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Pulsed blooms and persistent oil-degrading bacterial populations in the water column during and after the Deepwater Horizon blowout

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ABSTRACT

One of the defining features of the Deepwater Horizon oil spill was the rapid formation and persistence of a hydrocarbon plume in deep water. Here we use 16S rRNA gene clone libraries and pyrosequencing of 16S rRNA gene fragments to outline the temporal dynamics of the bacterial community in the water column near the Macondo wellhead. Our timeline starts with the pre-spill (March 2010) status of the water column bacterial community, continues through the bacterial enrichments dominating the hydrocarbon plume after the blowout (DWH *Oceanospirillales*, *Cycloclasticus*, *Colwellia* in late May 2010), and leads towards post-spill bacterial communities with molecular signatures related to degradation of phytoplankton pulses (September and October 2010; July 2011) in the water column near the Macondo wellhead. We document a dramatic transition as the complex bacterial community before the oil spill was temporarily overwhelmed by a few specialized bacterial groups responding to the massive influx of hydrocarbons in May 2010. In September and October 2010, this bacterial bloom had been replaced by a diversified bacterial community which resembled its predecessor prior to the spill. Notably, the post-plume 16S rRNA gene clone libraries and pyrosequencing datasets illustrated the continued presence of oil-degrading bacteria in the water column near the Macondo wellhead which we posit to represent an inherent signature of hydrocarbon catabolic potential to the Gulf of Mexico. The pyroseqencing results detected and tracked minority bacterial populations that were not visible in the conventional 16S rRNA gene clone libraries and allowed us to identify natural reservoirs of the Deepwater Horizon *Oceanospirillales* within and outside of the Gulf of Mexico.

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1. Introduction

The explosion and sinking of the Deepwater Horizon platform discharged oil and gas into the Gulf of Mexico and generated massive and long-lasting perturbations in its ecosystem (Schrope, 2011). One of the defining features of the Deepwater Horizon oil spill was the formation of a deepwater hydrocarbon-enriched plume during the multiphase ejection of gas and oil from the wellhead. The plume was positioned between approx. 1000 and 1300 m depth due to preferential entrainment of the soluble complex hydrocarbons within the deep, cold (5 °C) water, and consisted mostly of light alkanes (C_1 to C_3), BTEX, submicrometer-size oil droplets (Ryerson et al., 2012; Reddy et al., 2012); it also entrained the dispersant compound dioctyl sodium sulfosuccinate (DOSS) (Kujawinski et al., 2011). The deep plume was detected initially in early May 2010 (Diercks et al., 2010b), and its gradual spread was monitored throughout the summer of 2010 (Hazen et al., 2010, Camilli et al., 2010, Kessler et al., 2011, Joye et al., 2011a,b) by tracking local oxygen depletion and C-DOM fluorescence maxima as proxies for the presence of hydrocarbons and microbial activity (Diercks et al., 2010b; Wade et al., 2011). However, tracking the evolving composition of the bacterial community in the oil-impacted water column, including the deep hydrocarbon plume, during 2010 was an extraordinary challenge.

Initially, changes of the microbial community in the water column were inferred from Phylochip® analyses of oil degrading communities (Hazen et al., 2010), or from models of methane, ethane and propane dynamics (Valentine et al., 2010, Kessler et al., 2011). These studies did not provide exact information on

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Table 1
Samples collected on multiple research cruises near the Macondo wellhead with dates, water depths, and geographical coordinates.

Sample names with cruise-specific sampling codes in parentheses	Ship	Date	Depth (m)	Latitude (N)	Longitude (W)
Prespill-800m	R.V. *Pelican*	March 10, 2010	800	28°50.43	88°30.29
SurfaceOil-PE5	R.V. *Pelican*	May 5, 2010	0	28°44.175	88°22.335
Plumeprofile-800m (B11)	R.V. *Walton Smith*	May 31, 2010	800	28°41.686	88°26.081
Plumeprofile-1170m (B6)	R.V. *Walton Smith*	May 31, 2010	1170	28°41.686	88°26.081
Plumeprofile-1210m (B3)	R.V. *Walton Smith*	May 31, 2010	1210	28°41.686	88°26.081
Plumeprofile-1320m (B1)	R.V. *Walton Smith*	May 31, 2010	1320	28°41.686	88°26.081
Postplume I-800m (C4B8)	R.V. *Pelican*	Sept 12, 2010	800	28°41.713	88°26.073
Postplume I-1210m (C4B4)	R.V. *Pelican*	Sept 12, 2010	1210	28°41.713	88°26.073
Postplume II (GIP22)	R.V. *Cape Hatteras*	Oct 18, 2010	1052	28°40.503	87°39.250
Postplume III (E002)	R.V. *Endeavor*	July 3, 2011	1100	28°42.177	88°21.240

sampling times, water depths and geographical positions for their molecular data. Additional 16S rRNA gene clone library datasets were recently synthesized and published with precise sampling locations and times, in order to coherently survey the changing bacterial community composition over the lifetime of the deep hydrocarbon plume (Redmond and Valentine, 2012). In late May 2010, the plume-associated bacterial community was dominated by a specific cluster within the *Oceanospirillales*, subsequently termed Deep Water Horizon (DWH) *Oceanospirillales*, before changing in mid-June to a community where most clones grouped with the genera *Cycloclasticus*, obligate degraders of aromatic hydrocarbons, and *Colwellia*, known as a genus of psychrophilic marine heterotrophic generalists. By early September, the bacterial community had diversified considerably and included different *Alphaproteobacteria*, multiple lineages within the *Gammaproteobacteria*, *Flavobacteria*, and several other phylum-level lineages such as the *Actinobacteria*, *Planctomycetes*, *Chloroflexi*, and the SAR406 cluster (Redmond and Valentine, 2012).

Here we extend the timeline of microbial oil spill response with molecular analyses of samples from March 2010 to July 2011 (Table 1). By complementing clone libraries of nearly full-length 16S rRNA genes with pyrosequencing surveys of shorter 16S rRNA gene fragments, we combine the taxonomic precision of full-length 16S rRNA genes with the high-throughout resolution of bacterial community structure enabled by pyrosequencing. Specifically, we extend previous molecular analyses in three ways. (1) The pre-spill (March 10, 2010) water column bacterial community is compared to post-spill communities (September 12 and October 18, 2010; July 3, 2011) near the Macondo wellhead with 16S rRNA gene clone libraries. (2) A water column profile near the Macondo wellhead with samples above, within and below the deep hydrocarbon plume during its *Oceanospirillales*-dominated phase (May 31, 2010) is analyzed with conventional 16S rRNA gene clone libraries and by 16S rRNA gene fragment pyrosequencing. (3) The water column profile is compared to surface water samples contaminated with weathered oil from early May 2010 (May 5, 2010), and post-plume water samples (September 12 and October 18, 2010) from near the wellhead and east of the wellhead, using pyrosequencing.

2. Materials and methods

2.1. Sampling

Surface and water column samples were obtained during six research cruises (Table 1). The pre-spill sample (March 10, 2010) was obtained on R.V. *Pelican* by CTD cast at 800 m depth, ca. 10 nautical miles northwest of the Macondo wellhead (28°50.43N, 88°30.29W). The water column did not show any of oxygen or CDOM anomalies (Fig. S1). From May 5 to 9, Oil spill surface water samples were collected via bucket sampling from the R/V *Pelican*, and kept at ca. 4 °C during and after immediate transport to Chapel Hill. Surface water sampled ca. 0.5 nautical miles from the wellhead (28°44.175N, 88°22.335W, May 5, 2010) showed the strongest admixture of reddish-brown weathered oil sludge, and was used for DNA sequencing. These surface seawater samples are to the best of our knowledge the first samples collected on the earliest Rapid Response cruise to the Deepwater Horizon response zone (May 5 to 9, 2010; Diercks et al., 2010a). CTD surveys during the second cruise leg (May 10 to 16, 2010) provided the first evidence of the southwest-trending hydrocarbon plume in the deep water column (Diercks et al., 2010b). About three weeks later, a water column profile with four depths bracketing the deepwater plume was obtained by CTD approx. 4.7 nautical miles southwest of the wellhead (R/V *Walton Smith*, May 31, 2010; 28°41.686N, 88°26.081W). Water samples of approx. 500 ml were collected at 800, 1170, 1210, and 1320 m depth. Immediately after shipboard recovery, they were filtered through 47 mm diameter and 0.22 μm poresize Anodisc filters; the filters were placed on dry ice until DNA extraction in Chapel Hill. The 1170 m and the 1210 m samples of this profile represent the deepwater hydrocarbon plume, as indicated by localized oxygen depletion and increased water column fluorescence measured during the CTD cast (Fig. S2). On September 12, almost two months after the Macondo wellhead had been capped on July 15, 2010, water column filter samples were collected again at the same location (R/V *Pelican*; 28°41.713N, 88°26.073W) to evaluate the water column bacterial community at 800 and 1210 m depth (Postplume I). CTD profiles no longer detected the *in-situ* indicators (localized oxygen depletion coinciding with fluorescence maximum) of the deep hydrocarbon plume (Fig. S3), consistent with the deepwater circulation of the Gulf of Mexico that moved the deep hydrocarbon plume in a southwesterly direction already at the onset of the spill (Diercks et al., 2010b). A negative control sample (Postplume II) was obtained 37 nautical miles east of the wellhead (28°40.503N, 87°39.250W) at a depth of 1052 m (R/V *Cape Hatteras*, October 18, 2010). Due to the predominantly west and southwest deepwater current pattern in this area, this sample was unlikely to have been in contact with the Macondo wellhead and any residual hydrocarbon leakage at this location. In July 2011, the water column near the Macondo wellhead was sampled again (July 3; R/V *Endeavor*; 28°42.177N, 88°21.240W), to initiate a multiannual survey of water column microbial community structure (Postplume III). In the home laboratory, DNA extraction from filters (Teske et al., 2011), 16S rRNA gene amplification with previously described 16S rRNA gene primers (Teske et al., 2002), and clone library construction were performed using standard methods, detailed in the supplementary information.

2.2. Phylogenetic analysis

Near-complete 16S rRNA gene sequences were analyzed using Sequencher (Gene Codes, Ann Arbor, MI) and compared to other

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