Same same but different: ecological niche partitioning of planktonic freshwater prokaryotes

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ABSTRACT

Lakes and ponds harbour a high number of diverse planktonic microorganisms that are centrally involved in biochemical cycles and aquatic food webs. Although the open water body (pelagial) seems to be a uniform and unstructured environment, ecological niche separation of coexisting microbial taxa might be triggered by limiting resources (bottom-up control) and mortality factors (top-down control), leading to distinct spatial and temporal distribution patterns of different microbes. This review gives an overview of the most abundant prokaryotic populations by grouping them in specific ecological guilds *based on their life strategies.* Defense specialists *such as very small* Actinobacteria *or big filamentous bacteria mostly occur at times of highest grazing pressure by heterotrophic nanoflagellates, the main consumers of bacteria.* Oligotrophic ultramicrobacteria*, on the other hand, seem to be mostly adapted to nutrient depleted water layers during summer stratification, while* opportunistic bacteria *profit from material released during short-living algal blooms. Seasonal changes in abiotic and biotic factors may be the main causes for periodic reoccurring density maxima of different prokaryotes populations in the pelagial of temperate lakes, reflected in a distinct seasonality of the freshwater bacterioplankton.*

Key words: ecological niche, freshwater bacterioplankton, seasonality, spatial patchiness, bottom-up control, top-down control.

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PELAGIAL OF LAKES AND PONDS AS HABITAT FOR MICROBES

Freshwater microorganisms occur in high numbers and comprise an enormous genetic diversity: one mL of lake water contains approximately 10^6 prokaryotic cells (range: 10^5-10^7 mL^{-1}) and several thousand microbial genotypes (Newton *et al.,* 2011). While *Eukarya* (including animals and plants) represent only a small branch in the tree of life (Fig. 1) and are limited to a handful of nutritional modes, *Bacteria* and *Archaea* encompass virtually all genetic diversity and lifestyles. Moreover, lacustrine microorganisms possess key functions in all biochemical cycles and are therefore crucial for the functioning of lakes. The recycling of dissolved organic matter by microbes via the classical microbial loop and the channelling of carbon to higher trophic levels is the necessary basis of every aquatic food web (Azam *et al.*, 1983; Pomeroy, 1974; Sherr and Sherr, 1988).

Prokaryotes inhabit virtually every zone in lakes in the benthal (litoral and profundal) and pelagial, and special microbial habitats can be found at the boundary regions to air (neuston) and sediment, and at the surfaces or inside eukaryotes (animals, plants, and protists). Microorganisms in the pelagic realm of lakes and ponds can either live planktonic or attached to particles (lake snow) and many microbes can even switch from one lifestyle to the other (Grossart, 2010). This review focuses on the permanently free-living fraction of freshwater bacterioplankton in the oxygenated water body of temperate lakes and the differential microbial life strategies that can be found in such a seemingly unstructured and uniform environment. Niche separation of coexisting microbial populations triggered by growth and mortality factors may result in distinct *ecological guilds* of prokaryotes. Members of such guilds are frequently unevenly distributed in the pelagial, both on spatial (longitudinal as well as vertical) and temporal scales (*i.e.*, seasonality). Together with additional metabolic diversification of sympatric microbial populations (*i.e.*, resource partitioning and cross-feeding), this niche separation might be an explanation for the high diversity of pelagic microbes, analogous to Hutchinson's *paradox of the plankton* for phytoplankton (Hutchinson, 1961).

Niche partitioning of micro- and macroorganisms has already been intensely investigated in experiments focusing on the emergence and maintenance of species diversity (Gómez and Buckling, 2013; Lawrence *et al.*, 2012; Rainey *et al.*, 2000; Rainey and Travisano, 1998). Spatially structured environments were identified as important drivers for genetic diversification of microbes (Rainey and Travisano, 1998), as well as resource partitioning and cross-feeding on waste products of co-occurring species (Lawrence *et al.*, 2012). Moreover, spatio-temporal niches in experimental river biofilms have not only led to higher algal diversity but also to increased nutrient elimination and thus, improved water quality (Cardinale, 2011). Such examples of spatially,

seasonally, and physiologically driven niche separation in experimental systems might point at selective processes that led to the high diversity observed today. However, as many experimental studies focused on a few well-known model organisms (Rainey and Travisano, 1998; Turner *et al.*, 1996), a propagation of results to the pelagial of freshwater lakes is challenging. Here, numerous microbial taxa with largely unknown physiological capacities co-occur and we just started to get a glimpse of the overall biodiversity and the multitude of interplaying factors shaping freshwater microbes.

FACTORS SHAPING MICROBIAL GROWTH AND SURVIVAL IN THE PELAGIAL

Two key factors control microbial abundances in aquatic habitats: firstly, bacterial growth is limited by competition for available resources (bottom-up control) as well as by physical factors like temperature, pH, oxy-

gen, and light. Secondly, mortality is caused by grazing and viral lysis (top-down control). In lakes, top-down and bottom-up control have numerous complex interactions *in situ* and tend to co-occur (Grossart *et al.*, 2008; Salcher *et al.*, 2007; Šimek *et al.*, 2008).

All microbes are dependent on limiting resource of the dissolved organic matter (DOM) pool that consists of various different substances. The main components supporting microbial growth are simple mono- and oligomers like amino acids, carbohydrates, and carboxylic acids that are only present in nM concentrations in natural lake water (Meon and Jüttner, 1999; Zotina *et al.*, 2003) with fast turnover rates (Rosenstock and Simon, 1993; Sundh, 1992). Phytoplankton and cyanobacterial blooms are main sources of labile DOM as algae release a substantial fraction of exudates (Callieri *et al.*, 2007; Hama and Handa, 1987). Although the majority of exudates are polymers (Giroldo and Vieira, 2005), microbes utilize algal low molecular weight
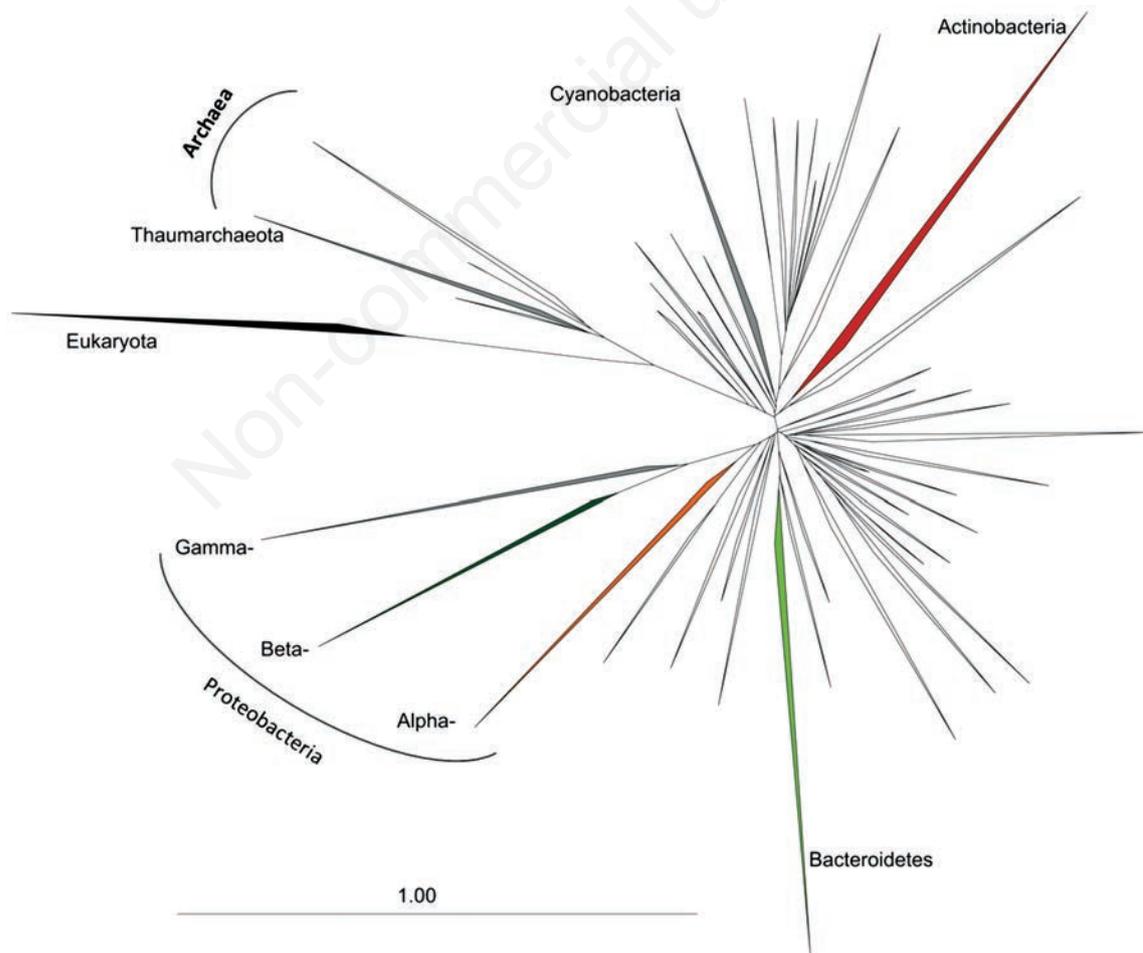
Fig. 1. Phylogenetic tree of the 16S rDNA of typical freshwater prokaryotes (including a branch of Eukaryota based on 18S rDNA). Phyla with populations further described in the text are highlighted.

(LMW) exudates more rapidly and to a much higher extent (Giroldo *et al.*, 2007). Moreover, some bacteria are specialized in the breakdown of algal polymers to small monomers that can be subsequently utilized by other microbes (Williams *et al.*, 2013). Allochthonous DOM input from terrestrial sources can be also an important carbon source for freshwater microbes, especially in small humic lakes with large catchment areas or short water retention times (Berggren *et al.*, 2010; Kritzberg *et al.*, 2004). Although this DOM type is considered to be a poor substrate for bacteria because of chemical recalcitrance, the higher amounts of DOM present in humic lakes might compensate for low degradation rates (Wetzel, 2001). Moreover, humic substances can be photochemically degraded to more bioavailable substrates such as carboxylic acids (Berggren *et al.*, 2010; Bertilsson and Tranvik, 1998).

Several excellent reviews deal with top-down control of the bacterioplankton by protistan grazing (Hahn and Höfle, 2001; Jürgens and Matz, 2002; Pernthaler, 2005; Pernthaler and Posch, 2009), and viral lysis (Weinbauer, 2004; Winter *et al.*, 2010). The main consumers of freshwater microbes are small protists such as flagellates and ciliates, however, also cladocerans and rotifers may occasionally graze on larger morphotypes such as filamentous bacteria (Lampert, 2006; Langenheder and Jürgens, 2001; Pernthaler *et al.*, 2004; Sanders *et al.*, 1989). Heterotrophic nanoflagellates (HNF) typically dominate grazing with ingestion rates of up to 77% of the daily bacterial production (Sanders *et al.*, 1989). Grazing by protists is predominately affecting medium-sized bacteria, as most flagellates and small ciliates are size selective (Andersson *et al.*, 1986; Chrzanowski and Šimek, 1990; Jürgens and Matz, 2002; Posch *et al.*, 2001), while very small cells and filamentous bacteria seem to be protected from ingestion (Pernthaler, 2005; Posch *et al.*, 1999). Viral-induced mortality also accounts for a significant, however, highly variable fraction of bacterial production in freshwaters (Weinbauer, 2004). Viral abundances are usually at least one order of magnitude higher than bacterial numbers and seasonally tightly coupled (Personnic *et al.*, 2009; Pradeep Ram *et al.*, 2010; Thomas *et al.*, 2011). As phage infection is host density dependent, viruses mostly affect competitive and highly abundant microbes, and thus, may even sustain species diversity by *killing the winner* (Thingstad and Lignell, 1997; Winter *et al.*, 2010). Moreover, viral lysis leads to a significant release of DOM, in turn stimulating microbial growth (Weinbauer, 2004).

COMMON BACTERIOPLANKTON TRIBES IN FRESHWATERS

Lakes and ponds harbour a high diversity of microbial species, however, most of them still lack cultured representatives (Hahn, 2006; Newton *et al.*, 2011). Cultivation-independent *in situ* analyses based on the 16S rRNA gene as phylogenetic marker are therefore useful tools to assess gross microbial diversity (fingerprinting methods) and identity (phylogenetic analyses), and to quantify distinct populations (fluorescence *in situ* hybridization (FISH) techniques, qPCR). High-resolution next-generation sequencing (454 pyrosequencing of short fragments of the 16S rDNA) commonly resulted in >1500 OTUs (operational taxonomic units at a cut-off of 97% sequence similarity, *i.e.*, different *species*) in the epilimnion of freshwater lakes (Eiler *et al.*, 2012; Peura *et al.*, 2012b) and even >3500 OTUs if hypoxic hypolimnia were included (Peura *et al.*, 2012a). However, as aquatic microbial communities are dominated by a few very abundant lineages and a high number of rare taxa, the *real* microbial diversity might be substantially higher (Pedrós-Alió, 2012). Moreover, all PCR based approaches for estimating microbial diversity are vulnerable to possible biases introduced during DNA isolation (Frostegard *et al.*, 1999), PCR amplification (Wintzingerode *et al.*, 1997), and an irregular number of 16S rRNA genes per cell (Farrelly *et al.,* 1995). In an excellent review by Newton *et al.,* (2011), >100 ubiquitous freshwater bacterial *tribes* (*i.e.*, monophyletic OTUs gained from at least 2 lakes) were identified. Such tribes, however, might include different subspecies or ecotypes, *e.g.*, the prominent *Betaproteobacteria Polynucleobacter* and *Limnohabitans* harbour ecotypes beneath the species level that differed in habitat preference, pointing to pronounced ecological micro-diversification (Jezbera *et al*., 2011, 2013). Moreover, further sequencing and subsequent quantitative analyses by *e.g.*, FISH might still lead to the detection of novel ubiquitous freshwater tribes and might help to unravel ecological properties of so far poorly studied populations, as was recently demonstrated for *e.g.*, *Chloroflexi* (Okazaki *et al.*, 2013) or the LD12 tribe of *Alphaproteobacteria* (Fig. 2; Salcher *et al.*, 2011b). Most studies have focussed on the identification, quantification, and the assignment of a potential ecological role of the most abundant microbial taxa in freshwaters, while rare species remain still widely unexplored (Pedrós-Alió, 2012). Members of the rare biosphere might be dormant most of the time acting as seed banks (Lennon and Jones, 2011; Williams *et al.*, 2013), to enable a rapid recruitment of species in response to environmental changes (*e.g.,* as degraders of specific short-living organic matter compounds). Such a contribution to compensatory dynamics of different species might be crucial for the overall stability of microbial communities (Fig. 3). Some studies suggest that rare species are disproportionally active and get selectively ingested by grazers, and thus, might act as an important link of carbon flow to higher trophic levels (Jones and Lennon, 2010; Zeder *et al.*, 2009) .

Typically, the most abundant planktonic freshwater prokaryotes (Fig. 1) are affiliated with the phyla *Actinobacteria*, *Proteobacteria* (mainly of the alpha- and

beta-subdivision), *Bacteroidetes* (*Flavobacteriales* and *Sphingobacteriales*), *Cyanobacteria*, *Verrucomicrobia*, *Thaumarchaeota*, and a handful of others are present in low or transient abundances (*i.e.*, *Acidobacteria, Chlorobi, Chloroflexi, Fibrobacteres, Firmicutes, Fusobacteria, Gemmatimonadetes, Lentisphaerae, Nitrospira, Planctomycetes, Spirochaetes*, and members of the uncultured phyla BRC1, OD1, OP10, SR1, and TM7).

DIFFERENT LIFE STRATEGIES OF LACUSTRINE BACTERIOPLANKTON POPULATIONS

Because of the enormous diversity of pelagic microbes, I will focus on some of the most abundant and well-studied populations and try to identify reasons for their success (*i.e.*, their specific niches) in freshwaters. A comprehensive de-
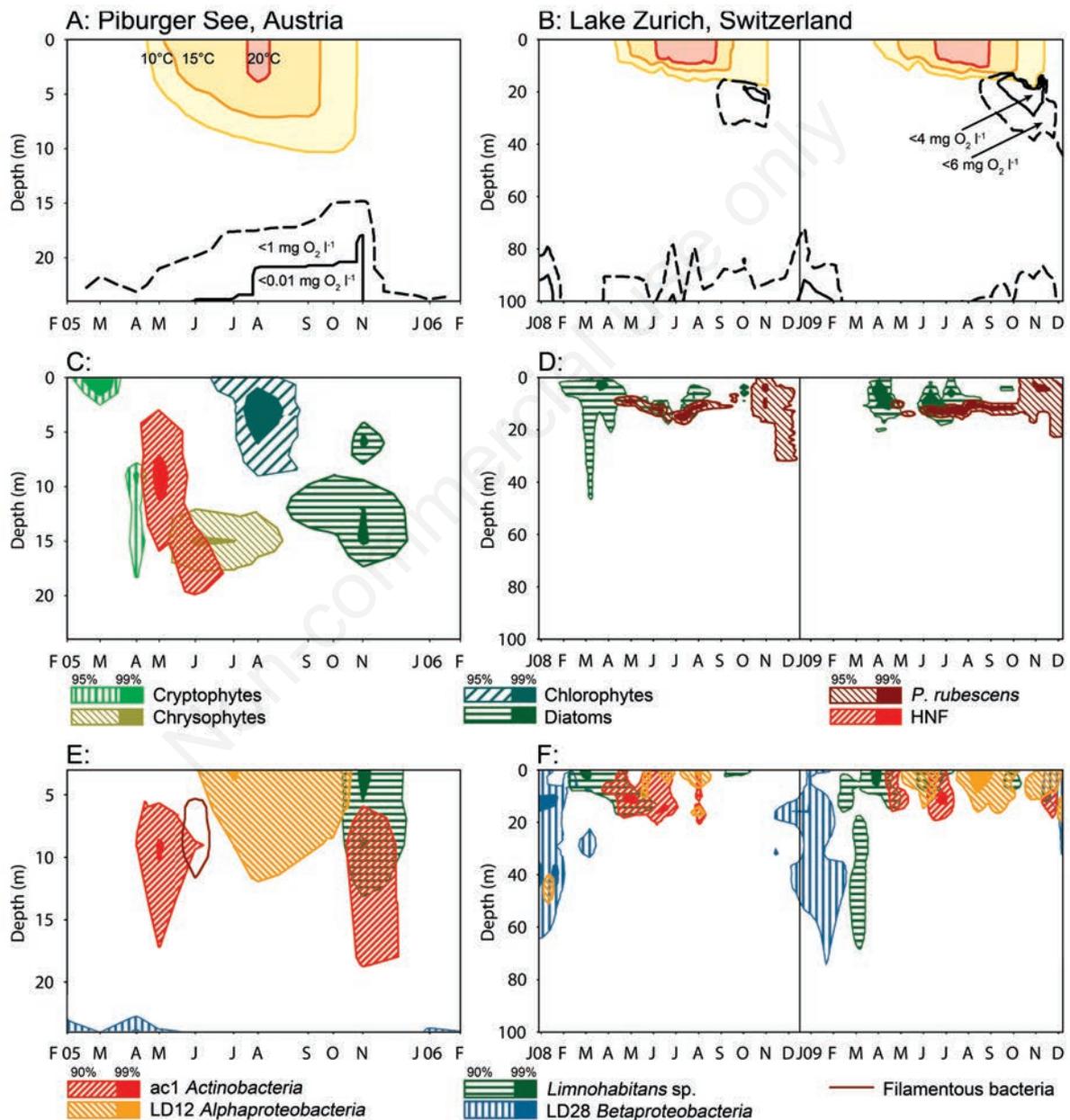
Fig. 2. Seasonal patterns of temperature, oxygen content (A,B), abundances of different algal groups, the cyanobacterium *Planktothrix rubescens*, heterotrophic nanoflagellates (C,D), and selected microbial populations (E,F) in Piburger See, Austria (A,C,E) and Lake Zurich, Switzerland (B,D,F). All biological data are presented as population maxima (percentiles are given in legend). Raw data were taken from Salcher *et al.* (2008, 2010, 2011), and *unpublished data*.

scription of the life strategies of these populations, however, is still challenging. Thus, they are grouped in distinct *ecological guilds* based on growth patterns, survival strategies, or specific physiological adaptations.

Defense specialists

The numerically dominant microbes in freshwaters are affiliated with *Actinobacteria* (Glöckner *et al.*, 2000; Zwart *et al.*, 2002), a phylogenetically diverse phylum with 9 ubiquitous freshwater lineages and >40 tribes (Newton *et al.*, 2011). The most abundant family-like lineage (ac1) can account for >50% of microbes in the pelagial of lakes (Warnecke *et al.*, 2005) and shows recurrent seasonal patterns with population maxima in spring and/or autumn (Fig. 2; Allgaier and Grossart, 2006; Salcher *et al.*, 2010). The spring maxima typically occur shortly after phytoplankton blooms contemporaneous with high numbers of HNF (Eckert *et al.*, 2012; Salcher *et al.*, 2010; Zeder *et al.,* 2009), pointing to specific adaptations to high grazing pressure. Freshwater *Actinobacteria* are of con-

spicuous small cell size [<0.1 μm³, *i.e.*, *ultramicrobacteria* (Posch *et al.*, 2009)], which *per se* might protect them from ingestion by size selective flagellates (Jezbera *et al.*, 2006; Pernthaler *et al.*, 2001). Even if ingested by HNF, these bacteria might not be digested, as they do not promote growth of flagellates (Šimek *et al.*, 2013), which is related to their specific gram+ cell wall properties (Tarao *et al.*, 2009). Moreover, ac1 *Actinobacteria* seem to profit from polymeric organic carbon sources released by the consumption of their grazing-vulnerable competitors (Beier and Bertilsson, 2011; Eckert *et al.*, 2013) and are involved in carbohydrate turnover (Buck *et al.*, 2009; Garcia *et al.*, 2013; Salcher *et al.*, 2013). Generally, freshwater *Actinobacteria* seem to have competitive disadvantages to opportunistic, fast-growing bacteria in nutrient and/or substrate enrichments; however, they can form highly persistent population numbers because of their grazing resistance (Šimek *et al.*, 2006). Within the ac1 lineage, some taxa are better adapted to alkaline lakes, while others prefer acidic conditions (Newton *et al.*, 2007) and even within the same lake, different tribes can occupy distinct niches
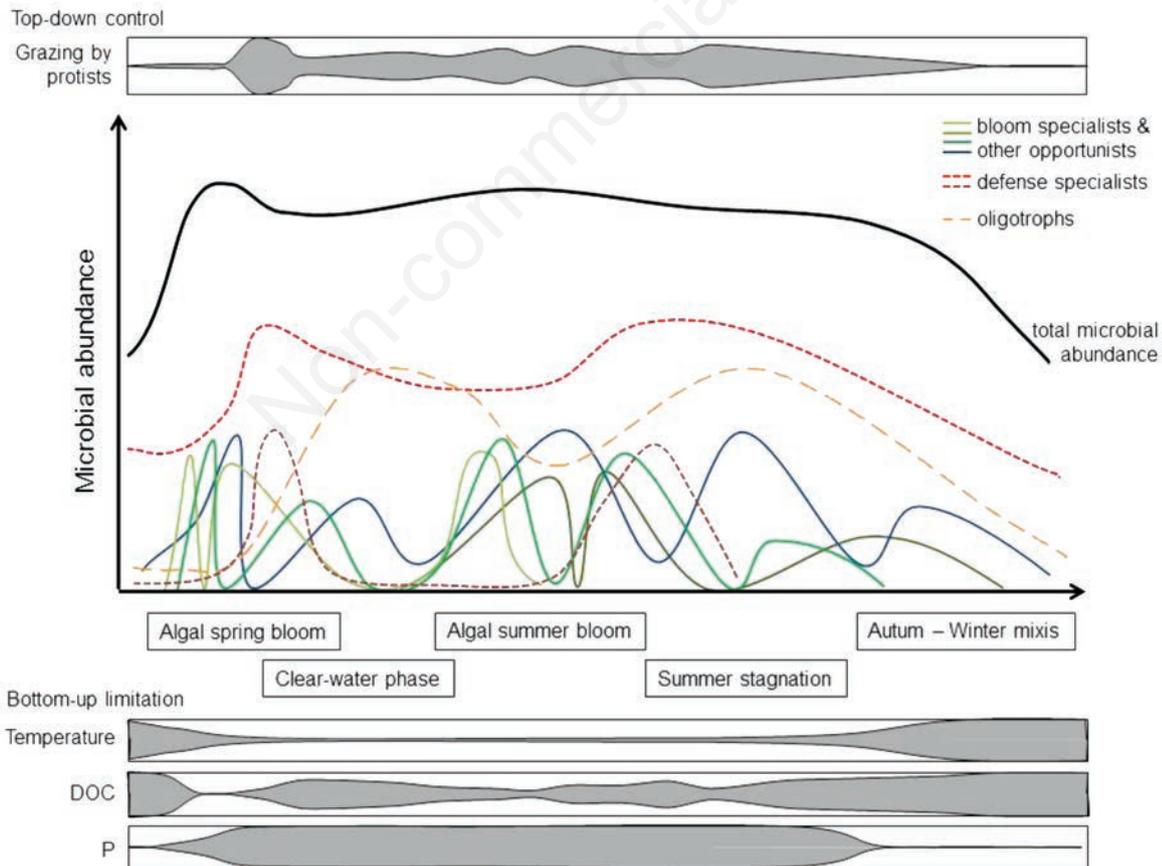
Fig. 3. Schematic view of seasonal successions of different microbial *guilds* in the epilimnion of lakes resulting in relatively stable total prokaryotic numbers. The main top-down and bottom-up limitations for microbes and typical seasonal phases in freshwaters are given for reference.

according to oxygen content and substrate preferences (Allgaier and Grossart, 2006; Buck *et al.*, 2009). So far, no pure cultures of ac1 *Actinobacteria* have been established; however, one representative was described as *Candidatus* Planktophila limnetica based on low but stable densities in co-cultures (Jezbera *et al.*, 2009). Some members of ac1 *Actinobacteria* have light driven proton pumps (rhodopsins) that might be important in energy generation to fuel, *e.g.*, membrane transporters (Garcia *et al.*, 2013; Sharma *et al.*, 2009; Wurzbacher *et al.*, 2012).

A special form of defense strategy against flagellate grazing can be attributed to filamentous bacteria: threadlike cells are beyond the handling and ingestion size limit of HNF (Hahn *et al.*, 1999; Jürgens and Stolpe, 1995; Šimek *et al.*, 2001). Filamentous bacteria are no coherent taxonomic unit, as members of different phyla (*e.g.*, *Proteobacteria*, *Bacteroidetes*) share this morphology (Hahn *et al.*, 1999; Salcher *et al.*, 2007; Schauer and Hahn, 2005). Although filaments appear to be numerically not very important, their contribution to overall microbial biomass is substantial due to their large biovolume (Corno *et al.*, 2008; Pernthaler *et al.*, 1998; Posch *et al.*, 2009; Schauer *et al.*, 2006). Some taxa are of obligate filamentous morphology [*e.g.*, *Candidatus* Aquirestis calciphila (Hahn and Schauer, 2007)], while others are morphologically variable [facultative filamentous bacteria, *e.g.*, *Flectobacillus* sp. (Hahn *et al.*, 1999; Šimek *et al.*, 2007) or *Comamonas acidovorans* (Hahn and Höfle, 1998)]. Such a morphological plasticity was hypothesized to be triggered by chemical cues released by predators (Corno and Jürgens, 2006). Typically, filamentous bacteria have recurrent seasonal population maxima at the decline of spring phytoplankton blooms (Fig. 2), during highest grazing pressure by HNF (Eckert *et al.*, 2012; Jürgens and Stolpe, 1995; Pernthaler *et al.*, 2004; Schauer *et al.*, 2006). This timing might be related to the grazing resistance of filaments and their subsequent enrichment in the community or even to a reduced risk of viral attacks (Šimek *et al.*, 2007). However, filamentous bacteria might also directly profit from algal exudates such as carbohydrates (Salcher *et al.*, 2013; Schauer *et al.*, 2006) or from recycled material released during predation on other microbes (Eckert *et al.*, 2013). Although they seem to occupy the same niche as ac1 *Actinobacteria,* filamentous bacteria differ substantially in their role in the carbon flow: spring maxima of filaments are typically rapidly terminated by filter-feeding crustaceans (esp. *Daphnia* sp.) during the clearwater phase, as filaments are within the size range of the filter apparatus of daphnids (Langenheder and Jürgens, 2001; Pernthaler *et al.*, 2004; Schauer *et al.*, 2006). Hence, these bacteria represent a substantial fraction of microbial biomass that is directly transferred to higher trophic levels in bypassing the microbial loop and might therefore be an important *link* in the carbon flow, while *Actinobacteria* might be more regarded as a *sink* for organic carbon.

Oligotrophic ultramicrobacteria

Besides *Actinobacteria*, also microbes of the LD12 tribe of *Alphaproteobacteria* are of conspicuous small cell size and occur in high numbers in freshwater lakes (Heinrich *et al.*, 2013; Salcher *et al.*, 2011b). So far, there is no evidence that these ultramicrobacteria are protected from grazing by flagellates in the same way as *Actinobacteria*. However, their annual population maxima were in parallel with neither HNF nor *Actinobacteria,* pointing to a different life strategy (Fig. 2). In fact, niche separation between LD12 *Alphaproteobacteria* and ac1 *Actinobacteria* has been proposed based on spatial (Salcher *et al.*, 2011a), temporal (Fig. 2; Eiler *et al.*, 2012), as well as ecophysiological properties (Salcher *et al.*, 2013). LD12 *Alphaproteobacteria* are the freshwater sister group of the dominant marine microbes, called SAR11 (Bahr *et al.*, 1996; Salcher *et al.*, 2011b; Zwart *et al.*, 2002). The family-like SAR11 clade includes several highly diversified marine, brackish, and freshwater tribes, whereof the marine representatives have attracted most attention (Giovannoni *et al.*, 2005a, 2005b; Morris *et al.*, 2002). Although transitions between marine, brackish and freshwaters have been rare during the evolution of this family (Logares *et al.*, 2010), all 3 phylotypes can co-occur in the same habitat [*i.e.*, the coastal Baltic Sea (Herlemann *et al.*, 2011; Piwosz *et al.*, 2013)] and share several ecological features (Salcher *et al.*, 2011b). Typically, LD12 *Alphaproteobacteria* have recurrent population maxima in the epilimnion in summer, at times of low phytoplankton biomass and nutrient availability (Heinrich *et al.*, 2013; Salcher *et al.*, 2011b). They follow an oligotrophic lifestyle with slow but efficient uptake of amino acids already at low substrate concentrations and are centrally involved in LMW substrate turnover (Salcher *et al.*, 2011b). Microbes of the marine SAR11 clade are characterized by streamlined genomes that encode a high number of membrane transporters and light driven proton pumps (rhodopsins; Giovannoni *et al.*, 2005a, 2005b). Similarly, LD12 *Alphaproteobacteria* seem to have reduced genomes and rhodopsins for photoheterotrophic energy acquisition (Atamna-Ismaeel *et al.*, 2008; Bertilsson, *unpublished data*).

Other ubiquitous ultramicrobacteria thriving in epilimnia of lakes are affiliated with *Polynucleobacter* sp. (*Betaproteobacteria*). These bacteria (esp. *P. necessarius* ssp. *asymbioticus)* can be readily enriched (Burkert *et al.*, 2003; Grossart *et al.*, 2008; Hutalle-Schmelzer *et al.*, 2010) and cultured (Hahn, 2003; Hahn *et al.*, 2009), they have short doubling times and are actively ingested by flagellates (Hahn *et al.*, 2012), pointing to an opportunistic life strategy. However, these microbes have a more passive lifestyle, as they do not incorporate algal exudates such as carbohydrates and are not associated with short-living algal blooms, but on the other hand specialized in the utilization of photooxidation products of humic substances, *e.g.*, carboxylic acids (Buck *et al.*, 2009; Hahn *et al.*, 2012). Therefore, *P.n.* ssp. *asymbioti-*

cus might be rather placed in the guild of oligotrophic ultramicrobacteria, as they have also very small cell sizes and streamlined genomes (Hahn, 2003; Hahn *et al.*, 2012). Moreover, some photoheterotrophic *Polynucleobacter* sp. use light as energy source (Martinez-Garcia *et al.*, 2012).

Opportunistic bacteria

Contrary to oligotrophic bacteria, some freshwater taxa can be characterized by their fast generation times and short-lived population maxima. These so called *opportunistic bacteria* (also known as *competition specialists*, *uptake specialists*, *growth specialists*, *copiotrophic bacteria*, or *feast and famine* bacteria) are typically specialized on short-living DOM sources (Šimek *et al.*, 2005; Thingstad *et al.*, 2005) and might also be found attached to particles (Grossart, 2010). Opportunistic bacteria may be rare in the pelagic zone (Šimek *et al.*, 2006), however, they act as an important link in the carbon flow to higher trophic levels because of their disproportional contribution to bacterial biomass production and their tight control by bacterivorous grazers (Kasalický *et al.*, 2013; Sherr and Sherr, 1988). Members of this bacterial guild are typically larger than ultramicrobacteria and therefore highly vulnerable to size selective grazing (Posch *et al.*, 2009; Šimek *et al.*, 2005; Zeder *et al.*, 2009). This selective mortality together with a fast depletion of transient carbon and nutrient sources may limit the dominance of opportunistic bacteria resulting in short-term *blooms* of these taxa (Fig. 3).

Probably the best studied opportunistic taxa are affiliated with *Limnohabitans* (*Betaproteobacteria*), a highly diversified genus composed of so far 4 described species (Hahn *et al.*, 2010; Kasalický *et al.*, 2013; Kasalicky *et al.*, 2010). *Limnohabitans* spp. are versatile in the incorporation of LMW substrates with a preference for simple organic acids and monosaccharides (Kasalický *et al.*, 2013; Salcher *et al.*, 2013) and typically show a quick response to nutrient enrichments (Pérez and Sommaruga, 2006; Peura *et al.*, 2012b; Šimek *et al.*, 2003). Moreover, these microbes seem to be tightly coupled to autochthonous carbon sources (Pérez and Sommaruga, 2006; Šimek *et al.*, 2011b). In temperate lakes, *Limnohabitans* spp. have annually recurrent population maxima during phytoplankton blooms (Fig. 2; Eckert *et al.*, 2012; Šimek *et al.*, 2008), that are rapidly terminated by HNF due to preferential ingestion (Jezbera *et al.*, 2006). However, the susceptibility to protistan grazing and viral lysis is species-specific (Šimek *et al.*, 2010) and even closely related strains of *Limnohabitans* may differ in food quality for flagellates (Šimek *et al.*, 2013).

Also some members of *Alphaproteobacteria* (esp. *Sphingomonadaceae*) and *Gammaproteobacteria* have a competitive and fast growing lifestyle as they can suddenly dominate microbial assemblages after nutrient enrichment and/or removal of grazers (Hutalle-Schmelzer *et al.*, 2010; Newton and McMahon, 2011). While *Sphingomonadaceae* seem to profit from algal derived carbon sources (Dziallas and Grossart 2011; Neuenschwander *et al.*, *unpublished data*), an enrichment of *Gammaproteobacteria* was only achieved at times of low phytoplankton biomass (Newton and McMahon, 2011; Peura *et al.*, 2012b; Neuenschwander *et al.*, *unpublished data*), indicating that their growth is induced by recycled or allochthonous DOM sources.

Flavobacteria and some populations of *Sphingobacteria (Bacteroidetes)* on the other hand are seen as typical *bloom specialists* favoured by phytoplankton bloom derived exudates or decay products (Newton and McMahon, 2011; Sarmento and Gasol, 2012). Member of this class can be enriched on algal exudates (Nelson and Carlson, 2012; Newton and McMahon, 2011), cultured on solid media (Cousin *et al.*, 2008), and are abundant during phytoplankton blooms (Eckert *et al.*, 2012; Eiler and Bertilsson, 2007; Salcher *et al.*, 2010; Zeder *et al.*, 2009). However, a consequent specialization seems likely, as even closely related populations of *Flavobacteria* showed striking seasonal patterns in enrichments during blooms of different algal species (Neuenschwander *et al.*, *unpublished data*), pointing to specific adaptations to different types of algal exudates. Marine *Flavobacteria* were specialized in the degradation of algal derived polymers, which in turn were released as by-products in the form of simpler compounds (simple sugars, acetate, ammonia) that can then be exploited by other microbes such as *Proteobacteria* (Teeling *et al.*, 2012; Williams *et al.*, 2013). A similar ecological role of *Flavobacteria* can be expected in freshwaters.

Physiologically specialized prokaryotes

Some microbes fulfill a conspicuous role in aquatic environments by acting as key players in the nitrogen cycle (*e.g.*, ammonia oxidizing *Thaumarchaeota*, denitrifying *Epsilonproteobacteria*), the sulfur cycle (*e.g.*, sulfate reducing *Deltaproteobacteria*, sulfur oxidizing *Epsilonproteobacteria*), or the carbon cycle (*e.g.*, methanotrophic *Gammaproteobacteria*, methylotrophic *Betaproteobacteria*) (Madigan, 2012). While most of these specialists are obligate or facultative anaerobes, ammonia oxidizing *Thaumarchaeota* and members of the methylotrophic LD28 tribe (*Betaproteobacteria*) dwell in oxygen saturated deep hypolimnia (Callieri *et al.*, 2009; Salcher *et al.*, 2008, 2011a; Urbach *et al.*, 2001). LD28 *Betaproteobacteria* are closely related to the marine OM43 tribe of *Methylophilaceae* (Giovannoni *et al.*, 2008; Halsey *et al.*, 2011). They are methylotrophs, *i.e.*, they use C_1-compounds such as methanol as sources of carbon and/or energy gain. Decaying phytoplankton blooms and allochthonous DOM might be the main

sources of methanol in freshwaters, as it is a degradation product of pectin and lignin (Halsey *et al.*, 2011). *Methylophilaceae* were recently identified to be involved in the degradation of microcystins, toxins released by bloom forming cyanobacteria (Mou *et al.*, 2013). Interestingly, LD28 *Betaproteobacteria* were repeatedly detected in deeper layers of lakes below the zone of primary producers, but were rare in the warm stratified water layers during summer (Salcher *et al.*, 2008, 2011a). Moreover, distinct maxima were reported during mixis in autumn-winter (Fig. 2; Eiler *et al.*, 2012), pointing to cold-stenothermic adaptation and a beneficial effect of specific resources that get enriched during mixis.

Also *Thaumarchaeota* thrive mostly in hypolimnia of deep lakes and have close relatives in marine realms (Callieri *et al.*, 2009; Urbach *et al.*, 2001). These Archaea are involved in ammonia oxidation and dark CO_2 fixation in the hypolimnia of deep lakes (Auguet *et al.*, 2012; Callieri *et al.*, 2014), similar to their marine counterparts (Könneke *et al.*, 2005). However, further knowledge about, *e.g.*, seasonality and mortality factors of these small prokaryotes is still scarce (Auguet *et al.*, 2011).

Photo(hetero)trophic bacteria

Most aquatic prokaryotes can use light for carbon fixation or energy generation ranging from pure photoautotrophy to photoheterotrophy. Cyanobacteria carry out oxygenic photosynthesis comparable to eukaryotic algae but use different light harvesting complexes, and some are even able to fix atmospheric nitrogen (Oliver *et al.*, 2012). Freshwater cyanobacteria are very diverse and their morphology ranges from small coccoid single cells (picocyanobacteria, *e.g. Synechococcus* sp.) (Callieri *et al.*, 2013) to large multicellular filaments (*e.g.*, *Planktothrix* sp., *Anabaena* sp.). They can form dense blooms, with some taxa being able to regulate their buoyancy by gas vacuoles or to produce toxins as grazing defense agents (Dokulil and Teubner, 2000; Posch *et al.*, 2012). There are several excellent reviews and books about the ecology of cyanobacteria that I would like to draw the readers' attention to (Callieri *et al.*, 2012; Callieri and Stockner, 2002; Dokulil and Teubner, 2000; Oliver *et al.*, 2012; Whitton, 2012).

Photoheterotrophy on the other side is the ability to utilize DOM and harvest light energy for ATP production. Two types of photoheterotrophs thrive in oxygenated freshwaters, *i.e.*, rhodopsin bearing bacteria (RBs) and bacteriochlorophyll containing aerobic anoxygenic phototrophs (AAPs). Rhodopsins (simple retinal-binding membrane proteins that act as light driven proton pumps) are widespread among freshwater and marine prokaryotes, including some of the most abundant taxa [*e.g.*, ac1 *Actinobacteria*, LD12 *Alphaproteobacteria*, several *Sphingo-* and *Flavobacteria* (Atamna-Ismaeel *et al.*,

2008; Martinez-Garcia *et al.*, 2012)]. Most likely, rhodopsins generate ATP to fuel membrane transporters in order to better survive in nutrient limited environments (Kirchman and Hanson, 2013). AAPs on the other side are not very abundant in lakes and restricted to some members of *Alpha-*, *Beta-*, and *Gammaproteobacteria* (Martinez-Garcia *et al.*, 2012; Salka *et al.*, 2008). However, as most AAPs are typical opportunists [*e.g.*, several *Limnohabitans* spp. (Zeng *et al.*, 2012)] with fast growth rates, bigger than average cell size, and high susceptibility to protistan predation, their contribution to microbial biomass and carbon flow are high (Mašín *et al.*, 2008). Although AAPs gain more light energy than RBs, also the costs of the more complex bacteriochlorophyll based light harvesting machinery are substantially higher. Therefore, the low synthesizing costs and simplicity of rhodopsins might be the main reason for the success of RBs (Kirchman and Hanson, 2013).

SPATIAL NICHES IN THE PELAGIAL OF LAKES

Planktonic microorganisms show distinct spatial patterns that can range from micro-scale (µm-mm) to large-scale (m-km) patchiness (Blackburn *et al.*, 1998; Salcher *et al.*, 2011a). Micro-scale heterogeneity of resources is a strong structuring factor for microorganisms, as dissolved and particulate organic matter in the water is present in small, ephemeral patches of *e.g.*, algal exudates, material released by viral lysis, autolysis, or sloppy zooplankton feeding, detritus, or sinking lake snow particles (Blackburn *et al.*, 1998; Stocker, 2012). Such micro-scale resource-rich patches in marine environments can be exploited by chemotactic motile bacteria (Taylor and Stocker, 2012), resulting in an accumulation of opportunistic bacteria (Barbara and Mitchell, 2003). Chemotaxis for inorganic nutrients (phosphorus, nitrate, and ammonium) of prominent freshwater bacterial populations has been demonstrated recently (Dennis *et al.*, 2013). Besides micro-scale distribution of microbes, also large-scale longitudinal changes in nutrient regimes, temperature, and phytoplankton assemblages can act as niche separators for microorganisms. A changing importance from allochtonous DOM resulting in net heterotrophy in inflow regions towards a more phototrophic assemblage with pronounced shifts in microbial activity and assemblage composition has been reported for large reservoirs and lakes (Comerma *et al.*, 2003; Reichart and Simon, 1996; Salcher *et al.*, 2011a; Šimek *et al.*, 2011a). The vertical structuring of the pelagial of stratified lakes is based on differences in temperature (epi-, meta-, and hypolimnion), light (euphotic and aphotic zone), and oxygen content (oxic and hypoxic zone; Wetzel, 2001). The vertical distribution of bacteria has been studied in detail, as oxygen gradients strongly influence organisms, thus, chemoclines and hypoxic hypolimnia provide niches for

specialized microorganisms [*e.g.*, sulphur oxidisers, fermenting or methanogenic bacteria (Madigan, 2012)]. Moreover, the well illuminated and – during summer stratification – warm surface water is inhabited by microorganisms that differ from those adapted to oxygenated hypolimnia due to several reasons. Firstly, temperature *per se* plays an important role, as total bacterial growth rates are tightly correlated to water temperature (Coveney and Wetzel, 1995; White *et al.*, 1991). Secondly, many bacteria live phototrophic or photo-heterotrophic and are therefore dependent on light. Thirdly, phytoplankton exudates are main carbon sources for microbes (Giroldo *et al.*, 2007; Hama and Handa, 1987) and some opportunistic taxa are well adapted to different epilimnetic phytoplankter (Eckert *et al.*, 2012; Eiler and Bertilsson, 2004; Šimek *et al.*, 2011b).

A SYNOPTIC VIEW ON THE SEASONAL SUCCESSION OF FRESHWATER MICROBES IN TEMPERATE LAKES

Temporal changes in the bacterioplankton are frequently referred to as another mode of niche separation besides spatial patchiness. Especially temperate lakes undergo strong seasonal changes in abiotic (*e.g.*, temperature, light, oxygen) and biotic characteristics, and therefore, also microbes show a distinct seasonality with reoccurring patterns. These seasonal changes mostly take place in the epilimnion and are tightly linked to the main factors shaping microbial assemblages in the pelagial of lakes and ponds. Based on data from 2 contrasting prealpine lakes (small, shallow, oligomesotrophic Piburger See, Austria; and large, deep, mesotrophic Lake Zurich, Switzerland; Fig. 2) and other relevant literature, I will try to summarize the characteristic seasonal succession of microbial populations (Fig. 3), analogous to the well-known PEG model for phyto- and zooplankton (Sommer *et al.*, 1986, 2012).

Typically, temperature and DOC are the limiting factors for microbial growth during winter (Figs. 2, 3). As soon as water temperature and solar radiation reach a certain threshold and an algal spring bloom develops (Sommer *et al.*, 2012), some fast growing opportunistic bacteria profit from phytoplankton derived DOM and grow to high densities (Eckert *et al.*, 2012; Salcher *et al.*, 2010; Zeder *et al.*, 2009; Zwisler *et al.*, 2003). Small transient populations of *Flavobacteria* might be responsible for polymer degradation (Teeling *et al.*, 2012; Williams *et al.*, 2013), while *e.g.*, *Limnohabitans* spp. (*Betaproteobacteria*) might grow on algal derived monosaccharides (Kasalický *et al.*, 2013; Salcher *et al.*, 2013; Šimek *et al.*, 2011b). Population maxima of such *bloom specialists* are usually only short-living due to depletion of resources (esp. phosphorus) and a rapid elimination by bacterivorous protists and viruses (Eckert *et al.*, 2012). Subsequently, grazing

resistant defense specialists with lower growth rates such as ac1 *Actinobacteria* and filamentous bacteria rise in abundance (Allgaier and Grossart, 2006; Eckert *et al.*, 2012; Salcher *et al.*, 2010). These microbes might also directly profit from algal derived DOM or from recycled carbon released during flagellate grazing or viral lysis (Eckert *et al.*, 2013; Salcher *et al.*, 2013). During the clear-water phase, filaments are eliminated by filter feeding daphnids (Langenheder and Jürgens, 2001; Pernthaler *et al.*, 2004; Schauer *et al.*, 2006), while small ac1 *Actinobacteria* might suffer from viral lysis or bottom-up limitation (Šimek *et al.*, 2006). LD12 *Alphaproteobacteria* thrive in such nutrient depleted situations and might moreover profit from increasing water temperatures and solar radiation (Eiler *et al.*, 2012; Salcher *et al.*, 2011b). In case of additional phytoplankton blooms during summer, these oligotrophic ultramicrobacteria get displaced by opportunistically growing microbes with another succession starting comparable to the one after spring blooms (Figs. 2, 3). However, as phosphorus is limiting in summer, population maxima might not be as pronounced as in spring. In late summer to autumn, also nitrogen sources get depleted, consecutively favouring oligotrophic ultramicrobacteria such as LD12 *Alphaproteobacteria* (Heinrich *et al.*, 2013; Salcher *et al.*, 2011b). At the onset of autumnal mixis, microbial populations get passively entrained in deeper water layers where suboptimal conditions prevail. Simultaneously, decreasing water temperatures and enhanced resource availability due to mixis might favour specialized populations such as LD28 *Betaproteobacteria* (Fig. 2; Salcher *et al.*, 2008).

The synoptic view on the seasonal succession of different bacterioplankton populations presented here, however, is definitely not complete, as most microbes so far lack cultured representatives and a correct assignment of their ecological role. Future work focusing on the isolation of some of the most abundant freshwater microbes (*e.g.*, ac1 *Actinobacteria*, LD12 *Alphaproteobacteria*) is needed to gain more information on their life-style, growth dynamics, and specific physiological adaptations (Giovannoni and Stingl, 2007). This, together with single-cell analyses such as MAR-FISH (Salcher *et al.*, 2013) or single amplified genomes (Blainey, 2013) and meta-omics approaches (Simon and Daniel, 2011) may further elucidate ecological functions of the dominant microbes and identify their driving forces, and thus, shed light on the reasons for their apparent success in freshwaters. However, the so far recognized recurrent spatio-temporal distribution patterns together with several ecophysiological properties already point to pronounced ecological niche separation of the dominant microbial populations, and thus, might be a reason for the high diversity, analogous to the *paradox of the plankton* for algae (Hutchinson, 1961).

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