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Title: Microbial Oxidation of Hg(0) - Its Effect on Hg Stable Isotope Fractionation and Methylmercury Production

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SUMMARY

In the 1950s and early 1960s, large amounts of mercury (Hg) were released into East Fork Poplar Creek as a result of the nuclear weapons production at the Oak Ridge Y-12 Plant in eastern Tennessee. Critical to predicting the impacts of the contamination is a mechanistic understanding of the processes that control mercury methylation along the hydrological flow path of East Fork Poplar Creek. The methylation of inorganic Hg is known to be mediated by microorganisms under anoxic conditions. Previous studies have elucidated the forms of mercuric Hg [Hg(II)] that are bioavailable to methylating microbes. It is generally assumed that elemental Hg [Hg(0)] is unavailable for biologic methylation, however the uptake and transformation of Hg(0) by anaerobic Hg-methylating bacteria have never been tested. In this project, we conducted laboratory experiments to examine the oxidation of Hg(0) by anaerobic bacteria, investigated the effect of microbial interactions on Hg(0)/Hg(II) transformations, and assessed Hg isotope fraction during methylmercury production.

In part I of our project, we investigated Hg(0) oxidation and methylation by anaerobic bacteria. We discovered that the anaerobic bacterium *Desulfovibrio desulfuricans* ND132 can oxidize elemental mercury [Hg(0)] (Colombo et al., 2013). When provided with dissolved elemental mercury, *D. desulfuricans* ND132 converts Hg(0) to Hg(II) and neurotoxic methylmercury [MeHg]. We also demonstrated that diverse species of subsurface bacteria oxidizes dissolved elemental mercury under anoxic conditions (Colombo et al., 2014). The obligate anaerobic bacterium *Geothrix fermentans* H5, and the facultative anaerobic bacteria *Shewanella oneidensis* MR-1 and *Cupriavidus metallidurans* AE104 can oxidize Hg(0) to Hg(II) under anaerobic conditions.

In part II of our project, we established anaerobic enrichment cultures and obtained new bacterial strains from the DOE Oak Ridge site. We isolated three new bacterial strains from subsurface sediments collected from Oak Ridge. These isolates are *Bradyrhizobium* sp. strain FRC01, *Clostridium* sp. strain FGH, and a novel *Negativicutes* strain RU4 (Wang et al., 2013; Shah et al., 2014; Choi et al., 2016). Strain RU4 is a completely new genus and species of bacteria (Choi et al., 2016). We also demonstrated that syntrophic interactions between fermentative bacteria and sulfate-reducing bacteria in Oak Ridge saprolite mediate iron reduction via multiple mechanisms (Shah et al., 2014). Finally, we tested the impact of Hg on denitrification in nitrate reducing enrichment cultures derived from subsurface sediments from the Oak Ridge site, where nitrate is a major contaminant. We showed that there is an inverse relationship between Hg concentrations and rates of denitrification in enrichment cultures (Wang et al., 2013).

In part III of our project, we examined in more detail the effects of microbial interactions on Hg transformations. We discovered that both sulfate reducing and iron reducing bacteria coexist in freshwater sediments and both microbial groups contribute to mercury methylation (Yu et al., 2012). We showed that mercury methylation by sulfate reducing and iron reducing

bacteria are temporally and spatially separated processes. We also discovered that methanogens can methylate mercury. We showed that *Methanospirillum hungatei* JF-1 methylated Hg at comparable rates, but with higher yields, than those observed for sulfate-reducing bacteria and iron-reducing bacteria (Yu et al., 2013). Finally, we demonstrated that syntrophic interactions between different microbial groups increase mercury methylation rates (Yu et al., in prep). We showed that Hg methylation rates are stimulated via inter-species hydrogen and acetate transfer (i) from sulfate-reducing bacteria to methanogens and (ii) from fermenters to the sulfate-reducing bacteria.

In part IV of the project, we studied Hg bioavailability and Hg isotope fractionation. We demonstrated that thiol-bound Hg is bioavailable to mercury resistant bacteria (Ndu et al., 2015). We found that uptake of Hg from Hg-glutathione and Hg-cysteine complexes does not require functioning glutathione and cystine/cysteine transport systems. We demonstrated that a wide range of methylmercury complexes (e.g. MeHgOH, MeHg-cysteine, and MeHg-glutathione) are bioavailable to mercury resistant bacteria. The rate of MeHg demethylation varies more between different species of mercury resistant bacteria than among MeHg complexes (Ndu et al., 2016). We showed that microbial demethylation of MeHg depends more on the species of microorganism than on the types and relative concentrations of thiols or other MeHg ligands present. Finally, we demonstrated that Hg methylation by *Geobacter sulfurreducens* PCA and *Desulfovibrio desulfuricans* ND132 imparts mass-dependent discrimination against ^{202}Hg relative to ^{198}Hg (Janssen et al., 2016). *G. sulfurreducens* PCA and *D. desulfuricans* ND132 have similar kinetic reactant/product Hg fractionation factors. Using the Hg isotope data, we showed that there are multiple intra- and/or extracellular pools provide substrate inorganic Hg for methylation.

INTRODUCTION

Mercury (Hg) associated with mixed waste generated by nuclear weapons manufacturing has contaminated vast areas of the Oak Ridge Reservation (ORR). Neurotoxic methylmercury (MeHg) has been formed from the inorganic Hg wastes discharged into headwaters of East Fork Poplar Creek (EFPC). Thus, understanding the processes and mechanisms that lead to Hg methylation along the flow path of EFPC is critical to predicting the impacts of the contamination and the design of remedial action at the ORR.

Redox transformations of Hg play an important role in controlling the distribution and bioavailability of inorganic Hg in EFPC waters. At ORR, extensive studies have been carried out to investigate the reduction of mercuric Hg [Hg(II)] by abiotic and microbial processes. Our previous ORR research has shown that aerobic microbes in the upper reaches of EFPC and anaerobic bacteria in subsurface sediments of the Integrated Field Research Challenge (IFRC) site reduce Hg(II) to its elemental form [Hg(0)]. The resulting Hg(0) is thought to be less toxic

and largely unavailable for uptake by biota. Because all known Hg substrates used by Hg-methylating bacteria are aqueous complexes of Hg(II), the reduction of Hg(II) to Hg(0) has the potential to limit the concentration of Hg available for methylation. However, little is known regarding the reverse redox reaction (i.e., the oxidation of Hg(0) to Hg(II)) on Hg bioavailability and on MeHg production.

This project was carried out in four parts. In part I, we investigated Hg(0) oxidation and methylation by anaerobic bacteria. In part II, we established anaerobic enrichment cultures and obtained new bacterial strains from the DOE Oak Ridge site. In part III, we examined in more detail the effects of microbial interactions on Hg transformations. And finally in part IV, we studied Hg bioavailability and Hg isotope fractionation. Our specific research activities and accomplishments are described below.

RESULTS

Part I: To determine if anaerobic bacteria oxidize and methylate Hg(0)

In part I of our project, we investigated Hg(0) oxidation and methylation by anaerobic bacteria. First, we conducted experiments to examine the oxidation and methylation of dissolved elemental mercury [Hg(0)] by the anaerobic bacterium *Desulfovibrio desulfuricans* ND132. Anoxic cultures of *D. desulfuricans* ND132 were exposed to a constant source of Hg(0) in the dark, and samples were collected and analyzed for the formation of non-purgeable Hg and MeHg over time. We found that *D. desulfuricans* ND132 rapidly converted dissolved gaseous mercury into non-purgeable Hg, with bacterial cultures producing approximately 40 μg/L of non-purgeable Hg within 30 min, and as much as 800 μg/L of non-purgeable Hg after 36 h. Derivatization of the non-purgeable Hg in the cell suspensions to diethylmercury and analysis of Hg(0)-reacted *D. desulfuricans* ND132 cells using X-ray absorption near edge structure (XANES) spectroscopy demonstrated that cell-associated Hg was dominantly in the oxidized Hg(II) form. Spectral comparisons and linear combination fitting of the XANES spectra indicated that the oxidized Hg(II) was covalently bonded to cellular thiol functional groups. MeHg analyses revealed that *D. desulfuricans* ND132 produced up to 118 μg/L of methylmercury after 36 h of incubation. We found that a major fraction of the methylated Hg was exported out of the cell and released into the culture medium. The results are reported in Colombo et al., (2013).

We also tested if diverse anaerobic bacteria were able to oxidize dissolved Hg(0) to Hg(II). Mercury oxidation experiments were carried out with the obligate anaerobic bacterium *Geothrix fermentans* H5, and the facultative anaerobic bacteria *Shewanella oneidensis* MR-1 and *Cupriavidus metallidurans* AE104. We found that all three bacterial strains reacted with dissolved gaseous Hg(0) to form non-purgeable Hg. In mass balance experiments, the formation of non-purgeable Hg corresponded to the loss of volatile Hg. Derivatization of non-purgeable

Hg to diethylmercury and the Hg L_{III}-edge position of the XANES spectra demonstrated that the reacted bacterial samples contained Hg(II). XANES analysis also revealed that cell-associated Hg(II) was covalently bound to bacterial functional groups, most likely to thiol moieties. Finally, experiments with metabolically active and heat-inactivated cells indicated that both live and dead cells oxidized Hg(0) to Hg(II). Hg(0) oxidation rates for metabolically active cultures increase in the order *S. oneidensis* MR-1 (1.6×10^{-4} fg/cell/min), *C. metallidurans* AE104 (2.5×10^{-4} fg/cell/min), and *G. fermentans* H5 (23.1×10^{-4} fg/cell/min). The results are reported in Colombo et al., (2014).

Part II: To obtain bacterial isolates and consortia from the DOE Oak Ridge site

In part II of our project, we established anaerobic enrichment cultures and obtained new bacterial strains from the DOE Oak Ridge site. The most interesting finding is the discovery of a new bacterial species, which we named *Anaerosporomusa substerrana* strain RU4. The new isolate is a spore-forming Gram-negative anaerobe belonging to the class *Negativicutes* isolated from saprolite collected at the Oak Ridge site. This is a fascinating microorganism because it is a rare Gram-negative bacterium in the *Firmicutes* phylum. We have characterized this bacterium and deposited the pure culture with the ATCC and DSMZ culture collections (Choi et al, 2016).

We also examined that syntrophic interactions between fermentative bacteria and sulfate-reducing bacteria in Oak Ridge saprolite mediate iron reduction via multiple mechanisms. We cultivated from Oak Ridge sediments an anaerobic consortium that was composed of a fermentative Fe-reducer *Clostridium* species (designated as strain FGH) and the novel bacterium strain RU4. In pure culture, *Clostridium sp*. strain FGH mediated the reductive dissolution/transformation of iron oxides during growth on peptone. When *Clostridium sp.* FGH was grown with strain RU4 on peptone, the rates of iron oxide reduction were significantly higher. Iron reduction by the consortium was mediated by multiple mechanisms, including biotic reduction by *Clostridium sp.* FGH and biotic/abiotic reactions involving biogenic sulfide formed by strain RU4. The *Clostridium* sp. FGH produced hydrogen during fermentation, and the presence of hydrogen inhibited growth and iron reduction activity. The sulfate-reducing partner strain RU4 was stimulated by the presence of H_2 and generated reactive sulfide which promoted the chemical reduction of the iron oxides. Characterization of Fe(II) mineral products showed the formation of nanoparticulate magnetite during ferrihydrite reduction, and the precipitation of iron sulfides during goethite and hematite reduction. The results are reported in Shah et al. (2014).

Finally, we tested the impact of Hg on denitrification in nitrate reducing enrichment cultures derived from subsurface sediments from the Oak Ridge site, where nitrate is a major contaminant. We observed an inverse relationship between Hg concentrations and onset and rates of denitrification in enrichment cultures containing between 53 nM and 1.1 µM of inorganic Hg; higher Hg concentrations irreversibly inhibited denitrification. A decline in the number of species in the subsurface community, indicated by the number of peaks in tRFLP patterns, occurred with increasing Hg concentrations. A single tRFLP peak observed for the 312

nM Hg treatment consisted of the 16S rRNA gene of *Bradyrhizobium* spp. A *Bradyrhizobium* sp. isolate from a nitrate enrichment reduced Hg(II) to Hg(0) and the translation product of its *merA* gene had a 97% identity to that of *Proteobacteria* and *Firmicutes*. The results are reported in Wang et al., (2013).

Part III: To understand the effects of microbial interactions on Hg transformations

In part III of our project, we examined in more detail the effects of microbial interactions on Hg transformations. First, we investigated microbial methylmercury production in sediments contaminated with Hg. We found that potential Hg methylation rates in samples collected at nine sites were low in late spring and significantly higher in late summer. Demethylation of was dominated by CH_4 production in spring, but switched to producing mostly CO_2 in the summer. Fine-grained sediments originating from the erosion of river banks had the highest MeHg concentrations and were potential hot spots for both methylation and demethylation activities. Sequencing of 16S rRNA genes of cDNA recovered from sediment RNA extracts indicated that at least three groups of sulfate-reducing bacteria (SRB) and one group of iron-reducing bacteria (IRB), potential Hg methylators, were active in SR sediments. SRB were confirmed as a methylating guild by amendment experiments showing significant sulfate stimulation and molybdate inhibition of methylation in SR sediments. The addition of low levels of amorphous iron(III) oxyhydroxide significantly stimulated methylation rates, suggesting a role for IRB in MeHg synthesis. The results are reported in Yu et al. (2012)

We also conducted studies to elucidate mercury methylation by methanogens. We showed that a methanogen, Methanospirillum hungatei JF-1, methylated Hg in a sulfide-free medium at comparable rates, but with higher yields, than those observed for some SRB and IRB. Phylogenetic analyses showed that the concatenated orthologs of the Hg methylation proteins HgcA and HgcB from *M. hungatei* are closely related to those from known SRB and IRB methylators and that they cluster together with proteins from eight other methanogens, suggesting that these methanogens may also methylate Hg. Because all nine methanogens with HgcA and HgcB orthologs belong to the class *Methanomicrobia*, constituting the late-evolving methanogenic lineage, methanogenic Hg methylation could not be considered an ancient metabolic trait. Finally we demonstrated that syntrophic interactions between different microbial groups increase mercury methylation rates. We showed that Hg methylation rates are stimulated via inter-species hydrogen and acetate transfer from sulfate-reducing bacteria to methanogens and from fermenters to the sulfate-reducing bacteria.The results are reported in Yu et al. (2013) and a paper in preparation (Yu et al., in prep)

Part IV: To elucidate Hg bioavailability and to quantify Hg isotope fractionation during methylation

In part IV of the project, we studied Hg bioavailability and Hg isotope fractionation. First, we conducted experiments with bacterial biosensors to evaluate Hg bioavailability. The Hg

uptake into the biosensors was quantified based on the intracellular conversion of inorganic mercury to elemental mercury by the enzyme MerA. We found that uptake of Hg from Hg-cysteine (Hg(CYS)2) and Hg-glutathione (Hg(GSH)2) complexes occurred at the same rate as that of inorganic complexes of Hg(II) into *Escherichia coli* strains with and without intact Mer transport systems. However, higher rates of Hg uptake were observed in the strain with a functioning Mer transport system. These results demonstrate that thiol-bound Hg is bioavailable to *E. coli* and that this bioavailability is higher in Hg-resistant bacteria with a complete Mer system than in non-resistant strains. No difference in the uptake rate of Hg from Hg(GSH)2 was observed in *E. coli* strains with or without functioning glutathione transport systems. There was also no difference in uptake rates between a wildtype *Bacillus subtilis* strain with a functioning cystine/cysteine transport system, and a mutant strain where this transport system had been knocked out. The results are reported in Ndu et al., (2015).

We also investigated the effects of thiol complexation on the uptake of MeHg by measuring the intracellular demethylation-reduction (transformation) of MeHg to Hg(0) in Hg-resistant bacteria. Short-term intracellular transformation of MeHg was quantified by monitoring the loss of volatile Hg(0) generated during incubations of bacteria containing the complete *mer* operon (including genes from putative mercury transporters) exposed to MeHg in minimal media compared to negative controls with non-*mer* or heat-killed cells. The results indicate that the complexes MeHgOH, MeHg-cysteine, and MeHg-glutathione are all bioavailable in these bacteria, and without the *mer* operon there is very little biological degradation of MeHg. In both *Pseudomonas stutzeri* and *Escherichia coli*, there was a pool of MeHg that was not transformed to elemental Hg(0), which was likely rendered unavailable to Mer enzymes by non-specific binding to cellular ligands. Since the rates of MeHg accumulation and transformation varied more between the two species of bacteria examined than among MeHg complexes, microbial bioavailability, and therefore microbial demethylation, of MeHg in aquatic systems likely depends more on the species of microorganism than on the types and relative concentrations of thiols or other MeHg ligands present. The results are reported in Ndu et al., (2016).

Finally, we assessed the extent of Hg stable isotope fractionation during Hg methylation by *Geobacter sulfurreducens* PCA and *Desulfovibrio desulfuricans* ND132. In both organisms, Hg stable isotope ratios of directly analyzed MeHg showed mass-dependent discrimination against ^{202}Hg relative to ^{198}Hg (lower δ^{202}Hg values), but no mass-independent fractionation (MIF) of Hg stable isotopes during Hg methylation. Despite differences in methylation rates and phylogenetic classification, *G. sulfurreducens* PCA and *D. desulfuricans* ND132 had similar kinetic reactant/product Hg fractionation factors ($\alpha r/p = 1.0009$ and 1.0011, respectively). Unexpectedly, after both organisms methylated 34% to 36% of the inorganic Hg to which they had been exposed, accumulated MeHg acquired an isotopic composition 0.4‰ greater than the initial value of reactant inorganic Hg. This indicates that a ^{202}Hg-enriched pool of inorganic Hg was preferentially utilized as a substrate for methylation by these organisms. In addition, the change in sign of Hg isotope fractionation during later stages of methylation by *D. desulfuricans*

indicates that multiple intra- and/or extracellular pools provided substrate inorganic Hg for methylation in this organism. The results are reported in Janssen et al., (2016).

CONCLUSIONS

We concluded that anaerobic bacteria can produce MeHg when provided with dissolved Hg(0) as their sole Hg source (Colombo et al., 2013). This is a previously unrecognized pathway in the mercury cycle, and may represent a significant route for the production of MeHg at ORR. Furthermore, diverse bacteria react with Hg(0) (Colombo et al., 2014), and thus passive microbial oxidation of Hg(0) can affect the redox transformation of mercury contaminants in subsurface environments.

Using enrichment cultures, we found that nitrate, iron-reducing and sulfate-reduction are major redox processes in Oak Ridge sediments. An important pathway for iron reduction and secondary mineralization by fermentative sulfate-reducing microbial consortia occurs through syntrophy-driven biotic/abiotic reactions with biogenic sulfide (Shah et al., 2014). Interesting, DOE Oak Ridge sediments harbor new bacteria species whose functions and phylogeny are hitherto uncharacterized (Choi et al., 2016). Furthermore, in subsurface sediment incubations, Hg inhibited denitrification which was restored at low Hg concentrations upon enrichment of Hg resistant denitrifying bradyrhizobia possessing horizontally transferred *merA* genes (Wang et al., 2013).

Diverse anaerobic microorganisms can produce methylmercury, and understanding the ecological and physiological controls on Hg methylation represents a major new frontier in mercury research. Sulfate-reducing bacteria and iron-reducing bacteria that co-exist in river sediments contribute to Hg methylation, possibly by temporally and spatially separated processes (Yu et al., 2012). Methanogens have been identified as a new guild of Hg-methylating microbes with a potentially important role in sulfate- and iron-limited anoxic freshwater environments (Yu et al., 2013). Finally, there are multiple intra- and/or extracellular pools provide substrate inorganic Hg for methylation. Using Hg isotope data, we can now examine the intracellular compartmentalization of Hg(II) in methylating microorganisms (Jansen et al., 2016).

List of Peer-reviewed Articles Delivered (including papers in preparation):

1. Wang Y., J.K. Schaefer, B. Mishra, and N. Yee (in prep) Intracellular Hg(0) oxidation and complexation in a mercury methylating bacterium.
2. Yu, R., J.R. Reinfelder, M.E. Hines, and T. Barkay (in prep) Syntrophic pathways for microbial mercury methylation.
3. Janssen, S.E., J.K. Schaefer, T. Barkay, and J.R. Reinfelder (submitted) Fractionation of mercury stable isotopes during microbial methylmercury production in pure cultures. *Environ. Sci. Technol.*

4. Choi J.K., Shah M., Yee N.* (submitted) *Anaerosporomusa subterraneum* gen. nov., sp. nov., a spore-forming obligate anaerobe isolated from saprolite. *International Journal of Systematic and Evolutionary Microbiology*
5. Ha J., Zhao X., Yu R., Barkay T., *Yee N. (2016) Hg(II) Reduction by Siderite ($FeCO_3$) (submitted)
6. Ndu, U., T. Barkay, A.T. Schartup, R.P. Mason, and J.R. Reinfelder (2016) The effect of aqueous speciation and cellular ligand binding on the biotransformation and bioavailability of methylmercury in mercury-resistant bacteria. *Biodegrad.* 27: 29-36.
7. Ndu, U., T. Barkay, R.P. Mason, A.T. Schartup, R. Al-Farawati, J. Liu, J.R. Reinfelder (2015) The use of a mercury biosensor to evaluate the bioavailability of mercury-thiol complexes and mechanisms of mercury uptake in bacteria. *PLoS ONE*, 10(9): e0138333.
8. Colombo M.J., Ha J., Reinfelder J.R., Barkay T., Yee N., (2014) Oxidation of Hg(0) to Hg(II) by Diverse Anaerobic Bacteria, *Chemical Geology*, 363, 334-340
9. Shah M., Lin C.C., Kukkadapu R., Engelhard M.H., Zhao X., Wang Y., Barkay T., Yee N. (2014) Syntrophic Effects in a Subsurface Clostridia Consortium on Fe(III)-(Oxyhydr)oxide Reduction and Secondary Mineralization, *Geomicrobiology Journal*, 31, 101-115
10. Colombo M.J., Ha J., Reinfelder J.R., Barkay T., Yee N., (2013) Anaerobic Oxidation of Hg(0) and Methylmercury Formation by *Desulfovibrio desulfuricans* ND132, *Geochimica et Cosmochimica Act* , 112, 166-177
11. Wang Y., Wiatrowski H.A., Ria J., Lin C.C., Young L.Y., Kerkhof L.J., Yee N., Barkay T. (2013) Impact of mercury on denitrification and denitrifying microbial communities in nitrate contaminated subsurface sediments, *Biodegradation*, 24, 33-46
12. Poulain, A.J., and T. Barkay. 2013. Cracking the mercury methylation code. *Science.* 339:1280-1281. doi: 10.1126/science.1235591
13. Yu, R.-Q, J. Reinfelder, M. Hines, and T. Barkay. (2013). Mercury methylation by the methanogen *Methanospirillum hungatei*. *Appl. Environ. Microbiol.* 79:6325-6330.
14. Yu, R.-Q, J. R. Flanders, E. E. Mack, R. Turner, M. B. Mirza, and T. Barkay. 2012. Coexisting Sulfate and Iron Reducing Bacteria Contribute to Methylmercury Production in Freshwater River Sediments. *Environ. Sci. Technol.* 46:2684-2691.

Conference Abstracts

Janssen, S., J.K. Schaefer, Tamar Barkay, and J.R. Reinfelder, "Fractionation of mercury stable isotopes during microbial methylmercury production in pure cultures," Geological Society of America Annual Meeting, Baltimore, Maryland, November 2015.

Yee N., Wang Y., Wang T., Schaefer J., Mishra B. Intracellular Mercury Oxidation and Complexation in Anaerobic Bacteria, Geological Society of America Annual Meeting, Baltimore, Maryland, NOVEMBER 2015.

Janssen, S., J.R. Reinfelder, "Controls on mercury methylation in the Hackensack River, NJ," Hudson-Delaware Chapter of the Society of Environmental Toxicology and Chemistry, Spring Meeting, New Brunswick, NJ, April 2015.

Janssen, S., T. Barkay, J.D. Blum, J.R. Reinfelder, "Stable isotopic composition of methylmercury in pure cultures of mercury methylating bacteria," Northeastern Geobiology Symposium, Princeton, NJ, February 2015.

Janssen, S., M.W. Johnson, T. Barkay, J.D. Blum, and J.R. Reinfelder, "Mercury stable isotopic composition of monomethylmercury in estuarine sediments and pure cultures of mercury methylating bacteria," American Geophysical Union, Fall Meeting, San Francisco, CA, December 2014.

Janssen, S. and J.R. Reinfelder, "Tracking sources of mercury in fish from the Hackensack River estuary, New Jersey, USA using mercury stable isotopes," Passaic River Symposium VI, Montclair, New Jersey, October 2014.

Reinfelder, J.R., Kritee, L. Motta, "Photomicrobial reduction and dark oxidation of mercury in marine surface waters," the 24th V.M. Goldschmidt Conference, Sacramento, CA, June 2014.

Colombo M., Yee N., Role of Microbial Growth on Hg(0) Uptake and Production of Methylmercury, Goldschmidt Conference, Sacramento, JUNE 2014

Yee N., Colombo M., Ha J., Interactions of Elemental Mercury with Microbial Biomass Goldschmidt Conference, Sacramento, JUNE 2014

Ndu, U., T. Barkay, J.R. Reinfelder, "The effects of thiol complexation, and Mer transport proteins on the bioavailability of methylmercury in Hg-resistant bacteria," Eleventh International Conference on Mercury as a Global Pollutant, Edinburgh, Scotland, UK, July-August 2013.

Colombo, M., Juyoung Ha, John Reinfelder, Tamar Barkay, Nathan Yee, "Oxidation of Hg(0) to Hg(II) by metabolically diverse anaerobic bacteria," Eleventh International Conference on Mercury as a Global Pollutant, Edinburgh, Scotland, UK, July-August 2013.

Colombo M.,Ha J., Reinfelder J.R., Barkay T., Yee N., Microbial production of methylmercurcury from Hg(0), Goldschmidt Conference, Montreal, JUNE 2012

Colombo M.,Ha J., Reinfelder J.R., Barkay T., Yee N., Microbial Uptake and Methylation of Dissolved Elemental Mercury, Goldschmidt Conference, Prague, AUG 2011

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