Bacterial Community Composition in Lake Tanganyika: Vertical and Horizontal Heterogeneity

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Vertical and latitudinal differences in bacterial community composition (BCC) in Lake Tanganyika were studied during the dry season of 2002 by means of denaturing gradient gel electrophoresis analysis of PCR-amplified 16S RNA fragments. Dominant bands were sequenced and identified as members of the Cyanobacteria, Actinobacteria, Nitrospirae, green nonsulfur bacteria, and Firmicutes divisions and the Gamma- and Deltaproteobacteria subdivisions. The BCC in the lake displayed both vertical and latitudinal variation. Vertical changes in BCC were related to the thermal water column stratification, which influences oxygen and nutrient concentrations. Latitudinal variation was related to upwelling of deep water and increased primary production in the south of the lake. The number of bands per sample increased with bacterial production in the epilimnion of the lake, suggesting a positive diversity-productivity relationship.

Since the first application of molecular tools to the study of the ecology of aquatic bacteria, bacterial community composition (BCC) has been studied in a wide variety of aquatic ecosystems, ranging from shallow to deep lakes to coastal seas and oceans. Molecular studies of BCC in lakes and rivers have revealed a consistent set of typical freshwater bacteria. Zwart et al. (51) discerned 34 putative phylogenetic clusters which contain the largest volume of anoxic freshwater in the world. This lake is anoxic below a depth of 100 to 200 m, and it contains the largest volume of anoxic freshwater in the world. The permanent temperature and oxygen gradients may affect nutrient concentrations in the epilimnion and result in differences in phytoplankton biomass between the north and south of the lake (4). So far, horizontal variation in BCC has been studied mainly in marine ecosystems rather than in lakes. Horizontal variation in BCC has been observed along transects crossing marine fronts (33) or in marine upwelling regions (18). The causes of horizontal differences in BCC were changes in nutrient concentrations and phytoplankton biomass or community composition.

For this study, samples from the entire water column were collected along a north-south transect in Lake Tanganyika during the dry season of 2002, and the BCC in these samples was analyzed using denaturing gradient gel electrophoresis (DGGE). The results of this study provide the first description of the bacterial community in Lake Tanganyika and are the first data on BCC in a tropical lake. Vertical and horizontal differences in the BCC were related to important environmental gradients in the lake.

MATERIALS AND METHODS

Study site. Lake Tanganyika is situated in East Africa and is bordered by Burundi, Tanzania, Zambia, and Congo. This lake is part of the East African rift valley. With a maximum depth of 1,470 m, it is the second deepest lake in the world. The lake measures 650 by 50 km (average width) and can be divided into three subsasins: the Kigoma basin in the north (1,310 m), the central Kalemie basin (800 m), and the East Marungu basin in the south (1,470 m) (4). The lake has an annually recurrent limnological cycle related to the monsoon season (35, 36). During the dry season (May or June to September or October), southeast monsoon winds tilt the thermocline toward the surface in the southern part of the lake. This causes an upwelling of deep water in the south of the lake and an...
accumulation of warm surface water in the north of the lake. When the monsoon winds subside during the rainy season, the thermocline exhibits dampened oscillations. These oscillations cause internal waves and alternated upwelling in the lake. When the monsoon ends in January to April, long-term monitoring suggests that the thermocline and upwelling of deep water are reduced north and south of the lake. The maximum stability of the lake is reached at the end of the rainy season in January to April. Long-term monitoring suggests that the thermocline and upwelling of deep water are reduced during El Niño years (34).

Field sampling. For this study, samples were collected on a 7-day cruise from the north to the south of the lake on 10 to 14 July, during the dry season of 2002. Water samples were collected at eight sites situated along a north-south transect in the lake (Fig. 1) using Hydrobios (5 liter) or Go-Flo (up to 12 liter) sampling bottles. At each site, samples were collected each 20 m down to 100 m. Below a depth of 100 m, samples were collected every 100 to 200 m down to 400 or 1,200 m, depending on the depth of the lake at the site. In some cases different hauls were required to collect large enough volumes for the different analyses. At each site, temperature, conductivity, dissolved oxygen, and pH depth profiles were recorded using a SeaBird 19 CTD (conductivity-temperature-depth) instrument. For determination of bacterial production, equal volumes of water samples from 0, 10, 20, and 30 m, representing the upper mixed layer of the water column, were pooled. Subsamples for nutrient analysis were stored refrigerated for analysis within 24 h on board the ship. For pigment analysis, equal volumes of water from depths of 0, 20, 40, and 60 m were pooled to obtain a composite epilimnetic sample. The pooled sample was filtered with a GF/F filter. Subsamples for enumeration of bacteria, phytoplankton (both <5 μm and ≥5 μm), heterotrophic nanoflagellates (HNF), and ciliates were fixed by the lugol-formalin-thio-
was carried out with ClustalX (45), and the aligned sequences were used with close relatives retrieved from GenBank. The alignment of the sequenced DGGE bands with representatives of related freshwater clusters as defined by Zwart et al. (51) and Warnecke et al. (49) and with close relatives retrieved from GenBank. The alignment was carried out with ClustalX (45), and the aligned sequences were used with PAUP* (44) to construct a 1,000× bootstrapped neighbor-joining tree rooted with the archaean Pyrodictium occultum.

Nucleotide sequence accession numbers. The sequences determined in this study have been deposited in the GenBank database under accession numbers AY845326 to AY845337.

RESULTS

Environmental variables. The surface water temperature declined from 26.5°C in the north to 25.2°C in the south of the lake. The thermocline depth simultaneously increased from 60 m in the north to about 120 m in the south of the lake (Fig. 2). At depths below 120 m, the temperature differences between the north and south of the lake were very small. As a result of the latitudinal variation in the thermocline depth, the PEA decreased from the north to the south of the lake (Fig. 3). The dissolved oxygen concentrations at the lake surface did not differ much between the north and the south of the lake. Anoxic conditions were reached at a depth of about 120 m in the north of the lake and at a depth of about 180 m in the south. The conductivity increased below the thermocline at all sites. The conductivity at the water surface was higher in the north than in the south of the lake (Fig. 2). The pH decreased below the thermocline at all sites and did not differ between the north and the south of the lake (Fig. 4). The SRP and TP concentrations (Fig. 4) increased below the thermocline throughout the lake. The epilimnetic concentrations of SRP were similar in the north and in the south of the lake, while the TP concentrations were slightly higher in the south. At depths below 700 m, the SRP and TP concentrations were slightly higher in the north than in the south of the lake. The concentrations of nitrate generally peaked between the thermocline and the oxycline. In the surface waters, the nitrate concentrations were higher in the south of the lake than in the north of the lake. Nitrate was absent at depths below 500 m due to conversion to ammonia in anoxic conditions.

Biological components. The total phytoplankton biovolume at a depth of 20 m was low at all sites (<50 mm$^3$ m$^{-3}$) and increased from the north to the south of the lake. The contribution of phytoplankton smaller than 5 µm in diameter to the total phytoplankton biomass increased toward the south of the lake (Fig. 3). The chlorophyll a concentrations measured in pooled samples obtained from depths of 0 to 60 m ranged from 0.3 to 1.0 µg liter$^{-1}$ and increased from the north to the south of the lake (Fig. 3). The concentrations in the euphotic zone were slightly higher (range, 0.5 to 1.3 µg liter$^{-1}$) (7). Using processing of pigment data with CHEMTAX, Cyanobacteria of the Synechococcus pigment type and Chlorophytes were identified as the main phytoplankton groups, contributing about 90% of the total chlorophyll a concentration. The biomass of heterotrophic nanoflagellates at a depth of 20 m ranged from 2.2 to 3.3 µg C liter$^{-1}$, and there was not a clear latitudinal trend. The mean size of the HNF was between 2 and 5 µm. The ciliate biomass at a depth of 20 m ranged from 0.1 to 8.8 µg C liter$^{-1}$ and was maximal at station TK1 and minimal at stations TK9 and TK11. The ciliate community was dominated by the peritrichous organisms Pseudohaplocaulus sp. and Vorticella aquadulcis.

The bacterial abundance ranged from $1 \times 10^6$ to $4 \times 10^6$ cells ml$^{-1}$ in surface waters and from $3 \times 10^6$ to $4 \times 10^6$ cells ml$^{-1}$ at depths below 200 m (Fig. 4). At depths below 200 m, colonies of filamentous bacteria were present in all samples. Due to the low numbers of filaments encountered during the counting, the total filament length varied greatly between samples ($1.6 \times 10^3$ to $8.8 \times 10^3$ µm ml$^{-1}$). The average total length of filaments for all hypolimnetic samples was $6 \times 10^5$ µm ml$^{-1}$.
bacterial abundance, the bacterial production in epilimnion samples also increased from the north to the south of the lake.

**DGGE analysis.** In the 56 samples that were analyzed by DGGE, 35 band classes were discerned. The number of bands encountered per sample varied between 4 and 19 and was on average 12. The number of bands generally increased from the lake surface to deep water. In the surface water the number of bands increased from the north to the south of the lake (Fig. 3).

**Band sequencing.** Eleven bands belonging to different band classes were sequenced. These sequenced bands accounted for on average 71% of the relative band intensity in the samples. Only five of the sequenced bands were closely related (≥98% similarity) to sequences deposited in the GenBank database (genotypes 1, 2, 3, and 6). The six remaining genotypes exhibited lower sequence similarity (92 to 97%; genotypes 5, 7, 8, 10, and 11). Phylogenetic relationships between our sequences and the database sequences are shown in Fig. 5. The distribution of the sequenced bands is shown in Fig. 6. Genotypes 1, 3, 4, 5, and 10 were almost exclusively found in the oxic epilimnion of the lake. These genotypes exhibited the highest similarity with *Gammaproteobacteria* (genotypes 1 and 5), *Actinobacteria* (genotype 3 and 10), and *Cyanobacteria* (genotype 4). Genotype 1 occurred mainly in the south of the lake, while genotypes 5 and 10 were more common in the north. The closest matches during a BLAST search for genotype 1 were a member of the *Gammaproteobacteria* isolated from ocean floor basalt (98% sequence similarity) (25) and an *Acinetobacter* sp. from effluent from a bioremediation site (99%). The closest relative of genotype 5 was a member of the *Gammaproteobacteria* belonging to the Legionellales isolated from a Swedish lake. Genotypes 3 and 10 exhibited high sequence similarity with *Actinobacteria* from Swedish lakes and belonged to the acl-B and acl-V-A clusters, respectively, as defined by Warnecke et al. (49). Genotype 4 was identified as *Synechococcus*. This genotype also occurred in some hypolimnetic samples. The short length of the sequence did not allow discrimination between freshwater (accession no. AY224198) and marine (accession no. AY135672) *Synechococcus* sequences.

Genotypes 2, 8, and 9 were found mainly in hypolimnetic waters and exhibited high similarity to the *Gammaproteobacteria* (genotypes 2 and 8) and *Deltaproteobacteria* (genotype 9). Genotype 2 exhibited high similarity (99%) to *Actinobacter calcoaceticus*. Genotype 8 exhibited the highest similarity (97%) to a member of the *Gammaproteobacteria* found on the roots of Proteaceae (accession no. AY827046) and the gammaproteobacterium *Stenotrophomonas* isolated from effluent from a water treatment plant (accession no. AY803991). Genotype 9 exhibited the highest similarity to an uncultured bacterium from deep groundwater (95%) and to a member of the *Deltaproteobacteria*.

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**Fig. 3.** Horizontal profiles (from south to north) of measured biotic parameters and the PEA. Each dot represents a sampling station, with TK11 on the left in the graph and TK1 on the right. (A) Horizontal changes in phytoplankton biomass at a depth of 20 m, obtained from inverted microscope (≥5 μm) and epifluorescence (<5 μm) counts. (B) Results of depth-integrated (0 to 60 m) chlorophyll a measurements and CHEMTAX analysis. Data for *Synechococcus*-like *Cyanobacteria*, *Chlorophytes*, and other phytoplankton groups are expressed as chlorophyll a equivalents determined by the CHEMTAX analysis. (C to H) HNF biomass (C), ciliate biomass (D), bacterial density (E), bacterial production (Bact. prod.) (F), number of DGGE bands (G), and PEA calculated for the upper 100 m (H).
Deltaproteobacteria isolated from uranium mining waste piles (94%).

Genotypes 6, 7, and 11 were abundant in the hypolimnion throughout the lake but were also detected in epilimnetic samples in the south of the lake. These genotypes were identified as Nitrospirae, green nonsulfur bacteria, and Firmicutes, respectively. Genotype 6 exhibited 99% sequence similarity to an unidentified member of the Nitrospirae detected in groundwater from a deep-well injection site. Genotype 7 exhibited the highest similarity (95%) to a green nonsulfur bacterium isolated from subsurface sediment from the Sea of Okhotsk (NT-B3 cluster) (16) and an uncultured genotype found in polluted groundwater. Genotype 11 exhibited 96% sequence similarity (74 of 93 bp) to an Alicyclobacillus sp. and an Alicyclobacillus vulcanalis sequence isolated from hot springs.

DISCUSSION

Lake Tanganyika is a meromictic lake characterized by permanent vertical temperature stratification. Many other environmental variables, like dissolved oxygen, pH, conductivity, and inorganic nutrient concentrations, were strongly linked to the vertical temperature gradient. Eight of the 11 sequenced band classes displayed a clear vertical zonation that was related to the water column stratification (Fig. 6). The number of bands in the DGGE analysis also differed for epilimnetic samples, with the hypolimnetic samples having a higher number of bands than the epilimnetic samples. Filamentous bacteria were observed in all samples from the anoxic hypolimnion but in no epilimnetic samples. As filamentous bacteria were excluded from the DGGE analyses due to prefiltration of the samples, differences in the BCC between the epilimnion and the hypolimnion were probably more pronounced than the DGGE data suggest.

As in most tropical temperature-stratified lakes, the vertical and horizontal temperature differences were relatively small in Lake Tanganyika (only 1.5 to 3°C). It is unlikely that such small temperature differences were responsible for the pronounced vertical and horizontal differences in the BCC. Therefore, the influence of vertical and latitudinal temperature differences in Lake Tanganyika on the BCC was probably indirect and due to regulation of the degree of mixing of deep and surface waters. Throughout the lake, the transition from epilimnion to hypolimnion was associated with a transition from oxic to anoxic conditions. As bacteria require different metabolic pathways to survive under oxic and anoxic conditions, differences in oxygen concentration may to a large extent explain differences in the BCC between the epilimnion and the hypolimnion. Genotype 9, which was closely related to a member of the Deltaproteobacteria, was found mainly in deep water samples. Deltaproteobacteria are known to occur mainly in benthic environments and are rarely found in oxygenated water columns (31). This suggests that differences in oxygen concentration indeed contributed to vertical differences in the BCC. Pronounced vertical differences in BCC have been observed previously in stratified lakes with anoxic deep waters. Konopka et al. (21) observed differences in BCC between oxic and anoxic water samples from 10 thermally stratified lakes in northeastern Indiana. Kizumi et al. (20) found important vertical changes in the BCC in the saline meromictic Lake Kaike. However, vertical differences in BCC were also observed in stratified lakes without an anoxic hypolimnion. Denisova et al. (6), for example, showed that there were significant differences in BCC with depth in Lake Baikal. Lindström et al. (23) observed greater dominance of Verrucomicrobia in the oxic hypolimnion of a Swedish lake.

Genotypes 6, 7, and 11 were found in anoxic deep waters throughout the lake but also occurred in the epilimnion in the south of the lake. This suggests that some genotypes are not restricted to either aerobic or anaerobic conditions. Instead of

![FIG. 4. Depth profiles over 1,200 m for conductivity, pH, SRP, TP, NO\textsubscript{3}, bacterial density, and the number of bands for the northern (open circles) and southern (solid circles) stations. The values are averages of the data for sites TK1, TK2, and TK3 for the northern sites and averages of the data for sites TK5, TK6, TK8, TK9, and TK11 for the southern sites.](http://aem.asm.org/v071/p5099/p5031-f004.jpg)
being linked to oxygen concentration, the distribution of these genotypes may be related to nutrient concentrations. Nutrient concentrations in Lake Tanganyika were high in the hypolimnion throughout the lake. Due to upwelling of deep nutrient-rich water, nutrient concentrations were also increased in the epilimnion in the south of the lake. This was particularly clear for nitrate. The occurrence of hypolimnetic bacteria in surface waters enriched with nutrients is in agreement with observa-
tions of Lindström et al. (23). These authors found that typical hypolimnetic bacteria appeared in epilimnetic samples to which nutrients were added. In a transplant experiment carried out in a eutrophic reservoir, a significant effect of nutrients on BCC has also been observed (13).

In addition to the pronounced vertical water column stratification of Lake Tanganyika we also observed a clear latitudinal environmental gradient in the epilimnion of this lake. From the north to the south of the lake, the thermo- and oxycline depth increased, the PEA decreased, and the nitrate concentration increased. This indicated that there was erosion of the thermocline and upwelling of deep water in the south of the lake. Upwelling of deep water in the south of Lake Tanganyika is an annually recurring phenomenon during the dry season that is related to a tilting of the thermocline by southeasterly monsoon winds (35). Upwelling of nutrient-rich water resulted in a higher phytoplankton biomass and, surprisingly, in increased importance of small phytoplankton (diameter, <5 μm) in the phytoplankton community. The upwelling event was also reflected in a latitudinal gradient in the BCC. Compared to the vertical gradient in the BCC, a smaller number of genotypes showed clear latitudinal variation (6 of the 11 band classes sequenced). The influence of spatial variations in water column stability or upwelling on BCC has to our knowledge not been studied previously in lakes. In marine ecosystems, however, local hydrodynamic phenomena like upwelling regions or fronts have also been found to influence BCC. Kerkhof et al. (18) observed changes in BCC during an upwelling event in the Mid-Atlantic Bight. Pinhassi et al. (33) observed strong changes in BCC along the Kattegat-Skagerak front in the North Sea. Schauer et al. (39a) related changes in BCC in a coastal embayment of the Mediterranean to upwelling of deep water from a submarine canyon. Upwelling of deep water in the south of Lake Tanganyika may influence the BCC directly by increasing nutrient concentrations in the epilimnion. However, the effect of nutrients on BCC in the upwelling region may also be indirect. Upwelling of deep, nutrient-rich water in the south of Lake Tanganyika was associated with an increase in the total phytoplankton biomass and a higher contribution of small (<5-μm) phytoplankton. Changes in the total biomass and community composition of phytoplankton may influence the quantity and quality of organic matter supplied to bacteria and in that way influence BCC (27). In a study of BCC in arctic lakes, the bacterial community was found to change with the dominant source of organic matter (5). In phytoplankton cultures, different bacterial communities are often associated with different phytoplankton species (48). In the epilimnion, the number of bands was higher in the south than in the north of

FIG. 6. Distribution of different genotypes throughout the lake. The panel numbers correspond to the band class numbers in Fig. 5. The sizes of the circles correspond to the relative band intensities of the genotypes on the DGGE gel.
the lake. The mean number of bands per sample in the epilimnion was positively correlated with bacterial production, suggesting that there is a positive diversity-productivity relationship. Yannarell and Triplett (50) also found a positive diversity-productivity relationship in different Wisconsin lakes. Horner-Devine et al. (15a), however, found that the responses of bacterial diversity to productivity in a mesocosm experiment were different for different major taxonomic groups.

In the hypolimnetic samples from Lake Tanganyika, the genotypes with the greatest relative band intensity were identified as members of the Deltaproteobacteria, Nitrospirae, green nonsulfur bacteria, and Firmicutes. The sequences exhibited similarity to genotypes isolated from other freshwater environments, albeit different from hypolimnetic lake water, ranging from deep groundwater to acidic hot springs. However, they were not included in the typical freshwater clusters defined by Zwart et al. (51). This is not surprising since anoxic environments were not included in the study of Zwart et al. (51). The genotypes with the highest relative band intensities in the epilimnion were identified as members of the Actinobacteria, Gammaproteobacteria, and Cyanobacteria. Actinobacteria are generally an important component of freshwater bacterial communities (31), and the Actinobacteria found in our study belong to the typical freshwater clusters defined by Zwart et al. (51). The representatives of the Gammaproteobacteria were not identified as members of the freshwater gamma I cluster (51), but they exhibited high levels of similarity to species observed in other freshwater systems, like Swedish lakes and effluent from a bioremediation site. The importance of Gammaproteobacteria in the epilimnion of Lake Tanganyika was rather unexpected, as these organisms are often of minor importance in freshwater ecosystems (31). Moreover, we did not detect Alpha- and Betaproteobacteria, which tend to be major components of bacterial communities in freshwater systems. The prevalence of Gammaproteobacteria and the lack of Alpha- and Betaproteobacteria in our samples, however, may be related to bias in the DGGE analysis. The relative band intensity of a genotype in a DGGE analysis does not necessarily reflect the relative abundance of the genotype in the prokaryotic community (22). For instance, Kirchman and Castle (19) detected Betaproteobacteria using fluorescent in situ hybridization but not using DGGE. The high relative band intensity for Synechococcus in our samples also illustrates this bias in the DGGE method. While Synechococcus often contributes more than 50% of the relative band intensity in DGGE profiles of the epilimnemic samples, epifluorescence counts indicated that the contribution of picocyanobacteria to the total prokaryotic cell numbers could not have been greater than 10%. Moreover, cell counts and pigment data indicate that there was an increase in picocyanobacteria, while the DGGE data revealed a decrease in the relative band intensity for Synechococcus.

Conclusions. This study demonstrated the presence of pronounced vertical and latitudinal gradients in the BCC in Lake Tanganyika during the dry season of 2002. Vertical gradients in the BCC could be related to vertical differences in oxygen and/or nutrient concentrations. As Lake Tanganyika is a permanently stratified lake, vertical gradients in the BCC are probably permanently present. Latitudinal gradients in the BCC were related to upwelling of deep water in the south of the lake. Upwelling may influence BCC by influencing nutrient concentrations and phytoplankton biomass and community composition. Latitudinal differences in BCC may be less pronounced at the end of the rainy season, when stratification is similar throughout the lake. Since 2002 was an El Niño year (although a weak event) and upwelling in Lake Tanganyika seems to be relatively weak during El Niño years (34), latitudinal differences in BCC may be more pronounced during the dry season of other years. Sequencing of the dominant bands in the DGGE gels revealed the presence of Actinobacteria and Gammaproteobacteria in the epilimnion, while Gammaproteobacteria, Nitrospirae, green nonsulfur bacteria, Actinobacteria, Deltaproteobacteria, and Firmicutes were observed in the hypolimnion. A thorough analysis of the BCC using clone libraries, fluorescent in situ hybridization, and/or reverse line blotting is required to obtain more detailed information on the occurrence of specific bacterial clusters in this lake.

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