Microbial community analysis of Deepwater Horizon oil-spill impacted sites along the Gulf Coast using functional and phylogenetic markers

by

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Abstract

The purpose of this study was to employ genomic approaches to determine if the oil spill affected the microbial population present along the Gulf Shore. Samples were collected along the coastal regions of Louisiana and Alabama based on their proximity to the oil spill site and being known as contaminated areas. Of these samples collected one was found to be contaminated based on the GC/MS analysis. The analysis showed that the sample from Bay Jimmy "South," LA (BJS) was contaminated with n-alkanes and contained similar spikes between 9 to 17 min retention time as compared to the gas chromatograph of the BP source MC - 252. This suggested that these alkanes came from the most recent spill in the Gulf. The PCR analysis revealed the presence of a microbial species, *Pseudomonas*, within the microbial community based on the *Pseudomonas* 16S rRNA gene and universal bacterial 16S rRNA gene targets that is known to contain the enzymes necessary for crude oil degradation. In addition, the PCR analysis confirmed the presence of alkane and PAH degrading genes within the samples, based on the *alkB*, P450, and PAH-RHD$_{\alpha}$ gene targets. The qPCR analysis revealed an observable difference between the functional gene quantifications and that of the *Pseudomonas* 16S rRNA gene target. This was correlated to the presence of other microbial species with degradative capabilities present within the samples based on the phylogenetic analysis. The statistical analysis conducted between the contaminated sample, non-contaminated sample, and the negative control soil showed a similarity between the samples, confirming previous studies which found these enzymes to be ubiquitous in the environment. However, the phylogenetic analysis of the

contaminated sample revealed a significantly larger amount of crude oil degrading bacteria, identified at the genus level, the majority of which are specific to degrading alkanes. The results obtained for the qPCR and Phylogenetic analyses suggests that only a small percentage of the bacteria present in the BJS sample may have the enzymes necessary for degradation. To determine whether or not these bacteria are actively breaking down the crude oil contaminants, further elucidation such as gene expression may be required.

Acknowledgments

There are many who have supported me throughout the trials of obtaining my masters at Auburn University. First, I would like to extend the utmost respect for my advisor Dr. Ahjeong Son. She has supported me in my quest for knowledge even as an undergraduate and over time became a great mentor. Without her wisdom, perseverance, and most of all support I could not have achieved or experienced what I have done in the past two and a half years. In addition, I would like to thank Dr. Dongye Zhao and Dr. Mark Liles who have both inspired me to do my best, whether in the classroom or in life. Their patience and encouragement has helped me get to this point.

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Last I would like to thank my friends and family. My mom and dad, Susan and Rick Pavek, have always stood behind me and expected my best. To my brothers Jake Pavek, Jimmy Hart, and Daniel Looper who have taken the time to bring a smile to my face during the stressful times. And to my friends Matthew Brooks, Bernardo Trindade, Jessica Henderson, and those mentioned above, thank you for confidence when I didn't have enough of my own.

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List of Symbols and Abbreviations

α	Alpha
AL	Sediment sample collected from Sandy Bay, AL
ATP	Adensosine triphosphate
BD	Core sample collected from Bayou Dulac, LA
BJN	Core sample collected from Bay Jimmy "North," LA
BJS	Sediment sample collected from Bay Jimmy "South," LA
BP	British Petroleum
C	Carbon
DNA	Deoxyribonucleic acids
dNTPS	Deoxynulceotide triphosphate
FDEP	Florida Department of Environmental Protection
GC	Gas chromatography
gDNA	Genomic DNA
MS	Mass spectrometry
NCS	Negative Control Soil sample collected from Auburn, AL
PAH	Polycyclic aromatic hydrocarbon
PC	Positive Control
PCR	Polymerase Chain Reaction
PPi	Pyrophosphate

qPCR	Quantitative PCR or Real-time PCR
RHD	Ring-hydroxylating dioxygenase
SW	Seawater sample collected from Sandy Bay, AL
TSA	Tryptic soy agar

Chapter One. Introduction

In the past 20 years the world has experienced two of the largest oil spills to date; the largest being the Kuwait oil spill in 1991 during the Gulf War and the second largest being the Deepwater Horizon oil spill in 2010 off the coast of the Gulf of Mexico (Casselman 2012). In the same amount of time the United States alone has seen an increase in the reported incidents. Initial approaches to contain and remove the oil consisted mainly of booms with skimmers (Casselman 2012). In the case of the Deep Water Horizon, burning off the oil and applying dispersants were also used. The problem with these approaches is that they are containment strategies and lack the capability of removing all of the oil from the contaminated site (Chauhan, Fazlurrahman et al. 2008; Das and Chandran 2011).

It is important that these contaminants be removed since many of the hydrocarbons found in crude oil can lead to temporary fatigue or drowsiness to more severe health effects such as paralysis and cancer depending on the length and method of exposure, and the contaminant itself (2008; 2008; Goldstein, Zempsky et al. 2011). In addition, some of the contaminants have the potential to persist in the environment, increasing the risk for the contaminant to move up through the food chain (Ahangar 2010; Aigner, Burgess et al. 2010).

As an alternative strategy, bioremediation has been used to contain and remove crude oil contaminants in soil and groundwater since the Hanahan Bioremediation Project of 1992, in which the indigenous population was biostimulated to help treat contaminated groundwater (Chapelle 1997). In general, bioremediation is the process of utilizing microorganisms capable of degrading contaminants into less harmful substances. This method has the potential to be non-invasive and is cost-effective as compared to other methods, such as adding biosurfactants or absorbants (Chauhan, Fazlurrahman et al. 2008; Das and Chandran 2011). However, whether or

not this method can be used at a specific site is heavily dependent on whether or not the indigenous microorganisms contain the specific enzymes required for the degradation pathway. In addition, the environmental conditions, such as the amount of nutrients and competitive levels at which these organisms thrive, must be maintained after exposure. While approaches such as bioaugmentation and biostimulation can be used to overcome such obstacles, natural attenuation remains a popular topic of study (Chauhan, Fazlurrahman et al. 2008; Das and Chandran 2011).

1.2 Objectives

The purpose of this study was to perform a functional gene analysis on oil-impacted sediments and seawater collected from contaminated sites along the gulf coast and determine the degradative capabilities of the indigenous microbial populations. Five gene targets were chosen based on genus- or function-specific genes pertinent to the degradation process. These results were then compared with the results obtained from a chemical analysis conducted using gas chromotography (GC)/mass spectrometry (MS) and a phylogenetic analysis conducted using 454-pyrosequencing. Based on the accumulative analysis it was determined whether or not the oil spill had an effect on the environment.

Chapter Two. Literature Review

2.1 Environmental Contamination

As technology and industry have evolved, more and more by-products of crude oil are utilized in today's market (i.e. gasoline, wax, and lubricants) which means an increase in mining and transportation efforts. Before the Deepwater Horizon oil spill in 2010, the majority of oil spills occurred between the 1980s and 1990s. Most of these spills were at the well head or during the transportation by large tankers. However, the largest oil spill to date happen in Kuwait during the Gulf War where about 300 million gallons of oil were intentionally exposed to the surrounding land and ended up flowing into the Persian Gulf. (Casselman 2012)

The hydrocarbons that make up crude oil form compounds, such as alkanes, polycyclic aromatic hydrocarbons (PAHs), and parrafins, are harmful to humans and the environment. These health effects depend largely on the contaminant, as well as, the method and length of exposure. Contaminants such as alkanes are more volatile meaning they are quickly transported through a given system. They typically cause minor fatige, skin irritation, and/or stomach pain. However, compounds such a PAHs are less volatile and can cause severe damage such as cancer. (2008; 2008; Goldstein, Zempsky et al. 2011)

Although there has been an overall decrease in oil spill accidents over the past 20 years, it is still estimated that an average of 1.3 million gals is spill near U.S. territory each year. However, this does not take into account the Deepwater Horizon oil spill which was leaking about 2.5 million gallons a day before being capped. The large amount of crude oil contaminants in which the Gulf Coast was exposed to led to thousands of deaths of marine life (Ahangar 2010; Aigner, Burgess et al. 2010). While initial removal strategies were put in place, it is estimated that 75% of the oil remained, leading to the necessity of an alternate strategy.

2.2 Removal Strategies and Bioremediation

Initial removal strategies can include controlled burning, booms and skimmers, absorbents, and dispersants (Chauhan, Fazlurrahman et al. 2008). However, these methods are ineffective at completely removing the contaminants. As secondary strategy, bioremediation has been used to contain and remove crude oil contaminants in soil and groundwater since the Hanahan Bioremediation Project of 1992, in which the indigenous population was biostimulated to help treat contaminated groundwater (Chapelle 1997). In general, bioremediation is the process of utilizing microorganisms capable of degrading contaminants into less harmful substances. This method has the potential to be non-invasive and is cost-effective as compared to other methods, such as adding biosurfactants or absorbants (Chauhan, Fazlurrahman et al. 2008; Das and Chandran 2011). However, whether or not this method can be used at a specific site is heavily dependent on whether or not the indigenous microorganisms contain the specific enzymes required for the degradation pathway. In addition, the environmental conditions, such as the amount of nutrients and competitive levels at which these organisms thrive, must be maintained after exposure. While approaches such as bioaugmentation and biostimulation can be used to overcome such obstacles, natural attenuation remains a popular topic of study (Chauhan, Fazlurrahman et al. 2008; Das and Chandran 2011).

2.3 Crude-oil Biodegradating Bacteria

Previous studies (Chadhain, Norman et al. 2006; Kloos, Munch et al. 2006; van Beilen, Funhoff et al. 2006; Wang, Wang et al. 2010) have been conducted on different bacterial and fungal species to determine their role in the degradation process of crude oil constituents, such as PAHs and alkanes. A recent study by Hazen et al. (2010) found that areas directly surrounding the oil plume contained a newly discovered species of bacteria closely related to *Oceanospiralles*

which had become highly adapted to the increased flux of contaminants and was degrading the oil at an unexpected rate. However, this species has not been identified in contaminated soils. Of the bacteria studied with the degradation capabilities, *Pseudomonas* (e.g., *Pseudomonas putida*) has been identified as the most abundant species in hydrocarbon contaminated soil and in some aquatic environments (Hazen, Alusi et al. 2010; Das and Chandran 2011). In addition, they have a high efficacy of utilizing hydrocarbons as a carbon and/or energy source and producing biosurfactants (Das and Chandran 2011). Particularly, *Pseudomonas putida* is a non-pathogenic species that contains both alkane monooxygenase and *PAH* dioxygenase, which are responsible for encoding the enzymes responsible for alkane and PAHs degradation, respectively.

2.4 Enzymes Required for Crude-oil Biodegradation

For the alkane degradation pathway, alkane monooxygenase is an enzyme that partakes in the terminal oxidation of the alkane degradation metabolic pathway (Kloos, Munch et al. 2006; van Beilen, Funhoff et al. 2006; van Beilen and Funhoff 2007). Several different genes, including *alkB*, cytochrome P450, sMMO, and pMMO (van Beilen and Funhoff 2005; Kloos, Munch et al. 2006; Das and Chandran 2011); have been found to encode this enzyme based on different metabolic pathways or different microbial genomes. The two chosen for this study were the *alkB* and *P450* genes. *alkB* was chosen because it encodes an integral membrane non-heme diiron alkane hydroxylase that is known for its high sequence diversity (Wang, Wang et al. 2010). It has been identified in around 45 bacterial species, including *Pseudomonas putida*, that have been capable of degrading C_3-C_{13} or C_{10}-C_{20} alkanes (Rojo 2010; Wang, Wang et al. 2010). On the other hand, P450 expresses a cytochrome, heme-thiolate protein, which has been identified in over 18 species from various microbial domains capable of degrading C_5-C_{12} alkanes (Rojo 2010; Wang, Wang et al. 2010). The enzyme encoded by P450 is considered

equally capable of alkane degradation as the alkane hydroxylase encoded by *alkB* and was recently discovered in *Pseudomonas putida* (Kubota, Nodate et al. 2005; Rojo 2010).

For the PAH degradation pathway, the ring-hydroxylating dioxygenase (RHD) enzyme is part of the alpha subunit in the terminal dioxygenase that incorporates the last oxygen into the aromatic nucleus. In particular the alpha subunit consists of the Rieske center and the iron containing catalytic domain. If just one of these conserved regions were to be selected as the gene target then the sequence would have to be highly selective for a given microbial species or loose specificity towards PAH dioxygenase. Therefore, the PAH-RHD$_\alpha$ gene was chosen based on its general specificity towards PAH degraders.

2.5 Gas Chromatography and Mass Spectrometry

Gas chromatography and mass spectrometry (GC/MS) is a method of identifying compounds within a given sample. Gas chromatography was first realized by Martin and James in 1952 but was not combined with mass spectrometry until 1959 by Gohlke (Bartle and Myers 2002). Since then the combination has been widely used in forensic science and the identification of contaminants in environmental samples.

Gas chromatography utilizes the boiling points of a compound's individual components to separate them. Carrier gases, such as, helium, argon, or nitrogen transport the gases through a column to a detection port (Fig. 2.1). There the spectral data is collected and the individual components are identified based on their retention time (Fig. 2.2). On the other hand, mass spectrometry uses ionization to amplify the individual charge of each component. Samples are placed into an ionization chamber where they are bombarded with electrons. The charged particles are then sent towards a series of amplification surfaces before being analyzed (Fig 2.3). (Hengstmann, Chin et al. 1999)

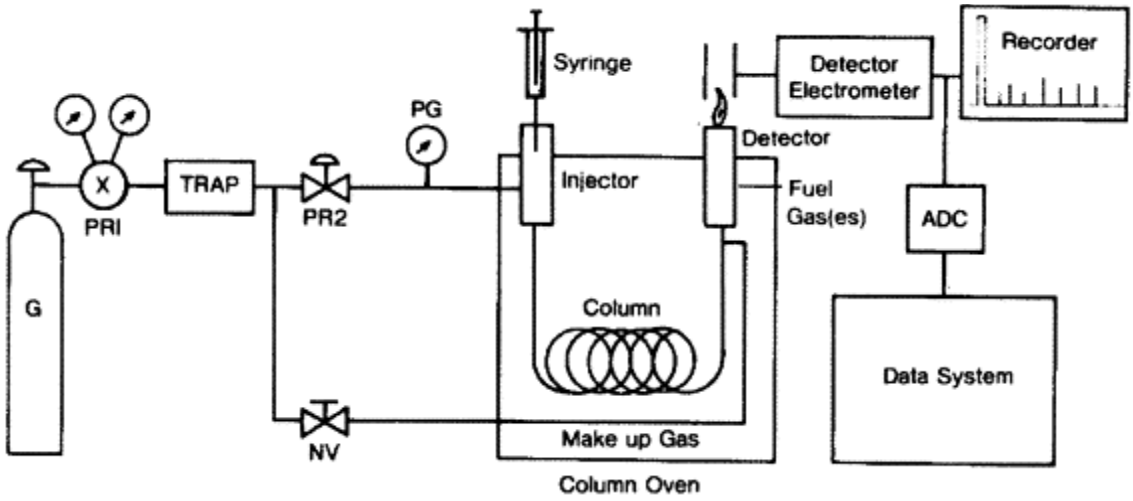

Figure 2.1. Schematic of a gas chromatograph. (Bartle and Myers 2002)

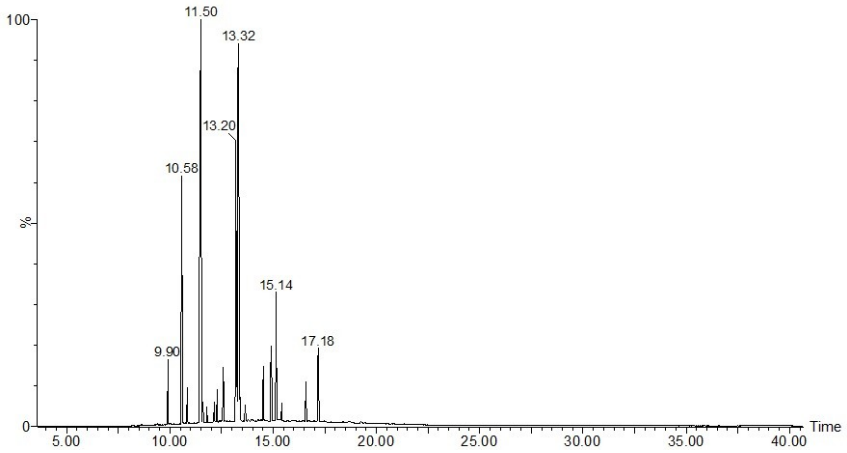

Figure 2.2. Example of a gas chromatograph. (This study)

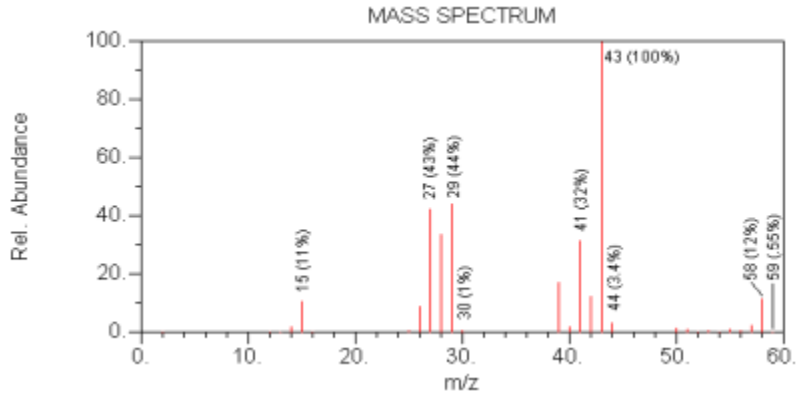

Figure 2.3. Example of mass spectrum. (Bartle and Myers 2002)

2.6 Polymerase Chain Reaction

Polymerase chain reaction (PCR) was developed by Kary Mullis in 1985 (NCBI, 2012). This process allows for specific targets sequence from the given DNA to be amplified and studied. Essentially, the dsDNA is placed in a master mix containing: taq polymerase, a forward and reverse primer, and dNTPs. As the temperature rises, the double-helix structure of the DNA is broken apart allowing for the primers to bind to a specific sequence that is unique to the intended target. As the temperature lowers, the taq polymerase binds the free dNTPs from solution to their complementary base pair. As this continues, eventually two identical DNA strands are formed from the original and then the process is repeated.

The PCR process is strictly qualitative. Results are analyzed once all the cycles are completed using gel-electrophoresis (Fig. 2.4). However, quantitative-PCR (qPCR) allows for the samples to be analyzed at each cycle. During the qPCR process samples are analyzed against a standard curve formed from the serial dilution of a product containing the specified target. The different concentrations will amplify at different cycles, higher concentrations amplyfing at earlier cycles than lower concentrations. When the sample are analyzed against the standard those samples having a higher quantity of the given target sequence will also show earlier signs of amplification. At any given threshold the amplification data for a sample can then be compared to the known quantity within the standard (Fig. 2.5).

The downside of these strategies is that they are sensitive to the presence of inhibitors found in environmental samples. This inhibitors, such as humic acids, are co-extracted along with gDNA and can result in false positives of gDNA concentrations (Frostegard, Courtois et al. 1999). In addition, these inhibitors interact with taq polymerase preventing proper amplification of the target sequence (Opel, Chung et al. 2009).

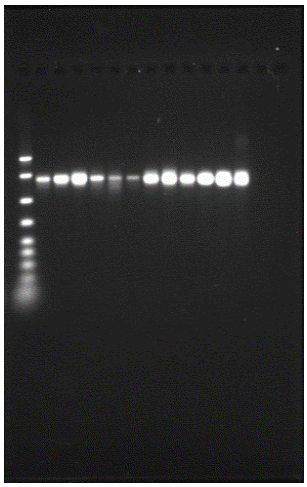

Figure 2.4. Example of PCR products imaged using gel-electrophoresis. (This study)

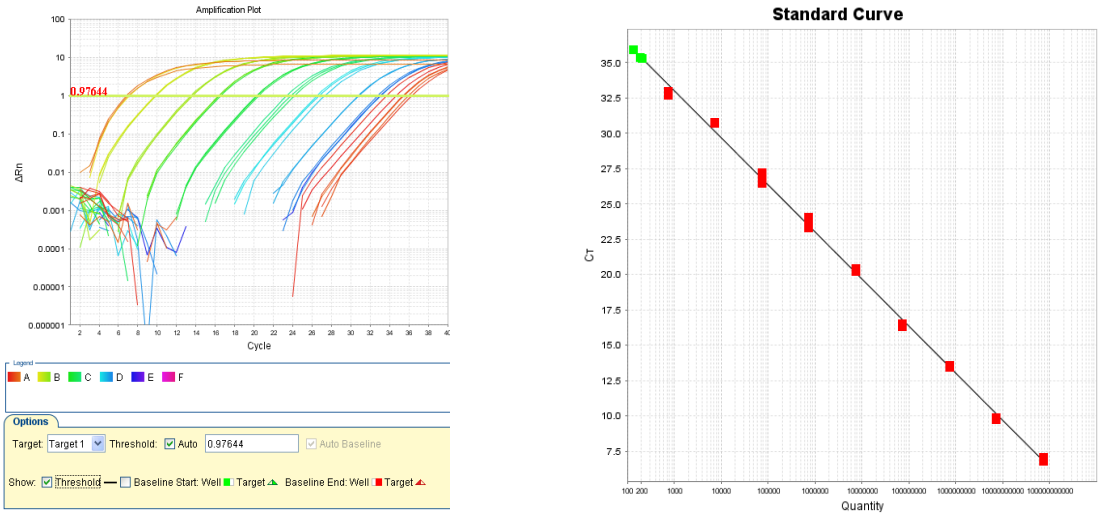

Figure 2.5. (Left) the amplification plot and (right) standard curve formed from the qPCR standard using the qPCR analysis. (This study)

2.7 Pyrosequencing

Next-generation sequencing was first introduced to the public in 2007. As opposed to Sanger sequencing, pyrosequencing offered a high-thoroughput system that was more sensitive, efficient, and accurate (Schuster 2008). It also allowed for parallel processing based on a system of barcoded primers that allowed for each sample and target to be labeled for individual identification.

Samples go through a PCR amplification process in which the primers and specific barcodes are attached to ssDNA within a given sample. Each dNTP is added individually. If it is complimentary then a pyrophosphate (PPi) is released and converted to ATP. The ATP is used to drive the light emission process. All of the un-utilized dNTP and ATP is continuously degraded allowing for the next dNTP to be added once the process is complete (Fig. 2.6). Nucleotide sequence is determined from the signal peaks in the Pyrogram trace (Fig. 2.7). (2004)

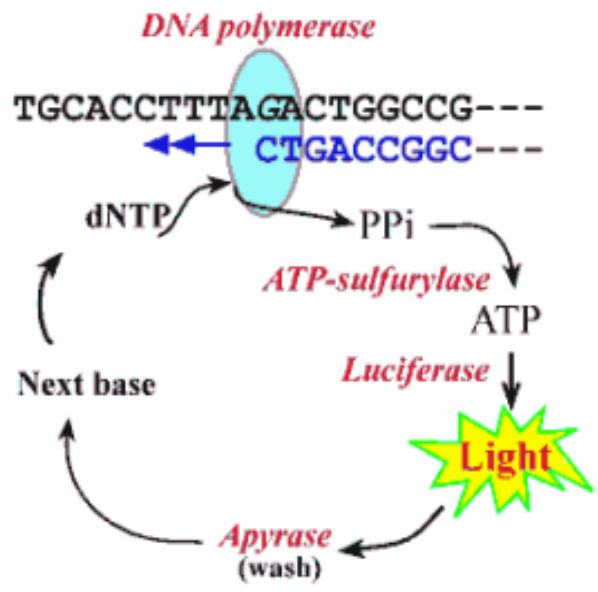

Figure 2.6. Pyrosequencing process. (2004)

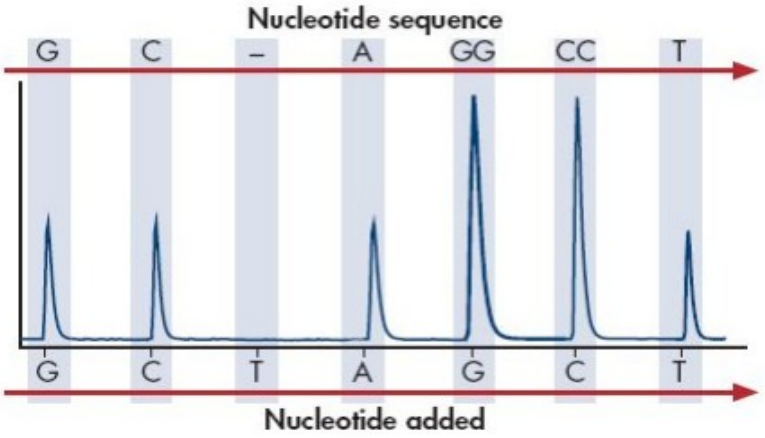

Figure 2.7. Example of pyrosequencing results. (2004)

Chapter Three: Microbial community analysis of Deepwater Horizon oil-spill impacted sites along the Gulf Coast using functional and phylogenetic markers

Abstract

We investigated the impact of the Deepwater Horizon oil spill on microbial assemblages in sediment, soil and seawater samples collected from sites along the Gulf Shore. Based on a GC/MS analysis only one sample from Bay Jimmy, LA, had detectable signs of hydrocarbon contamination, identified as n-alkanes similar to the GC/MS pattern of the Deepwater Horizon source oil (MC – 252). To identify changes in microbial assemblage structure and functional diversity in response to hydrocarbon contamination five genes were selected (bacterial 16S rRNA, *Pseudomonas*-specific 16S rRNA, *alk*B, P450, and PAH-RHD$_\alpha$) to determine phylogenetic affiliation and specific enzymes encoded by bacteria to degrade alkanes and polycyclic aromatic hydrocarbons (PAHs). A qPCR analysis revealed the presence of alkane and PAH-degrading genes in contaminated and non-contaminated samples, with no significant difference in gene content between the different samples. However, the ribotype analysis identified 17 bacteria genera known for their capacity to degrade hydrocarbons, including *Mycobacterium*, *Novosphingobium*, *Parvibaculum*, *Pseudomonas*, and *Sphingomonas*, with the highest relative abundance of these potential hydrocarbon degraders found within the contaminated soil sample. Furthermore, the contaminated sample had a very high relative abundance of 16S rRNA gene sequences affiliated with the genus *Parvibaculum*, members of which have been characterized for their degradative abilities. These data suggest that specific bacterial taxa within the genus *Parvibaculum* have the capacity for hydrocarbon degradation and

can use the hydrocarbons as a carbon and energy source, resulting in a dominant population within a hydrocarbon-contaminated soil.

Keywords

Bioremediation; GC/MS; PCR; quantitative PCR (qPCR); pyrosequencing; alkane monooxygenase; PAH dioxygenase; microbial community analysis

3.1. Introduction

In the past 20 years the world has experienced two of the largest oil spills to date; the largest being the Kuwait oil spill in 1991 during the Gulf War and second largest being the Deepwater Horizon oil spill in 2010 in the Gulf of Mexico (Camilli, Reddy et al. 2010; Casselman 2012). In both cases initial approaches to contain and remove the oil consisted mainly of booms with skimmers (Casselman 2012). In the case of the Deepwater Horizon spill, the oil was burned and dispersants were applied to reduce the ecological impact of hydrocarbon contamination. The problem with each of these approaches is that they are containment strategies and lack the capability of removing all of the oil from the contaminated site (Chauhan, Fazlurrahman et al. 2008; Das and Chandran 2011).

It is important that these contaminants be removed due to the toxic effects of crude oil to humans and the environment. Many of the hydrocarbons found in crude oil can cause temporary fatigue or drowsiness in humans; however, more severe health effects , such as paralysis and cancer, can result depending on the length and method of exposure and the specific type of contaminant (2008; 2008; Goldstein, Zempsky et al. 2011). In addition, some hydrocarbons

have the potential to persist in the environment, increasing the risk for the contaminant to move up through the food chain (Ahangar 2010; Aigner, Burgess et al. 2010).

As an alternative strategy, bioremediation has been used to contain and remove crude oil contaminants in soil and groundwater since the Hanahan Bioremediation Project of 1992, in which the indigenous population was biostimulated to help treat contaminated groundwater (Chapelle 1997). In general, bioremediation is the process of utilizing microorganisms capable of degrading contaminants into less harmful substances. This method has the potential to be non-invasive and is cost-effective as compared to other methods, such as adding biosurfactants or absorbants (Chauhan, Fazlurrahman et al. 2008; Das and Chandran 2011). However, whether or not this method can be used at a specific site is heavily dependent on the availability of the indigenous microorganisms which contain the specific enzymes required for hydrocarbon degradation. In addition, the environmental conditions, such as the amount of nutrients and competitive levels at which these organisms thrive, must be maintained after exposure. While approaches such as bioaugmentation and biostimulation can be used to overcome such obstacles, natural attenuation remains a popular topic of study (Chauhan, Fazlurrahman et al. 2008; Das and Chandran 2011).

Previous studies (Chadhain, Norman et al. 2006; Kloos, Munch et al. 2006; van Beilen, Funhoff et al. 2006; Wang, Wang et al. 2010) have been conducted on different bacterial and fungal species to determine their role in degrading crude oil constituents, such as PAHs and alkanes. A recent study by Hazen et al. (2010) found that areas directly surrounding the oil plume contained a newly discovered bacterial taxa affiliated with the *Oceanospiralles* that was at high relative abundance within the contaminated water column. However, this *Oceanospiralles* taxa has only been identified in marine samples (e.g., as a bacterial symbiont in bone-devouring

worms) and has not been identified in contaminated soils. Among the soil and sediment bacteria studied that have been found to contain hydrocarbon-degrading capabilities, members of the genus *Pseudomonas* (e.g., *Pseudomonas putida*) has been identified as the most abundant species in hydrocarbon-contaminated soils and in some aquatic environments (Hazen, Alusi et al. 2010; Das and Chandran 2011). In addition, *Pseudomonas* spp. are able to utilize hydrocarbons as a carbon and/or energy source and produce biosurfactants (Das and Chandran 2011). Particularly, *Pseudomonas putida* is a non-pathogenic species that expresses both alkane monooxygenase and PAH dioxygenase that are responsible for alkane and PAHs degradation, respectively.

For the alkane degradation pathway, alkane monooxygenase is responsible for the terminal oxidation step of the alkane degradation metabolic pathway (Kloos, Munch et al. 2006; van Beilen, Funhoff et al. 2006; van Beilen and Funhoff 2007). Several different genes, including *alk*B, cytochrome P450, sMMO, and pMMO (van Beilen and Funhoff 2005; Kloos, Munch et al. 2006; Das and Chandran 2011) have been related to alkane monooxygenase activity. The two chosen for this study were the *alkB* and *P450* genes. The *alkB* encodes an integral membrane non-heme di-iron alkane hydroxylase that is known for its high sequence diversity (Wang, Wang et al. 2010). It has been identified in around 45 bacterial species, including *Pseudomonas putida*, that are capable of degrading C_3-C_{13} or C_{10}-C_{20} alkanes (Rojo 2010; Wang, Wang et al. 2010). On the other hand, P450 expresses a cytochrome, heme-thiolate protein, that has been identified in over 18 species from various bacterial phyla and is capable of degrading C_5-C_{12} alkanes (Rojo 2010; Wang, Wang et al. 2010). The enzyme encoded by P450 is considered equally capable of alkane degradation as the alkane hydroxylase encoded by *alkB* and was recently discovered in *Pseudomonas putida* (Kubota, Nodate et al. 2005; Rojo 2010).

For the PAH degradation pathway, the PAH-RHDα gene found in gram negative bacteria was chosen based on its general specificity towards PAH degraders, such as *Pseudomonas*, *Ralstonia*, *Burkholderia*, and *Sphingomonas*. The ring-hydroxylating dioxygenase (RHD) enzyme is part of the alpha subunit in the terminal dioxygenase that incorporates the last oxygen into the aromatic nucleus. In particular the alpha subunit consists of a Rieske center and an iron-containing catalytic domain which make up a conserved region of the gene targetencoding specific enzymes including nahAc, ndoB, pahAc, phnAc, phnA1, etc.

The clean-up attempts after the 2010 Deepwater Horizon oil spill left behind an estimated 75% of the total oil spilled into the Gulf. Due to the expected effects from long-term exposure, an analysis needs to be conducted in order to access the crude oil degradative capabilities of the indigenous microbial populations at contaminated sites. Therefore, the objective of this study was to survey microbial assemblages in soil, sediment and seawater samples affected by the oil spill using both functional and phylogenetic markers.

3.2. Materials and Methods

3.2.1. Sample collection and storage

Samples were collected along the coastal regions of Louisiana and Alabama based on their proximity to the oil spill site and being known as contaminated areas (Aigner, Burgess et al. 2010) (Fig. 3.1), with sample information also collected at each site (Table 3.1). Samples (sediment and seawater) collected along the Alabama coastline were obtained in December 2010 with the help of the Dauphin Island Sea Lab in Alabama. The seawater sample was collected in a sealable semi-transparent 1 L container directly off shore from the banks of Sandy Bay, AL.

Samples collected from the Louisiana coastline were obtained from a collaboration with the Department of Geology (Dr. Ming-Kuo Lee) at Auburn University (Auburn, AL). Core samples were collected from Bay Jimmy "North" and Bayou Dulac, LA using a Wildco hand corer with a two-meter extension and stored in a clear plastic 50 cm sealable tube. The sample collected from Bay Jimmy "South," LA was a surface soil obtained from a highly contaminated bank and stored in a sealed, clear plastic bag at 4°C. Sediment and soil samples were stored at -20°C until further use and seawater samples were stored at 4°C upon arrival at the laboratory.

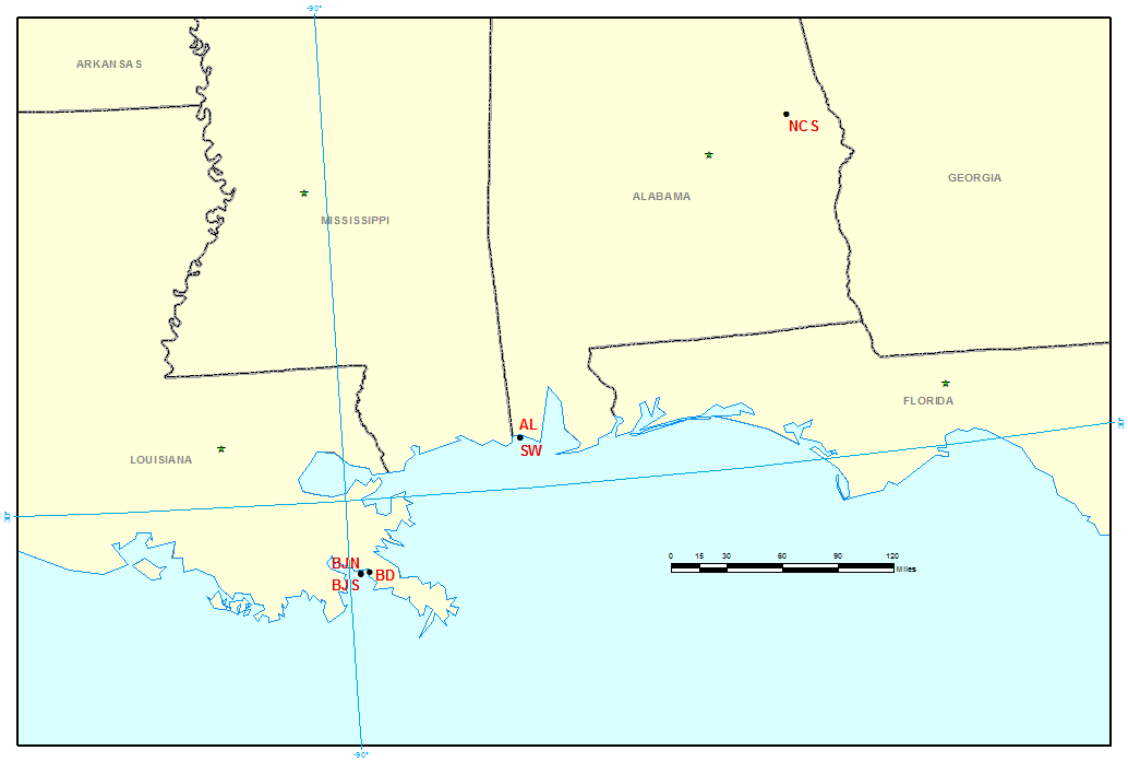

Figure 3.1. Locations of extracted environmental samples in reference to oil spill. (0) Deepwater Horizon, Gulf of Mexico; (1) Bay Jimmy "South," LA; (2) Auburn, AL; (3) Bay Jimmy "North," LA; (4) Bayou Dulac, LA; (5) Sandy Bay, AL.

Table 3.1. Sample identification and description.

Reference ID	Location	Sample Description
BJS	Bay Jimmy "South", LA (29˚26.683'N, 89˚53.454'W)	Soil sample collected off a vegetative bank coated in oil[1]
NCS	Auburn, AL (32˚35.457' N, 85˚29.579' W)	Garden soil collected from the grounds of Auburn University's Arboretum
BJN	Bay Jimmy "North", LA (29˚27.236'N, 89˚53.512'W)	Core sample of sediment collected offshore[2]
BD	Bayou Dulac, LA (29˚27.392'N, 89˚48.469'W)	Core sample of sediment collected offshore[2]
AL	Sandy Bay, AL (30˚22.644'N, 88˚18.900'W)	Sediment collected from the marsh region of the bay
SW	Sandy Bay, AL (30˚22.644'N, 88˚18.900'W)	Seawater collected just offshore of the bay

Note: Oil spill coordinates: 28° 44′ 11.86″ N, 88° 21′ 57.59″ W

[1]Triplicates made due to the high variability of the sample.

[2]Triplicates made based on 15 cm increments from the sediment surface. At each point 5 cm of sample was removed from the core and used as the experimental sample.

3.2.2. Bacterial Strains and Growth Conditions

Pseudomonas putida, strain DSM 8368 (DSMZ; Braunschweig, Germany) was selected as a positive control for containing enzymes necessary to degrade hydrocarbons (Guerin and Boyd 1995; Morasch, Richnow et al. 2002; Das and Chandran 2011). Cells were revived on Difco™ triptic soy agar (TSA) medium (Sparks, MD) and incubated at 30°C for 3 days. Colonies were transferred to Difco™ triptic soy broth (TSB) (Sparks, MD) and incubated at ambient temperatures in an orbital shaker (GallenKamp; Leicestershire, England) at 300 rpm for 4 days. For PAH-RHD$_\alpha$ gene, the *P. putida* culture was required to be enriched in the presence of naphthalene in order to obtain the target gene for the qPCR standard. The enrichment was implemented by transferring 10% of the inoculated medium into fresh minimal media containing various concentrations of naphthalene (150 or 200 mg/L) as the sole carbon source. Cultures were incubated at ambient temperatures in an orbital shaker set at 300 rpm and the bacterial growth was monitored using the absorbance by a Nanodrop spectrophotometer (Thermo Scientific; Barrington, IL). Once stationary growth was observed, typically reached after 5 days, cultures were transferred to fresh minimal media for further growth. At the point of each transfer, gDNA was extracted and PCR assays (for details see below) were conducted to verify the presence of the target gene.

3.2.3. Genomic DNA Extraction

Genomic DNA was extracted from the soil samples using the Ultra Clean DNA Isolation Kit for Soils (Mo Bio Laboratories; Solon, OH). Approximately 0.5 g (wet weight) of soil/sediment was used for each extraction. Pure cultures required an initial centrifugation at 6750 × g for 5 min. This allowed for the supernatant to be decanted and the concentrated pellet to be used for the

extraction process. Genomic DNA from the seawater sample was extracted according to the manufacturer's instructions for the Rapid Water DNA Isolation Kit (Mo Bio; Carlsbad, CA). DNA concentrations for all samples were obtained using the Nanodrop ND 1000 Spectrophotometer (Thermo Scientific; Barrington, IL). The optical density at 260 and 280 nm ($OD_{260/280}$), was monitored to identify whether potential inhibitors had been co-extracted. For samples showing an $OD_{260/280}$ value lower that 1.8, gDNA was re-extracted until optimal conditions were obtained.

3.2.4. Gas Chromatography and Mass Spectrometry Analysis

Organic substrates were extracted from the soil and seawater samples using the modified EPA method 3570. Additional modifications were made in order to increase the end yield. Samples were thawed at 4°C and homogenized by manual mixing. 3 g (wet weight) of sample were mixed with approximately 2.5 – 5 g of anhydrous sodium sulfate (Na_2SO_4). 10 mL of dichloromethane (CH_2Cl_2) was added and the vial was rotated on a Rugged Laboratory Rotator (Diagger; Vernon Hills, IL) for at least 24 hours. In order to liberate the liquid extract from the soil the vials were centrifuged at 3000 rpm for 10 min. The liquid extract was pipetted from the vial and passed through a 0.2 µm syringe filter to remove any remaining particulates before being left to dry under Nitrogen gas for approximately 30 min. The dried residual was then re-dissolved using 1.5 mL of the chromatography grade hexane and left to sit for 10 min. The final solution was then transferred to a 2 mL clear GC vial and stored at -20°C until analyzed.

The GC/MS analysis was conducted by the Mass Spec Center at Auburn University (Auburn, AL). Gas chromatography was conducted on a Waters 6890N (Waters; Milford, MA) using a DB5-MS column (J&W Scientific; Folsom, CA) combined with a Time of Flight Mass

Analyzer (Waters; Milford, MA). 3 µL was injected into the column with a temperature program of: 40°C to 100°C at 15°C/min, to 250°C at 8°C/min, to 300°C at 20°C/min. Electron fragmentation patterns (70 eV) with forward and reverse match scores above 800 and 90% or higher probability were considered matches to the compound library (NIST; Gaithersburg, MD). Identification was confirmed using a mass spectrometer with an internal calibrator of heptacosafluorotributylamine (Sigma Aldrich; Oakville, Ontario) set at a lock mass of 118.9919 m/z, and using isotope modeling by comparing the experimental and theoretical isotope distributions. In addition, the results for each sample were compared against the results for the uncontaminated negative control soil (NCS) and the BP source MC - 252 crude oil (positive control), obtained from Florida Department of Environmental Protection (FDEP) in collaboration with Auburn University's Geology Department, in order to identify contaminants that may have been related to the recent oil spill.

3.2.5. Primer Selection

Primers selected for this study were based on their overall relevance to the biodegradation process of crude oil contaminants, specifically alkanes and PAHs (Table 3.2). Genes that encode alkane degrading enzymes were identified based on two primer sets that target alkane monooxygenases. Two primer sets were chosen since bacteria have multiple metabolic pathways that utilize this specific enzyme (Kloos, Munch et al. 2006; van Beilen, Funhoff et al. 2006; van Beilen and Funhoff 2007). The first primer set targeting the *alkB* gene was *alkB*-1f (Kloos, Munch et al. 2006) (Table 3.2). The second primer set targeted the *P450* gene, part of the CYP153 gene, which consists of *P450*fw1 and *P450*rv3 (van Beilen, Funhoff et al. 2006) (Table 3.2). To identify the ability to degrade polycyclic aromatic hydrocarbons (PAHs), a primer set

was chosen that targets the gene which encodes the ring-hydroxylating-dioxygenase enzyme. The primer set consists of PAH-RHD$_\alpha$ GN F and PAH-RHD$_\alpha$ GN R (Cebron, Norini et al. 2007) (Table 3.2).

The *Pseudomonas* genus-specific 16S rRNA primer set targets a conserved domain of the small submit rRNA of several *Pseudomonas* species, including *Pseudomonas putida* that are have been identified as hydrocarbon degraders (Tsai and Olson 1992; Guerin and Boyd 1995; Morasch, Richnow et al. 2002; van Beilen, Funhoff et al. 2006; Hazen, Alusi et al. 2010; Das and Chandran 2011). The primer set chosen for this target gene included Ps-for and Ps-rev (Widmer, Seidler et al. 1998) (Table 3.2).

We also used a universal bacterial 16S rRNA gene primer set to characterize the structure of the bacterial assemblages in each of the environmental samples (Hazen, Alusi et al. 2010). To target the 16S rRNA gene among diverse members of the domain Bacteria, several primers were used , including 27F and 1492R for PCR (Martin-Laurent, Philipot et al. 2001), BACT1369F PROK1492R , and probe TM1389F for the qPCR analysis (Suzuki, Taylor et al. 2000), and the bar-coded primers V1-9F and V3-541R for the pyrosequencing analysis (Table 3.2).

Table 3.2. Detailed information about the primers and probes used in this study.

Gene and Primer Name	5'-3' Sequence	Size (bp)	Reference
Bacterial 16S rRNA			
Bact1369F	CGGTGAATACGTTCYCGG		
Prok1492R	GGWTACCTTGTTACGACTT	123	Suzuki, 2000[a, 1]
TM1389F (probe)	CTTGTACACACCGCCCGTC		
27F	AGAGTTTGATCMTGGCTCAG	1500	Martin-Laurent, 2001[2]
1492R	TACGGHTACCTTGTTACGACTT		
V1-9F	X-AC-GAGTTTGATCMTGGCTCAG	532	Chun, 2010[b, 3]
V3-541R	X-AC-WTTACCGCGGCTGCTGG		
Pseudomonas Specific 16S rRNA			
Ps-for	GGTCTGAGAGGATGATCAGT	990	Widmer, 1997
Ps-rev	TTAGCTCCACCTCGCGGC		
Alkane monooxygenase			
alkB-1f	AAYACNGCNCAYGARCTNGGNCAYAA	550	Kloos, 2006
alkB-1r	GCRTGRTGRTCNGARTGNCGYTG		
*P450*fw1	GTSGGCGGCAACGACACSAC	339	van Beilen, 2005
*P450*rv3	GCASCGGTGGATGCCGAAGCCRAA		
PAH dioxygenase			
PAH-RHD GN F	GAGATGCATACCACGTKGGTTGGA	306	Cébron, 2008
PAH-RHD GN R	AGCTGTTGTTCGGGAAGAYWGTGCMGTT		

Note: If not specified primer sets were used for both PCR and qPCR assays.

[a]qPCR assay was conducted with TaqMan Universal Master Mix (Life Technologies; Grand Island, NY), otherwise Fast SYBR Green Master Mix (Life Technologies; Grand Island, NY) was used.

[b]X denotes the 7~11 nucleotide long barcode and AC denotes a common linker for all bacteria.

[1]Primer used for qPCR assay.

[2]Primer used for PCR assay.

[3]Primers used for pyrosequencing assay.

3.2.6. PCR and qPCR assays

PCR assays were conducted using 25 µL reaction volumes. Results for each amplicon was confirmed through gel electrophoresis using Gel Logic 100 Imaging System (Kodak and Carestream Health; Rochester, NY) with a 1 – 2 % agarose gel ran at 100 V for 1 – 1.25 hr. However, since this analysis does not allow for a quantitative analytical comparison between samples, a quantitative polymerase chain reaction (qPCR) was conducted for each target gene. Samples were analyzed with the StepOne™ Real-time PCR system (Life Technologies; Grand Island, NY) using a SYBR Green Master mix (Life Technologies) unless otherwise specified. Results were normalized per the amount of soil or water used for each extraction. Based on these results the variation of coefficients (CV) was calculated by dividing the result of each duplicate by the average and multiplying by 100.

For the *alkB* gene, a touch-down PCR was conducted which contained 2.5 µL of 1× Takara PCR buffer without $MgCl_2$, 1.5 µL of 1.5 mM $MgCl_2$, 2 µL of 0.2 mM dNTPs, 2 µL of 0.8 mM each primer, 0.25 µL of 1.25 U of Takara *Ex Taq* polymerase, and 1 µL of gDNA at 10 – 50 ng/µL. The temperature cycle consisted of: 94°C for 4 min, followed by 10 cycles of 94°C for 30 sec; 65-56°C for 30 sec decreasing on a 1°C increment with each cycle; 72°C for 1 min, then 22 cycles of 94°C for 30 sec; 55°C for 30 sec; 72°C for 1 min, and a final extension with 72°C for 10 min. The qPCR assay used a 25 µL reaction volume that consisted of 12.5 µL of 1× Fast SYBR Green Master Mix, 1 µL of 0.5 µM of each primer, and 0.5 µL of gDNA. The temperature cycle consisted of: 95°C for 10 min, followed by 45 cycles of 95°C for 10 sec, 56°C for 30 sec, and the subsequent disassociation analysis.

For the P450 gene, the PCR was conducted using 2.5 µL of 1× PCR buffer, 2.5 µL of 2.5 mM $MgCl_2$, 2 µL of 0.2 mM dNTPs mixture, 1.25 µL of 0.5 mM each primer, 0.25 µL of 1.25 U

of *Taq* polymerase, and 2 µL of gDNA. The temperature cycle consisted of: 94°C for 4 min, followed by 32 cycles of 94°C for 45 sec; 58°C for 1 min; 72°C for 1 min, and the extension with 72°C for 5 min. The qPCR assay used a 20 µL reaction volume, which consisted of 10 µL of 1× Fast SYBR Green Master, 1 µL of 0.5 µM of each primer, and 5 µL of gDNA. The temperature cycle consisted of: 95°C for 10 min, followed by 40 cycles of 95°C for 10 sec, 58°C for 30 sec, and 72°C for 30 sec, followed by the disassociation cycle.

The PCR reaction for the PAH-RHD$_\alpha$ gene consisted of 2.5 µL of 1× Takara PCR buffer without $MgCl_2$, 1.5 µL of 2.5 mM $MgCl_2$, 2 µL of 0.2 mM dNTPs, 0.5 µL of 0.2 mM of each primer, 0.25 µL of 1.25 U of Takara Ex *Taq* polymerase, and 1 µL of gDNA at about 1 – 5 ng/µL. The temperature cycle consisted of: 94°C for 5 min, followed by 30 cycles of 94°C for 30 sec, 57°C for 30 sec, and 72°C for 30 sec, and a final extension with 72°C for 5 min. The qPCR assay used a 25 µL reaction volume consisting of 12.5 µL of 1× Fast SYBR Green Master, 1 µL of 0.4 µM of each primer, and 1 µL of gDNA. The temperature cycle of the qPCR assay consisted of: 95°C for 5 min, followed by 40 cycles of 95°C for 30 sec, 58°C for 30 sec, and 72°C for 30 sec, followed by one cycle of 80°C for 10 sec and one cycle of 72°C for 7 min, finished with the disassociation cycle.

The PCR procedure for the *Pseudomonas* genus-specific 16S rRNA target consisted of 5 µL of 1× Takara PCR buffer without $MgCl_2$, 3 µL of 2 mM $MgCl_2$, 2.6 µL of 0.3 mM dNTPs, 4 µL of 0.8 mM each primer, 0.3 µL of 0.75 U of Takara *Ex Taq* polymerase, and 1 µL of gDNA. The temperature cycle consisted of: 95°C for 5 min, followed by 30 cycles of 94°C for 45 sec; 66°C for 1 min; 74°C for 1 min, and a final extension with 74°C for 10 min. The qPCR assay used a reaction volume of 20 µL consisting of 10 µL of 1× Fast SYBR Green Master Mix (Life Technologies; Grand Island, NY), 1.4 µL of 0.7 µM of each primer, and 5 µL of gDNA. The

temperature cycle consisted of: 95°C for 15 min, followed by 40 cycles of 95°C for 10 sec, 65°C for 15 sec, and 72°C for 20 sec, following by a disassociation cycle of 95°C for 30 sec, 65°C for 1 min, 95°C for 30 sec.

For the PCR assay of the universal bacterial 16S rRNA gene the reaction consisted of 2.5 µL of 1× Takara PCR buffer without $MgCl_2$ (Fischer Scientific; Pittsburgh, PA), 2 µL of 2 mM $MgCl_2$, 4 µL of 0.4 mM dNTPs, 2.5 µL of 1 mM each primer, 0.3 µL of 1.5 U of Takara *Ex Taq* DNA polymerase (Fischer Scientific; Pittsburgh, PA), and 1 µL of gDNA at 2 ng/µL. The temperature cycle consisted of: 94°C for 5 min, followed by 30 cycles of 94°C for 1 min; 55°C for 1 min; 72°C for 2 min, and a final extension with 72°C for 15 min. The qPCR assay used a 20 µL reaction volume consisting of 10 µL of 1x TaqMan Universal Master Mix (Life Technologies; Grand Island, NY), 0.8 µL of 0.8 µM of each primer, and 5 µL of gDNA. The temperature cycle consisted of: 95°C for 2 min, followed by 40 cycles of 95°C for 1 min, 55°C for 1 min, and 72°C for 2 min.

3.2.7. Standard Curve Construction for qPCR Assay

The plasmid dsDNA standard for the *alkB* gene was kindly provided by the collaborator, Dr. Sinéad Ní Chadhain at the University of South Alabama. The three plasmid dsDNA standards were prepared for the P450, PAH-RHD_{α}, and universal bacterial 16S rRNA as follows. The gDNA were extracted from the sediment soil from Sandy Bay, AL; the pure *P. putida* culture grown with naphthalene-selective media; or the pure *P. putida* for the P450, PAH-RHD_{α}, and universal bacterial 16S rRNA gene targets, respectively. The PCR amplicons of these three genes were obtained from the amplification of gDNA with the gene-specific primer set as described above and listed in Table 3.2. The PCR products were excised from their gel molds and purified

using the Gel DNA Extraction Kit (Zymo Research; Irvine, CA). The quantity and the purity of the purified amplicons were obtained by the OD_{260} and $OD_{260/280}$, respectively. The PCR amplified and purified genes were ligated into the pCR - 2.1 TOPO vectors, and the plasmids were chemically transformed into the competent *E. coli* cells (TOP10F') using the Invitrogen TOPO TA Cloning® kit (Life Technologies; Grand Island, NY). The plasmid DNAs were extracted from *E. coli* clones using Qiagen Spin Mini-prep kit (Qiagen;Valencia, CA). Verification that the target genes were successfully inserted into the clones was performed by colony-PCR with M13F/R primers, restriction enzyme digestion with EcoR I (New England Biolabs, Ipswich, MA), and gene sequencing conducted by the Auburn University Sequencing Lab (Auburn, AL). The sequenced genes were confirmed by BLASTn comparison to the Genbank nr/nt database (NCBI). The copy numbers of the four plasmid DNAs were calculated from the DNA concentrations (at OD_{260}) and the combined molecular weights of the specified target gene and that of the TOPO vector plasmid. Each plasmid dsDNA was serially diluted for the construction of standard curves for the qPCR assay.

For the *Pseudomonas* genus-specific 16S rRNA gene the dsDNA gene standard was made directly from the PCR products (990 bp), which were obtained from the amplification of gDNA extracted from the pure *P. putida* bacterial culture (see details above). The copy numbers of the *Pseudomonas* genus-specific 16S rRNA gene was calculated from the DNA concentration determined by measuring absorbance at 260 nm and the molecular weight of the gene target. The dsDNA standard was serially diluted to be used for the standard curve construction for the qPCR assay targeting *Pseudomonas* genus-specific 16S rRNA genes.

3.2.8. Pyrosequencing

Genomic DNAs (gDNA) of six samples (BJS, BJN, BD, AL, SW, and NCS) were sent to the National Instrumentation Center for Environmental Management (Seoul, Korea) and sequenced using a 454 GS FLX Titanium Sequencing System (Roche, Mannheim, Germany). Pyrosequencing was implemented in a 50 μL reaction volume containing 1× PCR buffer (Roche, Mannheim, Germany), 0.2 mM of dNTPs, 400 nM of each primer, 1 mg/mL of bovine serum albumin (BSA) (Sigma-Aldrich, St. Louis, MO, USA), 1.25 U of Taq DNA polymerase (Roche, Mannheim, Germany) and 1 μL of 1:10 dilution of gDNA of sample. Thermal cycling followed a touch-down PCR method consisting of: 94°C for 5 min, followed by 10 cycles at 94°C for 30 sec, 60 - 56°C for 45 sec decreasing 0.5°C per cycle, and 72°C for 90 sec, followed by 20 cycles at 94°C for 30 sec, 55°C for 45 sec, and 72°C for 90 sec.

Results were analyzed with the MOTHUR software package (version 1.23.1) (Schloss, Westcott et al. 2009). Reads were clustered based on the PyroNoise algorithm (Quince, Lanzen et al. 2011) and chimeric sequences were removed (Wright, Yilmaz et al. 2012). Sequences were classified to the genus level using a 80% bootstrap cut-off value based on silva taxonomy (Pruesse, Quast et al. 2007), and to remove poor quality sequences. The program then merged sequences and calculated pair-wise distances based on the Neddleman algorithm. Sequences were clustered into operational taxonomic units (OTUs) with a 97% similarity or higher based on the furthest neighbor algorithm. Chao1 and Shannon's diversity index were formed using MOTHUR. Good coverage was calculated as $G = 1 - n/N$, where n is the number of individual phylotypes and N the number of total sequences. Phylogenetic trees were constructed by neighbor-joining analysis using Molecular Evolutionary Genetics Analysis (MEGA) 5.0 software with a bootstrap value of 500 replicates (Tamura, Peterson et al. 2011).

3.3. Results and Discussion

3.3.1. GC/MS Analysis

The chemical analysis by GC/MS indicated that despite reports of the sampling sites having been affected by the oil spill, only one sample, the Bay Jimmy South (BJS) sample from Louisiana (Fig. 3.2B), showed evidence of contamination by crude oil (Fig. 3.2A). The gas chromatograph of a negative control sample did not show any evidence of crude oil contamination (Fig. 3.2C). The peaks shown in the chromatogram of BJS sample (Fig. 3.2B) were identified as n-alkanes. When comparing the retention times of the BJS sample to that of the positive control (Fig. 2A), a similar peak pattern was observed around 9.90, 11.50, 13.20, 15.14, and 17.18 for the BJS sample. This indicated that the BJS sample was most likely contaminated by the BP source MC-252 crude oil. The other samples (BJN, BD, AL, SW) showed no indications of crude oil contamination and had a gas chromatograph more comparable to the negative control soil (Fig. 3.2D). However, a study conducted by Natter *et al*. (2012), was able to identify biomarkers suggesting BJN and BD were also contaminated in addition to the BJS sample. The study showed that surface samples had increased signs of biodegradation, volatilization, and dilution due to dispersants given the time lapse between environmental contamination and time of sampling (Ramseur 2010; Casselman 2012), and also showed overall lower levels of contamination for samples collected from Mississippi and Alabama, which may explain why our GC/MS analysis was unable to detect discernible contaminants. For the purpose of this study only the BJS sample was considered contaminated.

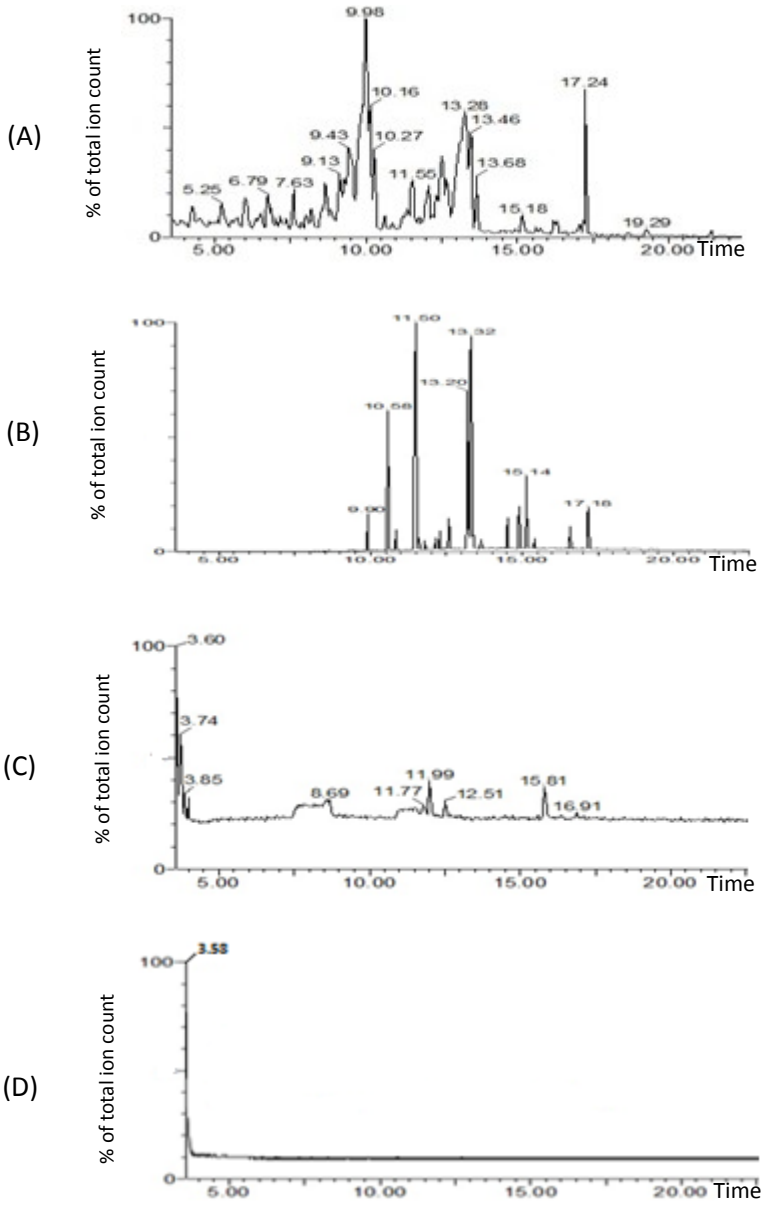

Figure 3.2. Analytical comparison of gas chromatographs of the (A) positive control crude oil from BP source MC-252; (B) the Bay Jimmy "South", LA sample, which was the only soil sample to show positive results; and (C) the negative control soil sample collected from Auburn, AL.

3.3.2. Quantitative gene analysis

All standard curves for qPCR assay were successfully constructed for the five genes. The *alkB* standard produced a curve that was linear (y = -5.52 x + 69.42, R^2 = 0.99, E = 50.72%) based on three orders of magnitude that ranged from 10^5 to 10^8 to gene copies per µL. The standard curve for the *P450* gene target was linear (y = -3.44 x + 42.33, R^2 = 0.99, E = 95.30%) based on seven orders of magnitude ranging from 10^3 to 10^{10} gene copies μL^{-1}. The standard curve for the PAH - RHD_α gene target was linear (y = -3.50 x + 43.62, R^2 = 0.99, E = 99.80%) based on seven orders of magnitude ranging from 10^2 to 10^{10} gene copies μL^{-1}. For the *Pseudomonas* 16S rRNA gene target, the standard curve was linear (y = -4.12 x + 41.78, R^2 = 0.99, E = 74.90%) based on seven orders of magnitude ranging from 10^1 to 10^8 gene copies per µL. The standard curve obtained for the universal bacterial 16S rRNA gene target was linear (y = -3.64 x + 55.77, R^2 = 0.99, E = 92.46%) based on five orders of magnitude ranging from 10^5 to 10^{10} gene copies per µL.

Gene quantification data based on qPCR results for samples were expressed in gene copies per gram of soil dw (dry weight) for all soil (or sediment) samples (BJS, NCS, BJN, BD, AL) and in gene copies per liter of water for the seawater sample (SW) (Fig. 3.3). For each analysis samples were split into duplicates and analyzed in triplicate to ensure reproducibility. The mean values for the duplicated samples are presented with the variation of coefficients (CV) ranging from 0.15 to 78.68% for each gene (Fig. 3.3).

Quantification of the three functional genes (*alk*B, P450, and PAH-RHD_α) was used to determine the abundance of the genes that encode degradative enzymes in each sample. The *alkB* gene quantity ranged from 10^9 to 10^{10} gene copies g^{-1} of soil dw (or L^{-1} of water) for contaminated (BJS), non-contaminated (BJN, BD, AL, SW), and the negative control soil (Fig. 3.3AA). The statistical analysis indicated that there was no significant difference between BJS

and the negative control sample or the non-contaminated samples except AL and BJN ($p = 0.001$, $n = 24$). The *P450* gene quantity (Figure 3b) for the BJS sample was 10^{11} gene copies per g of soil dw, ranged from 10^{9} to 10^{10} gene copies per g of soil (or L of water) for the non-contaminated samples and the NCS sample. The statistical analysis indicated that there was no significant difference between BJS and the non-contaminated samples, including NCS, except for BJN and BD ($p = 0.024$, $n = 24$). The PAH-RHD$_{\alpha}$ gene copy numbers ranged from 10^{6} to10^{7} gene copies g^{-1} of soil dw (or L^{-1} of water) for both BJS and the non-contaminated samples, with NCS resulting in 10^{5} gene copies g^{-1} of soil dw. For this gene target the statistical analysis did not show a significant difference ($p = 0.311$, $n = 24$) between any of the samples.

The quantification of *Pseudomonas* taxa was used to identify bacteria that are potentially involved in the biodegradation of crude oil contaminates (Alquati, Papacchini et al. 2005; Das and Chandran 2011). The quantity of *Pseudomonas* specific 16S rRNA gene within BJS and the non-contaminated samples was 10^{7} gene copies per g of soil dw (or L of water) and 10^{6} gene copies g^{-1} of soil dw for the negative control sample (Fig. 3.3DD). These values were significantly lower than the bacterial 16S rRNA amplification results, indicating the presence of other microbial taxa in the samples, and were typical of hydrocarbon degrading bacteria found within soils (Rojo 2010). The statistical analysis did not show any significant difference ($p = 0.423$, $n = 24$) between the contaminated samples and the non-contaminated samples or the negative control.

The quantity of universal bacterial 16S rRNA genes ranged from 10^{10} to 10^{11} gene copies per g of soil dw for all of the samples (Fig. 3.3EE). The results obtained from this study were on average 2-3 orders of magnitude higher than those found in past studies, 10^{7} to 10^{9} gene copies per gram of soil-sediment (Frostegard, Courtois et al. 1999; Lakay, Botha et al. 2007; Lloyd,

MacGregor et al. 2010). However, a study by Bashan *et al*. (2000) have shown that the presence of organic matter helps to facilitate microbial activity and may explain the higher values obtained in this study since these samples were on the upper range of the typical amounts of organic matter found in soil.

The results obtained for the functional genes, *alkB* and P450, were higher than the results obtained for the *Pseudomonas* specific 16S rRNA but remained lower than the results obtained from the universal bacterial 16S rRNA analysis. The PAH-RHD$_{\alpha}$ functional gene followed a similar pattern to that of the *Pseudomonas* specific 16S rRNA, with the exception that BJN was significantly higher. This suggested that other microbial taxa may be present in the samples that contain these genes that encode degradative enzymes and might be more indicative of the obtained values. (Das and Chandran 2011). However, the presence of the functional genes within the negative control sample collected from Auburn University's Arboretum verifies previous studies that found these genes to be ubiquitous in nature regardless of previous levels of contamination (Das and Chandran 2011). Based on these qPCR results, it could not be determined whether or not contamination by crude oil contaminants affected the indigenous microbial populations. The assay failed to differentiate the quantity of functional genes between the contaminated and non-contaminated samples.

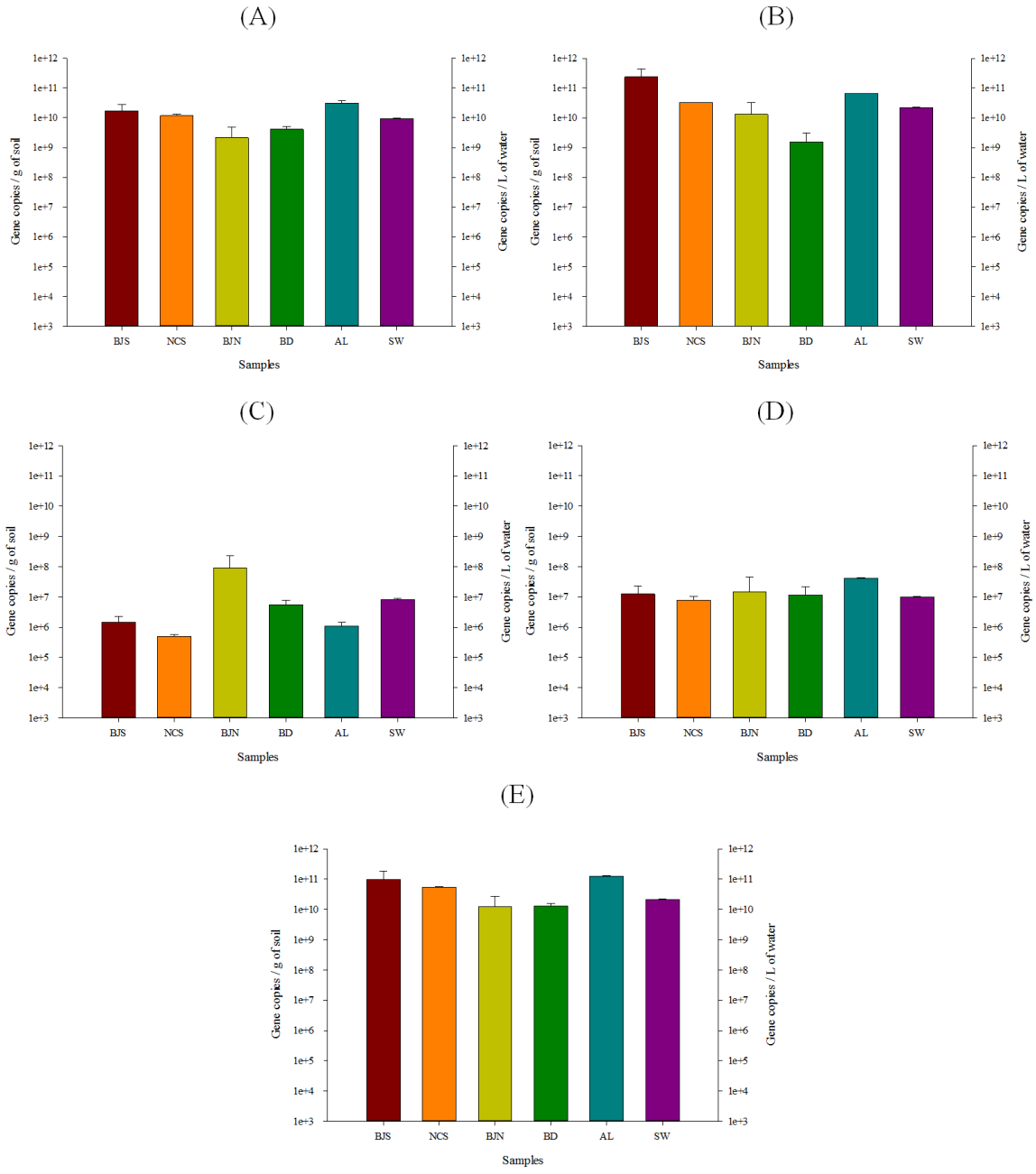

Figure 3.3. qPCR analysis of (A) alkB, (B) P450, (C) PAH-RHD, (D) Pseudomonas genus-specific16S rRNA, (E) universal bacterial 16S rRNA, based on the logarithimic value of the gene copies normalized to the amount of sample used for gDNA extraction prior to qPCR. Mean and standard values are based on duplicated samples during qPCR analysis.

3.3.3. Bacterial Assemblage Structure based on 16S rRNA gene pyrosequencing

The results obtained using 454-pyrosequencing of 16S rRNA genes were used to determine richness and diversity (Table 3.3), phylogenetic affiliations between contaminated and non-contaminated sites (Fig. 3.4), and to identify putative crude oil degraders (Fig. 3.5). On average there were 4,977 sequence reads (range of 2,240 to 11,159) per sample, with the contaminated sample (BJS) showing the largest number of reads and non-contaminated samples falling below the average. The number of operational taxonomic units (OTUs) ranged from 347 to 2502, with the largest value being represented by the negative control sample. The Good's coverage values of each sample, calculated at a 97% similarity cut-off, ranged from 64-93%. This value is indicative of whether the sample properly represents the entire population at each site. For BJS, with a value of 93%, this indicated that only 7 additional phylotypes would be discovered for every 100 additional sequencing efforts. In addition, BJN and the SW also had high Good's coverage values which was expected due to the proximity of BJN's sampling site to BJS and the lower number of OTUs for SW. However, the other non-contaminated samples, including the negative control sample, had lower values indicating that the number of pyrosequencing reads for each of these samples was insufficient to capture the overall bacterial diversity. The estimator of richness, Chao1, showed that the number of observed OTUs were considerable low, covering only 32-45% of the overall richness of the microbial population, with BJS showing the lowest percentage. Based on the values obtained for Chao1, there are between 430-4113 additional phylotypes left to be identified within the samples. The Shannon diversity index resulted in a range of 2.88-6.64 for each sample, with an average of 5.07. The BJS sample again had the lowest value, while the negative control sample had the highest. This value was used to

determine the ecological diversity of each sample but is also an uncertainty factor when predicting ribotypes.

The analysis grouped the microbial population obtained from the soil, sediment and seawater samples into 26 different bacterial phyla. Among the bacterial phyla known to contain studied crude oil degraders were the *Proteobacteria* (range of 14 - 84% relative abundance) , the *Actinobacteria* (range of 0.2 - 5.2% relative abundance), the *Bacteriodetes* (range of 3.2-6.9% relative abundance), and the *Firmicutes* (range of 0.4 - 7.2% relative abundance) (Fig. 3.4). Among the samples, *Proteobacteria* typically dominated; however, within the non-contaminated samples and the negative control sample it was observed that phyla previously associated with alkane or PAH degradation were at much lower relative abundance, whereas, in the BJS the putatively biodegrading bacteria were dominant.

A phylogenetic analysis was conducted to represent the overall diversity of sequences related to crude-oil biodegraders. Overall, there were 17 bacteria genera identified that are known to have taxa associated with the degradation of alkanes and PAHs (Kloos, Munch et al. 2006; van Beilen, Funhoff et al. 2006; Wang, Wang et al. 2010; Das and Chandran 2011). Less than 3% of these bacteria were found in the non-contaminated samples, including the negative control sample. On the other hand, the contaminated sample (BJS) was made up of about 45% of these potential degraders even though there was a low diversity within this group. Interestingly, the majority of the degraders were identified as *Parvibaculum* (Fig. 3.5A), a bacteria mainly associated with the degradation of alkanes, which was the contaminant identified within this sample based on GC/MS (Wang, Wang et al. 2010). Other studies have shown that contaminated samples typically are dominated by *Alcanivorax* and *Pseudomonas* which are both capable of alkane and PAH degradation (Röling, Milner et al. 2002; Alonso-Gutiérrez, Figueras et al. 2009;

Wang, Wang et al. 2010) . For comparison, the non-contaminated samples (BJN, BD, AL, SW) and the negative control soil showed a higher affiliation with genera such as, *Sulfitobacter*, *Dehalogenimonas*, *Clostridium*, *Sphingopyxis*, and *GP1*; respectively (data not shown). Among these genera, *Dehalogenimonas* and *Sphingopyxis* are the only two directly related to the degradation of either chlorinated alkanes or n-alkanes; respectively (Behlulgil and Mehmetoglu 2002; Röling, Milner et al. 2002; Alonso-Gutiérrez, Figueras et al. 2009; Yousafa, Andriaa et al. 2010; Maness, Bowman et al. 2012) While these samples did contain a larger diversity of bacteria with taxa known to contain the *alkB* and P450 gene targets, based on the presence of *Caulobacter*, *Bacillus*, *Burkholderia*, etc. (Fig. 3.5B and 3.5C) these bacteria were in low abundance relative to the overall microbial population present at these sites (Kloos, Munch et al. 2006; van Beilen, Funhoff et al. 2006; Cebron, Norini et al. 2007; Wang, Wang et al. 2010). Overall, there was no observable correlation with the non-contaminated samples, including NCS, between the relative abundance of specific degraders and any identifiable contaminants.

Since the BJS sample showed signs of selective growth on crude oil contaminants while the negative control and the non-contaminated samples failed to show any signs of growth under these conditions, this indicated that the oil spill enriched for specific microbial populations such as *Parvibaculum* spp. Further research will be necessary to isolate members of the *Parvibaculum* genus that have the capacity for alkane and/or PAH degradation, and to characterize their mechanism (s) for hydrocarbon degradation and utilization as a carbon and energy source. Furthermore, it will be of interest to study other contaminated sites and determine whether members of the *Parvibaculum* genus are similarly induced in their relative abundance.

Table 3.3. Summary of OTU richness, diversity indices, and estimated sample coverage for each sample.

Sample	Number of reads	Number of OTUs	Good's coverage	Richness estimator	Diversity index
	Raw			Chao1	Shannon
BJS	11159	747	0.93	2316.73	2.88
NCS	10232	2502	0.79	6615.61	6.64
BJN	2871	347	0.90	777.29	3.94
BD	2240	841	0.64	2930.81	5.86
AL	3629	1449	0.64	4993.17	6.46
SW	2315	457	0.83	1224.52	4.62

b Calculated at a 97% sequences similarity cut-off

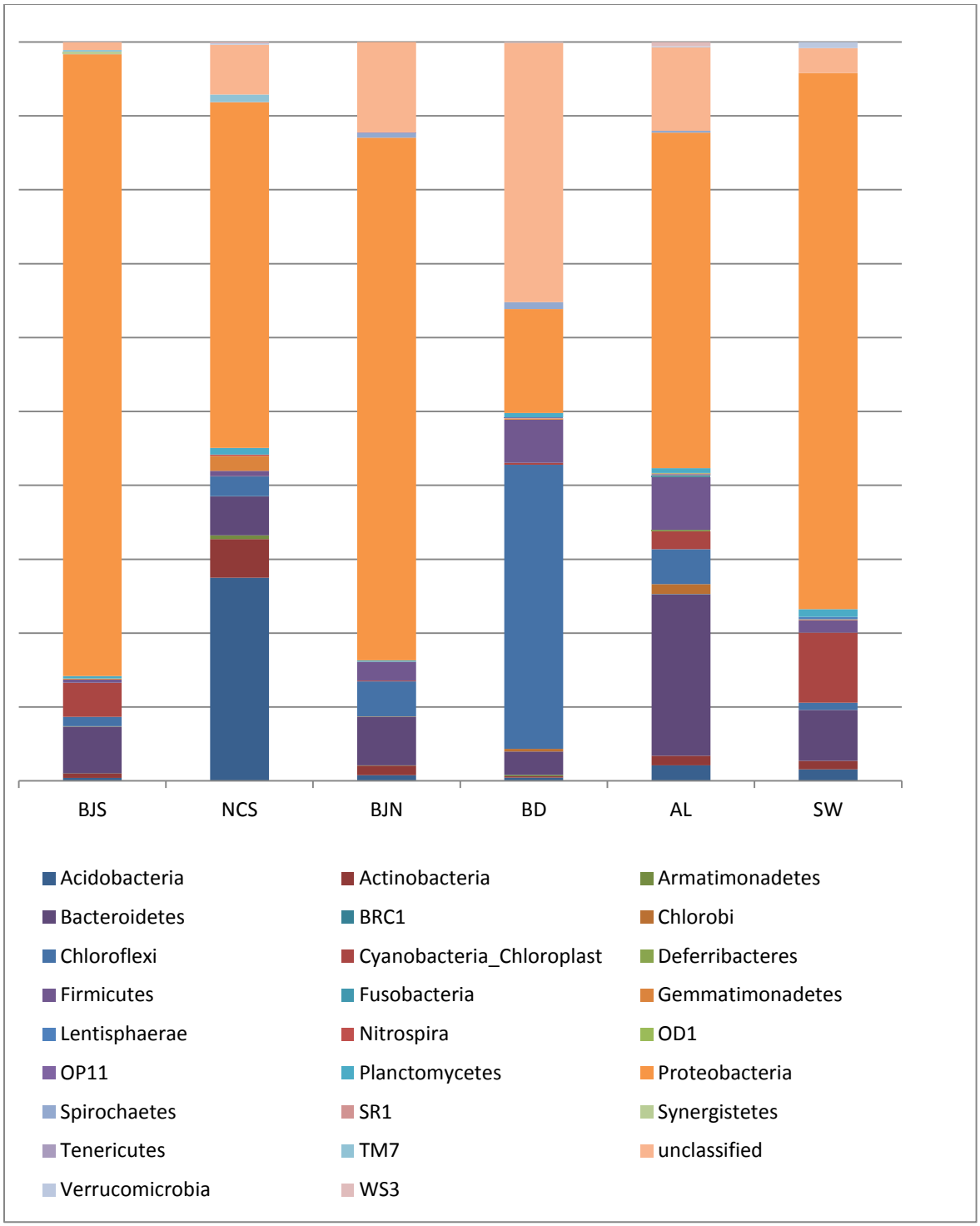

Figure 3.4. Relative abundance of bacterial phyla based on 16S rRNA gene sequences determined by 454 pyrosequencing of each sample.

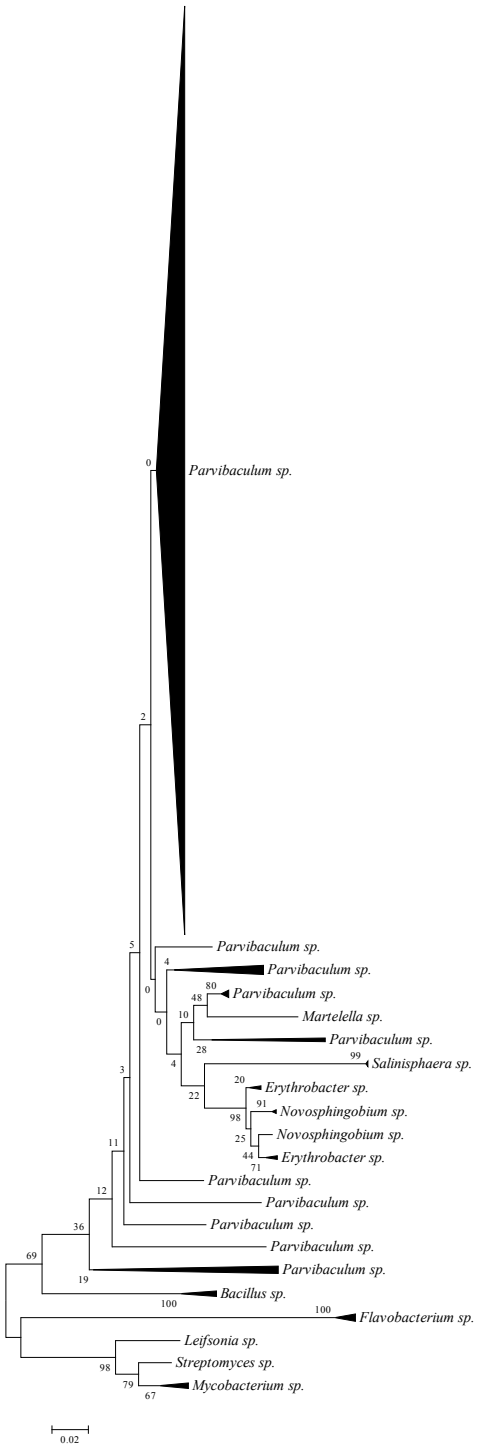

Figure 3.5A. Phylogenetic tree of Bay Jimmy "South" sample from Louisiana based on maximum likelihood statistical method with a phylogenetic test based on a bootstrap method.

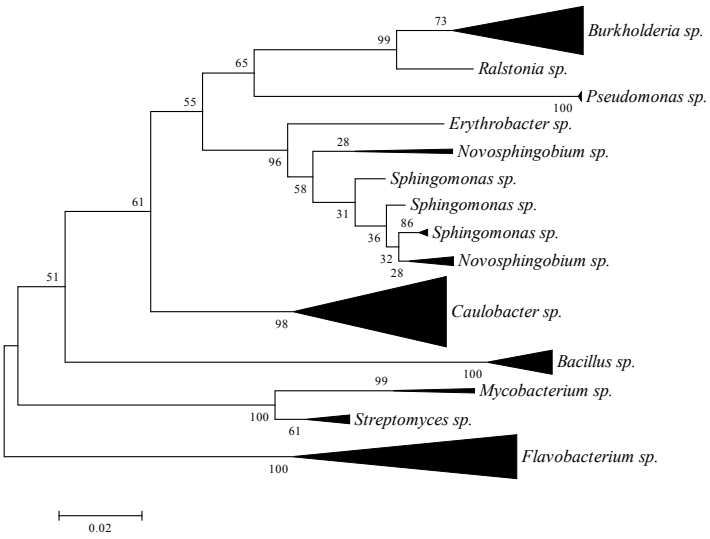

Figure 3.5B. Phylogenetic tree of the negative control soil sample based on neighbor-joining statistical method with a phylogenetic test based on a bootstrap method.

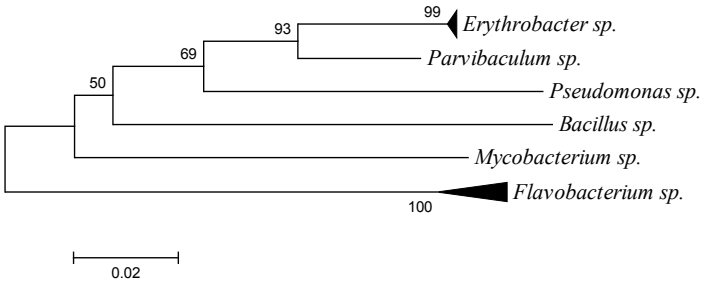

Figure 3.5C. Phylogenetic tree of the Bay Jimmy "North" sample from Louisiana based on neighbor-joining statistical method with a phylogenetic test based on a bootstrap method.

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3.4. Conclusion

In this study multiple approaches were used to study the impact of the Deepwater Horizon oil spill on a contaminated sampling sites. Among the many sediment, soil and seawater samples taken, only one soil sample was found to have objective evidence of crude oil contamination based on GC/MS analysis. A qPCR analysis of all samples demonstrated that the enzymes necessary for crude oil biodegration are ubiquitous in the environment. However, a phylogenetic analysis indicated that the contaminated soil sample had a higher relative abundance of sequences related to putative crude-oil biodegrading bacteria compared to the non-contaminated samples. In addition, the majority of these sequences were identified as putative alkane degraders, consistent with the nature of the contamination identified in the soil sample. Samples with no identifiable contaminates based on GC/MS analysis showed a higher predicted diversity of biodegrading bacteria but had a lower relative abundance of these populations based on the 16S rRNA gene analysis. Interestingly, the contaminated soil sample had a high relative abundance of *Parvibaculum* taxa, which have been previously associated with alkane degradation, suggesting that this bacterial population has increased its relative abundance due to crude oil contamination. This suggests a target bacterial population that may be useful for future biostimulation approaches to bioremediate soils and sediments that have been affected by oil spills.

Chapter Four. Additional Analyses

4.1. Introduction

This section contains additional information regarding the sample analysis and further pyrosequencing data. The purpose of the sample analysis was to verify the overall quality of the samples based on the yield, purity, and potential inhibitors due to the sensitivity of the PCR and qPCR processes (Frostegard, Courtois et al. 1999; Opel, Chung et al. 2009). The additional information regarding the pyrosequencing data was used to access the information provided in Chapter 3.

4.2 Materials and Methods

4.2.1 Genomic DNA Extraction

Genomic DNA was extracted from the soil samples using the Ultra Clean DNA Isolation Kit for Soils (Mo Bio Laboratories; Solon, OH). About 0.5 g (wet weight) of soil was used for each extraction. Pure cultures required an initial centrifuging at 6750 × g for 5 min. This allowed for the supernatant to be decanted and the concentrated pellet to be used for the extraction process. Genomic DNA from the seawater sample was extracted according to the manufacturer's instructions for the Rapid Water DNA Isolation Kit (Mo Bio; Carlsbad, CA). DNA concentrations for all samples were obtained using the Nanodrop ND 1000 Spectrophotometer (Thermo Scientific; Barrington, IL). Purity levels were measured based on the optical density of 260/280 ($OD_{260/280}$), which measures the concentration of DNA against any possible inhibitors.

4.2.2 Organic Matter Content

The content of organic matter at each sediment sample site was quantified through the Soils Lab at Auburn University (Auburn, AL). Quantification of organic matter was used as an indication

for potential signs of microbial life (Bot and Benites 2005). Variants between sample triplicates were assumed insignificant; therefore, sample sites were analyzed as a whole. The core samples were divided into two sections ranging from 0 – 15 cm and from 15 – 30 cm; therefore, results are presented as the ranges.

4.2.3 Humic Acids Analysis

Humic acids were extracted according to a study conducted by Ting et al. (2010). Quantification of humic acids was used to identify inhibitors which have the potential to prevent proper amplification during the PCR and qPCR assays. 10 g (wet weight) of soil sample was mixed with 30 mL of 1 M NaOH to be passed through a 0.45 μm vacuum filter. pH was monitored and diluted with 1 M HCl until the pH reached 2.0. This helps to facilitate the precipitation of humic acids during the centrifugation process, which was ran at 3000 x g for 30 min. Supernatant was decanted and the pellet was re-dissolved with 20 mL of 1 M NaOH. Solutions were re-centrifuged to confirm no precipitant formed. Quantification of humic acids was determined using a Spectramax M2 spectrometer (MDS; Sterling Heights, MI) at an excitation wavelength of 350 nm and an emission wavelength of 460 nm. Results higher than 200 RFU (relative fluorescence unit) were diluted with a 1:5 ratio using deionized (DI) water and re-analyzed based on an optimal range of 100-200 RFU (Wang 2011). Final results were converted to μg humic acids/mg of soil sample based on the calibration curve formed by Wang (2011).

4.2.4 PCR assay

See sections 3.2.5 and 3.2.6 for details.

4.2.5 Pyrosequencing

See section 3.2.8 for details on sample preparation and analysis.

4.3 Results and Discussion

4.3.1 Sample Analysis

The purpose of the sample analysis was to determine the usability of each sample in terms of the PCR and qPCR assay. These procedures required specific concentrations of template DNA in order to produce optimal results. In addition, they are highly sensitive to inhibitors which prevent proper amplification. To identify areas of concern gDNA concentrations were measured to ensure concentration ranges could be met. Measurements of organic matter content and humic acids were taken to identify inhibitors with the environmental samples. Then the gDNA concentrations were compared against their purity levels to determine if these inhibitors were co-extracted. The results of these experiments can be seen in Table 4.1.

Based on the results of the gDNA extraction process, there were several samples that were of concern. Results collected for the Bay Jimmy "South" sample from Louisiana were highly variable between 6.64-66.82 ng/ µL, which was expected due to the high variability of vegetative growth, organic content, and contaminants found with the given sample. For the *alkB* gene target, the Bay Jimmy "North" and the Bayou Dulac samples from Louisiana (i.e., 6.37 ng/ µL and 15.90 ng/ µL, respectively) did not meet minimum required specifications for concentrations; however, multiple extraction processes produced similar results. This posed a problem during the PCR assay (see PCR Analysis below). Regardless of these potential problems all samples was used for further experimentation as they were but taken into consideration during our analysis.

The results obtained from measuring the organic matter present within each sample showed that overall all of the soils' fell within a typical range from trace amounts to about 30%

(Bot and Benites 2005). Since organic matter is comprised of valuable nutrients essential to microbial life, levels closer to 30% indicate low decomposition of these nutrients by the microbial community, meaning the community is not thriving within its environment (Bot and Benites 2005). Samples collected from Louisiana had moderate to high levels of organic content, ranging from 12.7 to 28.7% (Table 4.1), suggesting that the microbial population in these regions, which received the highest impact from the 2010 oil spill was affected (Aigner, Burgess et al. 2010). On the other hand, samples from Alabama, an area with low to moderate exposure, showed lower percentages at 5.3 - 6.4% (Table 4.1) and also had higher extraction yields, indicating that these areas may not have been affected by the spill.

While the levels of organic matter are indicative of microbial activity, it was also used as an indicator of inhibitory organic compounds. Of the inhibitory compounds that may have been present specifically humic acids was chosen for measurement. Humic acids have been found to bind to DNA and interfere in the interaction between DNA and Taq polymerase, thereby preventing proper amplification during PCR. Based on a study conducted by Ogel et al. (1999) the soil typically contains 100 mg of humic acid per 5 mg of soil, or about 2% humic acids. Values obtained for this study were significantly lower than the typical value at < 0.11% (Table 4.1), with the largest percentage of humic acids pertaining to the Bay Jimmy "South" sample from Louisiana. However, these are based on a calibration curve prepared from a humic acid obtained from the International Humic Substances Society (IHSS), which does not represent the total number of environmental humic acids (Kim, Wang et al. 2011; Wang 2011). Therefore, it is possible that not all of the humic acids were accounted for. Regardless, in the case of the BJS sample, complications were seen during the qPCR assay which required lower dilutions to combat the problem.

To determine whether these levels posed a problem during future experiments, the optical density ratio of 260 over 280 nm ($OD_{260/280}$), which represents the purity of extracted gDNA, was measured. Lower ratios, between 1.10 - 1.62 (Table 4.1), obtained for samples BJN, BD, SW, and NCS indicated that inhibitory contaminants were in fact co-extracted along with gDNA from the samples. However, all of the other samples resulted in an optimal ratio of about 1.8 or higher, which is considered the optimum ratio according to the Nanodrop 1000 Spectrophotometer Manual (2008). For samples with below optimal ranges, multiple dilutions were tested for each experiment since these contaminants have the ability to absorb light and result in inaccurate readings (Ahn, Costa et al. 1996; Kim, Wang et al. 2011).

Table 4.1. Soil analysis based on the gDNA yield and purity levels after extraction, the amount of humic acids extracted from the soil, and amount of organic matter present in the soil.

Sample	gDNA Yield (ng / µL)	gDNA Purity ($OD_{260/280}$)	% Humic Acids (mg Humic Acids / mg Soil)	% Organic Matter
BJS	66.82	1.90	0.059	14.2
	37.52	1.72	0.057	
	6.64	1.72	0.112	
BJN	5.83	1.76	0.035	12.7-15.2
	7.15	1.87	0.029	
	6.12	1.36	0.045	
BD	11.90	1.78	0.039	26.8-28.7
	16.68	1.62	0.025	
	16.45	1.74	0.005	
AL	100.06	1.85	0.057	5.3
SW	19.47	1.10	N /A	N /A
NCS	110.81	1.61	0.054	6.4
PC	103.91	1.93	N /A	N /A

4.3.2 Qualitative Gene Analysis

The qualitative gene analysis was conducted using PCR assays specific to each gene target. The purpose of this experiment was to confirm the presence of the three functional genes within the environmental samples. To do this two genus-specific targets were chosen, Universal Bacterial 16S rRNA and *Pseudomonas* 16S rRNA, as verification of a specific population known to contain these functional enzymes within the microbial population as a whole. The results for each sample were compared against the positive control, *Pseudomonas putida*, and the negative control, NCS; the results for this analysis are presented in Figure 4.1.

Figures 4.1A and 4.1B, confirmed the presence of the target species, *Pseudomonas*, within the microbial population. Therefore, it was expected that the samples would also indicate the presence of the functional genes. Based on Figure 4.1A, all of the samples contained the bacterial 16S rRNA gene, showing a visible target band at around 1500 bp. However, the Bay Jimmy "North" sample from Louisiana, represented by sample BJN, resulted in a faint band at the target size. Similar results for this sample were obtained for the *Pseudomonas* specific 16S rRNA, *alkB*, and PAH-RHD$_{\alpha}$ genes targets with a faint or absent band observed at the target sizes of 990, 550, and 306 bp; respectively. As mentioned in previous sections, this sample had a average gDNA yield lower than the minimum requirement for the majority of the PCR assays and was therefore below the observable detection limit (Widmer, Seidler et al. 1998; Kloos, Munch et al. 2006). However, the other samples resulted in comparable bands.

Comparing the functional gene targets indicated that the *alkB* primers showed a higher specificity over the P450 primers towards targeting the gene encoding the alkane monooxygenase enzyme. In addition, the *alkB* PCR assay had a larger tolerance to various gDNA concentrations (Kloos, Munch et al. 2006) since there were only three samples (BJS, AL,

NCS) the met the minimum requirements for the P450 PCR assay (van Beilen, Funhoff et al. 2006). However, given that the P450 assay successfully amplified the gene target in the BJN sample indicates that the related metabolic pathway may be more prevalent in the microbial population within this sample. Since the PAH dioxygenase gene target resulted in faint bands for each sample, a proper comparison could not be made.

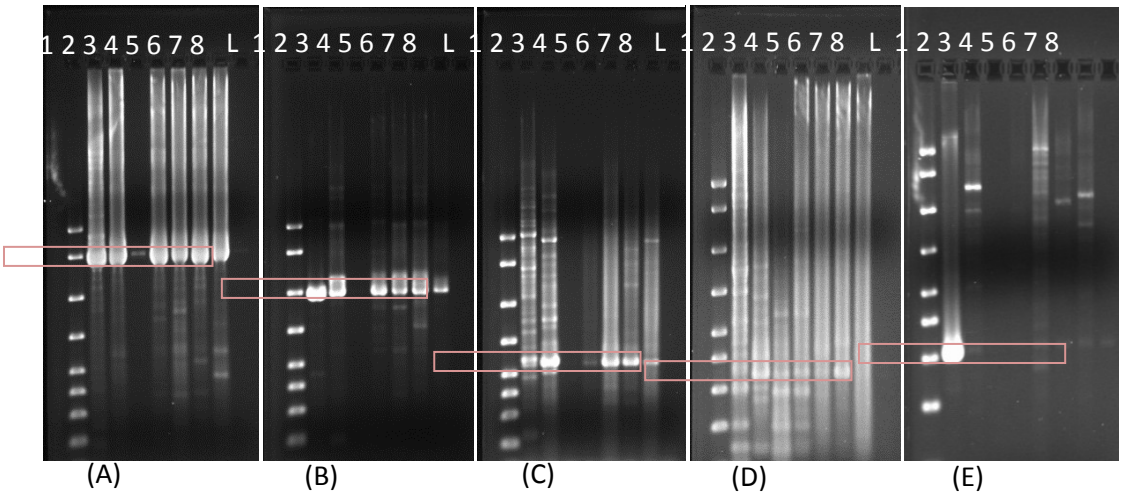

Figure 4.1. Gel electrophoresis image for (A) bacterial 16S rRNA gene at 1500 bp, (B) Pseudomonas specific 16S rRNA gene at 990 bp, (C) alkB gene at 550bp, (D) P450 gene at 339 bp, and (E) PAH-RHDα gene at 306 bp. Lane (L) is a 200-2000 bp molecular ladder followed by the PCR products for (1) *Pseudomonas putida* pure culture (positive control); (2) Bay Jimmy "South," LA; (3) Bay Jimmy "North," LA; (4) Bayou Dulac, LA; (5) Sandy Bay, AL sediment; (6) Sandy Bay, AL seawater; (7) soil from Auburn University Arboretum in Auburn, AL (negative control); and (8) negative control for PCR procedure.

4.3.3 Phylogenetic Analysis

In addition to the community analyses mentioned in Chapter 3, a community caparison analysis and rarefaction analysis were conducted. The community caparison analysis was used to indicate the relationship between the different samples. As was expected the microbial communities are highly dependent on geographical location (Fig. 4.2). The rarefaction curve was used to determine if the pyrosequencing data represented the microbial diversity found within each sample. As Figure 4.3 shows, the OTUs formed from the contaminated sample (BJS) represented the overall diversity within the sample leading to high percentages for the Good's coverage values. Similar patterns could be seen for the non-contaminated samples (BJN, SW), indicating that these samples not only had a low number of reads but a lower diversity compared to their high richness values (See section 3.3.3). However, the based on the increasing slope of the negative control sample (NCS), there were additional phylotypes within this sample that were not represented in the data. The non-contmainated samples (BD, AL) showed a similar pattern to NCS, indicating that these samples had a higher diversity.

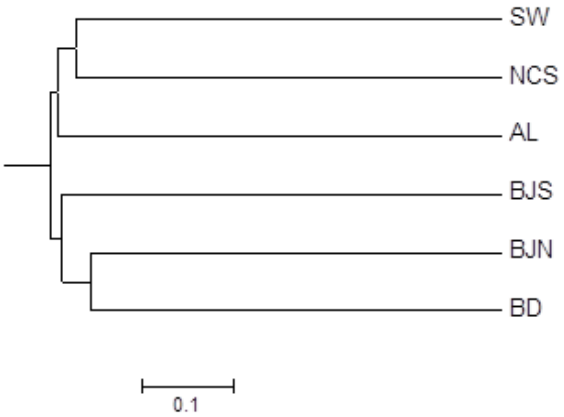

Figure 4.2. Phylogenetic Tree based on beta-diversity between the different environmental samples.

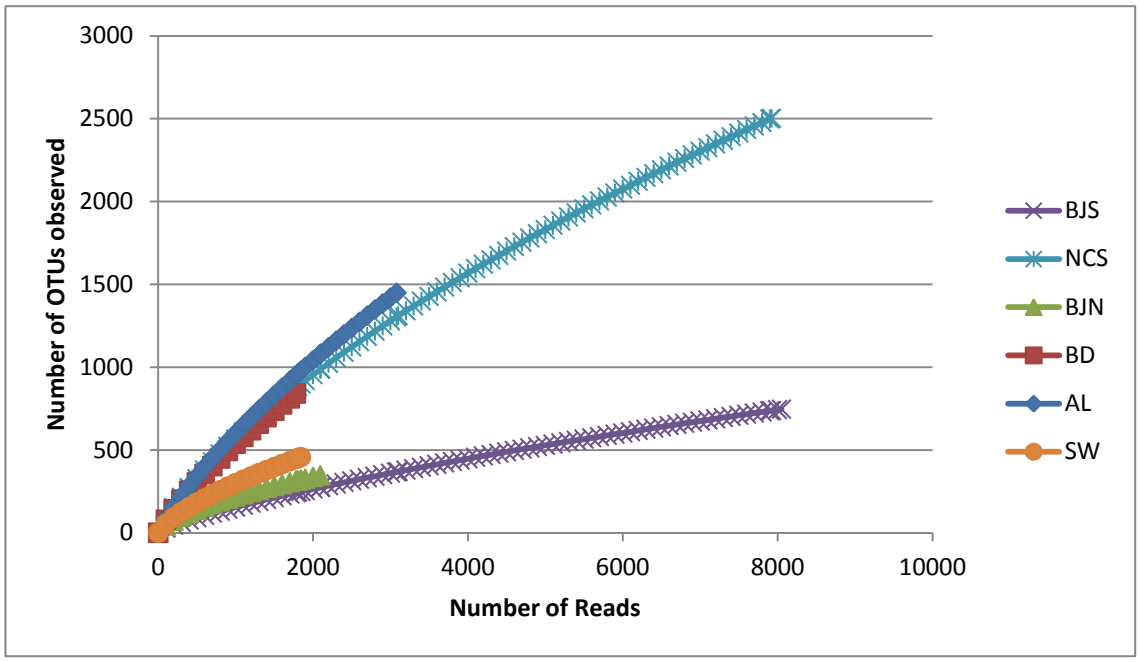

Figure 4.3. Rarefaction curves for the environmental samples clustering at a 97% similarity cut-off. The curves were generated using 1,000-random samplings without replacement.

Chapter Five. Conclusions and Future Work

5.1 Conclusions

Despite the fact that our GC/MS analysis was only able to confirm that one of the six samples was contaminated our results from the analyses of the functional and phylogenetic biomarkers were able to show:

1. Bacteria capable of biodegrading crude-oil contaminants are ubiquitous in the environment which confirmed the results found in previous studies based on the PCR and qPCR analysis.
2. Community analysis indicated there may have been a population shift as an affect of the oil spill based on the pyrosequencing data.

As a result of these findings it was determined that the PCR and qPCR alone were inadequate to determine if the oil-spill affected our selected sites is suggested. However, it is suggested that future studies utilize the pyrosequencing analysis as a screening method for the PCR and qPCR processes. In doing so, focus can be placed on specific bacterial communities and the specific enzymes by which they utilize crude oil contaminants.

5.2 Recommendations for Future Work

Given the data found in this study the following experiments are recommended in order to determine the full potential for bioremediation by the indigenous microbial populations at each site.

1. Conduct a RNA expression analysis. This will elucidate whether the functional genes were being expressed in the contaminated soil as compared to the non-contaminated samples.
2. Conduct a phylogenetic analysis based on each functional gene.This would allow us to identify specific species capable of biodegradation of crude oil contaminants.
3. Conduct a time lapse experiment on the samples.This will help to determine if there has been any change since the last sample collection.

With the finding of this complete analysis, it could be properly determined whether bioaugmentation, biostimulation, or allowing for natural attentuation would be the best plan of action along the gulf coast in response to the recent oil spill.

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Appendix A

The following is an example of the calculations used to convert gDNA concentrations into gene copies per reaction in preparation for the standard to be used in the qPCR process. In addition, sample calculations are also provided that show how the quantification data obtained from the qPCR analysis were normalized per g of soil (or L of water) used during the extraction of gDNA from the each sample.

Results of cloning the gene target:

Sample ID	ng/ul
Plasmid	263.28

qPCR details:

	Type	Stock	Final	RxN (uL)
AB TaqMan Universal Master mix		2x	1x	10.00
Primer F	BACT1369F	20μM	0.8μM	0.80
Primer R	PROK1492R	20μM	0.8μM	0.80
TaqMan probe	TM1389F	10μM	0.2μM	0.40
H2O				3.00
DNA sample				5.00
			Total volume	20.00

Thermal cycling:

50˚C	2 min	
95˚C	10 min	
95˚C	15 sec	40 cycles
56˚C	1 min	

Calculations to convert into gene copies per reaction:

$$Gene\ copy\ \#/\text{rxn.} = \frac{\left(concentration\ of\ gDNA \frac{g}{\mu L}\right)(6.02e23)(PCR\ DNA\ aliquot\ \mu L)}{\left(660 \frac{g}{mol \cdot bp}\right)(target\ length\ bp) + \ (\text{MW of TOPO-TA plasmid } \frac{\text{g}}{\text{mol}})} \quad Eqn.\ 1$$

$$= \frac{\left(263.28 \times 10^{-9} \frac{g}{\mu L}\right)(6.02e23)(5\ \mu L)}{\left(660 \frac{g}{mol \cdot bp}\right)(1500\ bp) + \ (2486846\ \frac{\text{g}}{\text{mol}})} = 2.28 \times 10^{11}$$

Sample data obtained from qPCR analysis:

Ct	Quantity
19.96705246	6.16982E+11

$$\frac{Gene\ copy\ \#}{g\ of\ soil} = \frac{\left(\frac{copies}{rxn}\right)(dilution)(vol.\ of\ elution\ buffer)}{(vol.\ used\ in\ qPCR)(g\ of\ soil\ used\ for\ extraction)}\ Eqn.2$$

$$= \frac{\left(6.17 \times 10^{11}\,\frac{copies}{rxn}\right)\left(1\,\frac{\mu L}{\mu L}\right)(50\ \mu L)}{(5\ \mu L)(0.4\ g\ dw)} = 2.40 \times 10^{11}$$

Appendix B

The following is the statistical data conducted on the qPCR data using ANOVA statistical analysis and a student t-test to compare samples.

Universal 16S rRNA

The GLM Procedure
Class Level Information

Class	Levels	Values
SAMPLES	6	AL BD BJN BJS NCS SW

Number of Observations Read 24
Number of Observations Used 24

The GLM Procedure
Dependent Variable: RESULTS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	4.5450862E22	9.0901725E21	4.79	0.0059
Error	18	3.4168529E22	1.8982516E21		
Corrected Total	23	7.9619392E22			

R-Square	Coeff Var	Root MSE	RESULTS Mean
0.570852	90.67058	4.35689E10	4.80519E10

Source	DF	Type I SS	Mean Square	F Value	Pr > F
SAMPLES	5	4.5450862E22	9.0901725E21	4.79	0.0059

Source	DF	Type III SS	Mean Square	F Value	Pr > F

SAMPLES	5	4.5450862E22	9.0901725E21	4.79	0.0059

The GLM Procedure

Tukey's Studentized Range (HSD) Test for RESULTS

NOTE: This test controls the Type I experimentwise error rate.

Alpha	0.05
Error Degrees of Freedom	18
Error Mean Square	1.898E21
Critical Value of Studentized Range	4.49442

Comparisons significant at the 0.05 level are indicated by ***.

SAMPLES Comparison	Difference Between Means	Simultaneous 95% Confidence Limits		
AL - BJS	2.79252E10	-8.513E10	1.4098E11	
AL - NCS	7.38848E10	-6.4579E10	2.12348E11	
AL - SW	1.05852E11	-3.2611E10	2.44316E11	
AL - BD	1.15086E11	2031099233	2.28141E11	***
AL - BJN	1.15557E11	2502267591	2.28612E11	***
BJS - AL	-2.7925E10	-1.4098E11	8.51298E10	
BJS - NCS	4.59596E10	-6.7095E10	1.59015E11	
BJS - SW	7.79271E10	-3.5128E10	1.90982E11	
BJS - BD	8.71609E10	7218929452	1.67103E11	***
BJS - BJN	8.76321E10	7690097811	1.67574E11	***
NCS - AL	-7.3885E10	-2.1235E11	6.45788E10	
NCS - BJS	-4.596E10	-1.5901E11	6.70955E10	
NCS - SW	3.19675E10	-1.065E11	1.70431E11	
NCS - BD	4.12013E10	-7.1854E10	1.54256E11	
NCS - BJN	4.16725E10	-7.1383E10	1.54728E11	
SW - AL	-1.0585E11	-2.4432E11	3.26113E10	
SW - BJS	-7.7927E10	-1.9098E11	3.5128E10	
SW - NCS	-3.1967E10	-1.7043E11	1.06496E11	
SW - BD	9233834999	-1.0382E11	1.22289E11	
SW - BJN	9705003357	-1.0335E11	1.2276E11	
BD - AL	-1.1509E11	-2.2814E11	-2.0311E9	***
BD - BJS	-8.7161E10	-1.671E11	-7.21893E9	***
BD - NCS	-4.1201E10	-1.5426E11	7.18537E10	
BD - SW	-9.23383E9	-1.2229E11	1.03821E11	
BD - BJN	471168358	-7.9471E10	8.04132E10	
BJN - AL	-1.1556E11	-2.2861E11	-2.50227E9	***
BJN - BJS	-8.7632E10	-1.6757E11	-7.6901E9	***
BJN - NCS	-4.1673E10	-1.5473E11	7.13825E10	
BJN - SW	-9.705E9	-1.2276E11	1.0335E11	
BJN - BD	-471168358	-8.0413E10	7.94708E10	

Pseudomonas 16S rRNA

The GLM Procedure
Class Level Information

Class	Levels	Values
SAMPLES	6	AL BD BJN BJS NCS SW

Number of Observations Read 24
Number of Observations Used 24

The GLM Procedure
Dependent Variable: RESULTS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	2.0160161E15	4.0320321E14	1.03	0.4276
Error	18	7.0175348E15	3.8986304E14		
Corrected Total	23	9.0335508E15			

R-Square	Coeff Var	Root MSE	RESULTS Mean
0.223170	117.7717	19744950	16765441

Source	DF	Type I SS	Mean Square	F Value	Pr > F
SAMPLES	5	2.0160161E15	4.0320321E14	1.03	0.4276

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SAMPLES	5	2.0160161E15	4.0320321E14	1.03	0.4276

The GLM Procedure

Tukey's Studentized Range (HSD) Test for RESULTS

NOTE: This test controls the Type I experimentwise error rate.

Alpha	0.05
Error Degrees of Freedom	18
Error Mean Square	3.899E14
Critical Value of Studentized Range	4.49442

Comparisons significant at the 0.05 level are indicated by ***.

SAMPLES Comparison	Difference Between Means	Simultaneous 95% Confidence Limits	
AL - BJN	18072538	-33162737	69307813
AL - BJS	28899814	-22335461	80135089
AL - BD	30095695	-21139580	81330970
AL - SW	31435104	-31315036	94185244
AL - NCS	33673927	-29076213	96424067
BJN - AL	-18072538	-69307813	33162737
BJN - BJS	10827276	-25401534	47056086
BJN - BD	12023157	-24205653	48251968
BJN - SW	13362566	-37872708	64597841
BJN - NCS	15601389	-35633885	66836664
BJS - AL	-28899814	-80135089	22335461
BJS - BJN	-10827276	-47056086	25401534
BJS - BD	1195881	-35032929	37424692
BJS - SW	2535290	-48699984	53770565
BJS - NCS	4774113	-46461162	56009388
BD - AL	-30095695	-81330970	21139580
BD - BJN	-12023157	-48251968	24205653
BD - BJS	-1195881	-37424692	35032929
BD - SW	1339409	-49895866	52574684
BD - NCS	3578232	-47657043	54813507
SW - AL	-31435104	-94185244	31315036
SW - BJN	-13362566	-64597841	37872708
SW - BJS	-2535290	-53770565	48699984
SW - BD	-1339409	-52574684	49895866
SW - NCS	2238823	-60511317	64988963
NCS - AL	-33673927	-96424067	29076213
NCS - BJN	-15601389	-66836664	35633885
NCS - BJS	-4774113	-56009388	46461162
NCS - BD	-3578232	-54813507	47657043
NCS - SW	-2238823	-64988963	60511317

***alk*B**

The GLM Procedure
Class Level Information

Class	Levels	Values
SAMPLES	6	AL BD BJN BJS NCS SW

Number of Observations Read	24
Number of Observations Used	24

The GLM Procedure
Dependent Variable: RESULTS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	1.6078412E21	3.2156823E20	7.59	0.0005
Error	18	7.6308884E20	4.2393824E19		
Corrected Total	23	2.37093E21			

R-Square	Coeff Var	Root MSE	RESULTS Mean
0.678148	68.67552	6511054003	9480895756

Source	DF	Type I SS	Mean Square	F Value	Pr > F
SAMPLES	5	1.6078412E21	3.2156823E20	7.59	0.0005

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SAMPLES	5	1.6078412E21	3.2156823E20	7.59	0.0005

The GLM Procedure
Tukey's Studentized Range (HSD) Test for RESULTS
NOTE: This test controls the Type I experimentwise error rate.

Alpha	0.05
Error Degrees of Freedom	18
Error Mean Square	4.239E19
Critical Value of Studentized Range	4.49442

Comparisons significant at the 0.05 level are indicated by ***.

SAMPLES Comparison	Difference Between Means	Simultaneous 95% Confidence Limits		
AL - BJS	1.72767E10	381507780	3.4172E10	***
AL - NCS	1.9723E10	-969391789	4.04153E10	
AL - SW	2.20781E10	1385717128	4.27704E10	***
AL - BD	2.73967E10	1.05015E10	4.4292E10	***
AL - BJN	2.93128E10	1.24176E10	4.62081E10	***
BJS - AL	-1.7277E10	-3.4172E10	-381507780	***
BJS - NCS	2446218695	-1.4449E10	1.93415E10	
BJS - SW	4801327611	-1.2094E10	2.16966E10	
BJS - BD	1.012E10	-1.82675E9	2.20667E10	
BJS - BJN	1.20361E10	89354975.5	2.39828E10	***
NCS - AL	-1.9723E10	-4.0415E10	969391789	
NCS - BJS	-2.44622E9	-1.9341E10	1.4449E10	
NCS - SW	2355108917	-1.8337E10	2.30475E10	
NCS - BD	7673767497	-9.22147E9	2.4569E10	
NCS - BJN	9589874182	-7.30536E9	2.64851E10	
SW - AL	-2.2078E10	-4.277E10	-1.38572E9	***
SW - BJS	-4.80133E9	-2.1697E10	1.20939E10	
SW - NCS	-2.35511E9	-2.3047E10	1.83372E10	
SW - BD	5318658580	-1.1577E10	2.22139E10	
SW - BJN	7234765266	-9.66047E9	2.413E10	
BD - AL	-2.7397E10	-4.4292E10	-1.0501E10	***
BD - BJS	-1.012E10	-2.2067E10	1826751710	
BD - NCS	-7.67377E9	-2.4569E10	9221471270	
BD - SW	-5.31866E9	-2.2214E10	1.15766E10	
BD - BJN	1916106685	-1.0031E10	1.38628E10	
BJN - AL	-2.9313E10	-4.6208E10	-1.2418E10	***
BJN - BJS	-1.2036E10	-2.3983E10	-89354975	***
BJN - NCS	-9.58987E9	-2.6485E10	7305364584	
BJN - SW	-7.23477E9	-2.413E10	9660473501	
BJN - BD	-1.91611E9	-1.3863E10	1.00306E10	

P450

The GLM Procedure
Class Level Information

Class	Levels	Values
SAMPLES	6	AL BD BJN BJS NCS SW

Number of Observations Read 24
Number of Observations Used 24

The GLM Procedure
Dependent Variable: RESULTS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	2.175185E23	4.3503699E22	3.41	0.0243
Error	18	2.2989398E23	1.2771888E22		
Corrected Total	23	4.4741247E23			

R-Square	Coeff Var	Root MSE	RESULTS Mean
0.486170	156.5033	1.13013E11	7.22111E10

Source	DF	Type I SS	Mean Square	F Value	Pr > F
SAMPLES	5	2.175185E23	4.3503699E22	3.41	0.0243

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SAMPLES	5	2.175185E23	4.3503699E22	3.41	0.0243

The GLM Procedure
Tukey's Studentized Range (HSD) Test for RESULTS
NOTE: This test controls the Type I experimentwise error rate.

Alpha	0.05
Error Degrees of Freedom	18
Error Mean Square	1.277E22
Critical Value of Studentized Range	4.49442

Comparisons significant at the 0.05 level are indicated by ***.

SAMPLES Comparison	Difference Between Means	Simultaneous 95% Confidence Limits		
BJS - AL	1.70008E11	-1.2324E11	4.6326E11	
BJS - NCS	2.01718E11	-9.1534E10	4.94969E11	
BJS - SW	2.12587E11	-8.0665E10	5.05839E11	
BJS - BJN	2.21697E11	1.43364E10	4.29057E11	***
BJS - BD	2.33033E11	2.5673E10	4.40394E11	***
AL - BJS	-1.7001E11	-4.6326E11	1.23244E11	
AL - NCS	3.17098E10	-3.2745E11	3.90868E11	
AL - SW	4.25791E10	-3.1658E11	4.01738E11	
AL - BJN	5.16889E10	-2.4156E11	3.44941E11	
AL - BD	6.30255E10	-2.3023E11	3.56277E11	
NCS - BJS	-2.0172E11	-4.9497E11	9.15341E10	
NCS - AL	-3.171E10	-3.9087E11	3.27449E11	
NCS - SW	1.08694E10	-3.4829E11	3.70028E11	
NCS - BJN	1.99791E10	-2.7327E11	3.13231E11	
NCS - BD	3.13157E10	-2.6194E11	3.24567E11	
SW - BJS	-2.1259E11	-5.0584E11	8.06648E10	
SW - AL	-4.2579E10	-4.0174E11	3.16579E11	
SW - NCS	-1.0869E10	-3.7003E11	3.48289E11	
SW - BJN	9109727190	-2.8414E11	3.02361E11	
SW - BD	2.04464E10	-2.7281E11	3.13698E11	
BJN - BJS	-2.217E11	-4.2906E11	-1.4336E10	***
BJN - AL	-5.1689E10	-3.4494E11	2.41563E11	
BJN - NCS	-1.9979E10	-3.1323E11	2.73273E11	
BJN - SW	-9.10973E9	-3.0236E11	2.84142E11	
BJN - BD	1.13366E10	-1.9602E11	2.18697E11	
BD - BJS	-2.3303E11	-4.4039E11	-2.5673E10	***
BD - AL	-6.3026E10	-3.5628E11	2.30226E11	
BD - NCS	-3.1316E10	-3.2457E11	2.61936E11	
BD - SW	-2.0446E10	-3.137E11	2.72805E11	
BD - BJN	-1.1337E10	-2.187E11	1.96024E11	

PAH - RHDα

The GLM Procedure
Class Level Information

Class	Levels	Values
SAMPLES	6	AL BD BJN BJS NCS SW

Number of Observations Read 24
Number of Observations Used 24

The GLM Procedure
Dependent Variable: RESULTS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	3.6024732E16	7.2049465E15	1.29	0.3111
Error	18	1.0046518E17	5.581399E15		
Corrected Total	23	1.3648991E17			

R-Square	Coeff Var	Root MSE	RESULTS Mean
0.263937	290.4798	74708761	25719086

Source	DF	Type I SS	Mean Square	F Value	Pr > F
SAMPLES	5	3.6024732E16	7.2049465E15	1.29	0.3111

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SAMPLES	5	3.6024732E16	7.2049465E15	1.29	0.3111

The GLM Procedure
Tukey's Studentized Range (HSD) Test for RESULTS
NOTE: This test controls the Type I experimentwise error rate.

Alpha	0.05
Error Degrees of Freedom	18
Error Mean Square	5.581E15
Critical Value of Studentized Range	4.49442

Comparisons significant at the 0.05 level are indicated by ***.

SAMPLES Comparison	Difference Between Means	Simultaneous 95% Confidence Limits	
BJN - SW	84607866	-109250511	278466242
BJN - BD	87261628	-49816944	224340201
BJN - BJS	91232135	-45846437	228310708
BJN - AL	91626241	-102232136	285484617
BJN - NCS	92212856	-101645521	286071232
SW - BJN	-84607866	-278466242	109250511
SW - BD	2653762	-191204614	196512139
SW - BJS	6624269	-187234107	200482646
SW - AL	7018375	-230408678	244445427
SW - NCS	7604990	-229822063	245032042
BD - BJN	-87261628	-224340201	49816944
BD - SW	-2653762	-196512139	191204614
BD - BJS	3970507	-133108065	141049080
BD - AL	4364612	-189493764	198222989
BD - NCS	4951227	-188907149	198809604
BJS - BJN	-91232135	-228310708	45846437
BJS - SW	-6624269	-200482646	187234107
BJS - BD	-3970507	-141049080	133108065
BJS - AL	394105	-193464271	194252482
BJS - NCS	980720	-192877656	194839097
AL - BJN	-91626241	-285484617	102232136
AL - SW	-7018375	-244445427	230408678
AL - BD	-4364612	-198222989	189493764
AL - BJS	-394105	-194252482	193464271
AL - NCS	586615	-236840437	238013667
NCS - BJN	-92212856	-286071232	101645521
NCS - SW	-7604990	-245032042	229822063
NCS - BD	-4951227	-198809604	188907149
NCS - BJS	-980720	-194839097	192877656
NCS - AL	-586615	-238	

Appendix C

BJS

>HTTFV6402IYN93
CGTGGGAACCTACCTAGGGGTACGGAATAACTCAGGGAAACTTGTGCTAATACCGTATACGACCTCAGGGTGAAAGATTTATCGCCCCTAGGTGGGCCCGCGTTGGATTAGCTAGTTG
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GTG----------
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G----------
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