569 documented shipwrecks (including 1583 tankers) were the result of World War II hostilities, and that they introduced 567 million to 4.5 billion gallons of oil into the oceanic environment. The environmental impacts of these WWII releases are undocumented.

The *Torrey Canyon* grounded off the coast of England in 1967, releasing 32 million gallons of oil (Smith, 1968). The public concern for such large oil spills grew after this event, leading to a significant increase in research on the fate and impacts of crude oil in the environment in the 1970s (Albers, 1995). As a result, a better understanding of the impacts of crude oil exposure on various marine organisms has been garnered (e.g., Peterson et al., 2003), particularly in cases where the local environment was already under study and baseline data were available before the oil spill (e.g., the *Tsesis*, *Florida*, and *Amoco Cadiz* spills; Teal and Howarth, 1984). Most of the documented impacts, however, were limited to coastal littoral and subtidal regions, with far less information gathered and analyzed on impacts to pelagic and planktonic organisms.

Despite the previous experiences and knowledge gained in earlier oil spills (including the *Exxon Valdez* in Prince William Sound, Alaska; Maki, 1991) and the significant efforts implemented to extract crude oil in the Gulf Mexico (Managi et al., 2005), the petroleum

industry, scientific community, and resource managers were under-prepared for the magnitude and complexity of the oil spill that occurred on April 20, 2010 in the northern Gulf of Mexico at the Macondo 252 production site. On this date, the *Deepwater Horizon* drilling rig exploded, resulting in the loss of eleven lives and the release of four million barrels (636 million L) of oil into the northern Gulf of Mexico over the next several months (Camilli et al., 2010). Oil was released at an average of 9.8+ million L of oil per day over an 84 day period (Chen and Denison, 2011). A legitimate concern is that the scale of this oil spill (likely the largest ever in U.S. territorial waters) has created a multitude of potentially catastrophic ecological impacts in the northern Gulf of Mexico for years to come.

The northern Gulf of Mexico harbors a highly productive coastal ecosystem, including the second largest U.S. fishery by weight (mainly Gulf menhaden, *Brevoortia patronus*), and the fifth largest by value (\$300–400 million per year; due primarily to the harvest of penaeid shrimps; de Mutsert et al., 2008). These substantial fishery yields are related (in part) to the large phytoplankton biomass generated by high nutrient loads supplied by the Mississippi River, primarily during the annual spring floods of the river (Lohrenz et al., 1997). The spring blooms are composed primarily of diatoms (Turner et al., 1998; Dortch et al., 2001), and are often dominated by the toxigenic genus, *Pseudo-nitzschia* (Dortch et al., 1997; Parsons et al., 1998; Parsons et al., 2013). Much of this phytoplankton biomass is consumed by grazers (Dagg, 1995), but phytoplankton biomass and zooplankton fecal pellets transport significant amounts of organic matter to the benthos (Dortch and Whitledge, 1992; Qureshi, 1995), fueling hypoxia in the calmer, warmer summer months (Rabalais et al., 2002, 2007). Phytoplankton growth rates can be high (up to 3 divisions day⁻¹; Fahnenstiel et al., 1995), but can be limited for diatoms by silica limitation (Dortch et al., 2001). A reduction in diatom biomass as a result of silica

limitation can cascade to higher trophic levels, for example causing a reduction in copepod biomass (Turner et al., 1998). In summary, research to date has demonstrated that diatoms dominate the coastal Louisiana phytoplankton assemblage (primarily in the spring months), and support higher trophic levels. When diatom growth is suppressed (e.g., in response to silica limitation), other phytoplankton groups dominate and higher trophic levels may be impacted (Turner et al., 1998). The *Deepwater Horizon* oil spill adds another stressor to the system - the toxic effects of oil on the phytoplankton.

Ozhan et al. (2014a) reviewed the studies on the effects of the Macondo oil spill on phytoplankton (i.e., those studies presented or published by spring 2014). Some studies reported evidence of an increase in phytoplankton biomass following the Macondo oil spill, as demonstrated by the higher chlorophyll concentrations in the northeastern Gulf of Mexico soon after the wellhead was capped (e.g., Hu et al., 2011). A relaxation of grazing pressures from micro- and macrozooplankton, however, cannot be discounted as the cause of the increase in phytoplankton biomass. Bacterial activity was also higher during and after the spill in surface and deeper waters (e.g., Hazen et al., 2010; Edwards et al., 2011; Ziervogel et al., 2012). Conversely, there is evidence that the oil spill could have been toxic to (some) phytoplankton (based on the *Pyrocystis lunula*-based QwikLite[®] assay; Paul et al., 2013), although laboratory- and microcosm-based studies indicate that the various phytoplankton species have different tolerance levels to the oil and/or dispersant (e.g., Ozhan and Bargu, 2014a, b). In summary, Ozhan et al. (2014a) concluded that the Macondo oil spill likely stimulated some phytoplankton species, while hindering the growth of others.

The Ozhan et al. (2014a) review demonstrated that there are no known published data examining *in situ* phytoplankton community responses to the Macondo oil spill. Phytoplankton

populations are notoriously patchy (both temporally and spatially), and so it can be difficult to obtain adequate baseline data to assess the impacts of the oil spill on the phytoplankton. Fortunately, the ongoing phytoplankton research described earlier has also produced a database of phytoplankton and associated environmental data for coastal Louisiana, of which 20 years (1990 – 2010) are now formatted for a long-term analysis (Parsons, in prep.). Portions of the database have been used in several publications related to harmful algal blooms and silica limitation (e.g., Dortch et al., 1997; Parsons et al., 1998; Dortch et al., 2001; Brown et al., 2006; Parsons et al., 2013), and several presentations addressing long-term trends have also been given (Maier et al., 2002; Parsons et al., 2007, 2008). Recent efforts have updated and formatted the phytoplankton database to allow for more long-term and baseline studies, including comparisons with the Macondo oil spill. The objective of this study, therefore, was to utilize this long-term dataset to determine if any differences were evident in the 2010 phytoplankton versus previous years, thereby recording possible impacts of the Macondo oil spill on the phytoplankton community.

2. Methods

2.1 Sample collection and preparation.

We collected surface (0 to 1 m depth) water samples from 1990 to 2010 at station C6* (C6, C6A, C6B, and C6C) on the Louisiana shelf (Fig. 1). This station was sampled most regularly, generally on a monthly basis, and was therefore the focus of this study. Water samples were prepared for microscopy following the methods of Dortch et al. (1997), in which aliquots were preserved in 0.5% glutaraldehyde, stained with 0.03% proflavine hemisulfate, and size-fractionated through 25 mm diameter polycarbonate 8, 3, and 0.2 μ m pore-size filters.

Microorganism counts from the 0.2 μm pore-size filters were not used in the present analysis because of concerns with reduced fluorescence due to a prolonged time between collection and processing of some samples in our target years (we rely heavily on fluorescence to detect the very small organisms usually encountered on the 0.2 μm filter and thus were concerned some organisms would be artificially under represented). The phytoplankton and heterotrophs on the 8 and 3 μm pore-size filters are less dependent on fluorescence for detection (larger cells) and thus were not compromised by delayed counts.

All cells were identified to the lowest practical taxonomic unit and enumerated on the filters using an Olympus BH2-RFCA epifluorescence microscope equipped with blue and green excitation light, and transmitted light when necessary. Only seven microscopists identified and enumerated phytoplankton since 1990, with W. Morrison (2000 to present) and M. Parsons (1996 to 1999) conducting the majority of the counts. An extensive identification logbook complete with descriptions and photographs has been maintained since 1990 and departing microscopists would always work with incoming microscopists to ensure that the counts and identifications were consistent. For those taxa where identifications could not be routinely made (e.g., small ($< 10 \mu\text{m}$ diameter) *Cyclotella* species versus other small centric species), a broader classification was adopted (e.g., centric diatom $< 10 \mu\text{m}$ diameter) to ensure consistency.

The abundance of phytoplankton and heterotrophic cells (cells L^{-1}) was calculated based on the number of fields counted per filter and volume of water filtered. The taxa were also sorted into higher taxonomic groupings, e.g., diatoms, dinoflagellates, cyanobacteria, etc. The relative abundance of each taxon and group was calculated by dividing the abundance of each taxon/group (cells L^{-1}) by the overall abundance of phytoplankton or heterotrophs (depending on which group the taxa belonged to). The relative abundance values are presented as percentages

of the total cell density. Shannon-Wiener diversity indices (Log_e) and species richness were calculated for the overall baseline data (i.e., the average abundance of each phytoplankton taxa across the baseline years for each month) and for the 2010 data to compare the baseline values versus 2010.

2.2 Environmental variables.

The environmental variables collected on the most consistent basis between 1990 and 2010 were temperature, salinity, and inorganic nutrients (nitrate, nitrite, ammonium, silicate, and phosphate). Temperature and salinity were measured at each site using a Seabird CTD. The concentrations of inorganic nutrients were determined using either a Technicon AutoAnalyzer II or an Alpkem RFA/2 Rapid Flow Analyzer and were reported in μM units.

2.3 Data analysis.

Environmental data from C6* (temperature, salinity, and nutrient variables) were arranged by month for each year in preparation for analysis. Sometimes samples were collected more than once per month, in which case the data would be averaged to provide a monthly value. The months between May and October were compared, because this time frame covers the beginning of oil spill (May) and post-oil spill months (September, October) that were sampled in 2010. No samples were collected in November 2010, and April samples were collected before the oil spill occurred and were, therefore, not included in the analysis. The environmental data were square-root transformed and normalized about parameter means. Using PRIMER 7, a resemblance matrix was generated using Euclidean distance calculations, and a group-average cluster analysis (CLUSTER) was conducted with a similarity profile test (SIMPROF) to determine which years

had the most similar environmental conditions to 2010 between the months of May and October. The SIMPROF test was conducted at an $\alpha = 0.05$.

Based on these results, phytoplankton and protozoan data from the years most similar (and not statistically different) from 2010 were then analyzed by averaging monthly data across the baseline years (e.g., averaging the May data from the baseline years to compare against data from May 2010). Only taxa that were present in at least 25% of these month periods were used in analysis (i.e., 3 out of the 12 month periods), to reduce the influence such infrequent species would have on the subsequent analyses (Clarke and Gorley 2014). The phytoplankton and protozoan data from the averaged baseline months were then compared to the monthly data from 2010 by creating a resemblance matrix (Bray-Curtis similarity), followed by the CLUSTER procedure (group-average) with SIMPROF testing to determine if the phytoplankton and protozoans from 2010 differed from the baseline months. Similarity percentages (SIMPER) analyses were then conducted to determine what taxa were most different between the baseline data and 2010. The plankton data were log-transformed ($\ln(\text{cells L}^{-1} + 1)$) prior to the PRIMER analysis.

3. Results

The results of the CLUSTER and SIMPROF analyses indicated that the years 1994, 1996, 1998, 2001, 2003, and 2008 were not statistically different ($p > 0.05$) from 2010 in terms of the environmental parameters tested (temperature, salinity, inorganic nutrients) between the months of May and October (Fig. 2). Additionally, the CLUSTER and SIMPROF results on the baseline-averaged monthly phytoplankton data versus the 2010 monthly phytoplankton data

indicated that the phytoplankton assemblage was different in 2010 compared to the baseline data (Fig. 3; $p < 0.05$).

The average dissimilarity between the baseline data and the 2010 phytoplankton assemblages was 38.58, with the taxa for which genus and/or species designations could be attributed are presented in Table 1. All diatom taxa analyzed were less abundant in 2010 versus the baseline, with *Chaetoceros affinis*, *Chaetoceros socialis*, and *Heterocapsa rotunda* responsible for most of the decrease between periods. All of the major taxa (i.e., those with species designations; Table 1) were less abundant in 2010 compared to the baseline assemblage, with many of them being absent altogether in 2010 (Table 1).

We classified the phytoplankton by higher taxa levels, and found that most groups were less abundant in 2010 compared to the baseline period (Table 2). Cyanobacteria, however, were more abundant in 2010 (39% higher; Table 2). Chlorophytes, ciliates, silicoflagellates, and coccolithophorids were entirely absent in the 2010 samples. Euglenoids and phytoflagellates were dramatically less abundant in 2010 versus the baseline (98% and 95%, respectively), whereas diatoms, cryptomonads, and dinoflagellates were moderately less abundant in 2010 (69%, 49%, and 47%, respectively). Overall, phytoplankton abundance was 85% lower in 2010 versus the baseline. Diatoms, cryptomonads, dinoflagellates, and cyanobacteria were proportionally higher in 2010 versus the baseline, mainly a result of the decreased representation of phytoflagellates in 2010 (Table 2). Phytoplankton were more diverse in 2010 versus the baseline ($H' = 2.135$ vs 1.503 ; 42% higher), although species richness was lower in 2010 versus the baseline (56 vs 67; 16% lower).

The SIMPER analysis on the protozoan data demonstrated that the protozoan assemblage from 2010 was not as different from the baseline as the phytoplankton were (protozoans had a

dissimilarity value of 24.88 versus the 38.58 for the phytoplankton). Five taxa were less abundant in 2010, whereas eight taxa were more abundant in 2010 versus the baseline (Table 3). Several of these taxa were not identified beyond being armored or naked, and by their size (length), which could be a cause of the ambiguity. Those taxa with higher-resolution identifications show the same result, however; some taxa increased (e.g., *Gyrodinium* spp. > 15 µm in length) whereas others decreased (e.g., *Amphidinium* spp.). *Hermesinium* (an Ebridian), heterotrophic ciliates, zooflagellates, and naked dinoflagellates < 15 µm in length were also more abundant in 2010 compared to the baseline period (Table 3). An examination at a higher taxa level reveals that heterotrophic ciliates were 62% more abundant in 2010 versus the baseline, whereas heterotrophic dinoflagellates were 33% less abundant in 2010, and zooflagellate abundance was not different in the two time periods (Table 4). The relative abundances among the groups did not change appreciably, with ciliates becoming more abundant as dinoflagellates were less abundant. Overall, the abundance of protozoans was 1% higher in 2010 compared to the baseline period (Table 4).

Our results are consistent with many, but not all, previous studies that we examined (Tables 5 and 6). Most studies reported a decrease in diatoms and phytoflagellates, and an increase in cyanobacteria, zooflagellates, and heterotrophic ciliates, all of which corroborate our results (Table 5). On a species level, our results were generally in agreement with previous studies, with some exceptions including the diatom, *Thalassionema nitzschioides*, and the dinoflagellate, *Prorocentrum minimum*, where the majority of studies reported an increase in abundance when exposed to oil versus our reported lower abundance in 2010 (Table 6).

4. Discussion

The overall results of this study suggest that in 2010, there was a dramatic reduction in phytoplankton concentrations (85%) coupled with a shift in the composition of the phytoplankton community (towards diatoms and cyanobacteria; away from ciliates and autotrophic flagellates). This study does not, however, directly link the Macondo oil spill to these results, although other (but not all) studies have reported a reduction of phytoplankton biomass following exposure to crude oil and/or dispersant (Table 5). A review of these other studies indicates that oil exposure can result in an increase in phytoplankton biomass in some cases (suppression of grazing, direct stimulation, and/or increase in nutrients), but not others (e.g., oil concentrations were too high or toxic compounds were present). González et al. (2013) suggest that the apparent lack of agreement among studies is (partly) due to the initial conditions of the phytoplankton community existing before the oil spill (i.e., if the composition is dominated by species sensitive to oil, one would expect an overall decrease in biomass). Additionally, the differing compositions of the various types of crude oil (and oil concentrations) can cause different phytoplankton responses, as can the presence of dispersants (reviewed in Ozhan et al., 2014a).

Although our study indicates that there was an overall decrease in phytoplankton biomass following the 2010 Macondo oil spill, the results were primarily due to phytoflagellates decreasing from 4.75×10^7 cells L^{-1} to 2.60×10^6 cells L^{-1} , which is a decrease of 95% (Table 2). Given that heterotroph biomass was not lower in 2010 versus the baseline (Table 4), grazing likely remained consistent and would not result in increased grazing pressure on the phytoflagellates. Additionally, baseline environmental conditions were similar to 2010, which cannot explain the lower phytoflagellate biomass in 2010. Rather, the large decrease in

269 phytoflagellate biomass suggests that the Macondo oil spill may have been detrimental to this
270 group. Many, but not all, studies corroborate this conclusion (Table 5).

271 All of the other phytoplankton groups, with the exception of cyanobacteria, also decreased in
272 abundance in 2010 (Table 2), resulting in a decrease of 65% when compared with the baseline
273 period when phytoflagellates are excluded from the calculation. This result suggests that while
274 the phytoflagellate impact was severe and caused most of the decrease in overall phytoplankton
275 abundance, the decrease was still significant for the other groups. The results of other studies
276 concur with these findings in most cases (Table 5). Interestingly, species diversity was higher in
277 2010 ($H' = 2.153$) versus the baseline ($H' = 1.503$), although species richness was lower (56
278 versus 67). These results suggest that there were fewer dominant species present in 2010, as
279 depicted by the lack of *Chaetoceros* species in 2010 (e.g., *C. affinis*, *C. socialis*, and *C. debilis*;
280 Table 1). Vargo et al. (1982) also observed higher phytoplankton diversity in the oil treatments
281 of their experiment, although Nomura et al. (2007) reported higher species richness in control
282 treatments versus oil and/or dispersant treatments in their study.

283 Our protozoan findings are opposite of the phytoplankton results, in that there was an overall
284 increase in these heterotrophs in 2010 versus the baseline period, albeit only a 1% increase
285 (Table 4). As was the case with the phytoplankton results, some previous studies were in
286 agreement with our results whereas others were not (Table 5). For example, Dale (1987)
287 observed a decline in heterotrophic ciliates exposed to oil, whereas we found higher numbers of
288 heterotrophic ciliates in 2010. Gertler et al. (2010), however, observed an increase in
289 heterotrophic ciliates exposed to oil (in line with our results), accompanied by an increase in
290 heterotrophic flagellates (in agreement with our findings). In mesocosm studies, Jung et al.
291 (2012) also documented an increase in heterotrophic flagellates, which they attributed to an

increase in bacteria (a food source) that were stimulated by the oil and oil + dispersant treatments. The lower numbers of heterotrophic dinoflagellates observed in our study suggests that these heterotrophs may have been hindered by potential exposure to oil (and possibly dispersant). The fact that heterotrophic ciliates and zooflagellates increased in abundance suggests that bacterial densities may have been higher in 2010, but the lack of bacterial density data (from the baseline years and 2010) prevents further examination of this possibility.

An examination of the literature revealed similar results for individual phytoplankton taxa; our results are corroborated by some, but not all, studies (Table 6). For example, only one out of four studies (Nomura et al. 2007) observed a decrease in the diatom *Thalassionema nitzschioides* when exposed to oil (Table 6). Similarly, only one out of three studies (Ozhan and Bargu 2014b) observed a decrease in the dinoflagellate, *Prorocentrum minimum* (Table 6).

The results of our analysis suggest that the Macondo oil spill may have had an impact on the phytoplankton community in Louisiana coastal waters west of the Mississippi River. The overall phytoplankton abundance was almost an order of magnitude lower (a decrease of 85%) compared to the baseline years, primarily due to lower numbers of phytoflagellates, although all phytoplankton groups decreased in abundance with the exception of cyanobacteria (Table 2). The trophic impacts of this decrease in phytoplankton biomass remain unknown, although such a large loss of trophic level one biomass would hypothetically cascade to higher trophic levels. Our results are in agreement with other studies in some cases, but are conflicting in others. Interestingly, our results are in almost complete disagreement with Nomura et al. (2007), which could be due to different oil sources (purported Macondo oil versus Bunker A), or experimental methods employed (*in situ* versus mesocosm). Such variability in methods and source oils

demonstrate the need to examine phytoplankton responses to oil (and dispersant) exposures on a case-by-case basis (Ozhan et al. 2014a).

Admittedly, this study is indirect, relying on an analysis of baseline data versus phytoplankton data collected during and immediately following the Macondo oil spill. There are means, however, to further examine the direct impacts of Macondo oil exposure to Louisiana phytoplankton, either through additional lab-based exposure experiments (e.g., Ozhan and Bargu, 2014a), or through the examination of additional field samples from 2010 (Parsons et al. in prep.). This study, however, represents the best opportunity to date of utilizing available baseline data to examine the impacts of the Macondo oil spill on local phytoplankton communities, and the results suggest that the impacts were plausible.

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Table 1. The results of a SIMPER (similarity percentage) analysis displaying the phytoplankton taxa for which genus and/or species designations could be attributed, and were moderately abundant in the samples ($>10^3$ cells L⁻¹ total abundance in baseline or 2010). The class of each phytoplankton taxon is given. The abundance values for the baseline and 2010 are displayed as cells L⁻¹, and were computed as total abundance across all months for the baseline and 2010. The average dissimilarity is based on Bray-Curtis similarity, and is computed by calculating the dissimilarity between the overall baseline average (i.e., species abundance averaged May – October across baseline years) versus the dissimilarity in 2010 for each species. The % contribution values indicate how much each taxon contributes to the overall dissimilarities between the two time frames.

taxon	class	baseline abundance	2010 abundance	average dissimilarity	% contribution
<i>Chaetoceros affinis</i>	diatom	5.94×10^7	0.00	1.14	2.95
<i>Chaetoceros socialis</i>	diatom	1.44×10^7	0.00	1.04	2.7
<i>Heterocapsa rotundata</i>	dinoflagellate	7.98×10^5	0.00	0.85	2.2
<i>Chaetoceros debilis</i>	diatom	6.60×10^5	0.00	0.83	2.16
<i>Chaetoceros diadema</i>	diatom	3.85×10^5	0.00	0.8	2.07
<i>Asterionellopsis glacialis</i>	diatom	2.68×10^5	0.00	0.77	2.01
<i>Dinophysis caudata</i>	dinoflagellate	2.45×10^5	0.00	0.77	1.99

<i>Chaetoceros laciniosus</i>	diatom	2.33×10^5	0.00	0.76	1.98
<i>Mesodinium rubrum</i>	ciliate	2.18×10^5	0.00	0.76	1.97
<i>Chaetoceros didymus</i>	diatom	1.75×10^5	0.00	0.75	1.93
<i>Asterionellopsis kariana</i>	diatom	1.61×10^5	0.00	0.74	1.92
<i>Chaetoceros lorenzianus</i>	diatom	1.40×10^5	0.00	0.73	1.89
<i>Hemiaulus sinensis</i>	diatom	1.05×10^5	0.00	0.71	1.84
<i>Chaetoceros constrictus</i>	diatom	9.20×10^4	0.00	0.7	1.82
<i>Eucampia cornuta</i>	diatom	2.43×10^4	0.00	0.61	1.59
<i>Ceratium fusus</i>	dinoflagellate	1.84×10^4	0.00	0.59	1.54
<i>Stauropsis membranacae</i>	diatom	1.90×10^4	0.00	0.6	1.54
<i>Ditylum brightwellii</i>	diatom	1.55×10^4	0.00	0.58	1.51
<i>Ceratium tripos</i>	dinoflagellate	1.16×10^4	0.00	0.56	1.46
<i>Prorocentrum micans</i>	dinoflagellate	1.21×10^6	3.65×10^2	0.55	1.42
<i>Cylindrotheca closterium</i>	diatom	4.74×10^5	3.65×10^2	0.48	1.25
<i>Rhizosolenia setigera</i>	diatom	4.17×10^5	7.28×10^2	0.43	1.11
<i>Skeletonema costatum</i>	diatom	5.84×10^6	2.20×10^4	0.38	0.97

<i>Chaetoceros decipiens</i>	diatom	9.65×10^5	4.11×10^3	0.37	0.95
<i>Torodinium</i> spp.	dinoflagellate	6.17×10^4	7.28×10^2	0.3	0.78
<i>Lioloma pacificum</i>	diatom	2.68×10^5	3.64×10^3	0.29	0.75
<i>Leptocylindrus danicus</i>	diatom	1.23×10^6	2.10×10^4	0.27	0.71
<i>Cerataulina pelagica</i>	diatom	3.58×10^6	7.92×10^4	0.26	0.67
<i>Karenia brevis</i>	dinoflagellate	4.39×10^4	1.09×10^3	0.25	0.65
<i>Prorocentrum gracile</i>	dinoflagellate	9.20×10^4	2.19×10^3	0.25	0.65
<i>Chaetoceros compressus</i>	diatom	1.56×10^6	4.09×10^4	0.25	0.64
<i>Dactyliosolen fragilissimus</i>	diatom	1.31×10^7	7.67×10^5	0.19	0.5
<i>Guinardia striata</i>	diatom	6.67×10^5	4.22×10^4	0.19	0.48
<i>Guinardia delicatula</i>	diatom	2.79×10^6	2.03×10^5	0.18	0.46
<i>Leptocylindrus minimus</i>	diatom	1.18×10^6	8.84×10^4	0.17	0.45
<i>Odontella sinensis</i>	diatom	1.05×10^5	9.41×10^3	0.16	0.42
<i>Gymnodinium</i> cf. <i>pulchellum</i>	dinoflagellate	2.58×10^5	2.56×10^4	0.16	0.4
<i>Ceratium hircus</i>	dinoflagellate	2.09×10^5	2.27×10^4	0.15	0.39
<i>Pseudo-nitzschia</i> spp.	diatom	2.21×10^7	2.42×10^6	0.15	0.38

<i>Proboscia alata</i>	diatom	1.34×10^6	2.22×10^5	0.12	0.32
<i>Prorocentrum minimum</i>	dinoflagellate	9.27×10^5	1.66×10^5	0.12	0.3
<i>Guinardia flaccida</i>	diatom	1.68×10^5	3.19×10^4	0.11	0.29
<i>Pseudosolenia calcar-avis</i>	diatom	2.36×10^5	5.42×10^4	0.1	0.26
<i>Trichodesmium</i> spp.	cyanobacteria	1.36×10^5	3.93×10^4	0.08	0.22
<i>Thalassionema nitzschioides</i>	diatom	1.30×10^6	3.62×10^5	0.09	0.22
<i>Akashiwo sanguinea</i>	dinoflagellate	3.45×10^4	1.05×10^4	0.08	0.21
<i>Heterocapsa niei</i>	dinoflagellate	3.70×10^5	1.23×10^5	0.07	0.19
<i>Chaetoceros curvisetus</i>	diatom	5.24×10^5	2.01×10^5	0.06	0.17
<i>Hemiaulus hauckii</i>	diatom	4.53×10^4	2.10×10^4	0.05	0.13
<i>Scrippsiella</i> spp.	dinoflagellate	1.68×10^5	1.11×10^5	0.03	0.07

Table 2. Summary of abundance changes of the phytoplankton classes differentiating the baseline assemblage versus 2010. The class abundance values are given as cells L⁻¹ and are summed across all six months analyzed in the study for the baseline and 2010. The % change was calculated by dividing the difference of the 2010 and baseline abundance by the baseline abundance for each class. Relative abundance values are the proportion of total phytoplankton represented by each class.

class	baseline abundance	2010 abundance	% change	baseline relative abundance	2010 relative abundance
autotroph – other	1.68 x 10 ⁵	0	- 100%	0.2%	0.0%
chlorophytes	1.08 x 10 ⁶	0	- 100%	1.5%	0.0%
ciliates	2.12 x 10 ⁴	0	- 100%	0.05%	0.0%
coccolithophorids	7.79 x 10 ²	0	- 100%	0.01%	0.0%
cryptomonads	3.35 x 10 ⁶	1.72 x 10 ⁶	- 49%	4.8%	16.2%
cyanobacteria	5.15 x 10 ⁵	7.18 x 10 ⁵	+ 39%	0.7%	6.8%
diatoms	1.71 x 10 ⁷	5.22 x 10 ⁶	- 69%	24.3%	49.3%
dinoflagellates	6.27 x 10 ⁵	3.34 x 10 ⁵	- 47%	0.9%	3.2%
euglenoids	7.23 x 10 ³	1.33 x 10 ²	- 98%	0.02%	0.0%
phytoflagellates	4.75 x 10 ⁷	2.60 x 10 ⁶	- 95%	67.5%	24.5%

silicoflagellates	1.89×10^3	0	- 100%	0.02%	0.0%
Total	7.04×10^7	1.06×10^7	- 85%	100%	100%

Table 3. The results of a SIMPER (similarity percentage) analysis displaying the total overall abundance of the heterotrophic taxa differentiating the baseline assemblage versus 2010. The class of each taxon is given. The abundance values are given as cells L⁻¹. The average dissimilarity is based on Bray-Curtis similarity, and is computed by calculating the dissimilarity between months (May – October) of the baseline versus 2010. The % contribution values indicate how much each taxon contributes to the overall dissimilarities between the two time frames.

taxon	class	baseline abundance	2010 abundance	average dissimilarity	% contribution
dinoflagellate – naked, > 15 µm in length	dinoflagellate	1.59 x 10 ⁵	0	5.68	23.19
dinoflagellate – other, > 15 µm in length	dinoflagellate	3.01 x 10 ⁴	0	4.89	19.97
<i>Protoperidinium</i> spp.	dinoflagellate	7.54 x 10 ²	0	3.14	12.83
<i>Amphidinium</i> spp.	dinoflagellate	7.41 x 10 ²	0	3.13	12.80
<i>Gyrodinium</i> spp. other	dinoflagellate	6.00 x 10 ²	0	3.03	12.39
<i>Hermesinium</i> spp.	Ebridian	1.80 x 10 ¹	2.00 x 10 ³	2.21	9.02
<i>Gyrodinium</i> spp. > 15 µm in length	dinoflagellate	5.79 x 10 ³	2.86 x 10 ⁴	0.76	3.09

<i>Gyrodinium</i> spp. < 15 µm in length	dinoflagellate	2.68 x 10 ³	8.53 x 10 ³	0.55	2.25
dinoflagellate – armored, < 15 µm in length	dinoflagellate	3.82 x 10 ⁴	9.02 x 10 ⁴	0.41	1.67
dinoflagellate – armored, > 15 µm in length	dinoflagellate	7.70 x 10 ³	1.50 x 10 ⁴	0.31	1.28
ciliate	ciliate	7.21 x 10 ⁴	1.17 x 10 ⁵	0.23	0.93
dinoflagellate – naked, < 15 µm in length	dinoflagellate	7.83 x 10 ⁴	1.04 x 10 ⁵	0.14	0.55
zooflagellate , < 10 µm in length	composite	7.87 x 10 ⁷	7.97 x 10 ⁷	0.01	0.02

Table 4. Summary of abundance changes of the heterotroph classes differentiating the baseline assemblage versus 2010. The abundance values are given as cells L⁻¹ and are summed across all six months analyzed in the study for the baseline and 2010. The % change was calculated by dividing the difference of the 2010 and baseline abundance by the baseline abundance for each taxon.

class	baseline abundance	2010 abundance	% change	baseline relative abundance	2010 relative abundance
ciliates	7.21 x 10 ⁴	1.17 x 10 ⁵	+ 62%	0.1%	0.2%
dinoflagellates	3.65 x 10 ⁵	2.46 x 10 ⁵	- 33%	0.5%	0.3%
zooflagellates	7.87 x 10 ⁷	7.97 x 10 ⁷	+ 1%	99.4%	99.5%
Total	7.92 x 10 ⁷	8.01 x 10 ⁷	+ 1%	100%	100%

Table 5. A comparison of the results of this study versus other studies conducted on phytoplankton and protozoan (higher taxa) exposures to crude oil and/or dispersant. For this study, a decrease refers to lower abundance in 2010 versus the baseline data (and vice versa for increase). For the other studies, a decrease indicates a lower abundance when exposed to oil (and/or dispersant) during a spill or in a mesocosm experiment. “Resistant” means the taxon was not affected by the oil. WAF = Water Accommodated Fraction; WSF = Water Soluble Fraction.

Taxa	This study	Other studies	Their results	Petroleum type	Comments
phytoplankton	decrease	Taş et al. (2011)	decrease	<i>Volgoneft-248</i> (heavy fuel oil)	
		Cabioch et al. (1981)	mixed	<i>Amoco Cadiz</i> (light crude oil)	Reduced biomass near spill; increase farther away
		Johansson et al. (1980)	increase	<i>Tsesis</i> (no. 5 fuel oil)	Increase could have been due to reduced grazing
		Hu et al. (2011)	increase	Macondo (MC) 252	River discharge could have played a role
diatoms	decrease	Taş et al. (2011)	decrease	<i>Volgoneft-248</i>	

				(heavy fuel oil)	
		Harrison et al. (1986)	decrease	Prudhoe Bay crude oil and Corexit [®] 9527	Mesocosm experiments; shift from diatoms to microflagellates
		Pérez et al. (2010)	decrease	naphthalene, phenanthrene, pyrene, fluoranthene	
		Gilde and Pickney (2012)	resistant	South Louisiana crude	
		Nomura et al. (2007)	decrease	Bunker A oil (and Corexit [®])	
		González et al. (2009)	resistant	<i>Prestige</i> - WAF	
		Ozhan and Bargu (2014a)	resistant	South Louisiana crude	
dinoflagellates	decrease	Taş et al. (2011)	increase	<i>Volgoneft-248</i> (heavy fuel oil)	

phytoflagellates	decrease	Sargian et al. (2007)	decrease	Patagonian crude oil - WSF	Smaller cells more sensitive
		Echeveste et al. (2010)	decrease	pyrene, phenanthrene	Smaller cells more sensitive
		Smith (1968)	decrease	<i>Torrey Canyon</i> (Kuwait crude oil)	Prasinophytes
		Harrison et al. (1986)	increase	Prudhoe Bay crude oil and Corexit [®] 9527	Mesocosm experiments; shift from diatoms to microflagellates
		Pérez et al. (2010)	decrease	naphthalene, phenanthrene, pyrene, fluoranthene	
autotrophic ciliates	decrease	Nomura et al. (2007)	increase	Bunker A oil (and Corexit [®])	
		Ortmann et al. (2012)	decrease	Corexit [®] 9500A and MC252 dispersed oil	Mesocosm experiments
		Pérez et al. (2010)	decrease	naphthalene,	

				phenanthrene, pyrene, fluoranthene	
cryptomonads	decrease	Gilde and Pickney (2012)	decrease	South Louisiana crude	
cyanobacteria	increase	Gilde and Pickney (2012)	increase	South Louisiana crude	
euglenophytes	decrease	Gilde and Pickney (2012)	resistant	South Louisiana crude	
		Nomura et al. (2007)	resistant	Bunker A oil (and Corexit [®])	
chlorophytes	decrease	Gilde and Pickney (2012)	resistant	South Louisiana crude	
heterotrophic flagellates	increase	Jung et al. (2012)	increase	Iranian heavy crude (and Hi-Clean dispersant)	Could have been stimulated by an increase in food (bacteria)
		Gertler et al. (2010)	increase		

heterotrophic	increase	Gertler et al. (2010)	increase	Ekofisk crude oil
ciliates		Dale (1987)	decrease	

Table 6. A comparison of the results of this study versus other studies conducted on phytoplankton and protozoan (species-level) exposures to crude oil and/or dispersant. For this study, a decrease refers to lower abundance in 2010 versus the baseline data (and vice versa for increase). For the other studies, a decrease indicates a lower abundance when exposed to oil (and/or dispersant) during a spill or in a mesocosm experiment. “Resistant” means the taxon was not affected by the oil. WAF = Water Accommodated Fraction; WSF = Water Soluble Fraction.

Taxa	This study	Other studies	Their results	Petroleum type
Diatoms				
<i>Cerataulina pelagica</i>	decrease	Varela et al. (2006)	decrease	<i>Prestige</i> (heavy fuel oil)
<i>Chaetoceros compressus</i>	decrease	Nomura et al. (2007)	resistant	Bunker A oil (and Corexit [®])
		Varela et al. (2006)	decrease	<i>Prestige</i> (heavy fuel oil)
<i>Dactyliosolen fragilissimus</i>	decrease	Nomura et al. (2007)	decrease	Bunker A oil (and Corexit [®])
<i>Skeletonema costatum</i>	decrease	Østgaard et al. (1984)	decrease	Ekofisk crude oil
<i>Thalassionema nitzschioides</i>	decrease	Nomura et al. (2007)	decrease	Bunker A oil (and Corexit [®])
		Varela et al. (2006)	increase	<i>Prestige</i> (heavy fuel oil)
		Jung et al. (2012)	increase	Iranian heavy crude (and Hi-Clean

				dispersant)
		González et al. (2009)	increase	<i>Prestige</i> - WAF
<i>Guinardia delicatula</i>	decrease	Nomura et al. (2007)	decrease	Bunker A oil (and Corexit [®])
		Jung et al. (2012)	increase	Iranian heavy crude (and Hi-Clean dispersant)
<i>Guinardia striata</i>	decrease	Varela et al. (2006)	decrease	<i>Prestige</i> (heavy fuel oil)
		Ozhan and Bargu (2014a)	decrease	South Louisiana crude
<i>Leptocylindrus danicus</i>	decrease	Ozhan and Bargu (2014a)	decrease	South Louisiana crude
<i>Leptocylindrus minimus</i>	decrease	Varela et al. (2006)	increase	<i>Prestige</i> (heavy fuel oil)
Dinoflagellates				
<i>Heterocapsa niei</i>	decrease	Varela et al. (2006)	decrease	<i>Prestige</i> (heavy fuel oil)
<i>Karenia brevis</i>	decrease	Ozhan and Bargu (2014b)	decrease	South Louisiana crude
<i>Prorocentrum micans</i>	decrease	Taş et al. (2011)	increase	<i>Volgoneft-248</i> (heavy fuel oil)
<i>Prorocentrum minimum</i>	decrease	Ozhan and Bargu (2014b)	decrease	South Louisiana crude
		Morales-Loo and Goutx (1990)	increase	Mexican crude (Isthmus Cactus – WSF)
		Okaichi (1983)	increase	Bunker C oil

<i>Torodinium</i> spp.	decrease	Varela et al. (2006)	increase	<i>Prestige</i> (heavy fuel oil)
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Ciliates

<i>Mesodinium rubrum</i>	decrease	Dale (1987)	decrease	Ekofisk crude oil
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List of Figures

Fig. 1. Coastal Louisiana showing the location of C6* sampled in this study. C6* includes stations C6, C6A, C6B, and C6C.

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Figure 1

Figure 2

Figure 3