

Drinking Water Microbiome

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Microbial communities interact with us and affect our health in ways that are only beginning to be understood. Microorganisms have been detected in every ecosystem on Earth, as well as in any built environment that has been investigated. Drinking water sources, drinking water treatment plants and distribution systems provide peculiar microbial ecological niches, dismantling the belief of the “biological simplicity” of drinking water. The assemblage of microbes within drinking water is referred to as the drinking water microbiota (“microbiome” when referring to the associated genetic information), and it accounts for about 10^6 – 10^8 cells/L. Recent DNA sequencing and meta-omics advancements allow a deeper understanding of drinking water microbiota.

Keywords: drinking water ; microbiome ; omics

1. Introduction

Drinking water quality is of direct relevance to human health because it is the primary source of human sustenance. Drinking water quality reflects the characteristics of raw water source, both from the physico-chemical and the microbiological point of view.

Often, a raw water source requires treatments before being considered potable. Furthermore, drinking water is delivered to the consumer through kilometers of pipes, and maintenance of water quality in these long ways to the tap is a prime concern for drinking water utilities.

Thus, providing safe and high-quality potable water can be a challenging task.

According to the Revised Drinking Water Directive (2020/2184), a total of 48 microbiological, chemical and indicator parameters must be monitored and tested regularly. However, considering specifically microbial safety, the focus is mainly on testing for the presence of bacteria indicating fecal contamination. These are measured using well-established culture-based tests, but with clear limits: they investigate for only specific microorganisms, without taking into account the wide range of microorganisms that constitute drinking water; moreover, those recalcitrant to growth in laboratory conditions are missed.

The assemblage of microbes within drinking water is referred to as the drinking water microbiota (“microbiome” when referring to the associated genetic information), and it accounts for about 10^6 – 10^8 cells/L ^[1].

In this context, exploring the whole microbial community of an ecosystem and its interactions with biotic and abiotic factors is pivotal. Advances in DNA sequencing technologies and computational analyses are fostering the application of DNA-based omics for understanding microbial community structure and dynamics to preserve and improve drinking water quality. High-throughput DNA sequencing (HTS) technologies (also called next generation sequencing technologies, NGS) are able to massively sequence millions or billions of DNA sequences with high sensitivity. This allows not only the detection of even DNA traces, but also the generation of an unprecedented amount of data, especially in the case of complex matrices (in terms of biodiversity), such as drinking water ^[2]. It is clear that the concept of biodiversity changed consequently to omics advances. Pioneering microbiome projects (e.g., Human Microbiome Project ^[3], Earth Microbiome Project ^[4], and many others) gave a boost in protocols development and DNA sequences acquisition, so that it is now possible to explore the biodiversity of an environmental sample in a time- and cost-effective manner. The inconceivable rise of omic tools has turned the exploration of such a peculiar ecosystem within reach ^[5].

2. Microbial Biodiversity in Drinking Water Treatment Plants (DWTPs) and Drinking Water Distribution Systems (DWDSs)

Groundwater and surface water are the two main types of source water to provide drinking water to the population. They have intrinsically different physical and chemical characteristics: groundwater are dark, oligotrophic environments, mostly known to be anoxic or anaerobic. The presence of iron, manganese, ammonia, sulfur compounds, methane, and dissolved organic carbon supports the growth of anaerobic communities without light sources [6][7][8]. On the other hand, surface waters are more affected by seasonal and environmental factors, such as weather and temperature, and thus, the concentration of certain chemicals is more variable. Being groundwater and surface water ecosystems with different characteristics, the microbial communities are also different [9]. Conversely, surface waters seem to be not dominated by these uncultivable, new-to-science microorganisms, but they show the presence of Cyanobacteria. Actinobacteria, Bacteroidetes, and Proteobacteria are shared by the two different water sources [10].

These microbial populations can seed downstream microbiota in the DWTP. The review of Zhou and colleagues exhaustively summarized the changes in the bacterial community and the influence of each treatment stage on microbial diversity in full-scale water supply systems [10].

Actually, potabilization processes involved in DWTPs are based on physical and chemical treatments to remove unwanted chemicals and microorganisms, such as coagulation and sedimentation, filtration through sand filters, granular activated carbon filters (GACs), and biological activated carbon filters, and finally disinfection. It is worthy to note that the seminal paper of Pinto and colleagues first shed light on the role of filtration in microbial community assembly in DWTP: carbon filters harbor a microbial community that can seed the downstream water [2][11]. Indeed, bacteria defined as “leaky colonizers” (e.g., *Hydrogenophaga*, *Acidovorax* and *Denitratisoma*) can colonize GAC/sand filters and can shape the drinking water microbiome downstream. Some studies also revealed the predominance of Bradyrhizobiaceae family and the enrichment in bacteria-carrying functions associated with aromatics degradation, many of which were encoded by Rhizobiales, in granular activated carbon filters [12]. Filter-specific occurrences have also been reported [12][13][14]. Disinfection through chlorination, chloramination, and UV can be employed to reduce the bacterial load. Generally, after disinfection, Alpha- and Beta-Proteobacteria are reported to be dominant in chlorinated water, whereas Beta-Proteobacteria are more abundant after chloramine disinfection than the other two processes [10].

Defining a conserved group of taxa characterizing drinking water exiting DWTP can be difficult, due to the variables related to water source and treatments mentioned above. However, at higher taxonomic levels, such as phyla and classes, a core microbiome constituted by Alpha- and Beta-Proteobacteria, and to a lesser extent of Gamma-Proteobacteria, Nitrospirae, Planctomycetes, Acidobacteria, Bacteroidetes and Chloroflexi, can be identified. At lower taxonomic level, Burkholderiaceae, Methylophilaceae, Comamonadaceae, and Rhodocyclaceae were abundant among Beta-Proteobacteria, whereas Sphingomonadaceae, Caulobacteraceae, and Methylobacteriaceae were dominant in Alpha-Proteobacteria [15].

The ecological dynamics occurring along the DWDS are well described in the review of Douterelo and colleagues [16]. Especially in DWDS, in addition to existing in a planktonic state (i.e., in the bulk-water), microorganisms can form a biofilm (eventually resistant to disinfectant) adhering to the pipe surfaces [17]. Biofilms are clusters of microorganisms that stick to nonbiological surfaces, such as rocks in a stream or pipes, as well as living forms (host-associated). Biofilm formation is spread in nature and serves as a defensive mechanism, produced by the microorganisms themselves or the host [18]. Resolving drinking water biofilms is a key aspect: biofilm formation can be easily seen in DWTPs and DWDSs because it represents a protected mode of growth that not only allows cells to survive in hostile environments but also to colonize new niches by dispersal of microorganisms from the microbial clusters [19]. After leaving DWTP, water reaches consumers after hours or days, depending on the system hydraulic retention time, a function of supply demands and network distances. A greater contact time with the DWDS infrastructure is likely to accelerate water quality degradation, and pipe material, dimension, and structure can affect biofilm formation [19][20]. Clearly, DWDS hosts extensive microbiomes with diverse biofilm communities, depending on several factors, such as flux and other hydraulic variables, but also the interaction with other microorganisms. A core microbiome is hard to be identified, considering differences in potabilization treatments, operational practices, and distribution system characteristics [5][21].

The meta-analyses conducted by Thom and colleagues [5] resolved the core microbiome of DWDS and proposed as prevalent taxa *Sphingomonas* (Alpha-Proteobacteria), an uncultured Rubinsphaeraceae (Planctomycetes), and *Hyphomicrobium* (Alpha-Proteobacteria) in DWDS bulk water and *Sphingomonas*, an uncultured Rubinsphaeraceae, and *Pseudomonas* (Alpha-Proteobacteria) in DWDS biofilm.

On the whole, the 25 most abundant genera considering the entire flow from source to the tap identified in this meta-analysis included organisms that are not usually tested for drinking water contamination but may have a role in drinking water quality. For instance, there were no coliforms identified in the core microbiome analysis or taxa profile for any meta-sample groups. It is worth noting that the most common genera in DWDS were less abundant in source and treatment, except *Nitrospira*, which was more abundant throughout treatment than in DWDS.

If many studies take a snapshot of specific points along the flow from the source to the tap and of specific moments, several works evaluate the microbiome considering its dynamics in space and time. For instance, omics strategies helped in disentangling spatial-temporal bacterial community in DWDSs in Northern China [22], exploring the UV/chlorine disinfection for the monitoring of potential opportunistic pathogens and the evaluation of risks caused by transregional water diversion to local water. Similar studies were conducted in Valencia [21], Paris [23], Milan [2], Zurich [13], more than one city in The Netherlands [24], Ann Arbor (US) [11], Urbana-Champaign (at the University of Illinois) [20], and many other.

On the whole, more and more data suggest that water treatments (in particular chlorination) significantly reduce overall species abundance and richness. Conversely, more stochastic processes governed the assembly of microbial communities in DWDS biofilm [5].

Beside the taxonomy characterization, also understanding microbiome functional properties is important to determine the behavior of a microbial community, mostly considering a predictive point of view. In this sense, shotgun metagenomics has revolutionized the way to study microbial dynamics, adding the information of functions. In this way, not only who are the actors (as in 16S rRNA sequencing approach), but also what they are doing can be explored. Moreover, shotgun metagenomics allows the monitoring and investigation of antibiotic resistance spread, an issue that is gaining increasing importance, considering the selective pressure that may be applied by potabilization processes [25][26]. Metagenomics-based approaches could also be used to identify “nonfunctional” microorganisms that play a key role in maintaining the stability of the whole microbial ecosystem. They underpin ecosystem functions, playing a crucial role in maintaining ecosystem equilibrium and health.

Although the effect of some microorganisms on human health are not well characterized, variations in microbial biodiversity and subsequently the bioactivity may affect the resilience of all other organisms and hence their ability to respond to anthropogenic pressure [27].

3. Microbial Dark Matter: Gap of Knowledge about the Uncultivable Majority

Considering the astonishing biodiversity that is emerging from microbiome studies, it would not be surprising if many of the microorganisms detected are unknown or poorly characterized. This also relies on the so-called Great Plate Count Anomaly [28]: in many environments, only 0.1–1% of microorganisms have been cultivated because of the difficulties to recreate in laboratory conditions the real environmental characteristics that allow the growth.

Nevertheless, unknown microbial life may be playing a crucial and even dominant role in ecosystem equilibrium. Borrowing the terms from astronomy, microbiologists have defined these still unknown microorganisms as “microbial dark matter” because they likely account for a large portion of the Earth’s biomass and biodiversity, yet their basic metabolic and ecological properties are not known. Phyla composed exclusively of uncultured representatives are referred to as Candidate Phyla (CP) [29][30][31].

The candidate bacterial superphylum Patescibacteria (also known as Candidate Phyla Radiation, CPR) and archaeal superphylum DPANN (Diapherotrites, Parvarchaeota, Aenigmarchaeota, Nanoarchaeota, and Nanohaloarchaeota) [32][33][34] are some of the uncultivable microorganisms uncovered in water ecosystems using high-throughput DNA sequencing techniques. It can be surely affirmed that the application of culture-independent methods has broadened the view of the tree of life [34][35][36], especially considering microorganisms which live in poorly understood environments as groundwaters. Due to their restricted metabolic capacity and unusual biology [33][35][37], it was suggested that Patescibacteria and DPANN are probably in a syntrophic relationship with other microorganisms, relying on them for complete redox transformations. The intricate pattern of dependencies between these microorganisms may explain the difficulty of their growth in laboratory conditions.

Patescibacteria are predominant in groundwater probably due to their thriving in oligotrophic environments and mobilization from soils [38]. Furthermore, recent studies [2][14] have found a high abundance of Patescibacteria in GACs as a possible consequence of groundwater seeding of carbon filters and filter morphology characteristics. The presence of microbial communities such as Patescibacteria influences the downstream water characteristics. Therefore, applying

stressors such as potabilization treatments to these oligotrophic ecosystems can greatly affect the selected microbial communities and the water people drink.

The catchy definition “microbial dark matter” contains imprecisions if compared with the astronomical “dark matter” [29]. However, it can help enhance the interest for the neglected microbial biodiversity harbored by unconventional environments, such as drinking water ecosystems [7].

4. Living in a Built Environment: DWTPs and DWDSs Ecosystems

The built environment (BE) encompasses all the environments that humans have constructed, including buildings, cars, public transport, and other human-built spaces, as well as DWTPs and DWDSs [39][40].

The built environments harbor unique microbial communities, different from those found in other environments on Earth. Often these constructed habitats are designed to be harsh for life, probably setting the conditions for a selective pressure that drives the built environment microbial assemblage [41].

Natural and constructed habitats are interconnected, especially in the case of water resources treated for human consumption, where drinking water source is collected from natural (sometimes pristine) environments and enters a manmade ecosystem. The flow has a direction from raw water upstream to treated water at the tap, and along this flow, multiple stressors can act on the microbial communities and their structures.

Microbial assemblage dynamics can be governed by both deterministic and stochastic processes in natural and built environments [42][43]. If deterministic factors are niche-based factors which can be controlled and manipulated, the effects of stochastic factors (such as genetic mutation, gene duplication, cell damage by radicals, die-off, interspecies interactions, emigration, immigration and random drift) on microbial assemblage are difficult to predict. For these reasons, DWTPs and DWDSs, as built environments, must be monitored and controlled taking into account those ecological processes that can relate to stochasticity in microbial assemblages [42]. For instance, opportunistic pathogens, such as *Legionella*, *Mycobacterium*, and *Pseudomonas*, find a favorable ecological niche in premise plumbings that are in effect a front line of human exposure [44].

Looking at a DWTP, microorganisms from drinking water source (groundwater and surface water) seed water downstream [11], colonizing the treatment units, such as granular activated carbon filters [2][14], surfaces and pipes [19][45], and can be released to subsequent processes and then to the DWDS. This directional movement is called migration (or immigration) and significantly contributes to microbial assemblage: in the neutral theory of biodiversity and biogeography, immigration is one of the key stochastic processes that change the community assemblage [46]. Moreover, water stagnation, intermittent supply, and the bi-directional migration from pipes to water and vice versa in the distribution network and indoor plumbing [20][47] must be taken into account. Mei and Liu [48] addressed the crucial question about to what extent immigration contributes to the assembly and function of the downstream community in DWTPs and DWDSs. What clearly appears is that commonly used methods, mainly based on culturing bacterial indicators and measuring chemical parameters, are not enough to quantitatively determine the microorganisms carrying out the process: to deeply understand these dynamics, an ecogenomics-based mass balance approach is proposed, an approach that couples a mass balance model with high-throughput DNA sequencing. Moreover, it can be coupled with machine learning to improve environmental variables identification [48].

Thus, monitoring, when stochasticity exists, is a technological challenge. De Vrieze and colleagues [42] proposed to first depict the initial status of the microbial communities, then to evaluate the deterministic processes (potentially) influencing the microbial community, and the (change in) input streams. The degree of microbial community dynamics, i.e., the change in microbial community composition in function of time, can be obtained on the genetic level through HTS-based microbiome analyses.

Linked to this, the estimation of the biological stability of drinking water, by the application of DNA-based omic technologies and powerful bioinformatic approaches, is a crucial node. Gomez-Alvarez and Revetta [49] demonstrated the potential of water microbiome profiles coupled with machine learning analyses as bioindicators for system stability in DWDS. This paves the way for the use of indicators that are microbiome-based: data-driven approaches can improve the predictive ability of the models applied to prevent risks, when classical bioindicators fail.

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