Marine microbial community responses related to wetland carbon mobilization in the coastal zone

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Scientific Significance Statement
Erosion of coastal habitats results in an export of 100s to 1000s of years old sediments and dissolved organic matter (DOM) into marine environments, reintroducing potentially reactive material into the modern carbon cycle. Research has suggested that the presence of highly reactive material, such as algal-derived DOM, which is often present in the coastal zone, can lead to increased rates of decomposition of less reactive material, a phenomenon called “priming,” although the mechanisms driving this process are unknown. This study provides evidence from a laboratory experiment that DOM transformations and microbial community composition and functional gene abundance respond uniquely when incubated with separate or combined additions of peat-derived and algal-derived DOM, with pathways for aromatic DOM decomposition and associated DOM transformations enhanced in the presence of both combined.

Abstract
Here, we examine how marine microbial communities respond when dissolved organic matter (DOM) is mobilized from coastal wetlands. Biological transformations of this DOM may increase in the presence of reactive substrates, such as algal-derived DOM (ADOM) in the coastal zone—a process known as priming. We performed laboratory experiments examining transformations of DOM derived from coastal wetland peat (PDOM) with and without the presence ADOM. Associated shifts in microbial community composition and functional gene abundance were

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Author Contribution Statement: TSB and NDW conceived of the experimental design. NDW and TZO collected the peat cores and performed the experiments at the Whitney Laboratory for Marine Bioscience. NDW performed CO2 analyses. ESM and AVO performed DNA extraction and interpretation of metagenomic results. AR-U performed LC–MS analysis and data interpretations. YL performed FT-ICR-MS analyses and data interpretations. The manuscript was prepared by NDW and ESM and was discussed/commented on among all authors.

Data Availability Statement: Data for the experiment are available in the figshare repository at https://doi.org/10.6084/m9.figshare.c.4201007.v2. Data for the metagenomic analyses are available in the National Center for Biotechnology Information (NCBI) Bioproject and database (Accession numbers: PRJNA441393-441404).

Additional Supporting Information may be found in the online version of this article.

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Blue carbon is defined as the organic carbon (OC) derived from and stored in coastal and marine environments and is recognized as a globally important OC sink relative to deep ocean sediments (Duarte and Prairie 2005; Mcleod et al. 2011; Hopkinson et al. 2012). Although buried blue carbon is often considered “stable” for thousands of years, molecular evidence has revealed that in certain habitats, such as seagrass meadows, substantial decomposition of vascular plant biomarkers (lignin) can occur both during and after deposition (Barry et al. 2018). In the case of salt marshes, historic conditions such as the age of current vegetation and preceding vegetation type can control rates of OC sequestration and conversely decomposition/export (Kelleway et al. 2017). Destabilization of coastal marsh habitats also results in the export of blue carbon to open estuarine waters as leached dissolved organic matter (DOM) in erosive environments such as the northern Gulf of Mexico (Wilson and Allison 2008; Bianchi et al. 2009; DeLaune and White 2012), but the fate of this DOM in open water environments is unknown. As shorelines continue to adjust to sea-level rise, stored blue carbon will become more vulnerable to coastal erosion, particularly in low relief settings such as the Florida coast, which contains a major fraction of the United States’ blue carbon reserves (Hinson et al. 2017).

Evaluating the fate of blue carbon in open water systems requires both experimental evidence of blue carbon-derived molecular transformations and a mechanistic understanding of the biotic and abiotic mechanisms that influence these transformations across the continuum from soils to the sea (Ward et al. 2017). For example, in both soils and open water environments, it has been suggested that mixing highly reactive substrates such as sugars and algal material with less reactive substrates such as lignocellulose (a prominent component of preserved blue carbon) enhances microbial decomposition of the less reactive substrate—a process known as the priming effect (Kuzyakov et al. 2000; Guenet et al. 2014; Bianchi et al. 2015). While three potential biological mechanisms for priming effects have been suggested (Bianchi 2011), observations of the magnitude of aquatic priming effects are noted to be “highly context-dependent in aquatic systems,” and little is known about the response of microbial communities to priming conditions (Bengtsson et al. 2018).

The aim of this study is to evaluate how marine microbial communities respond to the addition of various organic substrates in isolation or when added together and how this response influences DOM transformations and CO₂ production. Specifically, we ran dark incubations with various priming substrates and monitored CO₂ production, DOM transformations (via mass spectrometry), and changes in microbial community composition and function via metagenomic sequencing. Results were analyzed to determine: (1) what is the effect of substrate on CO₂ production; (2) what is the effect of substrate on DOM transformations; (3) does marine microbial community composition respond to different substrates; and (4) how do different substrate types influence the abundance of microbial functional genes.

**Methods**

**Experimental design**

Dark incubations were performed in 6-liter bottles with a ~1.7 liter N₂ headspace under four treatments with differing concentrations of algal- and peat-derived leachates (ADOM and PDOM, respectively): (1) seawater only (control); (2) seawater + 1³C-labeled ADOM (Algae; A); (3) seawater + PDOM (Peat; P); and (4) seawater + 1³C-labeled ADOM + PDOM (Peat + Algae; PA). Nine bottles were filled with raw seawater from the Whitney Marine Laboratory’s intake for each of the four treatments. Triplicate samples were filtered through 0.2 μm pore-size Sterivex filters (Millipore Sigma) for chemical and biological analyses at the onset of the incubations (time point [TP0]), after 1 d (TP1), and after 9 d (TP2) of incubating at 21–22°C. Filters and filtrate were frozen at –8°C. Gas samples were collected in 60 mL syringes from air-tight caps equipped with luer valves 1–4 times daily, and an equivalent amount of N₂ was injected into the headspace after gas sampling.

**Substrate preparation**

The PDOM leachate was prepared by collecting five 1-m deep sediment cores from a salt marsh near the Whitney Marine Laboratory. After processing (Supporting Information), the sediment was mixed with MilliQ water (12.5 g L⁻¹) and stirred at 22°C in the dark for 24 h then filtered with a 0.45 μm pore-size Geotech filter cartridge. The PDOM leachate had a total OC (TOC) and total nitrogen (TN) concentration of 3.3 mmol C L⁻¹ and 0.34 mmol N L⁻¹, respectively, and was added to P and PA treatments at a concentration of 101 μmol C L⁻¹.

For the ADOM substrate, 1³C-labeled lyophilized algal cells composed of 99% ¹³C were mixed with MilliQ water (0.84 g L⁻¹) and stirred at 22°C in the dark for 24 h, centrifuged, decanted, then filtered through a 0.2 μm pore size Sterivex filter. The ADOM leachate had a TOC and TN concentration of 1.2 mmol C L⁻¹ and 2.5 mmol N L⁻¹, respectively. ADOM was added to the A and PA treatments at a final concentration of 1.86 μmol C L⁻¹, TOC and TN of the ADOM
and PDOM leachates were measured via high-temperature catalytic oxidation with a Shimadzu TOCV-CSN, according to the method of Guo et al. (1994).

**Bulk geochemical conditions**

Gas samples were analyzed for partial pressure and stable isotopic composition of CO$_2$ ($p$CO$_2$ and $\delta^{13}$C-CO$_2$, respectively) within 5–30 min by injection into a Picarro G2201-i Cavity Ring-Down Spectrometer. $p$CO$_2$ values were corrected for dilution from N$_2$ added at the beginning of the experiment and after each sampling based on the common gas law. A linear regression of $p$CO$_2$ vs. time was performed for each replicate and unpaired Welch’s $t$-tests were performed to evaluate significant differences between treatments within a 95% confidence interval, and marginal significance was considered within a 90% confidence interval.

Initial pH, salinity, and dissolved O$_2$ levels were measured using a YSI Exo 2 sonde. Filtered water samples were analyzed for dissolved OC (DOC) and TN at each TP. The stable isotopic composition of the peat leachate was measured using a Thermo Electron DeltaV Advantage isotope ratio mass spectrometer coupled with a ConFlo II interface linked to a Carlo Erba NA 1500 CNS Elemental Analyzer.

**DOM characterization**

DOM from the filtered water was solid-phase extracted with Bond Elute PPL cartridges (Agilent) (Koch et al. 2008; Seidel et al. 2016). DOM composition was broadly characterized via Fourier-transform ion cyclotron resonance mass spectrometer (FT-ICR-MS), while liquid chromatography-mass spectrometry (LC–MS) was used to evaluate statistical differences in the abundance of molecules often associated with cellular metabolism. See Supporting Information for full details on analytical and statistical procedures.

For FT-ICR-MS data, averaged O : C and H : C values were calculated for spectra features for the ADOM, PDOM, undegraded (i.e., present in TP0 and TP2), and degraded (i.e., only present at the initial TP0, indicating that they were lost by TP2) features in A, P, and PA. A principal component analysis (PCA) was performed with the LC–MS data to evaluate variability between TP0 vs. TP2 and P vs. PA. Additionally, each detected metabolic feature was subjected to a one-way ANOVA to assess for statistical significance between P and PA at TP2 (Supporting Information Table S3). Subsequently, a Chi-square analysis comparing the observed vs. the expected number of metabolic features unique to or at significantly higher concentrations between P and PA was performed using an expected value of 50% of the total significantly changing compounds between treatments.

**Metagenome sample preparation, sequencing, and annotation**

DNA was isolated from the Sterivex filters (through which ~4.4 liters of water was filtered) using a phenol chloroform isoamyl alcohol extraction method, modified from Crump et al. (1999). DNA was shipped to the Joint Genome Institute (JGI) on dry ice, where libraries were prepared for Illumina Low Input Fragment sequencing (300 bp) with paired-end dual-indexing on an Illumina HiSeq 2500. Due to the low concentration of DNA, we only sequenced 12 metagenomes. All metagenome analyses were run within the Integrated Microbial Genomes & Microbiomes (IMG/M) portal, with additional analyses in R version 3.4.0 (see Supporting Information).

**Results**

**Bulk geochemical conditions**

$p$CO$_2$ values ranged from 841 to 1245 ppm throughout the experiment with a starting pH of 7.67, salinity of 36.4 psu, and dissolved O$_2$ concentration of 4.9 mg L$^{-1}$. $p$CO$_2$ decreased in all treatments for the first ~17 h while the headspace became equilibrated followed by a roughly linear increase for all treatments (Fig. 1). CO2Sys version 2.3 was used to calculate the initial distribution of inorganic carbon species (Pierrot et al. 2006), with 94.2% of the inorganic carbon existing as
HCO$_3^-$, 4.3% as CO$_3^{2-}$, and 1.5% as dissolved CO$_2$ (i.e., H$_2$CO$_3$).

After 19 h, pCO$_2$ in PA increased 1.2, 1.7, and 2.4 times more rapidly than A, P, and the control, respectively, based on linear regression (Table 1). The rate of pCO$_2$ increase for P and PA were not significantly different ($p = 0.068$), which was also the case for the control vs. P ($p = 0.059$), whereas A and PA both had significantly higher rates than the control and P (Table 1).

δ$^{13}$C-CO$_2$ remained fairly constant in the control and P, with average values of $-5.9\%$$_{oo}$ to $-0.9\%$$_{oo}$ and $-6.1\%$$_{oo}$ to $0.7\%$$_{oo}$, respectively. P became slightly more enriched throughout the experiment, varying from $-6.5\%$$_{oo}$ to $0.1\%$$_{oo}$ after 1.75 h to $-5.3\%$$_{oo}$ to $1.0\%$$_{oo}$ at the end of the experiment. The δ$^{13}$C signature of the peat leachate was $-27.7\%$$_{oo}$. In A and PA, δ$^{13}$C-CO$_2$ increased rapidly during the first 24 h, followed by a more gradual increase over the duration of the experiment (Fig. 1). A and PA reached final δ$^{13}$C-CO$_2$ values of 745$\%$$_{oo}$ to 2.5$\%$$_{oo}$ and 675$\%$$_{oo}$ to 12.5$\%$$_{oo}$, respectively.

Average DOC concentrations varied from 0.56 to 0.65, 0.58 to 0.61, 1.34 to 1.48, and 1.36 to 1.39 mg L$^{-1}$ for the control, A, P, and PA, respectively. t-tests results show that A was the only treatment with a statistically significant decrease in DOC between TP0 and TP2 ($p = 0.007$).

**DOM characterization**

FT-ICR-MS results showed a large overlap in O : C and H : C between peat- and algal-derived DOM on the van Krevelen diagram (Supporting Information Fig. S1). However, on average, peat-derived DOM was more oxidized (higher O : C) and less saturated (lower H : C) than ADOM (Fig. 2, left). Undegraded features from P and A had similar O : C and H : C characteristics to their respective endmembers. Undegraded features in PA were similar to the peat endmember, likely due to the fact that 54 times more PDOM was added compared to ADOM. All degraded features had lower O : C ratios than the undegraded features.

PCA of the LC-MS metabolite fingerprints clustered TP0 vs. TP2 and PA vs. P (Fig. 2, right), indicative of the presence of ADOM in PA. Principal component 1 (PC1) showed separation between TP0 and TP2, especially for PA and slightly for P. PC2 clustered P from PA. Univariate analyses at TP2 showed that 36% of the detected features were unique or in significantly higher concentration in PA with respect to P, whereas 46% were unique or in significantly higher concentration in P with respect to PA (Supporting Information Table S3). Chi-square test on the number of changing features between treatments at TP2 indicated that such changes were not random ($\chi^2 = 11.63$; $p = 0.00065$) and, thus, the treatment (addition of algae and peat) had a significant effect.

**Metagenome community composition**

The total gene count for metagenomes ranged from 128,175 (P, TP1) to 715,339 (PA, TP2; Supporting Information Table S4). Samples clustered based on TP and treatment, for both Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway categories and taxonomy (Fig. 3). The most

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**Table 1.** The slope and associated $R^2$ value for linear regressions of pCO$_2$ for each replicate and treatment from 19 h after initiation to the end of the incubation, and a statistical comparison between treatments.

| Treatment | Replicate | Slope (ppm h$^{-1}$) | $R^2$ | t-test comparisons | p value |
|-----------|-----------|---------------------|-------|-------------------|---------|
| SW        | #1        | 0.423               | 0.78  | SW vs. SWA        | 0.001   |
| SW        | #2        | 0.342               | 0.74  | SW vs. SWP        | 0.059   |
| SW        | #3        | 0.317               | 0.72  | SW vs. SWPA       | 0.001   |
| SW        | Average   | 0.361 ± 0.056       |       |                   |         |
| SWA       | #1        | 0.771               | 0.92  | SWA vs. SW        | 0.001   |
| SWA       | #2        | 0.812               | 0.94  | SWA vs. SWP       | 0.014   |
| SWA       | #3        | 0.689               | 0.9   | SWA vs. SWPA      | 0.068   |
| SWA       | Average   | 0.757 ± 0.062       |       |                   |         |
| SWP       | #1        | 0.421               | 0.8   | SWP vs. SW        | 0.059   |
| SWP       | #2        | 0.557               | 0.92  | SWP vs. SWA       | 0.014   |
| SWP       | #3        | 0.553               | 0.91  | SWP vs. SWPA      | 0.008   |
| SWP       | Average   | 0.510 ± 0.077       |       |                   |         |
| SWPA      | #1        | 0.848               | 0.9   | SWPA vs. SW       | 0.001   |
| SWPA      | #2        | 0.861               | 0.95  | SWPA vs. SWA      | 0.068   |
| SWPA      | #3        | 0.905               | 0.96  | SWPA vs. SWP      | 0.008   |
| SWPA      | Average   | 0.872 ± 0.030       |       |                   |         |
abundant phylum for all treatments and TPs was Proteobacteria, which comprised 56.4% (A TP2) to 94.1% (A TP1) of the total microbial community (Supporting Information Table S5). The most abundant Proteobacterial class was Gammaproteobacteria, which comprised 12.4% (PA TP0) to 96.5% (A TP1) of the Proteobacterial community. Betaproteobacteria was also abundant at TP0 (PA TP0; 76.9%) and in the peat-only treatment (P TP1; 84%; Supporting Information Table S5). Alteromonadales was the most abundant Gamma-proteobacterial order (Supporting Information Fig. S2).

Metabolic pathways

The most abundant metabolic KEGG orthology (KO) pathway categories were amino acid and carbohydrate metabolism, for all treatments and TPs (Fig. 4). At TP1 and TP2, pathways for amino acid and carbohydrate metabolism were significantly higher in the PA treatment when compared to the P treatment (D-rank abundance comparison, \( p < 0.05 \)). The majority of the clusters of orthologous groups (COGs) associated with amino acid and carbohydrate metabolism were associated with Proteobacteria and Actinobacteria (Supporting Information Fig. S3). There were 198 KOs associated with the degradation of aromatic compounds (Pathway Map 01220). There were 23 unique KOs found in the PA treatment, whereas A had one unique KO (KO16049) and P had no unique KOs associated with aromatic degradation (Supporting Information Table S6).

Discussion

What is the effect of substrate on CO₂ production?

There was no evidence for the decomposition of PDOM to CO₂ in the P treatment. However, there was evidence that decomposition of nonalgal DOM (i.e., either PDOM or DOM present initially in the seawater) was enhanced in PA. The rate of pCO₂ increase was 1.2 times greater for PA than P, which was marginally significant, and \( \delta^{13}C\text{-CO}_2 \) at the end of the experiment was on average 70.2‰ ± 12.7‰ lower for PA than P (Table 1). The higher pCO₂ and lower \( \delta^{13}C\text{-CO}_2 \) values imply enhanced decomposition of non-ADOM substrates in PA vs. P.

While we did not calculate the magnitude of priming effects, our observation of a marginally significant increase in nonalgal DOM decomposition is consistent with the average positive priming effect of 12.6% found across all aquatic
priming studies, which was not statistically different than zero (Bengtsson et al. 2018). High positive priming effects have been observed in some freshwater experiments, with vascular plant leachates decomposing 2–74 times more rapidly in the presence of priming substrates (Bianchi et al. 2015; Ward et al. 2016), but other experiments have shown zero to negative priming effects in different environments such as lakes, the hyporheic zone, and marine sediments (Gontikaki et al. 2013; Bengtsson et al. 2014; Catalán et al. 2015), illustrating the diversity in microbial responses to multiple substrates across environments. The diverse microbial responses to priming conditions necessitate standardized protocols for quantifying priming effects across environments, considering most studies to date use differing approaches. Likewise, priming effects may not always be detectable on a bulk level, necessitating more detailed molecular level evaluations of DOM transformations (more below).

**What is the effect of substrate on DOM transformations?**

The degraded material (i.e., compounds only present at TP0) in PA has H : C and O : C values closer to the ADOM leachate, suggesting that ADOM compounds or similar chemical characteristics present in PDOM were preferentially degraded. The fact that averaged H : C and O : C values of degraded features for A were substantially different than all other degraded features may suggest that degraded features in PA were not exclusively ADOM related, but in fact degradable PDOM features with similar characteristics as the initial ADOM leachate. This is supported by the fact that peat and algal endmembers have a large overlap in O : C and H : C values (Supporting Information Fig. S1). Additionally, it is known that direct infusion FT-ICR-MS analysis cannot distinguish structural isomers with the same elemental formulas even though they can be from completely different compound classes (Sleighter and Hatcher 2008).

If priming effects were completely nonexistent in marine waters, we would expect no overall differences between P and PA. However, from the relative abundance point of view, LC–MS analyses showed clearly distinct metabolic profiles between P and PA and TP0 and TP2 (Fig. 2, right). Furthermore, the metabolic distance between TP0 vs. TP2 was considerably larger in PA than in P along the PC1. These results suggest distinct metabolic activity between treatments and that, indeed, larger metabolic changes occurred in PA with respect to P during the incubation period. Additionally, the significantly higher number of metabolic features unique or in higher concentration in P with respect to PA ($\chi^2 = 11.63; p < 0.001$) suggests potential enhancements in DOM respiration with presence of algae. LC–MS results are in accordance
with FT-ICR-MS analyses; however, we cannot definitively conclude with mass spectrometry data alone if such differences are linked to priming, per se.

Other studies have shown that algal exudates can drive enhanced microbial activity and DOM transformation in peatlands (Wyatt and Turetsky 2015). For example, Morling et al. (2017) observed a consistent decomposition of aliphatic molecules with a H : C greater than 1.5 with and without algae present, and enhanced decomposition of oxidized and unsaturated molecules with H : C less than 1.0 and O : C greater than 0.4 with the presence of algae. Morling et al. (2017) saw a net increase of bulk DOC concentrations, concluding that molecular-level analyses are needed to determine transformations due to priming, similar to our findings of no significant DOC decrease. Understanding the drivers of molecular-level DOM transformations and when/where such transformations may occur requires a deeper probing of the microbial communities and genomic functions associated with the utilization of different substrates.

Does microbial community composition differ in treatments with different substrate types?

Sample clustering of metagenomes (Fig. 3) indicated that the composition of microbial taxa and functional genes changed over the course of the incubation and differed between treatments. The prevalence of Gammaproteobacteria in our samples agrees with previous literature, which has described members of the Gammaproteobacteria as important DOC cyclers in aquatic systems (Poretsky et al. 2010). Changes in the dominant Gammaproteobacterial orders over the course of the incubation indicate that microbial communities shift, likely due to changes in substrate availability, with Alteromonadales dominating the initial TP, but with a more diverse community developing by the second TP (Supporting Information Fig. S2).

Soil studies have seen similar shifts in microbial community composition due to priming based on 16S pyrosequencing (Pascual et al. 2013) and phospholipid fatty acids (Bastida et al. 2013; Wang et al. 2014). Models of Fontaine and Barot (2005) invoke concepts of r- and K-populations that metabolize fresh organic matter vs. more stable bulk pools, respectively, suggesting that the key enzyme producers might be those populations that have evolved to rapidly exploit readily available substrates, while bulk organics are mineralized by populations that maximize numbers/biomass at the expense of growth rate. Pascual et al. (2013) used the related concepts of copiotrophic and oligotrophic nutritional strategies to describe populations that respond to priming substrates vs. those that mineralize bulk organics, respectively. Members of Alteromonadales have been characterized as copiotrophs in the marine environment (Lauro et al. 2009), suggesting that copiotrophs may be involved in priming effects in aquatic systems, although further characterization of their growth rates and activities under priming conditions is necessary.

How do different substrate types influence the abundance of microbial functional genes?

The overall high abundance of pathways for amino acid and carbohydrate metabolism is likely due to the prevalence of housekeeping genes in these KO pathways. The increased abundance of these pathways in the PA treatment relative to the A treatment suggests that microbial activity may be enhanced when microorganisms are in the presence of both a “labile” and “recalcitrant” substrate. In addition, the prevalence of Proteobacteria in the COGs associated with amino acid and carbohydrate metabolism/transport suggests that the most abundant taxa in this system are likely the most metabolically active. The high number of unique genes for the degradation of aromatic compounds within the PA treatment suggests that there may be greater turnover of aromatic compounds within this treatment, although this may be driven by the higher number of reads within the PA treatment, and further work is needed to investigate the activities of microbial communities under priming conditions.

Conclusions

Here, we provide an initial evaluation of how marine microbial communities respond to the addition of peat and/or algal-derived DOM along with associated DOM transformations and bulk geochemical changes. Considering that the Florida coastal ecosystems studied here are experiencing both increasing rates of sea-level rise and have recently been impacted by hurricanes several years in a row (i.e., Matthew in 2016 and Irma in 2017), quantifying the impact of long-term and rapid export of carbon from wetlands to the sea is of critical importance. We show that microbial community composition and functional gene abundance are altered in the presence of both a “recalcitrant” and “labile” substrate, resulting in more rich DOM transformations. However, further work is required to investigate alterations in microbial activity, interactions, and chemical composition, to better understand the mechanisms driving microbial conversion of blue carbon to CO₂ in coastal systems.

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Acknowledgments

Funding was provided by the University of Florida Jon L. and Beverly A. Thompson Endowment. A portion of this research was performed under the Facilities Integrating Collaborations for User Science initiative (#49505) and used resources at the DOE Joint Genome Institute and the Environmental Molecular Sciences Laboratory, which are DOE Office of Science User Facilities. Both facilities are sponsored by the Office of Biological and Environmental Research and operated under Contract DE-AC02-05CH11231 (JGI) and DE-AC05-76RL01830 (EMSL). A portion of this research was also conducted as part of the PREMIS Initiative at Pacific Northwest National Laboratory (PNNL) under the Laboratory Directed Research and Development Program at PNNL, a multiprogram national laboratory operated by Battelle for the U.S. Department of Energy under Contract DE-AC05-76RL01830. We would like to thank Derrick Vaughn and Ana Arellano for assistance in sample preparation and bulk chemical analyses.

Submitted 25 April 2018
Revised 22 October 2018
Accepted 28 October 2018