Chapter 27
Bacterial Communities: Their Dynamics and Interactions with Physicochemical Factors

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27.1 Bacterial Communities in Lakes

In both soil and aquatic systems, bacterial communities perform key functions in ecosystem processes, such as material cycle, the decomposition of organic matter, and the breakdown of pollutants (Pesce et al. 2008; Gonzalez et al. 2012). Lakes are excellent systems for investigating bacterial community dynamics because lakes have not only a sharp boundary definition but also strong environmental gradients (Linz et al. 2017). Thus, lakes are biologically complex freshwater ecosystems that create habitats for a wide range of macro- and microorganisms (Carpenter et al. 2011; see also Chaps. 31, 32, 33 and 34). Lake water and sediments of different environmental habitats with their unique characteristics result in their unique bacterial community composition (BCC), and such difference accounts for different microbial biogeographies in lake environments (Lindström and Langenheder 2012; Yang et al. 2016). On the other hand, the establishment of BCC in environmental water may vary from location to location depending on community adaptation, community interactions, environmental factors, hydrology, and human activities (Newton et al. 2011; Wang et al. 2018). For instance, BCC varies with different physicochemical characteristics (Zwart et al. 2002; Chang et al., 2020) among lakes (Van der Gucht et al. 2005; Yang et al. 2016) and across space and time that represents habitat heterogeneity (Shade et al. 2008).

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Tonle Sap Lake (TSL) has a unique and dynamic flood-pulse ecosystem driven by seasonal flooding from the Mekong River (Holtgrieve et al. 2013; see also Chap. 1), and TSL is arguably known as one of the world's most productive freshwater lake ecosystems (Daly et al. 2020; see also Chaps. 31, 32, 33 and 34). As a result, the water volume change, flow direction, mixing of water and sediments, and others affecting BCC must be considered. A better understanding of the drivers and controls of bacterial communities (on spatial and longtime scales) would improve both our knowledge of the fundamental properties of those communities and our ability to predict community states (Linz et al. 2017). However, compared with that in temperate environmental water, the shifting of BCC in tropical environmental water as found in lakes has not been well understood (Ung et al. 2019). Furthermore, the comprehensive dataset of the shifting of BCC in water column and sediment in aquatic ecosystems is limited since studies have focused either on surface waters or sediments (Liu et al. 2013; Li et al. 2015; Chen et al. 2016; Hengy et al. 2017; Li et al. 2017; Wan et al. 2017).

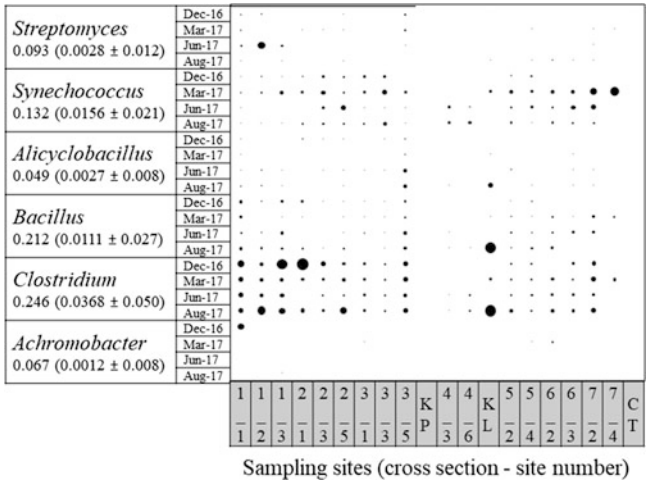## 27.2 Dominant Genera and their Spatiotemporal Distribution

The water and sediment samples in the TSL were collected at cross sections (CS) 1, 2, 3, and 4 (northwestern part); CS 5, 6, and 7 (southeastern part); and at three floating villages (Kampong Plouk (KP), Kampong Luong (KL), and Chhnok Tru (CT)). The surface water samples were collected using a water sampler (General Oceanics, Miami, FL, USA), while sediment samples were collected using a core sampler (Rigosha & Co., Ltd., Saitama, Japan). This sampling was conducted four times in December 2016 (Dec-16, dry season), March 2017 (Mar-17, the transition from dry to rainy season), and June and August 2017 (Jun-17 and Aug-17, rainy season) (see map of the study area (Fig. 1, Ung et al. 2019), published in Science of the Total Environment 664: 414-423. doi.org/10.1016/j.scitotenv.2019.01.351, as well as the detailed methods to measure physicochemical parameters and microbial communities).

The range (i.e., maximum–minimum) for the water depth of TSL was approximately 9.3 m (mean ± standard deviation, 3.9 ± 2.2), while, respectively, varied temperature of the surface water, 8.7 m (29.7 ± 1.8); electrical conductivity (EC), 21.5 mS/m (12.8 ± 2.3); dissolved oxygen (DO), 8.5 mg/L (6.8 ± 1.7); pH, 2.4 (7.9 ± 0.5); oxidation–reduction potential (ORP), 454 mV (213 ± 86); total dissolved solids (TDS), 95.3 mg/L (36.8 ± 33.1); and turbidity, 337 Nephelometric Turbidity Unit (NTU) (31 ± 58.5).

Based on the 16S rRNA gene sequence results from next-generation sequencing analysis, microbial communities in the lake water and sediment were chosen at the genus level for the major lineages set greater than 5% (see Figs. 27.1 and 27.2, respectively). Most of the genera were widely distributed in the lake water and
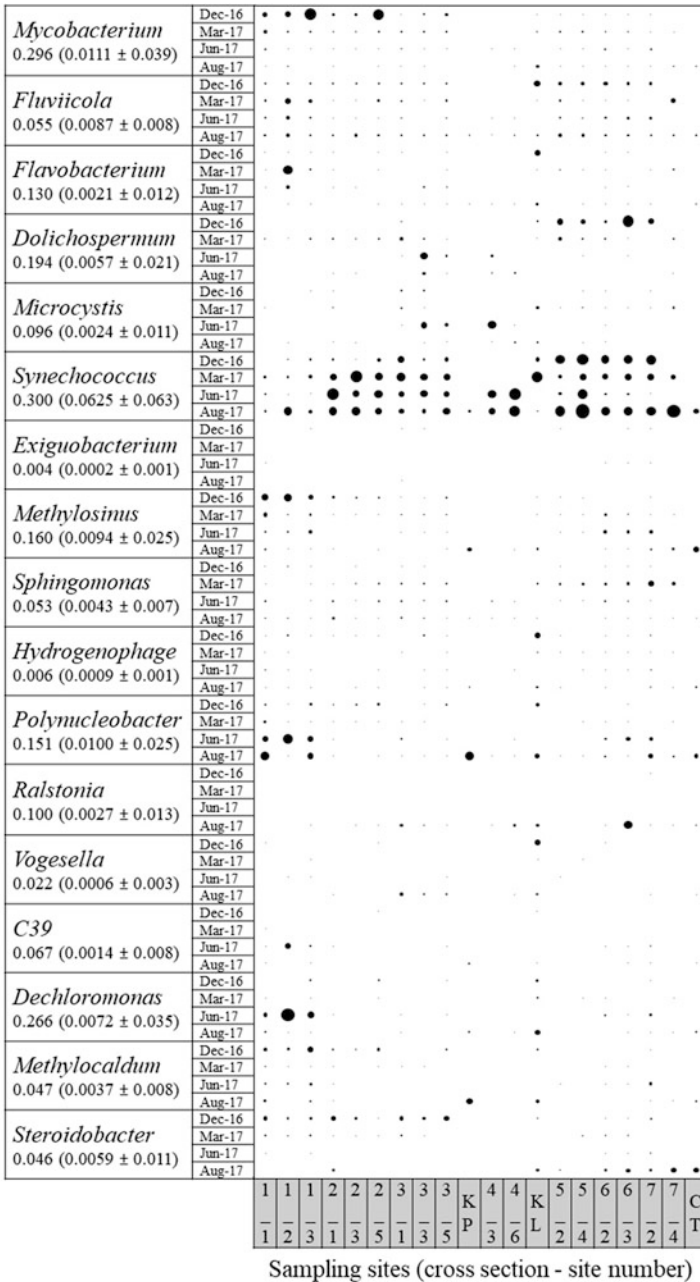
Fig. 27.1 Spatiotemporal patterns of assigned major genera on bubble charts, with the range value (mean ± standard deviation), showing their relative abundance in the surface water of the lake. Blank spaces represent low detection or no data available. Kampong Plouk (KP), Kampong Luong (KL), and Chhnok Tru (CT) are the sampling sites at the floating villages

Streptomyces 0.093 (0.0028 ± 0.012)	Dec-16 / Mar-17 / Jun-17 / Aug-17		
Synechococcus 0.132 (0.0156 ± 0.021)	Dec-16 / Mar-17 / Jun-17 / Aug-17		
Alicyclobacillus 0.049 (0.0027 ± 0.008)	Dec-16 / Mar-17 / Jun-17 / Aug-17		
Bacillus 0.212 (0.0111 ± 0.027)	Dec-16 / Mar-17 / Jun-17 / Aug-17		
Clostridium 0.246 (0.0368 ± 0.050)	Dec-16 / Mar-17 / Jun-17 / Aug-17		
Achromobacter 0.067 (0.0012 ± 0.008)	Dec-16 / Mar-17 / Jun-17 / Aug-17		

Sampling sites (cross section - site number): 1–1, 1–2, 1–3, 2–1, 2–3, 2–5, 3–1, 3–5, KP, 4–3, 4–6, KL, 5–2, 5–4, 6–2, 6–3, 7–2, 7–4, CT

Fig. 27.2 Spatiotemporal patterns of assigned major genera on bubble charts, with the range value (mean ± standard deviation), showing their relative abundance in the sediment of the lake. Blank spaces represent low detection or no data available. Kampong Plouk (KP), Kampong Luong (KL), and Chhnok Tru (CT) are the sampling sites at the floating villages

sediment; however, their abundance depended on location and season. With relative abundance about 30%, *Synechococcus* was the most abundant and widely distributed genus in the lake water (Fig. 27.1). Considered as an important contributor to primary production in many freshwater lakes (Ruber et al. 2018), *Synechococcus* (also called *picocyanobacteria*; diameter, 0.2–2 μm; cell wall, Gram-negative type; see Hoiczyk and Hansel 2000; Bell and Kalff 2001; and Callieri et al. 2007) belongs to *Cyanobacteria* at the phylum level. In the study of Ung et al. (2019), the abundance of *Cyanobacteria* was highly measured during the high-water-level season (Dec-16 and Aug-17) in the southeastern part (CS 4–3 to 7–4) of the lake. Conversely, its high abundance was measured during the low-water-level season (Mar-17 and Jun-17) in the northwestern part (CS 1–1 to 3–5). These results seem to suggest that the water flow from the Tonle Sap River (TSR) to the TSL during rainy season and from the TSL to the TSR during dry season strongly affects the abundance of *Cyanobacteria*. Similarly, *Cyanobacteria* was also dominantly found in some freshwater lakes in the world, such as Lake Loosdrecht (the Netherlands), Lake Ijssel (the Netherlands), and Lake Soyang (South Korea) (Yadav et al. 2019). Moreover, the biodiversity of bacteria found in other freshwater lake ecosystems shows the existence of *Synechococcus* and *Microcystis*. In addition, they appear to mix with other genera, such as *Aphanizomenon*, *Planktothrix*, and *Polynucleobacter*, in lakes Loosdrecht (the Netherlands), Baikal (Russia), and Tanganyika (Africa).

Synechococcus was not only dominant in this lake water but also in its sediment (Fig. 27.2). *Synechococcus* in the sediment was highly observed during dry season (Mar-17), especially in the northwestern part of the lake, probably due to the water

flow exchanges at the junction of the TSR and TSL. Those exchanges might play a role in the mixing process of the surface water and sediment in other parts of the lake. Another process was previously reported by Weisse (1993), in which a great interannual variability of *Synechococcus* was associated with the differences in weather conditions causing different spring mixing regimes and water column stabilization timing. Further characterization of these dynamics is necessary to truly understand the role of *Synechococcus* in environmental change, as well as that of other related microorganisms in this river–lake system.

On the other hand, *Mycobacterium*, *Flavobacterium*, *Polynucleobacter*, *Methylosinus*, *Dechloromonas*, and *Methylocaldum* were relatively dominant in the lake water of the northwestern part. *Methylosinus* and *Methlocaldum*, as methane-oxidizing bacteria, were highly detected in the northwestern part; this may be caused by the high concentration of methane, which is due to the methane fermentation of a high concentration of organic compounds and a low concentration of DO. It means that the northwestern part is the dead end of the lake, although a little water flow exists during the transition from dry to rainy season, and the area may tend to be a reductive environment. *Dolichospermum* and *Sphingomonas* were present in high abundance in the lake water of the southeastern part. *Microcystis* was also found in lake water, and its abundance increased during the transition from dry to rainy season in Jun-17. As shown in a recent study, during the bloom of *Cyanobacteria* in Lake Chaohu, *Microcystis* and *Dolichospermum* were the two major genera (Guan et al. 2020); specifically, the ranges of the cell diameter and colony size of *Microcystis* were small throughout the whole year, but those of *Dolichospermum* significantly changed over time and in different parts of the lake. It seems to be true that both genera coexist with the abundance of *Cyanobacteria*, which was also abundantly found in the water column of this river–lake system (Ung et al. 2019). Meanwhile, the most abundant genus in the sediment in Aug-17 is the *Clostridium*, which appeared in the northeastern part of the lake and is close to the floating village of KL. Generally, *Clostridium* sp. is known as a facultative anaerobic bacterium that can survive not only in the surface water but also in the sediment as fermentative microbes.

27.3 Relationships between Dominant Genera and their Physicochemical Factors

Most of the dominant genera significantly correlated with the physicochemical factors of lake water, especially with DO and pH (Table 27.1). In addition to both variables, *Mycobacterium* (individually, still determined by ORP), *Methylosinus* (by ORP and EC), and *Methylocaldum* were determined by temperature, TDS, and turbidity; *Steroidobacter* was significantly correlated with water depth, temperature, EC, and TDS; and *Hydrogenophaga* with turbidity. It is possible that these microbes are adsorbed to the surface of minute solids such as inorganic and organic substances

Table 27.1 Pearson's r correlation coefficients between the relative abundance of the dominant genera and physicochemical factors

	Water depth	Temperature	EC	DO	pH	ORP	TDS	Turbidity
Mycobacterium		−0.34**		−0.60**	−0.32**	0.46**	−0.40**	−0.38**
		(107)		(107)	(107)	(107)	(50)	(50)
Fluviicola					−0.28**			
					(107)			
Dolichospermum				0.21*				
				(107)				
Microcystis		0.30**			0.34**			
		(107)			(107)			
Synechococcus		0.35**		0.43**	0.30**	−0.24*		
		(107)		(107)	(107)	(107)		
Methylosinus		−0.26**	−0.40**	−0.56**	−0.42**	0.33**	−0.41**	−0.41**
		(107)	(107)	(107)	(107)	(107)	(50)	(50)
Sphingomonas	−0.28**				0.23*			
	(114)				(107)			
Hydrogenophaga				−0.29**	−0.34**			−0.29*
				(107)	(107)			(50)
Polynucleobacter			0.20*	−0.36**	−0.36**			
			(107)	(107)	(107)			
Dechloromonas			0.22*	−0.21*	−0.26**	0.43**	−0.45**	
			(107)	(107)	(107)	(107)	(50)	
Methylocaldum		−0.34**		−0.74**	−0.50**		−0.45**	−0.40**
		(107)		(107)	(107)		(50)	(50)
Steroidobacter	0.27**	−0.48**	−0.45**	−0.26**	−0.32**		−0.38**	
	(114)	(107)	(107)	(107)	(107)		(50)	

The significant levels (two-tailed) of the correlations are 0.01 (**) and 0.05 (*). Sample sizes are in bracket. *EC* electrical conductivity, *DO* dissolved oxygen, *ORP* oxidation–reduction potential; and *TDS* total dissolved solids. Blank spaces are not statistically significant

present in lake water. Therefore, as the concentration of TDS and/or turbidity increases, the abundance of those genera in lake water decreases. Besides DO and pH, *Dechloromonas* was also significantly related to EC, ORP, and TDS. As the physiological function of *Dechloromonas* is thought to be a reductive dichlorination from chlorine-containing materials, the abundance of this genus was related to ORP. In our further study, the relationships between the abundance of *Dechloromonas* and the original source or the concentration of chlorinated compounds in lake water must be verified.

Dolichospermum showed a significant correlation with DO in the water of TSL. This genus was also observed, in Missisquoi Bay (Lake Champlain), following low chlorine and mid-$KMnO_4$ (287.7 mg·min/L) exposure (Moradinejad et al. 2020). *Microcystis* significantly correlated with temperature and pH, and in addition to these variables, *Synechococcus* significantly correlated with DO and ORP (Table 27.1). It means that their photosynthesis is significantly affected by these physicochemical factors. However, although pH showed a significant correlation with *Microcystis* and *Synechococcus*, it is difficult to directly relate them because of the complexity of pH. However, the consistency of trends remains seen; for example, in Western Lake Erie, the shifts of cyanobacterial community composition dominated by OTUs of *Microcystis* and *Synechococcus*, which dynamically fluctuated during the bloom, could be partitioned into components predicted by pH, temperature, chlorophyll a, and water mass movements (Berry et al. 2017).

Key Points

- *Synechococcus* was the most detected genus in both lake water and sediment, while *Microcystis* increased its dominance in lake water during the transition from dry to rainy season.
- Most of the genera in lake water were statistically related to physicochemical factors, especially DO and pH.
- The succession of dominant species and their abundances might be regulated by the hydrodynamics of this river–lake system.
- The microbial communities in lake water are sensitive to environmental fluctuations.

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