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Review

Biodiversity and ecology of microorganisms in high pressure membrane filtration systems

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ABSTRACT

High-pressure membrane filtration (reverse osmosis and nanofiltration) is used to purify different water sources, including wastewater, surface water, groundwater and seawater. A major concern in membrane filtration is the accumulation and growth of micro-organisms and their secreted polymeric substances, leading to reduced membrane performance and membrane biofouling. The fundamental understanding of membrane biofouling is limited despite years of research, as the means of microbial interactions and response to the conditions on the membrane surface are complicated. Here, we discuss studies that investigated the microbial diversity of fouled high-pressure membranes. High-throughput amplicon sequencing of the 16S rRNA gene have shown that *Burkholderiales*, *Pseudomonadales*, *Rhizobiales*, *Sphingomonadales* and *Xanthomonadales* frequently obtain a high relative abundance on fouled membranes. The bacterial communities present in the diverse feed water types and in pre-treatment compartments are different from the communities on the membrane, because high-pressure membrane filtration provides a selective environment for certain bacterial groups. The biofilms that form within the pre-treatment compartments do not commonly serve as an inoculum for the subsequent high-pressure membranes. Besides bacteria also fungi are detected in the water treatment compartments. In contrast to bacteria, the fungal community does not change much throughout membrane cleaning. The stable fungal diversity indicates that they are more significant in membrane biofouling than previously thought. By reviewing the biodiversity and ecology of microbes in the whole high pressure membrane filtration water chain, we have been able to identify potentials to improve biofouling control. These include modulation of hydrodynamic conditions, nutrient limitation and the combination of cleaning agents to target the entire membrane microbiome.

Contents

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1. Introduction

The amount of water that can be obtained from natural sources is sufficient to satisfy the global freshwater demand but water scarcity exists due to mismanagement and spatial and temporal inequalities in the amount of natural supplied water (Mekonnen and Hoekstra, 2016). The global demand for freshwater has been growing due to urbanisation, changing consumption patterns, pollution and population increase and poses an important challenge today and in the future (Mekonnen and Hoekstra, 2016; Savenije, 2000). Assessment of water availability at high temporal and spatial resolution shows that two thirds of the global population suffers from water scarcity at least one month per year (Mekonnen and Hoekstra, 2016). Water scarcity prevails in areas with high population density or in highly irrigated districts, or in areas with a combination of these. The global increase in temperature will substantially increase the challenge to provide sufficient fresh water to the worldwide population (Postel et al., 1996; Schewe et al., 2014).

High pressure membranes, including nanofiltration (NF) and reverse osmosis (RO), remove most solutes, producing clean and biological stable water as well as a waste stream called concentrate. High-pressure membrane filtration has become attractive for water purification. Improved material design has led to progress in membrane functionality (permeability and selectivity) and applicability (mechanical and chemical stability) (Lee et al., 2011). High-pressure membrane filtration now provides the option to remove most impurities, such as hardness, colour and disinfection products in a single purification step (Warsinger et al., 2018; Werber et al., 2016). Other advantages include low purchase costs and low space requirements, membrane units can easily be scaled up and can be operated continuously and automatically (Bartels et al., 2005; Guo et al., 2012; Lin and Elimelech, 2015). This explains why membrane filtration has become the most important technology for seawater desalination (Caldera and Breyer, 2017). The use of high-pressure membranes for purification of water sources other than seawater is growing and is stimulated by tightened discharge standards and concerns for micropollutants (Barbosa et al., 2016; Fu and Wang, 2011; Sahinkaya et al., 2018).

A major challenge in membrane water filtration is to tackle fouling, which decreases membrane performance due to the accumulation of particles and growth of microbes at the membrane surface (Peña et al., 2013). A general classification of membrane fouling includes colloidal fouling (suspended particles such as silica), organic fouling (natural organic matter), inorganic fouling (salts) and biofouling (microorganisms) (Peña et al., 2013). Colloidal fouling can be reduced by e.g. sand bed filtration or by low-pressure membrane filtration, such as microfiltration (MF) and ultrafiltration (UF) (Voutchkov, 2010). For inorganic scalants several removal possibilities exist, such as acid precipitation, lime softening or addition of scale inhibitors (antiscalants) (Badruzzaman et al., 2019). Organic fouling of high-pressure membranes can be reduced by implementation of low-pressure membrane filtration or by fluctuating the pH of the feed water to stimulate solubilisation (high pH followed by low pH or vice versa) preferably combined with a surfactant (Voutchkov, 2010). Biofouling is difficult to prevent and control (Flemming et al., 1997). Pre-treatment systems, including MF and UF membranes, are unable to remove all microorganisms and those that pass may colonize the membrane (Badruzzaman et al., 2019; Greenlee et al., 2009). As a consequence, frequent membrane cleaning in place (CIP) is required for most membrane installations to remove recalcitrant biofilms and safeguard product quantity (Beyer et al., 2014). Membrane cleaning is unwanted because it leads to operational costs and labour for maintenance, membrane downtime and membrane damage (Greenlee et al., 2009; Shirazi et al., 2010). Membrane damage decreases selectivity and reduces product quality. Ultimately the membrane has to be replaced to certify consumers safety (Judd, 2017). To better understand membrane biofouling, many studies have described the microbiota present on membranes. The focus of this review is to outline the membrane surface as selective microbial environment and the strategies that microbes use to survive, grow and profit in this ecosystem.

Abbreviations

CF	Cartridge filters
CIP	Cleaning in place
DM	Dual media
EPS	Extracellular polymeric substances
GGE	Gradient gel electrophoresis
HMW	High molecular weight
MAG	Metagenome-assembled genomes
MF	Microfiltration
NGS	Next generation sequencing
NF	Nanofiltration
NOM	Natural organic matter
QS	Quorum sensing
RO	Reverse osmosis
SDI	Silt density index
T-RFLP	Terminal restriction fragment length polymorphisms
UF	Ultrafiltration

2. The membrane surface ecosystem

The conditions at the membrane surface result from operational

parameters and processes inherent to membrane filtration (Radu et al., 2012). These include feed water characteristics such as nutritional levels and temperature, hydrodynamic changes due to the feed spacer geometry and the arrangement of membrane modules in pressure vessels (Dreszer et al., 2014; Farhat et al., 2016; Radu et al., 2014; Shirazi et al., 2010; Suwarno et al., 2012). In addition, the local conditions on the membrane surface change during membrane operation and membrane cleaning (Nagaraj et al., 2017a). Hence, a broad range of conditions exist in a membrane module providing biotic and abiotic differences. This complexity makes it difficult to link shifts in microbial composition to particular process parameters.

2.1. A broad range of conditions can be encountered in membrane pressure vessels

Most high pressure membranes are spirally wound around a permeate tube to obtain a high membrane-area to volume-ratio and are arranged in membrane modules. To increase the volume of produced water per volume of feed water, multiple membrane modules are serially connected. Membrane modules are surrounded by a pressure vessel to provide mechanical stability. Within a pressure vessel, the feed water enters at the lead module, passes through the following modules and ultimately leaves the tail module as concentrate. The flow rate and flow velocity of the feed water inherently decrease along the membrane module as water is pressed through the membrane, while the concentration of inorganics and other solutes in the feed stream increases (Radu et al., 2010; Shirazi et al., 2010). Inorganic fouling for the latter reason commonly disrupts filtration of the tail modules (Khan et al., 2014; Peña et al., 2013). In addition, fluid friction decreases the feed pressure and velocity along all the membrane modules (Farias et al., 2014).

Membrane permeation also creates a drag force that moves organics, inorganics and microbes to the membrane surface (Fig. 1) (Eshed et al., 2008; Subramani and Hoek, 2008). This results in the accumulation of solutes, nutrients and microbes at the membrane surface (Semião et al., 2014; Song and Elimelech, 1995). Commonly biofilm embedded bacteria grow slower than free floating bacteria because the extracellular polymeric substances (EPS) embedded cells are limited of nutrients and oxygen due to diffusion limitation (Stewart, 2003). Permeation of the feed water across the membrane overcomes this limitation and biofilm embedded cells therefore grow faster at the membrane surface compared to free floating bacteria (Herzberg and Elimelech, 2007). In spite of enhanced cell attachment and stimulated growth, biofilm formation is not initiated on the entire membrane (Picioreanu et al., 2009; Vrouwenvelder et al., 2009). When membranes are operated under cross flow filtration, the flow also moves parallel to the membrane surface (Fig. 1). In contrast to the drag force, high shear stress restricts biofilm growth on the membrane surface (Ying et al., 2013). Biofilm growth is therefore initially preserved to locations close to the feed spacer where shear stress is lower (Radu et al., 2014). Membrane shear forces, which can be modulated by changing the cross-flow velocity, have a strong effect on the membrane microbiota (Al Ashhab et al., 2014a). Bacteria that produce EPS or appendages that prevent membrane removal by frictional fluid forces will maintain themselves at the membrane or in the membrane associated biofilms (de Vries et al., 2019; Rehman et al., 2019). Differences in physiochemical conditions can therefore be found between different membrane plants as well as between different membrane modules within the same pressure vessel (Nagaraj et al., 2017a).

2.2. Feed water quality plays a significant role in the progression of membrane biofouling

To colonize synthetic membranes bacteria have to obtain nutrients and withstand the challenges that are present on the membrane surface under filtration conditions, such as high shear stress and changes in pH (Chen et al., 2013; Radu et al., 2014; Yu et al., 2017). The feed water quality plays a significant role in the progression of membrane biofouling, but the ability to control membrane biofouling by modulating this factor has remained largely unexplored (Beyer et al., 2014). A CIP interval of once a month is generally considered as imperative for stable membrane operation to purify surface water or seawater (Warsinger et al., 2018). By exception, the performance of membranes that are fed with anoxic groundwater is stable for extended time periods due to the low concentration of dissolved oxygen and nutrients. CIP frequencies of less than once a year are common practice for membranes filtering anoxic groundwater (Beyer et al., 2014). In most source water types the availability of oxygen and nutrients, mainly in the form of natural organic matter (NOM), is sufficient for bacteria to rapidly colonize and grow on the membranes and as a consequence deteriorate membrane performance (Park et al., 2018). Lakes and rivers and their discharge locations in seas and oceans are rich in NOM that originates from terrestrial inflow (Matilainen et al., 2011). Marine environments are rich in NOM that originates from primary production (Arndt et al., 2013; Fabris et al., 2008). High molecular weight (HMW) compounds, such as phenols, lignins, tannins and humic substances are readily available in surface and marine water because, due to their insolubility and size, a limit number of micro-organisms are able to degrade these

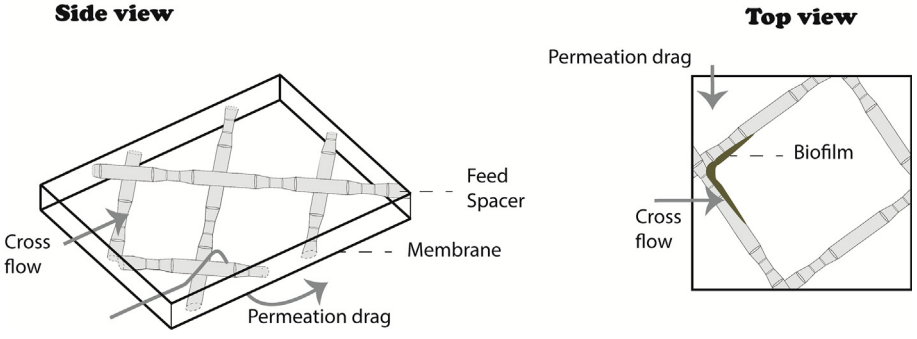

Fig. 1. Schematic diagram illustrating the two main forces that affect biofilm formation on the membrane: i) the permeation drag force, which acts perpendicular to membrane, pushes organics, inorganics and microbes to the membrane surface; ii) cross flow, the passage of the feed water parallel to the membrane surface, removes bacteria from the membrane surface. Due to the combined effect of the permeation drag force and the cross flow, biofilm formation is in the initial biofilm stage restricted to locations close to the feed spacer where the flow velocity and shear stress are low.

molecules (Matilainen et al., 2011; Simon et al., 2013). Although these compounds are usually rather efficiently removed by pre-treatment systems they still can cause organic fouling (Lee et al., 2004; Seidel and Elimelech, 2002). Hence, feed water quality determines to a great extend which nutrients accumulate at the membrane surface, irrespectively of the pre-treatment system. Proteins and carbohydrates are readily biodegradable and are, except during algal blooms, generally present at low concentrations compared to HMW compounds (Guastalli et al., 2013; Jeong et al., 2016; Simon et al., 2013). Micro-organisms that are able to degrade HMW compounds therefore have a profound advantage on the membrane surface (Corvini et al., 2006; Kurzbaum et al., 2017; Pandit et al., 2016; Vashi et al., 2018).

3. The microbiomes of synthetic membranes

The diversity and abundance of bacterial groups on high pressure membranes has been investigated and confirmed using different techniques (Fig. 2). Most of these studies have used molecular techniques such as quantitative PCR, PCR-gradient gel electrophoresis (GGE) and terminal restriction fragment length polymorphisms (T-RFLP). In recent years, next generation sequencing (NGS) has greatly expanded the ability to uncover microbial community compositions of diverse environments. Studies using NGS have shown that certain bacterial taxa frequently occur in membrane biofouling and that membrane surfaces often have their own microbiome. The number of studies using culture dependent techniques, aiming to understand the physiological traits of bacteria involved in membrane fouling is limited (de Vries et al., 2019; Nagaraj et al., 2019; Pang et al., 2005). From those studies it was not well feasible to reveal how bacteria interact and respond to conditions on the membrane surface. How the membrane surface behaves as ecosystem, a community together with its environment, functioning as a unit, remains enigmatic.

3.1. Bacterial identification techniques

The recognition of ribosomal RNA (rRNA) as phylogenetic marker by Carl R. Woese and George E. Fox led to a paradigm shift to evolutionary biology (Woese and Fox, 1977). Identification of bacteria, archaea and fungi was conventionally based on phenotypical characteristics and was laborious and time consuming, but less valuable for reliable identification (Amann et al., 1995; Woese et al., 1990). Cultivability, however, is the only secure and operational definition of viability, and enables direct biochemical, phylogenetic and physiological characterisation of a single strain. 16S rRNA gene sequences provide an objective tool to delineate bacteria and archaea. Rational taxonomic boundaries have been described to distinguish their taxonomical ranks, such as species (≥98.65% gene sequence similarity) and genus (≥94.5% gene sequence similarity) (Stackebrandt, 2006; Stackebrandt and Goebel, 1994, Yarza et al., 2017). Taxonomic classification of the fungal kingdom has conventionally been hampered by the large physiological diversity of its members and by the morphological transitions of many fungal species (Berbee et al., 2017; Geiser et al., 2006; Hibbett et al., 2007). The fungus kingdom includes moulds, mushrooms, lichens, rusts, smuts and yeasts (Stajich et al., 2009). Unlike bacteria and archaea, selection of the most appropriate genetic marker for taxonomic classification is still under debate for the fungal kingdom (Schoch et al., 2012).

The use of marker genes, such as the 16S and 18S rRNA gene, has led to development of quantitative and semi-quantitative

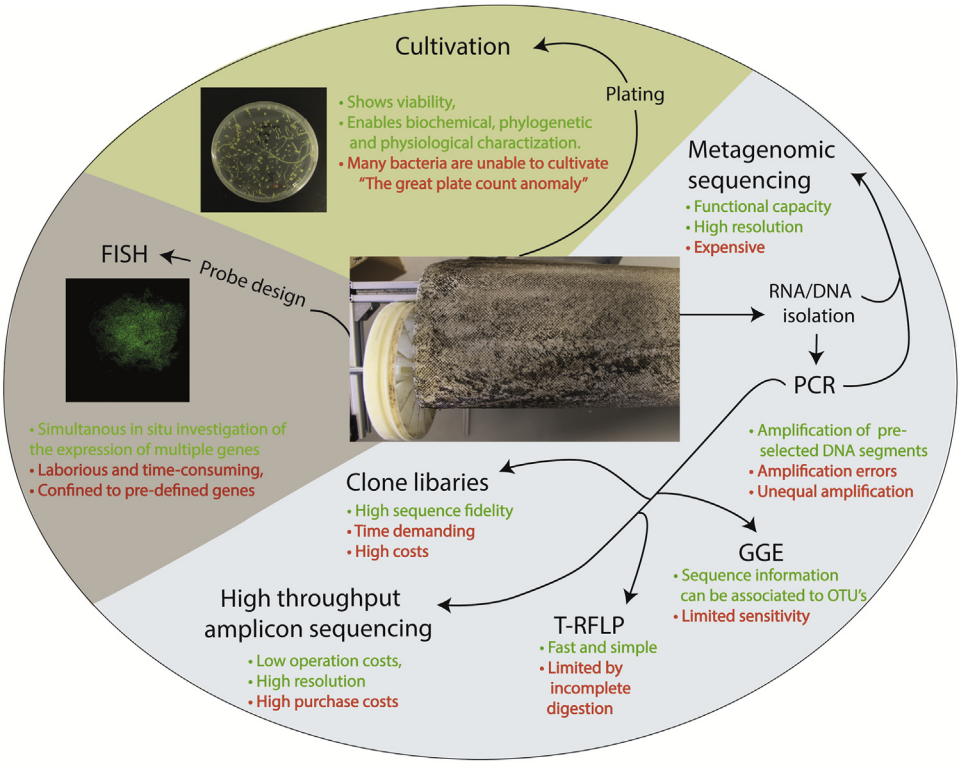

Fig. 2. Schematic diagram displaying frequently used approaches used to study the microbial community composition of fouled membranes. These include (clockwise):, cultivation, high throughput sequencing, polymerase chain reaction (PCR) dependent approaches as gradientgel electrophoresis (GGE), and terminal restriction fragment length polymorphisms (T-RFLP), clone librariesand fluorescent *in situ* hybridization (FISH),. Color coding indicates advantages (in green) and disadvantages (in red) of the identification approach. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

molecular identification techniques. Including the polymerase chain reaction (PCR), fluorescent *in situ* hybridisation (FISH) and next generation sequencing (NGS) (DeLong et al., 1989; Metzker, 2010; White et al., 1989). PCR revolutionized biological science because it enabled to amplify preselected segments of DNA or RNA to quantities which permit sequencing (White et al., 1989). Standard PCR alone is unreliable for DNA quantification, but in combination with other techniques it can be used for quantitative or semi-quantitative identification. Examples of such technologies are quantitative PCR (qPCR), PCR-gradient gel electrophoresis (GGE) and terminal restriction fragment length polymorphisms (T-RFLP) (Marsh, 1999; Nakatsu, 2007; Tabit, 2016; Thies, 2007). T-RFLP, qPCR and GGE are laborious, time-consuming and have low resolving power. Hence, many low abundant microbes will remain undetected using these identification methods. NGS platforms provide the ability to study bacterial community compositions in a culture-independent and high throughput manner (Metzker, 2010; Shokralla et al., 2012). These techniques identify microorganisms via comparative analysis, which enables to study the relationship between micro-organisms and their environment in an expeditious manner.

Many NGS platforms are available, launched by Roche 454 pyrosequencing (from 2013 this platform stopped); Illumina, including MiSeq, HiSeq and NextSeq; Oxford Nanopore Techniques with Nanopore sequencing; Pacific Biosystems with PacBio sequencing; and Ion Torrents with the Ion Proton sequencer (Claesson et al., 2010; Glenn, 2011; Goodwin et al., 2016; Metzker, 2010). Each platform has its advantages and disadvantages that are outside the scope of this review, but have been reviewed by Metzker (2010). The microbiota of high-pressure membranes have been investigated using pyrosequencing, Illumina sequencing and the ion proton sequencer (Table 2). Disadvantages of NGS techniques is that analysis is time-consuming and the purchase costs are still rather high, although prices get lower. Without additional sample preparation, NGS platforms cannot provide information about the spatial organization of the microorganisms present. Fluorescent *in situ* hybridisation (FISH) is based on hybridisation of a fluorescently labelled probe to its target RNA and is therefore linked to metabolic activity (Amann et al., 1995; Frickmann et al., 2017). FISH probes commonly target RNA of ribosomal marker genes but also the RNA of key functional genes have been used (Frickmann et al., 2017; Wagner et al., 2003). FISH provides the major advantage that expression of multiple functional genes can simultaneously be investigated *in situ* (Frickmann et al., 2017; Wagner et al., 2003). A disadvantage is that this method is laborious, time-consuming and its applicability is limited to organisms from which sequence data is available (Amann et al., 1995; Frickmann et al., 2017).

Technological advances and method optimization provide opportunities to further increase the understanding of fouled membranes as microbial environment. Although 16S rRNA gene amplicon sequencing delivers high throughput output, it is limited to characterise microbial diversity. Instead, by sequencing all available genomes or available RNA transcripts, metagenomic and metatranscriptomics approaches reveal the functional potential and the functional activity of the microbiome, respectively (Simon and Daniel, 2011). In the first and hitherto only study applying a metagenomic approach to characterise the microbial community in a full-scale RO plant, 25 metagenome-assembled genomes (MAGs) were recently recovered from a fouled membrane (Rehman et al., 2019). Comparison of these 25 MAGs to the 6 MAGs recovered from the intake seawater and brine revealed that the bacterial membrane microbiome carries quorum quenching genes, but no quorum sensing genes. Hence, implying that quorum quenching is a successful bacterial strategy to outcompete bacteria that use signalling molecules to regulate biofilm formation and membrane colonization (Rehman et al., 2019). Metatransciptomics has so far not been used to analyse fouled membranes but provide the ability to characterise the functional activity of the membrane microbiome and hence its response to different selection pressures in high spatial and temporal resolution (Moran et al., 2013). One general disadvantage of molecular techniques is that identification of the identified genes is always limited by the reference database.

3.2. The orders Burkholderiales, Pseudomonadales, Rhizobiales, Sphingomonadales and Xanthomonadales are frequently dominant on fouled membranes

Within the bacterial domain six taxonomic levels are defined. From high to low taxonomic level these include: phylum, class, order, family, genus and species. The lowest taxonomic level that can be determined by molecular techniques is dependent on the identification method and has changed over time due to technical innovations (Glenn, 2011; Goodwin et al., 2016; Metzker, 2010). Published studies therefore do not uniformly present the bacterial community composition at the same taxonomic level and this makes comparison of bacterial diversity between different studies cumbersome. For this review, we compared 33 studies that investigated bacterial communities on fouled high-pressure membranes and we have classified the identified bacteria at the order level (Table 1 and Supplementary Table S1). When possible the lower taxonomic levels are also discussed. In total, 35 bacterial orders were documented from these fouled high-pressure membranes. These orders were used as benchmark to compare the microbial diversity of feed water, pre-treatment compartments and fouled membranes and disclose the role of particular selection pressures on the microbial composition.

Bacteria belonging to the orders *Burkholderiales, Pseudomonadales*, *Rhizobiales* and *Sphingomonadales* and *Xanthomonadales* are most frequently detected on fouled membranes. *Burkholderiales* and *Xanthomonadales* were not detected in earlier studies but NGS studies have frequently detected these orders on fouled membranes. In this review, we refer to the *Burkholderiales, Pseudomonadales*, *Rhizobiales*, *Sphingomonadales* and *Xanthomonadales* orders as frequently detected taxa. Many of the early studies used methods that were biased in their identification ability, for instance towards cultivable organisms. More recent studies using NGS commonly describe the taxa with the highest relative abundance, but do not report on the rare taxa. Hence, the actual bacterial community composition of fouled high pressure membranes is more diverse than will be possible to describe here.

3.3. Biofilm formation: a strategy to grow and increase resilience

Biofilm formation constitutes a lifestyle in which microorganisms adopt a multicellular behavior and has been acknowledged to be the main cause of membrane biofouling (Flemming et al., 1996; Stewart et al., 2001). The self-produced matrix progresses biofilm embedded cells into sophisticated spatial organizations that vary in oxygen and nutrient concentration, pH values and viscosities (Costerton et al. 1994, 1995; Glud et al., 1998). The ecological organization of biofilms is complex and facilitates bacterial survival in a variety of environmental niches (Flemming et al., 2016). Because the EPS layer acts as a physical barrier, it alleviates the embedded cells to, for instance the perturbing effects of cleaning agents containing chlorine, and strong pH changes (Chen and Stewart, 1996; Jang et al., 2006; Nadell et al., 2016). The versatile binding sites within the EPS matrix provide biofilm embedded cells advantages under oligotrophic conditions as different substrates become entrapped (Battin et al., 2016). A part of the biofilm population,

Table 1
Overview of the bacterial diversity at the taxonomic order level detected on high-pressure biofouled membranes using different methods.

Order	Total	Number of encounters								References
		Culture-dependent	Clone Libraries	T-RFLP	FISH	DGGE	Ion torrent	Pyrosequencing	Illumina	
Actinobacteria	7	0	0	1	0	1	0	4	1	(Al Ashhab et al., 2014a; Ayache et al., 2013; Bereschenko et al., 2011; Chiellini et al., 2012; Khan et al., 2013b; Kim et al., 2014) (Inaba et al. (2018)
Aeromonadales	1	0	0	0	0	0	1	0	0	Baker and Dudley (1998)
Alteromonadales	2	0	0	0	0	0	0	2	0	(Jeong et al., 2017; Kim et al., 2014)
Bacillales	4	2	0	0	0	1	0	1	0	(Baker and Dudley, 1998; Belgini et al., 2018; Khan et al., 2015; Ridgway et al., 1983)
Bdellovibrionales	1	0	0	0	0	0	0	0	1	Zheng et al. (2018)
Burkholderiales	17	0	1	1	0	4	0	4	7	(Al Ashhab et al. 2014a, 2014b, 2017; Ayache et al., 2013; Bereschenko et al. 2008, 2010; Chun et al., 2012; Ivnitsky et al., 2005, 2007; Manes et al., 2011b; Nagaraj et al., 2017a; Tan et al., 2017; Zheng et al., 2018; Zodrow et al., 2014) (Inaba et al. (2018)
Caulobacterales	3	0	0	1	0	1	0	0	1	(Bereschenko et al., 2008; Chiellini et al., 2012; Nagaraj et al., 2017a)
Cellvibrionales	1	0	0	0	0	0	0	1	0	Kim et al. (2014)
Chitinophagales	1	0	0	0	0	0	0	0	1	Zheng et al. (2018)
Chroococcales	1	0	0	0	0	0	0	1	0	Jeong et al. (2017)
Chromatiales	2	0	0	1	0	1	0	0	0	(Belgini et al., 2018; Manes et al., 2011b)
Clostridiales	1	0	0	0	0	1	0	0	0	Chiellini et al. (2012)
Corynebacteriales	3	1	0	1	0	0	0	1	0	(Baker and Dudley, 1998; Barnes et al., 2015; Chiellini et al., 2012)
Cytophagales	2	0	1	0	0	1	0	0	0	(Herzberg et al., 2010, Ivnitsky et al., 2005)
Enterobacterales	2	1	0	0	0	0	0	1	0	(Khan et al., 2015; Ridgway et al., 1983)
Flavobacteriales	4	2	0	0	0	1	0	0	1	(Al Ashhab et al., 2017; Baker and Dudley, 1998; Ivnitsky et al., 2005; Ridgway et al., 1983)
Holophagales		0	0	0	0	1	0	0	0	Chen et al. (2004)
Legionellales	2	0	0	0	0	0	0	2	0	(Al Ashhab et al., 2014a; Levi et al., 2016)
Micrococcales	3	2	0	1	0	0	0	0	0	(Baker and Dudley, 1998; Chiellini et al., 2012; Ridgway et al., 1983)
Nitrosomonadales	3	0	0	0	0	2	0	1	0	(Barnes et al., 2015; Bereschenko et al. 2008, 2010)
Myxococcales	1	0	1	0	0	0	0	0	0	Chun et al. (2012)
Nitrospirales	1	0	0	0	0	0	0	0	1	Yu et al. (2017)
Phycisphaerales	1	0	0	0	0	0	0	0	1	Jeong et al. (2017)
Planctomycetales	3	0	0	0	0	1	1	0	1	(Bereschenko et al., 2008; Hong et al., 2016; Yu et al., 2017)
Pseudomonadales	14	2	0	0	0	5	0	2	5	(Al Ashhab et al. 2014a, 2014b; Baker and Dudley, 1998; Belgini et al., 2018; Bereschenko et al., 2010; Ivnitsky et al., 2005, 2007, Khambaty and Plumb, 2011; Khan et al., 2015; Ridgway et al., 1983; Tan et al., 2017; Yu et al., 2017; Zodrow et al., 2014)
Rhizobiales	9	0	0	1	1	1	0	4	2	(Al Ashhab et al. 2014a, 2014b; Ayache et al., 2013; Barnes et al., 2015; Bereschenko et al. 2008, 2010, Nagaraj et al., 2017a; Pang and Liu, 2007; Zheng et al., 2018)
Rhodobacterales	9	0	0	1	0	0	1	5	2	(Hong et al., 2016; Jeong et al., 2017; Khan et al. 2013a, 2013b, 2015; Levi et al., 2016; Zhang et al., 2011; Zheng et al., 2018; Zodrow et al., 2014) (Inaba et al. (2018)
Rhodocyclales	1	0	0	0	0	1	0	0	0	Chen et al. (2004)
Rhodospirillales	5	0	0	0	0	1	0	3	1	(Barnes et al., 2015; Bereschenko et al., 2010; Jeong et al., 2017; Khan et al., 2015; Zheng et al., 2018)
Saprospirales	1	0	1	0	0	0	0	0	0	Herzberg et al. (2010)
Sphingobacteriales	1	0	0	0	0	0	0	1	0	Nagaraj et al. (2017a)
Sphingomonadales	17	0	0	2	1	4	1	4	5	(Al Ashhab et al. 2014a, 2014b; Ayache et al., 2013; Barnes et al., 2015; Bereschenko et al. 2008, 2010; Chen et al., 2004; Chiellini et al., 2012; Hong et al., 2016; Ivnitsky et al., 2007; Khan et al., 2013b; Khambaty and Plumb, 2011; Nagaraj et al., 2017a; Tan et al., 2017; Zhang et al., 2011; Zheng et al., 2018; Zodrow et al., 2014) (Inaba et al. (2018)
Streptosporangiales	1	0	0	1	0	0	0	0	0	Chiellini et al. (2012)
Thiotrichales	1	0	0	0	0	0	0	1	0	Kim et al. (2014)
Xanthomonadales	8	0	0	0	0	1	0	3	4	(Al Ashhab et al. 2014a, 2014b; Khambaty and Plumb, 2011; Khan et al., 2015; Nagaraj et al., 2017a; Tan et al., 2017; Yu et al., 2017)

called the persister cells, is tolerant for biocides because they are metabolically inactive (Spoering and Lewis, 2001). Persisters are a small part of the whole community, but their offspring may become abundant after they shift to an actively growing state when most of the other cells of the biofilm have been killed, during for instance membrane cleaning (Hall-Stoodley et al., 2004).

Synergistic interactions and metabolic dependency generally increase the overall biomass produced in multispecies biofilms (Burmølle et al., 2014; Giaouris et al., 2013; Liu et al., 2018; Ren et al., 2015; Van der Veen and Abee, 2011). Due to their multispecies composition, natural biofilms are composed of phenotypically distinct bacteria that can either cooperate or compete for resources (Nadell et al., 2016). A regulatory network is therefore important for each cell to fine-tune its investment costs in profitable cooperative traits while antagonistic competitors are opposed. Quorum sensing (QS) – the secretion and response to signal molecules called autoinducers, provide bacteria the tool to assess local cell densities and act accordingly by expressing the most suitable set of genes. This signaling circuit is used by clonal clusters of genetically identical cells to limit exploitation within multispecies biofilms: bacteria within clonal clusters secrete and sense the same QS signals and respond uniformly so that exploitation by competitors is

Table 2
Abundance of bacterial taxa in feed water and the corresponding high-pressure membranes.

Feed water	Most abundant taxa in feed water Lowest detected taxonomic rank (Order)	Most abundant taxa on high-pressure membrane Lowest detected taxonomic rank (Order)	Reference
Seawater	*Synechococcus* (*Synechococcales*) *Marinovum* (*Rhodobacterales*) *Pelagibacter* (*Pelagibacterales*)	*Antarctobacter* (*Rhodobacterales*) and *Roseobacter* (*Rhodobacterales*)	(Khan et al. 2013a,b)
	Pelagibacteraceae (*Pelagibacterales*) *Octadecabacter* (*Rhodobacterales*) *Sediminicola* (*Flavobacteriales*) *Loktanella* (Rhodobacterales)	*Rhodobacteraceae* (Rhodobacterales) *Pseudomonas* (*Pseudomonadales*) *Ralstonia* (*Burkholderiales*)	Zodrow et al. (2014)
	Mycobacteria (*Actinobacteria*), *Ensifer* (*Rhizobiales*), *Sphingomonas* (Sphingomonadales), *Pelomonas* (*Burkholderiales*), *Bradynorhizobium* (*Rhizobiales*), *Mycobacterium* (*Corynebacteriales*)	*Mycobacteria* (*Actinobacteria*), *Ensifer* (*Rhizobiales*), *Sphingomonas* (*Sphingomonadales*), *Pelomonas* (*Burkholderiales*), *Methylibium* (*Burkholderiales*)	Ayache et al. (2013)
Wastewater effluent	*Rhizobiales, Sphingomonadales and Burkholderiales*	*Comamonadaceae* (*Burkholderiales*), *Rhizobiales, Sphingomonadales, Pseudomonadales, Xanthomonadales*	Al Ashhab et al. (2014b)
Surface water	*Burkholderiales*, *Janthinobacterium, Sphingomonadales*	*Sphingomonas* (*Sphingomonadales*), *Afipia* (*Rhizobiales*), *Hyphomicrobium* (*Rhizobiales*), *Caulobacter* (*Caulobacterales*), *Pedomicrobium* (*Rhizobiales*), *Sphingopyxis* (*Sphingomonadales*) *Acidovorax* (*Burkholderiales*) *Burkholderia* (*Burkholderiales*) *Janthinobacterium* (*Burkholderiales*) *Nitrosomonas* (*Nitrosomonadales*)	Bereschenko et al. (2008)

avoided (Nadell et al., 2016). QS has shown to effectively reduce biofilm formation under laboratory conditions, but metagenomic analysis of indicates that genes involved in quenching QS signals, rather than genes required for QS, are identified in biofilms on fouled RO membranes.

How survival strategies simultaneously mediate community assembly on the membrane and whether such strategies are conserved within certain bacterial taxa is not understood. Moreover, a limited number of studies has investigated the molecular changes in EPS composition during the membrane operation (Nagaraj et al., 2017b). Bereschenko et al. (2011) investigated the effect of conventional cleaning treatment and occurrence and development of biofouling in RO membrane units (Bereschenko et al., 2011). Over a period of 6 months membrane surfaces were cleaned once a week with a conventional acid cleaner. Only *Sphingomonas* species that are typically localized at the biofilm base were able to survive the chemical cleaning procedures (Bereschenko et al., 2011). Members of the *Sphingomonas* genus are versatile bacteria that are widely spread in natural water environments and man-made water systems (Balkwill et al., 2006; Glaeser and Kämpfer, 2014). Amongst the bacterial community, they are strong competitors in scavenging a variety of nutrients under oligotrophic conditions, and they contribute to cleaning-associated stability of bacterial biofilms (Bereschenko et al. 2010, 2011; Lal et al., 2006; Stolz, 2014; Waigi et al., 2017). Moreover, they secrete sphingans (a group of structurally closely related EPS) that effectively protect bacteria against extreme pH, temperature, salinity and pressure (García et al., 2018; Pollock, 1993; Xu et al., 2015). This provides a further explanation for the selection of EPS-producing bacteria by membrane cleaning agents. Therefore EPS quality and not quantity could be a determining factor in occurrence of cleaning−associated biofilms (Nagaraj et al., 2017b).

The long search for alternative membrane cleaning strategies is just one example that illustrates the difficulty of controlling biofilms (Flemming et al., 1996). Examples of alternative strategies to alleviate membrane biofouling include: nutrient limitation, surface modification, quorum quenching and biological control via bacteriophages and microfaunal predators. Based on the current knowledge, it appears that membrane surface modifications are in fact incompatible to control biofilm formation in full-scale membrane operations due to drag force that transferrers bacteria and nutrients to the membrane surface. As different components are transferred by the drag force to the membrane surface, it is swiftly covered and membrane surface modifications are rendered less effective.

Governing bacterial communication by quenching QS signals could switch the biofilm condition in aquatic environments in terms of controlling and replacing the microbes (Hong et al., 2012; Wood et al., 2016). QS permits bacteria to effectively regulate biofilm formation under static conditions, but this process becomes less efficient when the signal molecules are removed by the flow under turbulent settings (Purevdorj et al., 2002). Hence, the use of quorum quenching natural agents is a promising approach to control biofouling although it remains to be established which role QS circuits plays in membrane biofouling (Kalia and Purohit, 2011). In that context the development of less- or selectively toxic antibacterial agents capable of clearing biofilms would be timely. Here, the use of bacteriophages, that effect phage-mediated biocontrol of bacteria (phage therapy); purified phage-encoded enzymes that digest bacterial cell-wall material (endolysins); or phage-encoded enzymes that digest the EPS (EPS depolymerases) (Chan and Abedon, 2015). These agents have been shown to reduce the bacterial density of a diversity of biofilms and, in many cases, tend to be non-toxic (Chan and Abedon, 2015). Although reports on such alternatives provide promising perspectives, their success to alleviate membrane biofouling over prolonged periods still has to be established on multispecies models. This is a particularly important quest, due to the potential selective pressure they; microfaunal predators and bacteriophages exert on the bacterial community (Jousset, 2012; Scanlan and Buckling, 2012). Bacteria producing filaments and aggregates, but also small bacteria, have a strong selective advantage and higher survival rate in the presence of bacterial grazers such as nematodes (Jousset, 2012). Similarly, lytic phages select for bacteria to develop mucoid biofilms that are difficult to control (Scanlan and Buckling, 2012). The naturally high abundant bacteriophages in marine water raises question about their infection rates and how their success in alleviating membrane biofouling can be increased (Scanlan and Buckling, 2012).

4. Colonization of high pressure membranes

The membrane surface can be colonized by microbes transported by the feed water. Comparison of the bacterial community composition of pristine (unused) membranes to fouled membranes has shown that most bacteria causing membrane fouling have a feed water origin, and are absent on the pristine membranes (Nagaraj et al., 2017a). The frequently detected taxa are commonly present at low relative abundance in the different feed water types and in the different pre-treatment compartments.

4.1. The bacterial diversity on the membrane and in the feed water is different

High-pressure membranes are operated using a variety of feed

water types, including seawater, surface water, groundwater and wastewater effluents. In marine environments, the relative abundance of bacterial taxa is affected by seasonal changes, such as temperature differences, day length, nutrient composition and concentration (Fuhrman et al., 2015). In the upper marine layers, where light and oxygen easily penetrate, the phototrophic SAR11 (e.g. *Pelagibacterales*), SAR86, SAR116 clusters and the cyanobacteria *Prochlorococcus* and *Synechococcus* are dominant during spring blooms (Fuhrman et al., 2015; Morris et al., 2002). Table 2 shows the bacteria in marine environments that are typically abundant in the feed waters of high pressure membranes. The relative abundance of these microbes, however, is low at the surface of high-pressure membranes (Table 2) (Khan et al. 2013a, 2013b; Levi et al., 2016; Manes et al., 2011b; Zodrow et al., 2014). These differences in occupancy suggest that the conditions at the membrane surface are selective for certain bacterial phenotypic traits.

The dominant bacteria in secondary and tertiary effluent streams that originate from wastewater sources do not become dominant members of the biofilm community at the membrane surface (Table 2) (Al Ashhab et al., 2014a; Ferrera et al., 2015). Al Ashhab et al. (2014a) compared the bacterial diversity of an RO membrane biofilm with the artificial tertiary wastewater that was used as feed water, and showed that the bacterial community on the RO membrane clustered separately from the feed water communities. The orders that were abundant in the feed waters (*Burkholderiales, Rhizobiales* and *Sphingomonadales* with a cumulative relative abundance of 45.6%) were also present on the membrane, although at a much lower relative abundance (17.5%) (Al Ashhab et al., 2014a).

In feed water originating from surface and groundwater *Burkholderiales*, *Janthinobacterium, Sphingomonadales* were dominant (Table 2) (El-Chakhtoura et al., 2015; Forbes et al., 2016; Lin et al., 2014; Liu et al., 2014; Navarro-Noya et al., 2013; Shaw et al., 2015). These orders correspond to those found on fouled membranes that are fed with these water types, suggesting that ground water and surface water serve as inoculum for membrane biofilms (Bereschenko et al. 2008, 2010, 2011; Chiellini et al., 2012). Bereschenko et al. (2008) compared the bacterial diversity of the surface water and the membrane community and it was concluded that that the biofilm was actively formed on the membrane surface, rather than being a concentration effect of bacteria. Overall, the composition of the bacterial community on the membrane is generally different from the feed water as only a fraction of the bacterial feed water diversity accumulates at the membrane surface, indicating that the membrane surface provides bacterial selection pressures (Bereschenko et al., 2008). However, Hörsch et al. (2005) found that the bacterial composition of a mature fouling layer was similar to the composition of the feed water and concluded that, in contrast to the study of Bereschenko et al. (2008), growth played a minor role in the biofouling process (Hörsch et al., 2005). The difference between these studies is the identification technique and the resolution to which the bacterial community composition was delineated. Hörsch used FISH to distinguish bacteria at the at the phylum level, while Bereschenko identified bacteria at the species level via clone libraries of the 16S rRNA gene sequence. This exemplifies that the microbial diversity should be targeted and delineated to lower taxonomic levels, such as to species or at least family level to understand ongoing microbial processes.

4.2. Feed water pre-treatment strategies and their effect on bacterial communities

The composition of the feed water determines which pre-treatment strategy is most appropriate to control membrane fouling (Voutchkov, 2010). Two parameters that are commonly reported to assess the feed water quality are the silt density index (SDI) used as a measure for the amount of submicron particulates and turbidity to measure water clarity (Badruzzaman et al., 2019). Conventionally, feed water pre-treatment for high-pressure membrane filtration is typically performed by a combination of processes: coagulation and flocculation, followed by granular media filtration (e.g., anthracite coal, silica sand, or garnet) and cartridge filtration (Fig. 3) (Voutchkov, 2010). Biocides such as chlorine and peracetic acid, but also ozone or UV can be applied when biofouling is a concern (Bucs et al., 2018). Pre-treatment strategies are designed to remove the microbial load on high-pressure membranes, but could scavenge nutrients and potentially provide a suitable environment for microbial growth. Comparison of the bacterial community composition can therefore answer whether pre-treatment compartments serve as inoculum for high-pressure membranes.

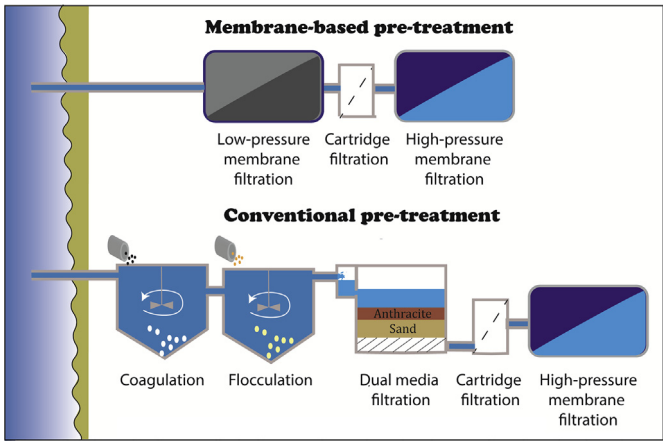

Fig. 3. Schematic diagram illustrating membrane-based and conventional pre-treatment systems for high-pressure membrane filtration.

In conventional pre-treatment systems, cartridge filters (CF) are commonly used as final step to remove suspended solids (Fig. 3) (Alawadhi, 1997). Commonly cartridge filters with micron ratings between 1 and 10 μm are used. These filters remove bacteria incompletely but, depending on the feed water quality and the micron rating, cartridge filtration may remove suspended solids (Chua et al., 2003; Leparc et al., 2007). The bacterial community of CF is commonly different from that of the succeeding RO membrane, at least in in full-scale facilities. (Bereschenko et al., 2008; Chun et al., 2012; Levi et al., 2016; Zhang et al., 2011). Comparison of the bacterial community composition between different compartments of fourteen full scale water desalination plants has shown that the dominant bacteria on the RO membrane are absent from or are a minor component of the bacterial community of the preceding cartridge filters (Zhang et al., 2011). Similarly, Chun et al. (2012) detected that members of the *Ruegeria, Pseudoruegeria, Parvularcula, Legionella* and *Shigella* are the only bacterial groups shared between the CF and RO membrane (Table 3). *Phaeobacter, Leisingera, Kangiella and Bacillales* are abundant on the CF, while *Haliangium* and *Limnobacter* are abundant on the RO membrane. On the cartridge filters, the presence of bacteria belonging to taxa harbouring facultative and obligate chemolithotrophs, such as *Geobacter*, *Desulfuromusa* and *Thioalkalivibrio*, seems to indicate that the pre-treatment compartments effectively removed certain nutritional compounds, such as ferrous iron or sulfur (Chun et al., 2012). This removal can account for the different bacterial community composition between the CF and the RO community.

Table 3
Abundance of bacterial taxa in pre-treatment compartments and the corresponding high-pressure membranes.

Pretreatment compartment	High abundant taxa pre-treatment step Lowest detected taxa (Order)	High abundant taxa high-pressure membrane Lowest detected taxa (Order)	Reference
Cartridge filtration	Phaeobacter (Rhodobacterales), Leisingera (Rhodobacterales), Kangiella (Oceanospirillales), Bacillales.	*Haliangium* (Myxococcales), *Limnobacter* (Burkholderiales).	Chun et al. (2012)
	SAR 11	*SAR 11*, *Legionellales, Rhodobacterales*	Levi et al. (2016)
Dual media filtration	*Hyphomonas* (*Rhodobacterales*), *Erythrobacter* (Sphingomonadales) *Trichodesmium* (Oscillatoriales) *Nitrospira* (*Nitrospirales*)	*Thalassospira* (*Rhodospirillales*) *Alteromonas* (*Alteromonadales*) *Marinobacter* (*Alteromonadales*), *Algisphaera* (*Phycisphaerales*), *Oceanicola (Rhodobacterales)*,*Cyanobacterium* (*Chroococcales*)	Jeong et al. (2017)
Low-pressure membrane filtration	*Rhizobium* (*Rhizobiales*), *Agrobacterium* (*Rhizobiales*), *Zoogloea* (*Rhodocyclales*), *Mesorhizobium* (*Rhizobiales*), *Caulobacter* (*Caulobacterales*), *Bradyrhizobium* (Rhizobiales) and *Bosea* (Rhizobiales)	*Bradyrhizobium* (*Rhizobiales*), *Rhodopseudomonas* (*Rhizobiales*) and *Sphingomonas* (*Sphingomonadales*)	Chen et al. (2004)
	Planococcus (*Planococcaceae*), *Aeromonas (Aeromonadales), Pseudomonas (Pseudomonadales), Acinetobacter (Pseudomonadales)*	*Erythrobacter* (*Sphingomonadales*), *Ruegeria* (*Rhodobacterales*), *Planctomycete* (*Planctomycetales*),	Hong et al. (2016)
Continous biocidal cleaning	*Alcaligenaceae* (*Burkholderiales*) *Cyclobacteriaceae* (*Cytophagales*) and *Rhizobiales*	*Pseudoxanthomonas* (*Xanthomonadales*) *Thermomonas* (*Xanthomonadales*) *Stenotrophomonas* (*Xanthomonadales*) *Sphingopyxis* (*Sphingomonadales*) *Pseudomonas* (*Pseudomonadales*)**	Tan et al. (2017)
	Ralstonia (*Burkholderiales*), *Diaphorobacter* (*Burkholderiales*), *Stenotrophomonas* (*Xanthomonadales*), *Enterobacteriaceae* (*Enterobacterales*)*	*Bacillales, Enterobacteriaceae (Enterobacterales) Pseudomonas (Pseudomonadales), Silicibacter (Rhodobacterales) Streptococcus (Lactobacillales) Staphylococcus (Bacillales) Acidocella (Rhodospirillales)*	Khan et al. (2015)

Members of the SAR11 cluster have been found in high relative abundance on both the cartridge filter and the RO membrane (Table 3). The relative abundance of this cluster varied seasonally between 10% to 30% and 64%–77% on the CF and RO membrane, respectively (Levi et al., 2016). Because the relative abundance of the SAR11 cluster was low in the compartments that preceded the CF membrane (rapid sand filtration; relative abundance of 0.4–8.4%), the CF might have stimulated growth of members of the SAR11 cluster and as such function as inoculum for the high-pressure membranes. SAR11 is ubiquitous in marine environments and found in near-shore waters to depths of 3.000 m (Hanson et al., 2012; Morris et al., 2002; Sunagawa et al., 2015). Physiological traits of these bacteria are largely unknown because, despite being ubiquitous, members of the SAR11 cluster have rarely been isolated (Henson et al., 2018; Giovannoni and Vergin, 2012; Rappé et al., 2002). The SAR11 bacteria are among the smallest free-living cells in culture with cell length of 0.37–0.89 μm and have limited metabolic flexibility (Henson et al., 2018; Giovannoni and Vergin, 2012; Rappé et al., 2002). Based on these morphological traits, it was concluded that the size of these bacteria might have provided them a benefit to access the high pressure membranes as they might more easily pass the CF compared to larger bacteria (Levi et al., 2016).

Dual media (DM) filters are conventionally used to remove soluble organics and are typically composed of a 1.0–2.0 m layer of sand covered by 0.4–0.8 m of anthracite (Badruzzaman et al., 2019). Granular activated carbon can be used instead of anthracite to reduce high levels of organics (Naidu et al., 2013; Anis et al., 2019). DM filters and RO membranes harbour different biofilm communities (Jeong et al., 2017). On the DM filter, phototrophic and nitrite-oxidizing bacteria, such as *Trichodesmium* and *Nitrospira* are abundant, but their relative abundance is below detection level on the RO membrane (Table 3). The bacterial community composition of DM and RO filter becomes more similar when they are continuously cleaned by chlorination. Under these conditions, *Erythrobacter* and *Sphingomonas* and *Hyphomonas* increase in relative abundance and become dominant on DM filters and downstream RO membranes. Whether the DM filters served in this case as inoculum is unknown, but these results indicate that the selection pressure on the bacterial diversity caused by continuous chlorination overcomes the selection pressures imposed by the different media types (e.g. DM filters and RO filters) (Jeong et al., 2017).

Low-pressure membranes (MF and UF) are applied as pre-treatment systems for high pressure membranes and their use has increased in recent years due to capital cost reductions (Huang et al., 2009; Wolf et al., 2005). Typically, low-pressure membranes filtration systems remove particles at ≥0.1 μm (MF membranes) or ≥0.01 μm (UF membranes) and may reduce SDI values to below 2 (Anis et al., 2019). Low pressure membranes remove bacteria with log reduction values of 4 and biofouling is therefore reduced but not prevented (Ghayeni et al., 1999; Jacangelo et al., 1989; Molelekwa et al., 2014).

The communities of MF and UF compartments have a different bacterial composition compared to the downstream high-pressure membranes (Table 3) (Chen et al., 2004; Ghayeni et al., 1998; Herzberg et al., 2010; Lee et al., 2010; Manes et al., 2011a). Similarly to the CF community, the MF filter harbours facultative and obligate chemolithotrophs, including the iron reducing *Geothrix fermentans* and the homoacetogen *Holophaga foetida* (Chen et al., 2004). This suggests that nutritional conditions are a determining factor for the bacterial community compositions of the MF and RO. When UF is used as pre-treatment step the genera *Erythrobacter*, *Planctomycete* and *Ruegeria* become dominant on downstream RO membranes (Table 3). Members of these genera are below detection limit on the UF membrane and in the UF effluent, confirming that the relative abundance of bacterial groups in the UF effluent does not correlate with the microbial community of the downstream RO membranes (Chen et al., 2004).

Chlorine is the most widely used disinfectant due to its ease of use and low cost (Du et al., 2017). In this review we distinguish between continuous dosing of chlorine as pre-treatment process and intermitted chlorination as membrane cleaning process. Chlorination effectively kills biomass on the RO membrane but, based on molecular analysis, some bacterial groups appear to tolerate this biocide. Bacterial classes that are well-known to resist chlorine due to their ability to sporulate are *Bacilli* and *Clostridia* (Wyatt and Waites, 1975). These classes, and in particular *Bacilli*, have been identified on fouled membranes that in many cases used chlorination as pre-treatment step Baker and Dudley (1998), Belila et al., (2016), Chen et al., (2004), Chiellini et al., (2012), Ivnitsky et al., (2007), Khan et al., (2015), Lee et al., (2009), Ridgway et al., (1983), Zodrow et al., (2014).

The use of the biocides K5030 (isothiazoline based) and FR110 (inorganic base type of combined chlorine agent) to UF effluent led to major bacterial community shifts on the downstream RO membrane (Tan et al., 2017). The *Alcaligenaceae* family, *Cyclobacteriaceae* family and the *Rhizobiales* order are dominant when biocide dosing is not part of the pre-treatment process are effectively removed when K5030 and FR110 are dosed (Table 3). Instead, *Pseudoxanthomonas*, *Stenotrophomonas* and *Thermomonas*, *Pseudomonas* and *Sphingopyxis* increase in relative abundance when biocides are dosed (Table 3).

4.3. Different membrane cleaning agents select for distinct bacterial communities

Membrane biofouling layers can be removed using alkaline or acid solutions, metal chelating agents, surfactants, enzymes and oxidizing agents (Li and Elimelech, 2004). Base/acid cleaning removes organic foulants on membranes and destroys the microbial cell walls (Ang et al., 2006). Metal chelating agents and surfactants can be used to disintegrate EPS layers by removal of divalent cations and solubilisation of macromolecules, respectively (Al-Amoudi and Lovitt, 2007). The efficiency of cleaning agents to remove biofouling is limited because the EPS layer is recalcitrant against cleaning agents. Improvement of cleaning efficiency is difficult, particularly for aged biofilms.

Membrane cleaning frequently removes only part of the fouling layer and cleaned membranes therefore provide a suitable environment for swift microbial colonization (Beyer et al., 2017). Membranes used in full-scale operation therefore have to be cleaned frequently. After the membrane is cleaned, the bacterial diversity of the membrane more closely resembles the feed water community compared to the membrane community before cleaning (Yu et al., 2017). From this point onwards, the bacterial diversity at the membrane surface increases till it is moderately fouled, but then declines till the membrane is cleaned again (Al Ashhab et al., 2017). These fluctuations in bacterial diversity indicate that the conditions on the membrane surface change during membrane fouling (Khan et al., 2015). Initially, nutrients are abundantly present on cleaned membranes, but when the biofilm matures, community members have to compete for resources as nutrients become limiting, leading to overgrowth of well adapted bacteria (Kim et al., 2014). Availability and depletion of nutrients could, together with the membrane cleaning events, therefore provide an explanation for the changes in species richness of fouling membranes.

Different bacterial groups have shown to succeed and thrive when membranes are cleaned intermitted with different cleaning agents (Al Ashhab et al., 2017; Bereschenko et al., 2011; Chun et al., 2012; Jeong et al., 2017; Khan et al., 2015; Oh et al., 2018; Tan et al., 2017; Yu et al., 2017). Inclusion of citric acid led to a different community composition compared to when chlorine was used alone (Khan et al., 2015). *Acinetobacter*, *Ralstonia, Comamonadaceae* and *Diaphorobacter*, *Stenotrophomonas* and *Enterobacteriaceae* are dominant on membranes that are cleaned by chlorination. When chlorination is combined with citric acid cleaning, *Silicibacter* and *Rhodobacteraceae*, *Pseudomonas*, *Pedobacter* and *Janthinobacterium* became abundant. Based on physiological features assigned to taxonomically related bacteria and ATP concentrations, it was suggested that spore-formers, Gram-positive bacteria and acidophiles better resist citric acid treatment (Khan et al., 2015). These suggestions have to be regarded with caution, as no evidence was provided that any of identified bacteria is recalcitrant against citric acid (Khan et al., 2015).

5. Eukaryotic and archaeal diversity

Most studies investigating the membrane microbiota of fouled high-pressure membranes have focussed on bacteria and neglected the archaeal and eukaryotic diversity (Al Ashhab et al., 2017; Baker and Dudley, 1998; Belgini et al., 2018; Chiellini et al., 2012). Those studies that did investigate the archaeal diversity show that it is – similar to the bacterial diversity – high in the feed water and decreases within the high pressure membranes (Al Ashhab et al., 2014b). Archaeal communities on the RO membrane are dominated by the phyla *Crenarchaeota* and *Euryarchaeota* (Al Ashhab et al., 2014b). Terminal restriction fragment length polymorphism analysis of the 18S rRNA gene sequences has shown that the eukaryotic community of a RO membrane used for river water purification was composed for 34% of fungal and 53% of amoebozoa (Chiellini et al., 2012). Unlike the bacterial and archaeal community, the fungal community composition of fouled RO membranes is comparable to that of the feed water community and remains the same during membrane cleaning (Al Ashhab et al., 2017). This evenness in fungal diversity indicates either that the membrane surface after cleaning is rapidly colonized by the same fungal taxa or that membrane cleaning removes fungi less effectively compared to bacteria.

5.1. Members of interkingdom biofilms benefit from cross-protection

Studies investigating the microbial community composition using NGS have shown that when tertiary wastewater is used as feed water, the fungal community of the high-pressure membrane is dominated by *Ascomycota*, *Basidiomycota* and *Glomeromycota* (Al Ashhab et al., 2014b). In a study that used clone libraries, which identified fungi to the genus level, the identified genera belong to the phylum *Ascomycota* (Belgini et al., 2018). During membrane cleaning, the relative abundance of *Ascomycota* increases at the expense of *Basidiomycota*. Abundant fungal *Ascomycota* classes on cleaned membranes include: *Eurotiomycetes*, *Saccharomycetes* and *Dothideomycetes* (Al Ashhab et al., 2017).

Diverse fungi are capable of biofilm growth or develop biofilm-like communities (Blankenship and Mitchell, 2006). Inter-kingdom biofilms containing both fungi and bacteria are ubiquitously present in nature and lead to close interactions, which can either be mutualistic or symbiotic (Hogan and Kolter, 2002; Romano and Kolter, 2005). Bacteria and fungi become highly recalcitrant for most of the antibiotics in inter-kingdom biofilms and are recognized as a serious problem especially in clinical settings due to cross-protection (Adam et al., 2002; Shirtliff et al., 2009). Whether inter-kingdom biofilms also provide cross-protection for biocides is not well studied, but it is known that microbial susceptibility towards biocides differs greatly per kingdom (Russell, 2003). Many bactericidal biocides, including chlorine, are less effective against fungi (Pereira et al., 2013). This is in line with the culturable microbial diversity obtained from more than a hundred membrane autopsies, which showed that problematic membranes biofilms (which were ineffectively removed using chlorine) had a higher fungal incidence (Baker and Dudley, 1998). Recalcitrant fungi pose a potential problem for the food industry, medical centres, pharmaceutical cleanrooms and for drinking water facilities as they increase the chance for recalcitrant infections and biofouling (Al-gabr et al., 2014; Cauda, 2009; Sandle et al., 2014; Videla, 2002). In clinical settings, inter-kingdom biofilms are frequently composed of the fungal genus *Albicans* and the bacterial genus *Pseudomonas* (Cauda, 2009; Harriott and Noverr, 2011). It appears that inter-kingdom biofilms on fouled membranes are composed of the same genera (Al Ashhab et al. 2014b, 2017). The interactions

between fungi and bacteria might affect membrane cleaning efficiency and consequently biofouling control. However, studies investigating these interactions are lacking.

The role that fungi play in membrane biofouling may have been underestimated due to their relative low number compared to bacteria (Al Ashhab et al., 2017). This has recently been shown for RO membranes used in the food industry (Vitzilaiou et al., 2019). The relationship between relative abundance and contribution to community ecology has, at least for bacteria, been questioned (Liu et al., 2017). Low abundant bacterial species may shift the relative abundance of other bacteria substantially and play therefore an important role in the fate of the multispecies biofilm (Liu et al., 2017). Cell count is an ambivalent measure to express contribution to membrane biofouling when comparing bacteria with fungi, particularly due to the typical differences in cell-volume between members of these kingdoms (Bloem et al., 1995). Besides tolerance towards chlorine, other physiological traits will most likely provide fungi advantages on the membrane surface. Members of the *Saccharomycetes* produce melanins: cell wall pigments that confer resistance against multiple stressors, including extreme temperatures, desiccation and radiation (Muggia et al., 2016). One member of the *Saccharomycetes*, - *Aureobasidium pullulans* - thrives in a wide range of conditions and is able to attach to moisturized plasticized surfaces using its hyphae, which might aid in membrane colonization (Webb et al., 1999). *A. pullulans* has the ability to form biofilms and grows under hypersaline, acidic and alkaline conditions and at different nutrient concentrations (Muggia and Grube, 2018). But the large number of unclassified fungi and the high physiological diversity between order members makes physiological predictions prone to inaccuracies (Stajich et al., 2009; Yarza et al., 2017).

6. Conclusions

The role of bacteria in membrane biofouling of high-pressure membranes is unequivocal and has been confirmed using a variety of techniques. NGS platforms have been fundamental for determining the composition of the membrane bacterial biota. A broad range of conditions can be found within a single pressure vessel and the effect of these abiotic and biotic variations is reflected by the abundance of many different bacteria taxa along membrane elements. As biofilm formation on membrane surfaces is complex, it is important for future studies to include a description about the cleaning agent, cleaning frequency, feed water temperature, location of the membrane element in the pressure vessel and on the sampling location at the membrane.

Because molecular techniques are limited by the reference database, taxonomical features of the detected microbes will only lead to accurate prediction of physiological features once representative members have been functionally characterized. The low number of physiologically characterized bacteria isolated from fouled membranes therefore provides a major limitation to understand how they interact and respond to the conditions at the membrane surface. Reference genomes are important for capturing information on metabolic properties. The use of metagenome-assembled genomes could therefor generate valuable physiological information from uncultivated bacteria. This approach was only recently used for the first time to characterise the microbial community in a full-scale RO plant (Rehman et al., 2019).

Most studies so far have neglected the archaeal and fungal community present on fouled membranes. As interkingdom biofilms commonly benefit cross protection, the understanding of the complete collection of microbial interactions at the membrane surface may be important for the design of more efficient cleaning strategies. Particularly fungi might contribute more to the membrane biofouling problem than previously anticipated as they are more recalcitrant against bacterial biocides.

The cleaning frequency of fouled membranes can be reduced by using anoxic groundwater. Seawater below the epipelagic zone is poor in NOM and the lower temperature and oxygen concentrations might in analogy to anoxic groundwater pose an opportunity for desalination purposes. But, although oxygen is limited, sulphide provides bacteria an electron donor and alternative energy source and biofouling is therefore to be expected. This review made clear that different cleaning agents select for distinct bacterial communities. Further research is required to determine whether cocktails with different antimicrobial activities can be designed that effectively remove all microbes and their EPS that prevent swift microbial regrowth.

Besides illustrating that the fundamental understanding of membrane biofouling has remained limited despite years of research, this review highlights that opportunities exists that may provide universal answers to the biofouling problem of high-pressure membranes and demand further investigation. The hydrodynamic conditions have repeatedly been shown to have a strong effect on the bacterial community composition and membrane biofouling. Improved material design has led to progress in membrane functionality and applicability, but development of improved spacer design is lacking behind. The effect of nutrient levels and possible manners to control membrane biofouling via nutrient limitation poses another potential solution for many membrane installation and should be further investigated.

7. Outlook

Although written records of the treatment of fouled ship bottoms as early as the 5th century B. C. have been found, the search for biofouling control strategies undoubtedly began with even earlier ships about which there is little information. Since the initial exploration of RO membranes in the 1950s, membrane biofouling mechanisms and control strategies have been investigated. In multiple momentous articles, Hans-Curt Fleming recognized in the 1990s the importance of biofilm formation in membrane fouling and suggested several options to circumvent it (Flemming et al., 1996; Flemming et al., 1997, Flemming 1997). The major concerns on biofouling mitigation in high pressure membrane filtration have since then been shifted from optimization of operating conditions to regulation of microbial, and in particular bacterial behaviour. Especially, a combination of emerging advanced analytical tools and developing molecular microbiology allows us to better resolve the characteristics of microbial relevant foulants.

Hitherto NGS tools have mainly been used to decipher bacterial communities. The role of bacteriophages, nematodes and other eukaryotes in the ecology of fouled membranes has remained elusive. Such information would bring insights into the applicability of dosing such organisms to control biofouling. Other examples include membrane surface modifications to mitigate microbial attachment or growth, nutrient limitation, or the use of bacterial predators such as bacterial grazers. But reports of successful implementation of these alternative strategies in full-scale operations are scarce.

Although the understanding of membrane biofouling has substantially improved, biofilm formation remains the main obstacle for high pressure membrane filtration. Hitherto, cleaning in place lingers the only universal method to effectively reduce membrane biofouling of high-pressure membranes, although several alternatives have, for many years, been pursued to replace it. A critical literature evaluation leads to the conclusion that a thorough understanding of the complete ecological organization of membrane biofilms that focusses on inter-kingdom interactions is required to

predict the effectiveness of alternative biofouling control strategies. This illustrates the need for multidisciplinary approaches and collaboration to advance biofouling research. An important factor that might explain the slow integration of prospective biofouling control strategies is the incomprehension to predict the effectiveness of alternative biofouling control strategies in full-scale installations. This might have hampered the decision-making process for implementation of alternative cleaning strategies. A standard method to grow and quantify membrane biofouling under reproducible conditions is therefore required to compare the effectiveness of different strategies between different laboratories. The membrane fouling simulator approaches such a reference method most closely, but lacks so far intra-laboratory reproducibility.

Author contributions section

Hendrik J. de Vries drafted the manuscript. All authors contributed to obtain the final version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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