PLANKTON OF INLAND WATERS

EDITOR

GENE E. LIKENS

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A DERIVATIVE OF ENCYCLOPEDIA OF INLAND WATERS

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EDITOR

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EDITOR

Professor Gene E. Likens is an ecologist best known for his discovery, with colleagues, of acid rain in North America, for co-founding the internationally renowned Hubbard Brook Ecosystem Study, and for founding the Institute of Ecosystem Studies, a leading international ecological research and education center. Professor Likens is an educator and advisor at state, national, and international levels. He has been an advisor to two governors in New York State and one in New Hampshire, as well as one U.S. President. He holds faculty positions at Yale, Cornell, Rutgers Universities, State University of New York at Albany, and the University of Connecticut, and has been awarded nine Honorary doctoral Degrees. In addition to being elected a member of the prestigious National Academy of Sciences and the American Philosophical Society, Dr. Likens has been elected to membership in the American Academy of Arts and Sciences, the Royal Swedish Academy of Sciences, Royal Danish Academy of Sciences and Letters, Austrian Academy of Sciences, and an Honorary Member of the British Ecological Society. In June 2002, Professor Likens was awarded the 2001 National Medal of Science, presented at The White House by President G. W. Bush; and in 2003 he was awarded the Blue Planet Prize (with F. H. Bormann) from the Asahi Glass Foundation. Among other awards, in 1993 Professor Likens, with F. H. Bormann, was awarded the Tyler Prize, The World Prize for Environmental Achievement, and in 1994, he was the sole recipient of the Australia Prize for Science and Technology. In 2004, Professor Likens was honored to be in Melbourne, Australia with a Miegunyah Fellowship. He was awarded the first G.E. Hutchinson Medal for excellence in research from The American Society of Limnology and Oceanography in 1982, and the Naumann-Thienemann Medal from the Societas Internationalis Limnologiae, and the Ecological Society of America's Eminent Ecologist Award in 1995. Professor Likens recently stepped down as President of the International Association of Theoretical and Applied Limnology, and is also a past president of the American Institute of Biological Sciences, the Ecological Society of America, and the American Society of Limnology and Oceanography. He is the author, co-author or editor of 20 books and more than 500 scientific papers.

Professor Likens is currently in Australia on a Commonwealth Environment Research Facilities (CERF) Fellowship at the Australian National University.

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CONTENTS

PROTISTS, BACTERIA AND FUNGI: PLANKTONIC AND ATTACHED

ALGAE (INCLUDING CYANOBACTERIA): PLANKTONIC AND ATTACHED

ZOOLPLANKTON

ECOSYSTEM INTERACTIONS

INTRODUCTION TO THE PLANKTON OF INLAND WATERS

The tiny floating, suspended, or weakly swimming biota of inland waters are collectively called plankton. The plankton of aquatic ecosystems are largely dependent on water movements for distribution and are highly diverse in form and function (Wetzel, 2001). The plankton of lakes, reservoirs, and rivers consist of protists, bacteria, fungi, cyanobacteria, algae, and tiny animals. The very small, often microscopic, photosynthetic, or chemosynthetic organisms of the plankton are at the base of aquatic foodwebs, and as such, are exceedingly important to the function of the aquatic ecosystems of inland waters. They are preyed upon by the animal component of the plankton, the zooplankton. Attached or sessile forms of these same groups are also considered in this volume.

Populations comprising the plankton of inland waters are highly diverse taxonomically. But, single-species blooms of cyanobacteria, such as *Microcystis* spp., can produce nuisance or toxic conditions in freshwater and coastal ecosystems in response to excessive enrichment of the key nutrients – nitrogen and phosphorus – (eutrophication) from waste-water runoff and/or atmospheric deposition (e.g., Conley et al., 2009; Allan and Castillo, 2007; Xu et al., 2010).

This volume contains five sections: first, a brief introduction to the plankton of inland waters; second, the protists, bacteria, and fungi, both planktonic and attached; third, the algae (including Cyanobacteria), both planktonic and attached; fourth, the so-called zooplankton, the animal component of the plankton; and fifth, the functional and system interactions of the planktonic and attached forms in aquatic ecosystems.

The articles in this volume are reproduced from the Encyclopedia of Inland Waters (Likens, 2009). I thank the authors of the articles in this volume for their excellent and up-to-date coverage of this important limnological topic.

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PROTISTS, BACTERIA AND FUNGI: PLANKTONIC AND ATTACHED

Contents

Archaea

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Introduction: Archaea the Unseen Third Domain of Life

Archaea are a relatively newly identified group of prokaryotic microorganisms that constitute the third phylogenetic domain of life together with the more well-known Bacteria and Eukarya. Only a few years ago, archaea were thought to be mostly restricted to extreme and anoxic environments but it has recently been established that archaeal biodiversity, abundance, and metabolic capabilities are substantially larger than the previously assumed. Thus, in a very short time two major changes in our perception of prokaryotic world have occurred. What was the basis for such marked changes now widely accepted? What makes archaea one of the most exciting current topics in microbial aquatic research?

First, over 30 years ago, Carl Woese and colleagues started the revolution by analyzing phylogenetic molecular markers (ribosomal RNA) instead of how organisms look or act. The comparison of 16S rRNA gene sequences showed that a group of prokaryotes had genetic differences as high as those observed between prokaryotes and eukaryotes. These results encouraged more detailed studies, including genome sequencing, leading to the conclusion that life is split in three big Domains instead of the previously recognized two of prokaryotes and eukaryotes.

A second contributor to the revolution in understanding was the recognition that laboratory cultures strongly biased views of the archaeal potentials. The phenotypic range of cultivated archaea indicated that these microorganisms were restricted to habitats with extreme values of temperature, pH, salinity, or anaerobic environments for methanogens. Thus, their metabolic diversity and ecological distribution seemed to be more limited than those of other prokaryotes. After considerable recent effort, a couple of new species of aerobic nonextremophilic archaea have been cultured in the laboratory, enabling detailed study of their metabolism and opening a race to bring into culture some of the most enigmatic microbes in freshwater environments.

Finally, widespread use of environmental ribosomal RNA sequencing has unveiled that unseen archaea were present in freshwater ecosystems and that the vast majority of them (excluding methanogens) were unrelated, or at best distantly related, to counterparts known from culture collections. Therefore, the known metabolic capabilities of the Domain Archaea have increased significantly. Unfortunately, the ecological significance, biochemistry, physiology, and impact on freshwater biogeochemical cycles of archaea still remain largely unknown.

To understand the ecology of archaea, a combination of new cultivation strategies, high-resolution molecular technologies, more detailed geochemical analytical techniques, traditional microbiological methods, and bioinformatics analyses on genomic data will be required. As soon as some of these organisms become cultivated and their metabolic and genetic potentials are studied in detail, a wide range of new physiological and ecological phenotypes will be discovered. In the meantime, scientists are profiting from new molecular genome-based technologies and from some special

features of archaea, e.g., the specific archaeal membrane lipids that have ether-linkages instead of ester-linkages typical of bacteria and eukaryotes. Some of these lipids can be used as biomarkers to trace the occurrence of different archaeal communities in ancient sediments or as paleotemperature proxies, useful to extrapolating water temperatures and climatic transitions. Altogether, the study of archaea is certainly a timely and exciting topic with strong evolutionary, ecological, and biogeochemical implications.

Archaeal Habitats in Inland Waters

The Domain Archaea comprises four main groups (Kingdoms): Crenarchaeota and Euryarchaeota are the two main Kingdoms; Korarchaeota (detected only by 16S ribosomal gene sequences obtained from a variety of marine and terrestrial hydrothermal environments, such as the hot spring Obsidian Pool in Yellowstone National Park) and Nanoarchaeota (represented by a nanosized hyperthermophilic symbiont originally found in a submarine hot vent as well as in the Obsidian Pool) are less widespread and diverse.

Cultivated species of crenarchaeota have thermo-acidophilic phenotypes and, in theory, occur in peculiar hot freshwater environments with an active sulfur cycle such as sulfureta and thermal springs. Uncultivated mesophilic crenarchaeota are in turn abundant in other natural environments and evidence exists that the largest proportion and greatest diversity of this group is present, surprisingly, in cold environments.

In contrast, euryarchaeota consists of cultured organisms that are more diverse in their physiology, metabolic capabilities, and habitat occurrence. This group includes well-known obligate anaerobic and widespread methanogens, the extreme halophiles from salt lakes, the hyperthermophiles, and the thermoacidophiles (i.e., the Thermoplasmata group lacking cell walls from hot springs and sulfuretic fields). Again, widespread noncultured mesophilic and cold-adapted phylotypes have been described for euryarchaeota in different freshwater ecosystems (**Table 1**).

Springs

Freshwater aerobic archaea have been traditionally associated with fresh waters influenced by hydrothermal activity (hot-water vents and fumaroles). Geothermally heated water percolates through volcanic material, which strongly influences the chemical composition. The emerging water is often enriched in reduced molecules such as sulfide, methane, and H_2, which yield energy for archaeal chemolithotrophic activity. These high-temperature ecosystems are interesting but unusual freshwater habitats. However, they may be useful model systems for understanding life under extreme environments on earth as well in relation to astrobiological studies. In addition, thermophilic archaea (both euryarchaeota and crenarchaeota) and bacteria (e.g., *Thermus aquaticus*) inhabiting these systems with optimum temperatures around $85\,°C$, are natural sources of biotechnological products, e.g., DNA polymerases.

Recently, sulfidic streamlets from emerging cold water (around $10\,°C$) in a nongeothermal environment have been reported to support the growth of a unique microbial community. A string-of-pearls-like, macroscopically visible structure, mainly composed of a non-methanogenic euryarchaeota, occurs in these streamlets and is viable at temperatures ranging from -2 to $20\,°C$ in close association with a sulfide-oxidizing bacteria. In this case, close links between archaea and the sulfur cycle arise in meso- to psychrophilic environments that compliment the better known associations of thermal environments.

Salt Lakes

Salt lakes, another extreme environment, are significant components of global inland waters. Salt lakes are complex and heterogeneous with distinct variation of salinity, alkalinity, and other physical/chemical as well as biological properties. Athalassohaline lakes are inland saline lakes with ionic proportions different from those lakes with salt composition similar to seawater. The conventional salinity value of $3\,g\,l^{-1}$ is taken as the dividing line between fresh and saline waters. The range of salinity encountered in inland waters can reach up to $350\,g\,l^{-1}$ and even beyond in certain lakes. The diversity of aquatic haline environments is enormous around the world, but the prokaryotes thriving in inland saline lakes are poorly known.

Considerable differences are apparent in the structure of archaeal communities along salinity gradients. At the lower end of the range ($\sim50–70\,g\,l^{-1}$), bacteria are the predominant components of the prokaryotic plankton, and mesohaline uncultured euryarchaeota distantly related to haloarchaea are found. This group is widespread in mesohaline freshwater environments surveyed so far but no representatives are available in culture to allow ecophysiological studies. At the highly saline end ($>200\,g\,l^{-1}$) the microbial community is dominated by extremely halophilic archaeal cells of square-shaped morphology that account for up to 75% of total prokaryotes beyond $350\,g\,l^{-1}$. These calcium and magnesium chloride saturated brines are one of the most extreme habitats

Table 1 Distribution of main groups of archaea in inland water ecosystems

Environment	Archaeal group	Comments
Lakes	Nonthermophilic Crenarchaeota (uncultured)	Distribution throughout the whole water column Biogeochemical role unknown
	Euryarchaeota (uncultured, non methanogens)	Distributed mainly in oxic and suboxic zones of the water column Biogeochemical role unknown
	Methanogens	Anoxic hypolimnia and sediments Methanogenesis
	ANME (uncultured anaerobic methane oxidizers)	Mainly in sediments but also in plankton Occurring either as syntrophic consortia with sulphate-reducing bacteria or as archaeal aggregates
Rivers	Eury- and Crenarchaeota	Most clones relate to soil archaea
Estuaries	Eury- and Crenarchaeota	Highly diverse communities due to inputs from different sources (e.g. rivers, coastal waters, marshes, soil).
Marshes	Methanogens Nonthermophilic Crenarchaeota	Mainly associated to rizosphere. Most clones related to soil archaea
Sediments	Methanogens	Highly diverse environments with different physicochemistry and nutrient loads
	ANME Nonthermophilic Crenarchaeota	High archaeal abundance and richness
Sulfureta and hot springs	Thermophilic chemolithotrophic Eury- and Crenarchaeota	Main source for Crenarchaeota cultured strains Extreme thermophiles and acidophiles Important players in the sulphur cycle
Salt and Soda Lakes, Solar Salterns	Halophilic and extreme Halophilic Euryarchaeota	Microbial communities dominated by archaeal representatives at the highest salinities. Important sources for novel genera and species of extreme haloarchaea
Acid Mine Drainage	Acidophilic chemolithotrophic Eury-(mainly Thermoplasmata) and Crenarchaeota	Extreme acidophiles Important players in biogeochemical cycling of sulphur and sulphide metals
Symbionts	Methanogens Crenarchaeota	Anaerobic freshwater protozoa (methanogens) Freshwater sponges?

ANME: Anaerobic methane oxidizers.

in the world, but cell concentrations at the higher salinities are towards the high end of the range found in any natural planktonic system, reaching up to 10^8 haloarchaeal cells ml^{-1} in some cases. High cell densities produce a visible pink-red color, due to their carotenoid pigments. In these environments, haloarchaea are very abundant but grow at very low specific growth rates, similar to a laboratory culture in stationary phase.

Haloarchaea are well known from a wide range of available pure cultures. They use two photosynthetic pigments to successfully develop in haline environments: bacteriorhodopsin (a light-driven proton pump that captures light energy and uses it to move protons across the membrane out of the cell creating a proton gradient that generates chemical energy) and halorhodopsin (which uses light energy to pump chloride through the membranes to maintain osmotic pressure). In addition, haloarchaea contain high concentration of salts internally and exhibit a variety of molecular characteristics, including proteins that resist the denaturing effects of salts, and DNA repair systems that minimize the deleterious effects of desiccation and intense solar radiation. Crenarchaeota lack most of this special enzymatic equipment and are not present in hypersaline environments.

Rivers and Estuaries

Rivers and estuaries transport materials and energy from both terrestrial and aquatic sources to the marine environment. Activity and diversity of microbial communities change strongly along this transit, especially in the mixing zone where fresh and saline waters meet. Rivers are characterized by spatial heterogeneity and variability imposed by differences in water flow and geomorphology. Accordingly, the structure of microbial communities greatly differs among the different river zones and it is also strongly influenced by water velocity. Although there is a

wealth of information on the structure of microbial communities in rivers, studies focusing on archaeal occurrence, diversity, and abundance are scarce. However, the small number of studies do provide a valuable comparison between the riverine communities and the associated estuarine/coastal waters (**Table 2**).

Benthic (sediments and biofilms) microbial riverine communities are complex and active, although archaea usually represent a minor fraction of the prokaryotic assemblages. However, archaeal phylotypes' richness is usually high, mainly in the particle-attached fraction, supporting the idea that rivers act as collectors of allochthonous archaea from catchments and neighboring ecosystems. Studies on archaeal diversity in rivers from diverse geographic locations with very different physichochemical conditions have revealed both euryarchaeota and

Table 2   Overall diversity and distribution of archaeal communities studied in different lotic habitats

Site	Main characteristics	Archaeal diversity[a]	Observations	Year	Source
Columbia (USA)	Temperate river It drains into a estuary	Marine and freshwater Crenarchaeota Euryarchaeota in the estuary	Mainly associated with particulate matter ('particle-attached archaea')	2000	1
Sinnamary (French Guiana)	Tropical river Interrupted by a dam (Petit Saut)	Euryarchaeota (Methanogens and Thermoplasmatales)	Detected in all sampling river stations downstream the dam	2001	2
Duoro (Portugal)	Temperate river Study carried out in estuary sediments	Archaeal community dominated by nonthermophilic Crenarchaeota (marine cluster)	Most of the sequences were obtained from surface sediment layers	2001	3
Rio Tinto (Spain)	Acidic (pH 2.2), high metal content	Euryarchaeota (Thermoplasma and Ferroplasma)	Extreme chemolithotrophic acidophilic archaea	2003	4
Aquifer (Idaho, USA)	Oxic, basalt aquifer	Euryarchaeotal clones related to methanogens and extremophiles. Crenarchaeota closer to freshwater clones	First report on Archaea inhabiting oxic temperate ground water	2003	5
Mackenzie (Canada)	Arctic river (mean temperature 3 °C), particle-rich waters	Mainly Euryarchaeota (methanogens and uncultured)	High diversity compared to other rivers	2006	6
		Marine Group I.1a Crenarchaeota	Clones related to archaea from soil and sediments Possible allochthonous origin		
Yangtze River estuarine region of East China Sea (China)	Temperate estuary	Sequences related to marine clones of both uncultured Euryarchaeota and Crenarchaeota (autotrophic ammonia-oxidizer *Nitrosopumilus maritimus*).	Remarkable spatial differences in archaeal composition	2007	7
	Planktonic samples analyzed		Low abundance but high diverse archaeal communities		

[a]Phylogenetic identity of the main clones of 16S rRNA genes recovered.

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crenarchaeota that are highly similar in their 16S rRNA gene sequence with uncultured archaea from soils, rice fields, marshes, and anoxic sediments from lakes (**Table 2**). These comparisons suggest an allochthonous origin for riverine archaea. Methanomicrobiales and uncultured methanogens from soils and anoxic sediments are predominant euryarchaeotal components among the archaea, and high nutrient loading combined with hypoxic conditions in river sediments may favor their growth and activity. In turn, most of the crenarchaeotal sequences obtained from rivers affiliate with either marine planktonic or soil crenarchaeota. Therefore, riverine archaea seems to be more related to both sediment decomposition and passive transport. Exceptions arise in rivers with extreme conditions, such as the Rio Tinto (Spain), an acid river (pH 2.2 along nearly 100 km) where the combination of an active sulfur–iron cycle with high amounts of dissolved metals (Fe, Cu, Zn) favor the presence of the iron oxidizing chemolithoautotroph *Ferroplasma* (Thermoplasmata). Again in this example as for the sulfidic streamlets discussed above, a linkage between archaea and the sulfur–iron metabolism arise in a mesophilic environment.

The structure and dynamics of the microbial communities thriving in estuarine waters are more complex than in rivers due, in part, to the mixing regime of these environments. Estuaries have strong spatial and temporal gradients imposed by the contact between fresh water and marine waters, the geomorphology of the area, the influence zone of the freshwater input, wind mixing, and tidal action. Moreover, the estuary usually receives high inputs of organic matter from the river and from the coastal marine environment. As a consequence, estuarine microorganisms are a mixture of riverine and marine components. Although archaeal phylotypes from plankton and sediments belong mostly to the nonthermophilic marine crenarchaeota, methanogens have also been detected in the sediment (**Table 2**). These results point to a main influence of marine waters on estuarine archaea although remarkable spatial differences are observed among and within systems.

Lakes

Stratified lakes   Stratified lakes with seasonal or permanent oxic–anoxic interfaces have been subject of intense research by microbial ecologists because of the environmental conditions imposed by the vertical physichochemical gradients and pronounced changes in oxygen concentration. Stratification results in well-defined water compartments with different conditions suitable for growth of distinct and highly diverse microbial assemblages that play different roles in biogeochemical cycles. Archaea have been found to change along the vertical profile: archaeal richness, identity, and abundance change between oxic, oxic–anoxic, and anoxic zones for most studied lakes. This is a first indication that uncultured phylotypes are autochthonous and metabolically active *in situ*. Another indication can be found in humic stratified boreal lakes. Humic lakes receive large inputs of allochthonous (terrestrially derived) organic material, and consequently foreign archaeal populations are entering in the lake. However, uncultured planktonic phylotypes are distantly related to their counterparts from boreal forest soils suggesting these populations are lacustrine.

In the upper and well-oxygenated water layers, nonthermophilic freshwater crenarchaeota and several phylotypes of the uncultured euryarchaeota (mainly related to uncultured freshwater and marine clones and also distantly related to the Thermoplasmata and relative groups) have been frequently detected (**Table 3**), although they usually constitute a minor fraction of the picoplankton. At the oxic–anoxic interface, complex microhabitats with sharp gradients that favor the activity of different microbial populations exist. Anoxic layers in the water column as well as anoxic sediments have a combination of anaerobiosis, low redox potentials, and an accumulation of dissolved sulfur- and nitrogen-reduced compounds, as well as methane. Different studies carried out in stratified lakes have shown that archaeal abundance increase with depth. Uncultured euryarchaeota are frequently found at the oxic/anoxic interfaces whereas methanogens and non-thermophilic crenarchaeota are found in the anoxic waters and sediments (**Table 3**).

Cultivation has remained elusive for these new archaeal groups and there is very little understanding of their metabolism and roles within the ecosystem. Concerning nonthermophilic freshwater crenarchaeota, recent findings indicate that although they have been generally found in plankton and sediments from very different lakes, they may be less abundant than their marine and soil counterparts. Also, the richness of nonthermophilic crenarchaeota in suboxic and anoxic water layers is low, yielding very few phylotypes distantly related to the ubiquitous crenarchaeota from marine water and sediments or soils. Phylotypes detected at and below the oxycline affiliate with marine benthic groups. This latter cluster has been properly named as Miscellaneous Crenarchaeota Group (MCG) since it includes a large diversity of sequences retrieved from different environments such as soils, terrestrial environments, deep-paleosoils and forest lakes.

Table 3 Overall diversity and distribution of archaeal communities studied in different lakes

Site	Main characteristics	Archaeal diversity	Observations	Year	Source
Alpine and polar lakes					
Gossenköllesee (Austria); Crater Lake (Oregon, USA); Pyrenean lakes (Spain)	High-altitude, ultraoligotrophic lakes	High archaeal richness among lakes	Archaeal abundance among lakes from 1% to 37% of total prokaryotic counts	1998, 2001, 2007	1, 3, 4, 5
	Completely oxygenated	Spatial segregation between crena- and euryarchaeota	Higher abundance of Archaea in autumn and after ice-cover formation (early winter) in alpine lakes		
	High UV-radiation	The most abundant Crenarchaeota are closely related to nonthermophilic marine planktonic groups	Crenarchaeota more abundant either at the air–water interface and in deep waters (300–500 m depth)		
Fryxell (Antarctica)	Permanently frozen	Mainly Euryarchaeota (methanogens and uncultured)	Coexistence of cold-adapted methanogenic and methanotrophic archaea in the anoxic bottom waters	2006	2
	Active methanogenesis and sulfate reduction in the sediment	Crenarchaeota related to uncultured marine benthic group			
Great and large lakes					
Michigan, Lawrence (WI, USA)	Oligo- to mesotrophic lakes	Euryarchaeota (methanogens)	Crenarchaeotal 16S rRNA up to 10% of total environmental RNA extracted	1997	6, 7
	Sediment samples analyzed	Crenarchaeota related to the marine group			
Laurentian Great Lakes (USA): Erie, Huron, Michigan, Ontario and Superior Onega; Ladoga (Russia); Victoria (Africa)	Temperate to cold waters	All sequences clustered with marine nonthermophilic planktonic Crenarchaeota	Archaeal rRNA accounted for 1 to 10% of total planktonic rRNA	2003	8
	Oligo- to mesotrophic lakes				
	Different climatic and geographic conditions covered		Presence of cosmopolitan crenarchaeotal phylotypes		
	Planktonic samples analyzed				

Stratified lakes					
Sælenvannet (Norway); Vilar (Spain); Pavin (France)	Meromictic sulfide-rich lakes	Euryarchaeota (methanogens, methanogens endosymbionts of anaerobic ciliates, and populations distantly related to Thermoplasmata)	Archaeal abundance increase with depth and maximal abundance below the chemocline	1997	9, 13, 16
	Moderate to cold temperatures	Crenarchaeota (nonthermophilic related to the marine and freshwater groups)	Seasonal dynamics, with higher relative abundance of Crenarchaeota in autumn and winter	2001 2007	
Charca Verde (France)	Freshwater pond	Methanogens, populations distantly related to Thermoplasmata and anaerobic methane-oxidizing archaea	Possible cooccurrence of methanogenic and methanotrophic (ANME-related) archaea in the anoxic water column	2007	18
	Sulfide-rich waters	No Crenarchaeota detected			
Valkea Kotinen (Finland)	Boreal forest lake	Methanogens and uncultured euryarchaeota distantly related to Thermoplasmata	Archaea up to 7% of total microscopic counts	2000	11
	Anoxic hypolimnion with methane	Crenarchaeota of the nonthermophilic freshwater group	No significant changes in abundance along season Freshwater crenarchaeota not related to soil crenarchaeota		
Stratified lakes					
Solar Lake (Sinai, Egypt)	Hypersaline lake	Methanogens and uncultured populations distantly related to Thermoplasmata	Archaeal community dominated by haloarchaea (salinities >10%)	2000	12
	Sulfide-rich hypolimnion Active methanogenesis at the bottom	No Crenarchaeota detected	Halophilic methanogens present		
Rotsee (Switzerland); Dagow (Germany); Biwa (Japan); Kinneret (Israel)	Samples from anoxic sediments	Methanogens, methanogenic endosymbionts of anaerobic ciliates and uncultured euryarchaeota distantly related to Thermoplasmata	Archaeal abundance (methanogens) accounted for 1 to 7% of total prokaryotes	1999; 2004; 2007	10, 14, 15, 17
	Mesoeutrophic lakes with anoxic hypolimnion	Crenarchaeota detected only in sulfurous sediments (freshwater nonthermophilic group)	Methanogenic endosymbionts up to 1%		

Sources

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