Comammox Nitrospira are abundant ammonia oxidizers in diverse groundwater-fed rapid sand filter communities

The recent discovery of completely nitrifying Nitrospira demands a re-examination of nitrifying environments to evaluate their contribution to nitrogen cycling. To approach this challenge, tools are needed to detect and quantify comammox Nitrospira. We present primers for the simultaneous quantification and diversity assessment of both comammox Nitrospira clades. The primers cover a wide range of comammox diversity, spanning all available high quality sequences. We applied these primers to 12 groundwater-fed rapid sand filters, and found comammox Nitrospira to be abundant in all filters. Clade B comammox comprise the majority (~75%) of comammox abundance in all filters. Nitrosomonadaceae were present in all filters, although at low abundance (mean=1.8%). Ordination suggests that temperature impacts the structure of nitrifying communities, and in particular that increasing temperature favours Nitrospira. The nitrogen content of the filter material, sulfate concentration and surface ammonium loading rates shape the structure of the comammox guild in the filters. This work provides an assay for simultaneous detection and diversity assessment of clades A and B comammox Nitrospira, expands our current knowledge of comammox Nitrospira diversity and demonstrates a key role for comammox Nitrospira in nitrification in groundwater-fed biofilters.
Comammox Nitrospira are key nitrifiers in diverse groundwater-fed drinking water filters

Nitrification is a dominant process in groundwater-fed rapid sand filters (RSFs) used for drinking water purification. Near complete removal of ammonium and nitrite is required in the EU and Denmark due to strict regulatory limits that enable high water stability in the distribution system. RSFs are a unique environment harboring diverse microbial communities including a range of ammonia oxidizers (AOs); Betaproteobacterial ammonia oxidizers (Nitrosomonas, Nitrosospira), ammonia oxidizing archaee, diverse heterotrophs and a large fraction of Nitrospira spp., which in one studied filter have been shown to comprise both nitrite oxidizers as well as complete nitrifying (comammox) Nitrospira spp. (Palomo et al. 2016). We developed a new qPCR assay for the quantification of the comammox Nitrospira amoA gene which amplifies both clades A and B and applied this assay to the study of 12 drinking water treatment plants across Denmark. We further sequenced amplicons of the 16S rRNA gene of total Bacteria and amoA gene of Nitrospira to examine the microbial biodiversity present in the filters. Our results show that comammox Nitrospira are present in high abundance making up an average of 19% of the microbial communities in the examined filters. While members of both clades A (41 sequence variants) and B (47 sequence variants) were both present in high abundance, the majority of comammox diversity (70-90% in each filter) was made up by clade B. Ordination analysis with variance partitioning was performed on the total
microbial communities and the comammox Nitrospira communities to identify physicochemical parameters of the influent water, filter material, or operational parameters which influenced the community structures in an effort to understand the success of comammox Nitrospira in these filters. Temperature as well as the sulfate and calcium content of the influent water made significant contributions towards explaining both the total and comammox community structures, while the iron content of the filter material made a significant contribution to explaining only the structure of the comammox Nitrospira communities. Further examination of groundwater-fed RSFs with higher variability in microbial communities and physicochemical parameters may provide further information on the ecology of comammox Nitrospira and explain their success in the groundwater-fed filters examined in this study. Together this work provides a new assay for the simultaneous detection of clade A and B comammox Nitrospira and expands our current knowledge of the diversity of comammox Nitrospira, while attempting to explain the success of comammox Nitrospira in these groundwater-fed filters.

**General information**

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Organisations: Department of Environmental Engineering, Water Technologies
Authors: Fowler, J. (Intern), Palomo, A. (Intern), Smets, B. F. (Intern)
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**Discovery and description of complete ammonium oxidizers in groundwater-fed rapid sand filters**

Microbial communities are directly linked with process performance in several engineered systems. In the last century, intense study of microorganisms has contributed to optimize important environmental biotechnologies such as the activated sludge process or anaerobic digestion. However, less attention has been paid to the role of microorganisms in drinking water treatment technologies. In contrast, much effort has been devoted to eliminate potential pathogens in the drinking water treatment and supply systems. Nevertheless, the role of microbes in some drinking water treatments systems as biological filtration has long been acknowledged and recently been investigated. Biological filtration technology is widely used around the world and is especially important in Denmark as groundwater is the main source water for drinking water production. Because the groundwater has a relative high-quality, aeration followed by biological filtration is the only required treatment before distribution. In the last years, the microbial communities in rapid gravity sand filters, the typical biological filter used in Denmark, have been characterized, but little knowledge had been required about their physiological activity and roles in compound removal from the source water.

This PhD project focused on a comprehensive investigation of the microbial communities in rapid sand filters beyond their purely taxonomical identification. For this purpose, samples collected from a rapid sand filter were subjected to metagenomics analysis and genome recovery to identify the genetic capacities of the dominant types in the microbial community. Fourteen near-complete population genomes representing the dominant community were recovered comprising the capacity to grow on the typical compounds found in groundwater. The identified population genomes contained capabilities to oxidize ammonium, nitrite, methane, hydrogen sulfide, iron and manganese as well as to assimilate organic compounds. A composite population genome was assigned to Nitrospira. This genus had previously been found in multiple rapid sand filters at an unexplained high abundance. Nitrospira spp. are known to perform the second step of nitrification: oxidation of nitrite to nitrate. The two-step nitrification process disclosed at the end of the 19th century was assumed to be carried out by two different functional groups, ammonia oxidizing prokaryotes and nitrite oxidizing bacteria. Strikingly, the Nitrospira composite population genome not only contained the genes to oxidize nitrite to nitrate, but also the genetic potential to execute the first step of nitrification. Exhaustive bioinformatics investigation ruled out the possibility of genomic contamination and confirmed that the Nitrospira composite population genome harboured the complete ammonium oxidation (comammox) pathway. At the same time, evidence of a single microbe’s capacity to carry out complete nitrification was obtained by three other groups; in all cases the comammox type belonged to the Nitrospira genus.

To further investigate the genomic capacities of comammox Nitrospira, the Nitrospira composite genome was separated into individual population genomes using a differential coverage binning approach. As a result, five individual genomes were recovered, four of them containing the complete ammonium oxidation pathway. These genomes together with 11 high-quality publically available Nitrospira genomes (seven comammox and four strict nitrite oxidizers) were subject to a comparative genomics analysis. This examination showed specific genomic features for comammox, strict nitrite oxidizers and the two comammox clades. Thus, comammox Nitrospira harbour a higher variety of genes related to adaptation to nutrient-limited environments. The two comammox clades differ in their ammonium uptake affinity systems. Additionally, comammox Nitrospira genomes lack the genetic capacity to use nitrite as the only nitrogen source. The evolutionary history of comammox Nitrospira was also examined based on protein dissimilarity, gene arrangement and reconciliation analysis. We detected a high probability of horizontal gene transfer events from betaproteobacterial ammonia oxidizers to comammox Nitrospira for genes belonging to the ammonium oxidation pathway as well as from comammox clade B to clade A for a subset of genes.

I investigated the abundance of comammox Nitrospira in rapid sand filters at 12 different waterworks in Denmark. As these
new microorganisms are taxonomically similar to strict Nitrospira nitrite oxidizers, we developed specific primers to exclusively target comammox based on their gene encoding the ammonia monoxygenase subunit A. With these primers, we detected comammox Nitrospira as the dominant nitrifier in the biofilters with an abundance typically one order of magnitude higher than canonical ammonium oxidizing prokaryotes.

Lastly, I carried out lab-scale experiments with filter material from the top and bottom layers of a rapid sand filter containing different proportions of comammox Nitrospira, and strict nitrite and ammonia oxidizing prokaryotes under different loading conditions. Specifically, I exposed the filter material to distinct ammonium loading, under presence or absence of external carbon source as well as under oxygen limitation. In relation to the nitrifying community three main findings were made: (i) simultaneous growth of comammox Nitrospira and ammonium oxidizing prokaryotes; (ii) lower fitness of ammonium oxidizing archaea at higher temperatures; (iii) selection of comammox clade A over clade B at increasing ammonium loadings at reference temperature.

Overall, this PhD has provided insights into the genomic capabilities of the main types in the microbial community of a groundwater-fed biological filter. Moreover, the previously observed high abundances of Nitrospira spp. in rapid sand filters, has now been explained, by the discovery of complete ammonium oxidizing (comammox) Nitrospira from metagenomics analysis. In addition, this thesis presents the first extensive analysis of the genomic capabilities of comammox Nitrospira compared to canonical ammonium and nitrite oxidizers.

General information
State: Published
Organisations: Department of Environmental Engineering, Water Technologies, Department of Bio and Health Informatics, Metagenomics
Authors: Palomo, A. (Intern), Smets, B. F. (Intern), Sicheritz-Pontén, T. (Intern), Rasmussen, S. (Intern), Bælum, J. (Intern)
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Diversity, structure, and novel physiologies in microbial communities in rapid sand filters

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Organisations: Department of Environmental Engineering, Water Technologies, Department of Bio and Health Informatics, Metagenomics, Technical University of Denmark
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Dramatic loss of comammox Nitrospira associated with long-term nitrite feeding
Until recently, nitrification was thought to be a strict two-step process where ammonia was first oxidized to nitrite by ammonia-oxidizing bacteria and/or archaea, and subsequently to nitrate by nitrite oxidizing bacteria (NOB). Recent studies in NOB metabolism, however, have revealed that certain Nitrospira are capable of performing both steps, resulting in complete ammonia oxidation (comammox) by single microorganisms. These comammox Nitrospira have been detected in drinking water (Pinto et al., 2015; Palomo et al., 2016) and aquaculture systems (van Kessel et al., 2015), as well as deep oil exploration wells (Daims et al., 2015). The discovery of comammox Nitrospira has significantly changed our
understanding of biogeochemical nitrogen cycle. The goal of this experiment was to determine the extent of competition between comammox Nitrospira and canonical Nitrospira in ammonium scarce environment, with nitrite as the main energy source. Community assembly was monitored on well-established biofilms formed on the grains of rapid sand filter (RSF) for drinking water production. RSF sand was placed in laboratory scale column bioreactors and subjected to continuous feeding of tap water spiked with NO2- (1 mg-N/L) for 250 days. The biofilms were then characterized by Illumina MiSeq platform, targeting the 16S rRNA gene. The relative abundance of a putative comammox clade B Nitrospira sequence variant (with 100% 16S rRNA gene similarity to comammox CG24_A assembled genome) identified in the initial RSF sand (Palomo et al., unpublished) at a relative abundance of 12.4±1.1%, was not detected in 4 out of 6 replicates after 250 days. Similar trend was observed for other putative comammox clade B Nitrospira sequence variants. In contrast, we observed significant increase (padj<0.001) in canonical Nitrospira sequences (100% similarity to uncultured Nitrospira sp. clone KCS36101 (Pester et al., 2014)). These observations indicate different behavior of Nitrospira in the absence of ammonia and point to a possible competitive advantage of canonical Nitrospira in environments where nitrite is the sole nitrogen, as well as energy source. In addition, the results suggest that other comammox Nitrospira could also be unable to grow in the only presence of nitrite as it was observed for comammox Ca. Nitrospira inopinata (Daims et al., 2015).

General information
State: Published
Organisations: Department of Environmental Engineering, Water Technologies
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Niche differentiation and evolution of comammox Nitrospira through a comparative genomics analysis
Nitrification, the biological oxidation of ammonium to nitrate, is a fundamental process in the nitrogen cycle and plays an important role in natural and engineered systems. Throughout the last century, nitrification was assumed to be a two-step process executed by two different functional groups, ammonia oxidizing prokaryotes (AOP) and nitrite oxidizing bacteria (NOB). Recently, several articles have shown the capability of a single microorganism, belonging to the genus Nitrospira, to carry out the complete oxidation of ammonia to nitrate (comammox). Nitrospira spp. are widespread in both natural and engineered ecosystems associated with nitrogen cycling and different species are frequently observed to coexist in the same environment. Besides recent discoveries pointing towards versatile metabolism in some Nitrospira species, little is known about the functional potential of the two comammox Nitrospira clades, and the factors involved in niche-partitioning between comammox and canonical Nitrospira.

A comparative genomics analysis was conducted with five genomes recovered from a groundwater-fed rapid sand filter (including both comammox clades and a nitrite-oxidizing Nitrospira population genome) and high quality published Nitrospira genomes, to reveal distinct genomic features within Nitrospira. In addition, we investigated the evolution of the ammonia oxidation pathway in comammox Nitrospira. This analysis revealed distinct genetic capabilities of the different comammox clades and canonical Nitrospira which can help to explain the coexistence and niche partitioning of Nitrospira spp. These divergences range from the nitrogen source utilization capacity to the ability for electron donor versatility, and other characteristics such as stress response. With respect to the evolutionary history of comammox Nitrospira, our analysis indicates transfer events with betaproteobacterial ammonia oxidizers. In addition, transfer events between comammox clade A and clade B were also detected for genes belonging to the ammonium oxidation pathway.

Together, these results expand the actual knowledge of the ecology and evolution of the recently discovered comammox Nitrospira.

General information
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Organisations: Department of Environmental Engineering, Water Technologies, Department of Biotechnology and Biomedicine, Department of Bio and Health Informatics, Disease Intelligence and Molecular Evolution, Metagenomics
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Publication date: 2017
Event: Abstract from ICoN5: 5th International Conference on Nitrification, Vienna, Austria.
Main Research Area: Technical/natural sciences
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Metagenomic analysis of rapid gravity sand filter microbial communities suggests novel physiology of Nitrospira spp

Rapid gravity sand filtration is a drinking water production technology widely used around the world. Microbially catalyzed processes dominate the oxidative transformation of ammonia, reduced manganese and iron, methane and hydrogen sulfide, which may all be present at millimolar concentrations when groundwater is the source water. In this study, six metagenomes from various locations within a groundwater-fed rapid sand filter (RSF) were analyzed. The community gene catalog contained most genes of the nitrogen cycle, with particular abundance in genes of the nitrification pathway. Genes involved in different carbon fixation pathways were also abundant, with the reverse tricarboxylic acid cycle pathway most abundant, consistent with an observed Nitrospira dominance. From the metagenomic data set, 14 near-complete genomes were reconstructed and functionally characterized. On the basis of their genetic content, a metabolic and geochemical model was proposed. The organisms represented by draft genomes had the capability to oxidize ammonium, nitrite, hydrogen sulfide, methane, potentially iron and manganese as well as to assimilate organic compounds. A composite Nitrospira genome was recovered, and amo-containing Nitrospira genome contigs were identified. This finding, together with the high Nitrospira abundance, and the abundance of atypical amo and hao genes, suggests the potential for complete ammonium oxidation by Nitrospira, and a major role of Nitrospira in the investigated RSFs and potentially other nitrifying environments.

General information
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Organisations: Department of Systems Biology, Department of Environmental Engineering, Water Technologies, Center for Biological Sequence Analysis, Metagenomics
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Metagenomics and single-cell genomics reveal high abundance of comammox Nitrospira in a rapid gravity sand filter treating groundwater

The recent discovery of complete ammonia oxidizing (comammox) Nitrospira has revealed that the metabolic division of labor in nitrification is not obligate as was assumed during the last century. Despite the detection and enrichment of comammox Nitrospira from different nitrifying environments, the ecological relevance of comammox remains unknown. In this study, we analyzed the microbial communities from various locations within a groundwater-fed rapid sand filter (RSF), where Nitrospira were at very high relative abundances. Through metagenomics, a highly abundant composite multi-genome of Nitrospira genus was recovered harboring metabolic capacity for complete ammonia oxidation. We developed a cell extraction strategy that enables the disruption of Nitrospira cell clusters attached to the mineral coating of the sand. Individual cells were identified via fluorescent in situ hybridization (FiSH) with Nitrospira-specific 16S rRNA probes and sorted via fluorescence-activated cell sorting (FACS). Sorted cells were screened and selected Nitrospira spp. were subject to whole-genome sequencing. The single cell genomes confirmed the genomic presence of a complete ammonia oxidation pathway and revealed clear taxonomic differences with the recently described comammox Nitrospira genomes. The high abundance of comammox Nitrospira spp. together with the low abundance of canonical ammonia oxidizing prokaryotes in the investigated RSF system suggests the essential role of this novel comammox Nitrospira in the RSFs and potentially other nitrifying environments.

General information
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Organisations: Department of Environmental Engineering, Water Technologies, Department of Systems Biology, Center for Biological Sequence Analysis, Metagenomics, Department of Bio and Health Informatics, Aarhus University
Stable isotope probing and dynamic loading experiments provide insight into the ecophysiology of novel ammonia oxidizers in rapid gravity sand filters

Nitrification is often the dominant microbial process in rapid gravity sand filters (RSF), used to treat aerated groundwater to produce drinking water. RSFs harbor diverse microbial communities including a range of ammonia oxidizing clades; Betaproteobacteria (Nitrosomonas, Nitrosospira), Archaea, diverse potentially ammonia oxidizing heterotrophs and abundant Nitrospira spp., recently shown to comprise both canonical nitrite oxidizing as well as complete ammonium oxidizing (comammox) types. We examined the contributions of the different ammonia oxidizers to in situ ammonia oxidation, and aimed to elucidate the differences in ecophysiology between the ammonia oxidizing clades that enable them to co-exist in this unique environment. Experiments were conducted using sand columns designed and operated to mimic the conditions in the full-scale parent RSF. RNA and DNA stable isotope probing based on 13C-bicarbonate incorporation during continuous feeding with either ammonium or nitrite as sole energy source implicated Nitrospira spp. and certain ‘heterotrophic’ bacteria in addition to Nitrosomonas spp. in autotrophy during ammonium oxidation in RSFs. Further experimentation aimed to elucidate the ecophysiology of each ammonia oxidizing clade in RSFs, in particular comammox Nitrospira for which little is currently known. Columns were fed with RSF effluent spiked with various concentrations of ammonium ranging from 0.1- 5.0 mg/L delivered at different loading rates to examine the effects of both ammonium loading and oxygen limitation on ammonia oxidizers. Our observations indicate that the native conditions in the RSF used in this study foster the enrichment of comammox Nitrospira, which provides a preliminary step in the description of their ecophysiology.
Metagenomic analysis of microbial communities in rapid sand filter treating groundwater. Community diversity and metabolic potential

General information
State: Published
Organisations: Department of Environmental Engineering, Water Technologies, Department of Systems Biology, Center for Biological Sequence Analysis, Technical University of Denmark
Authors: Palomo, A. (Intern), Rasmussen, S. (Ekstern), Sicheritz-Pontén, T. (Intern), Smets, B. F. (Intern)
Number of pages: 1
Publication date: 2015
Taxonomic and metagenomic profiling of rapid sand filter microbiome reveals a high Nitrospira incidence

QPCR quantification of ammonia oxidizing bacteria: What should the target be?

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Publication: Research - peer-review › Conference abstract in proceedings – Annual report year: 2015

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Organisations: Department of Systems Biology, Department of Environmental Engineering, Urban Water Engineering, Center for Biological Sequence Analysis, Metagenomics
Authors: Palomo, A. (Intern), Gülay, A. (Intern), Rasmussen, S. (Intern), Sicheritz-Pontén, T. (Intern), Smets, B. F. (Intern)
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Organisations: Department of Environmental Engineering, Urban Water Engineering
Authors: Musovic, S. (Intern), Palomo, A. (Intern), Diwan, V. (Intern), Dechesne, A. (Intern), Smets, B. F. (Intern)
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Event: Abstract from The Danish Microbiological Society Annual Congress 2014, Copenhagen, Denmark.
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Relations
Activities:
Functional gene approach to study nitrifier diversity
Projects:

The structure and functional role of microbial communities in rapid sand filters

Department of Environmental Engineering
Period: 01/01/2014 → 30/09/2017
Number of participants: 7
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Diversity, structure, and novel physiologies in microbial communities in rapid sand filters
Period: 9 Jul 2017 → 13 Jul 2017
Barth F. Smets (Invited speaker)
Arda Gülay (Other)
Alejandro Palomo (Other)
Jane Fowler (Other)
Thomas Sicheritz-Pontén (Other)
Department of Environmental Engineering
Water Technologies
Department of Bio and Health Informatics
Metagenomics
Degree of recognition: International
Documents:
fems 2

Related event

The Federation of European Microbiological Societies
09/07/2017 → 13/07/2017
Valencia, Spain
Activity: Talks and presentations › Conference presentations
ESOF Marie Skłodowska-Curie actions Conference  
Period: 2014  
Alejandro Palomo (Participant)  
Department of Environmental Engineering  
Urban Water Engineering  

Related event  
ESOF Marie Skłodowska-Curie actions Conference  
19/06/2014 → 20/06/2014  
Copenhagen, Denmark  
Activity: Attending an event › Participating in or organising workshops, courses, seminars etc.

Nordic Environmental NUcleotide Network  
Period: 2014  
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Department of Environmental Engineering  
Urban Water Engineering  

Description  
Functional gene approach to study nitrifier diversity  

Related event  
Nordic Environmental NUcleotide Network  
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