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Bacterial Predation on Cyanobacteria

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Bacteria · Cyanobacteria · Survival strategies · Predatory bacteria · Predation

Abstract
Predatory bacteria gained interest in the last 20 years. Nevertheless, only a few species are well characterized. The endobiotic predator *Bdellovibrio bacteriovorus* invades its prey to consume it from the inside, whereas *Myxococcus xanthus* hunts as a whole group to overcome its prey. Both species were described to prey on cyanobacteria as well. This minireview summarizes the findings of the last 20 years of predatory bacteria of cyanobacteria and is supplemented by new findings from a screening experiment for bacterial predators of the model organism *Anabaena variabilis* PCC 7937. Known predatory bacteria of cyanobacteria belong to the phyla Proteobacteria, Bacteroidetes, and Firmicutes and follow different hunting strategies. The underlying mechanisms are in most cases not known in much detail. Isolates from the screening experiment were clustered after predation behaviour and analyzed with respect to their size. The effect of predation in high nitrate levels and the occurrence of nitrogen-fixing cells, called heterocysts, are addressed.

Introduction to Microbial Predation and Its Impact

Life on earth is a sensitive system of countless species that live together in a certain balance. They interact with each other through all domains of life, and the interactions can be beneficial, disadvantageous, or even neutral (Fig. 1). Mutualism describes a win-win situation of the participating organisms. By digestion, synthesis, or photosynthesis, they provide each other nutrients, growth factors, or energy. They can also act as a shield to environmental changes or even enemies [Boucher et al., 1982]. In commensal and amensal relationships, one organism benefits (commensal) from or is harmed (amensal) by the other. The latter is not affected at all. During competition, both organisms harm each other. In marine sponges for example, Esteves et al. found that a *Bacillus subtilis* strain degrades the host sponge. This reduces the living environment for commensal *Pseudovibrio* strains, which in turn inhibit *B. subtilis* or its degrading enzymes [Esteves et al., 2017].

Besides sharing benefits like in mutualism or commensalism, in interactions such as parasitism and predation, one organism benefits and harms the other. In the literature, the terms predator and parasite are not clearly delimited from each other. In this article, predation describes the straightforward killing of a prey to use its com-

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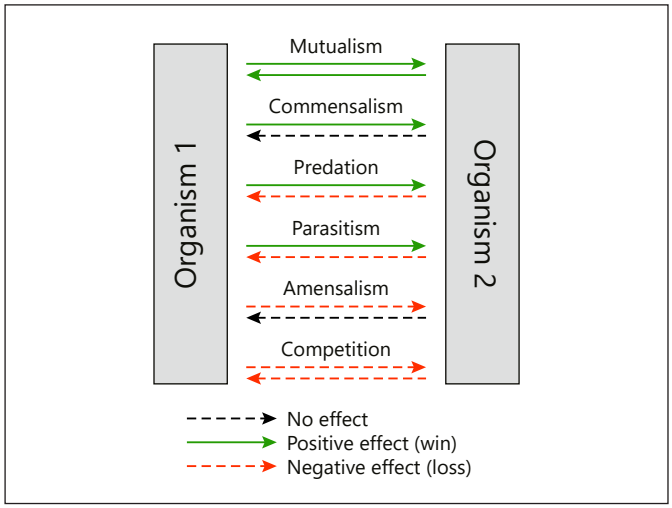

Fig. 1. Possible interactions between two organisms. Relations can be beneficial or harmful to one or both organisms. In some cases, only one organism is affected.

ponents as nutrients. Parasitism, on the other hand, defines a prolonged exploitation of a host metabolism. Well-known examples of parasites are worms and ticks with animals as hosts.

Microbacterial communities are complex ecosystems that are affected by many different factors. The dynamics of populations is determined by environmental factors like dissolved organic matter, temperature, light, and pH. An increase in nitrate levels due to agricultural fertilization can contribute to cyanobacterial bloom formation. Blooms pose a risk for humans, animals and the whole ecosystem [reviewed by Huisman et al. [2018]. Microbacterial communities, which blooms are, can be regulated top-down by grazers, viruses, and predatory bacteria. Gilbert et al. [2012], for example, showed that differences in day length during the seasons account for 65% of the changes in populations on a marine coastal site. Another study identified salinity as a driver for population changes [Bouvier and del Giorgio, 2002]. To predict multispecies relationships, the generalized Lotka-Volterra model is used, which describes the growth rates of populations of prey and predator over time [Gonze et al., 2018]. According to this model, the numbers of prey and predator depend on reproduction rates and the interaction between the species. In simple systems of only two species, the populations of prey and predator oscillate with a phase shift, indicating a rising number of predators as a result of a previous rise in the number of prey cells. This is followed by a drop of the prey numbers and then of the predator. The presence of a predator in a microbial community affects the population of the prey and probably of other bacteria, as well. But following the Lotka-Volterra model, the populations will be balanced in an oscillating way, if no other unpredicted events like fertilization, invasion of foreign species, or climate change happen.

The ability to perform photosynthesis and to fix atmospheric nitrogen makes cyanobacteria an excellent source of nutrients. Many organisms such as diatoms, sponges, corals, lichens, and mosses benefit from this (reviewed by Usher et al. [2007]). Predation of cyanobacteria by grazing protozoa, like amoeba for example, was reported many times [Wright et al., 1981; Dryden and Wright, 1987; Simkovsky et al., 2012; Ma et al., 2016]. Fungi prey on cyanobacteria, too. The white-rot fungi *Phanerochaete chrysosporium* (phylum: Basidiomycota) preys on *Oscillatoria* spp. and *Microcystis aeruginosa* using direct cell-cell contact. *Rhizosiphon* spp. (phylum: Chytridomycota) infiltrate *Anabaena macrospora* to reproduce over several infection stages [Gerphagnon et al., 2013; Zeng et al., 2015; Zeng et al., 2020]. So far, no predatory archaea are known.

The presence of predatory bacteria, however, has only gained attention the last 20 years (results for "predatory bacteria" rose from 10 results in 2000 to 83 in 2020, in PubMed, December 9, 2020).

Predatory bacteria depend on living prey (obligate predator) or can also live from lysed prey cells (saprophytic). Facultative predatory bacteria do not depend on prey and can grow in a nutrient-rich environment. To lyse the prey, predatory bacteria follow different hunting strategies: endobiotic predation, epibiotic predation, and the predations as a group.

Endo- and Epibiotic Predation: Examples of the Genus *Bdellovibrio*

One of the best known predatory bacteria is the endobiotic predator *Bdellovibrio bacteriovorus*. While searching for bacteriophages, it was isolated by Stolp and Petzold [1962] as a lytic bacterium. A year later, Stolp and Starr [1963] defined the lytic bacterium as *B. bacteriovorus*. Until 3 years ago, it was assigned to the Deltaproteobacteria, but in 2017 the order Bdellovibrionales was reclassified to Oligoflexia in the phylum Proteobacteria [Hahn et al., 2017]. *B. bacteriovorus* lyses exclusively Gram-negative bacteria like *E.coli* or the cyanobacterium *Phormidium luridum* [Burnham et al., 1976], but the prey spectrum varies from isolate to isolate [Stolp and Starr, 1963]. *B. bacteriovorus* follows a two-stage predation

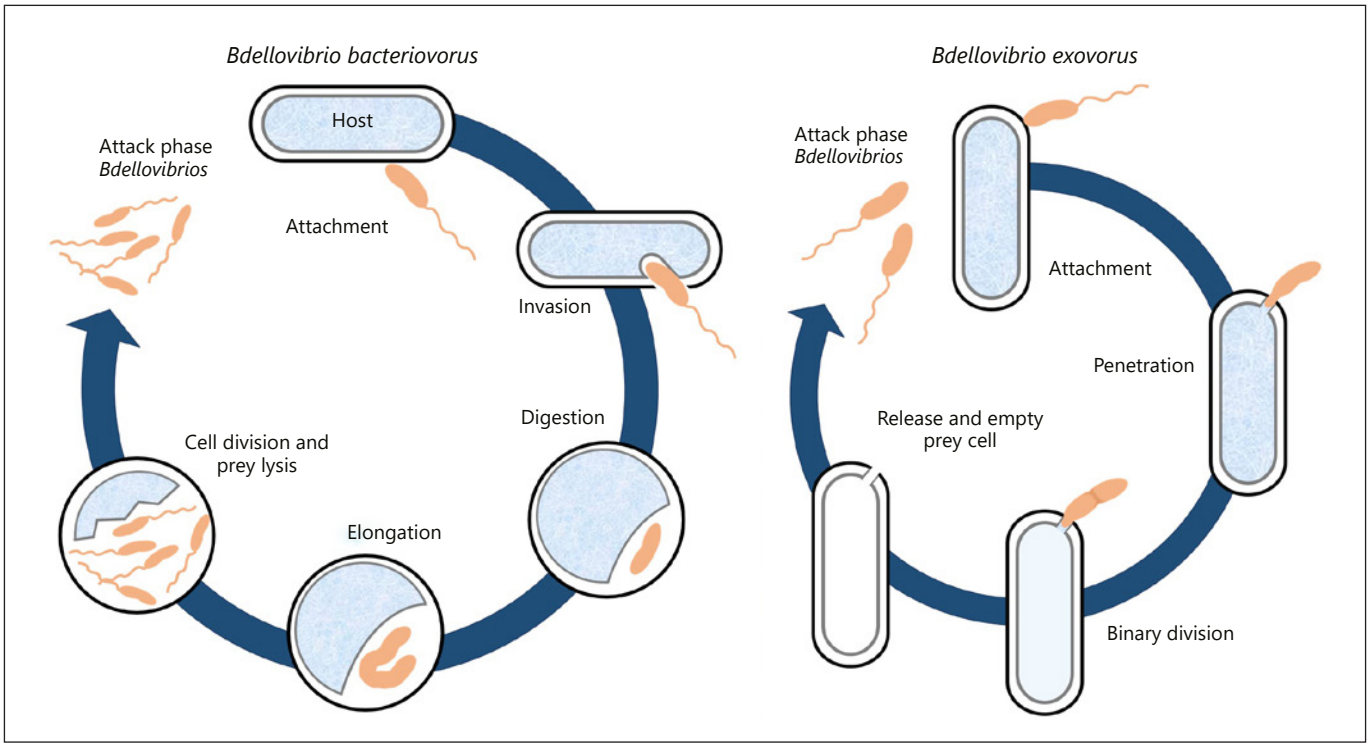

Fig. 2. Life cycle of *B. bacteriovorus* and *B. exovorus*. *B. bacteriovorus* follows an endobiotic lifestyle: it penetrates the periplasm of the prey cell and consumes it from the inside, elongates, divides, and sets the progeny free by lysing the host cell. *B. exovorus* is an epibiotic predator: it attaches on the surface of the prey cell and consumes the cytoplasm from the outside. While being attached to the prey cell, *B. exovorus* reproduces by binary fission. After division, it leaves the empty prey behind.

strategy starting with an attack phase, which leads up to a periplasmic growth phase (Fig. 2). In the attack phase, *Bdellovibrio* swims rapidly to find randomly new prey following chemoattractants. These compounds signal bacterial populations but not necessarily prey [Straley and Conti, 1977; Straley et al., 1979]. As soon as it finds its prey, it starts excreting enzymes like glycanase and peptidase to enter the cell [Thomashow and Rittenberg, 1978b]. Kuru et al. [2017] showed the formation of a "reinforced circular port-hole" through which the predator enters the prey. As a signal that is later needed for lysing exclusively the host, deacetylases alter the host-cell wall [Thomashow and Rittenberg, 1978a]. From the inside, that is, the periplasm, *B. bacteriovorus* degrades the cellular components and consumes them to reproduce itself. Due to the activity of endopeptidases that cleave crosslinks in the peptidoglycan, the prey cell changes its shape to a sphere. The so called bdelloplast prevents from double infection [Lerner et al., 2012]. After a phase of elongation, *Bdellovibrio* separates into single cells that leave the prey by producing the lysozyme DslA. This specifically destroys the previously deacetylated host cell wall, which prevents self-destruction of the predator [Harding et al., 2020]. The released progeny starts the cycle again. Although *Bdellovibrio* is regarded as an obligate predatory bacterium, there are variants that grow host independent in nutrient-rich media. As type IV pili are essential for predatory activity of *Bdellovibrio* [Evans et al., 2007], Capeness et al. [2013] proposed that a reduced type IV pili formation led to the host-independent lifestyle.

The complete genome of *B. bacteriovorus* covers 3.8 mega base pairs (Mbp) on one chromosome. Over 250 hydrolytic enzymes were found, including 150 proteases/peptidases [Rendulic et al., 2004]. In a recent study, the authors ran a genome-scale metabolic model. They also included metabolic information from genome annotation and biochemical data. The metabolic reactions were clustered into 12 different functional categories. The largest category included catabolic reactions (37%) like the degradation of peptidoglycan and other reactions of the cell envelope metabolism [Herencias et al., 2020]. An in silico analysis found 14 auxotrophies for amino acids and

several cofactors like riboflavin, nicotinamide, putrescine, and lipoate [Herencias et al., 2020]. This shows how important it is for *Bdellovibrio* to overcome its prey and to be able to compensate for the auxotrophies.

Bdevollvibrio exovorus is an epibiotic predator and follows another strategy. It was isolated from sewage in Canada, living on *Caulobacter crescentus* and was described as a novel species of *Bdellovibrio* in 2013 [Koval and Hynes, 1991; Koval et al., 2013]. The life cycles of the *Bdellovibrios* are similar. The difference is that *B. exovorus* does not enter the prey cell but attaches outside of it and consumes the cytoplasm. While being attached to the prey cell it reproduces by binary fission. After division, it leaves the empty prey behind (Fig. 2). The cell shape of the prey remains the same and no bdelloplast is formed. In contrast to *B. bacteriovorus*, the prey range of *B. exovorus* is limited to *Caulobacter* spp. [Koval et al., 2013]. Besides the known *Bdellovibrios*, there are *Bdellovibrio* and Like Organisms (BALOs). BALOs are small obligate predators that follow the same hunting strategy as *B. bacteriovorus* and *B. exovorus* [Rotem et al., 2014]. Caiola and Pellegrini [1984] isolated a BALO strain that can prey on the cyanobacterium *Microcistis aeruginosa*. Like *B. bacteriovorus*, it penetrates the prey cell to lyse it from within.

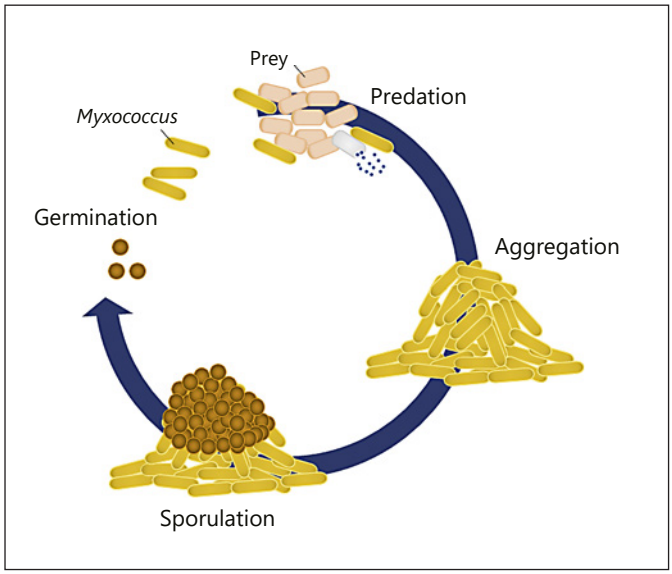

Fig. 3. Life cycle of *M. xanthus*. Gliding *Myxococcus* cells find prey and lyse them. When conditions get unfavourable, cells start to aggregate, and sporulation starts. Spores are released and germinate if conditions are favourable.

Hunting as a Group: The Example *Myxococcus xanthus*

An example of group-hunting predatory bacteria is the well-described *Myxococcus xanthus,* a rod shaped, Gram-negative soil bacterium belonging to the Deltaproteobacteria. It has auxotrophies for valine, leucine, and isoleucine [Bretscher and Kaiser, 1978] and needs to take up those amino acids from prey cells. However, as a saprophytic bacterium, it is also able to grow on dead prey bacteria [Shimkets, 1984]. The prey spectrum spans from soil bacteria including the plant pathogen *Pectobacterium carotovorum*, over the cyanobacterium *P. luridum*, to clinically relevant species like *Klebsiella pneumoniae* or *Candida albicans* [Burnham et al., 1981; Rosenberg and Varon, 1984; Morgan et al., 2010; Livingstone et al., 2017]. Because of this broad prey spectrum, Thiery and Kaimer [2020] suggested the involvement of different lysis mechanisms, which act alone or together. For successful lysis of prey, a direct physical contact is necessary [McBride and Zusman, 1996; Pan et al., 2013; Zhang et al., 2020]. The life cycle of *M. xanthus* comprises four main steps: free living *Myxococci* swarm out to find prey bacteria, consume the prey, aggregate when nutrients diminish and form myxospore containing fruiting bodies. Those germinate when the conditions are favourable again (Fig. 3). To find prey, *Myxococci* follow acyl homoserine lactones (AHLs), which are used from different bacteria as quorum sensing signals. In presence of AHLs, *M. xanthus* sporulation is hindered and germination is promoted, both leading to an increase in predatory active cells [Lloyd and Whitworth, 2017]. Because *Myxoccoci* need to find the prey actively, motility is an important feature in predation. *Myxococcus* uses two kinds of motility: social or S-motility is a movement of multiple cells and is mediated by retracting type IV pili (TFP) at one cell pole [Kaiser, 1979; Merz et al., 2000; Sun et al., 2000]. *Myxococcus* cells are covered with an extracellular matrix (ECM) consisting of the TFP, lipopolysaccharides, and fibrils [Bowden and Kaplan, 1998]. The fibrils are formed by proteins and exopolysaccharides (EPS) and connect the cells to each other [Behmlander and Dworkin, 1994]. The carbohydrates of the EPS are the point of attachment for the TFP. In case of attachment, the TFP retract, which leads to a movement towards the other cell [Li et al., 2003]. The presence of EPS is crucial for S-motility and fruiting body formation. S-motility, in turn, is necessary for efficient predation [Lu et al., 2005; Pérez et al., 2014]. Adventurous or A-motility is a single cell movement by gliding and intends to explore the environment and to

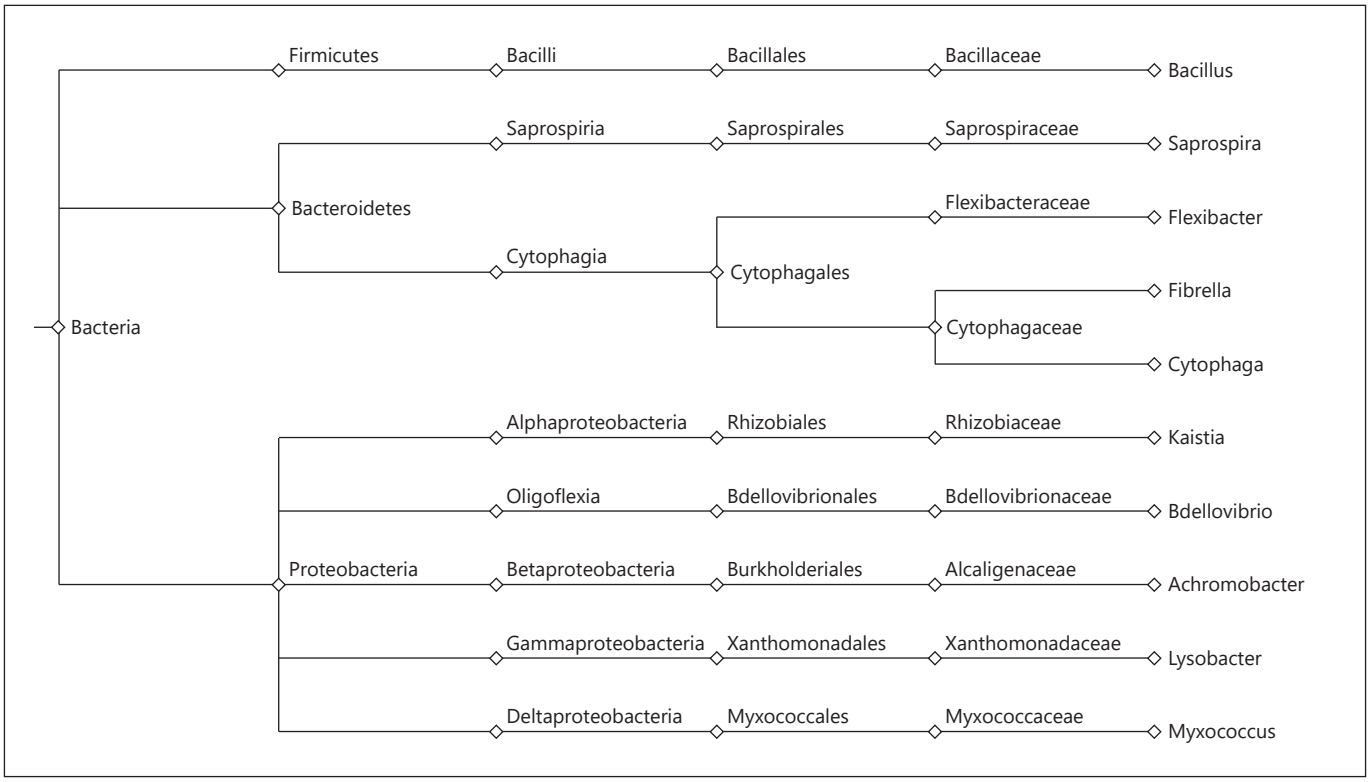

Fig. 4. Cladogram of predatory bacteria of cyanobacteria. Most predatory bacteria of cyanobacteria belong to the phyla Bacteroidetes and Proteobacteria, except *Bacillus* sp., which belong to the phylum Firmicutes. Tree by NCBI CommonTree. Tree Viewer: Dendroscope [Huson and Scornavacca, 2012].

find new habitats. The underlying mechanism is not completely clear yet. One hypothesis was that Myxobacteria glide by the extrusion of slime resulting in a jet propulsion and a thrust forward [Wolgemuth et al., 2002; Spagnolie and Lauga, 2010]. But experiments with motility mutants showed that slime is also produced in non-motile cells and does not necessarily lead to motility [Ducret et al., 2012]. The slime trails from A-motile cells can be tracked by S-motile cells via the TFP. Following the trails, S-motile cells also find the new favourable habitats [Muñoz-Dorado et al., 2016].

The Variety of Predatory Bacteria of Cyanobacteria

Predatory bacteria like *Bdellovibrio* and *Myxococcus* have been the focus of intense research efforts. In contrast, bacterial predators of cyanobacteria remain largely uncharacterized. The following part summarizes the current state of knowledge about predatory bacteria described to use cyanobacteria as prey. Most of them belong to the phyla Bacteroidetes and Proteobacteria, with the exception of *Bacillus cereus*, assigned to the Firmicutes (Fig. 4). *B. cereus* is able to lyse a variety of cyanobacteria within the species *Aphanizomenon flos-aquae*, *Microcystis viridis*, *Microcystis wesenbergi*, *Microcystis aeruginosa*, *Oscillatoria tenuis*, *Nostoc punctiforme*, *Anabaena flos-aquae*, and *Arthrospira maxima*. The lysing mechanism is not clear, but in case of *A. flos-aquae*, *B. cereus* attaches to the prey cell [Shunyu et al., 2006]. In contrast to that, in another study the supernatant of *B. cereus* was sufficient to lyse *Microcystis* [Nakamura et al., 2003], suggesting that *B. cereus* may use different strategies to kill different prey.

Within the phylum Proteobacteria, in addition to *Bdellovibrio* and *Myxococcus*, there are three genera with predators of cyanobacteria. The genus *Kaistia* belongs to the Alphaproteobacteria. Two strains of so-called ultramicrobacteria lyse *Acidovorax* spp., *Bacillus* spp., and several cyanobacteria. Ultramicrobacteria have a cell volume smaller than 0.1 μm^3 and a genome size of ~3.2 to ~0.58 Mb, and the cell size of the bacteria remains small regardless of the cultivation [Duda et al., 2012]. These facultative epibiotic predators of *Kaistia* lyse *Anabaena variabilis*,

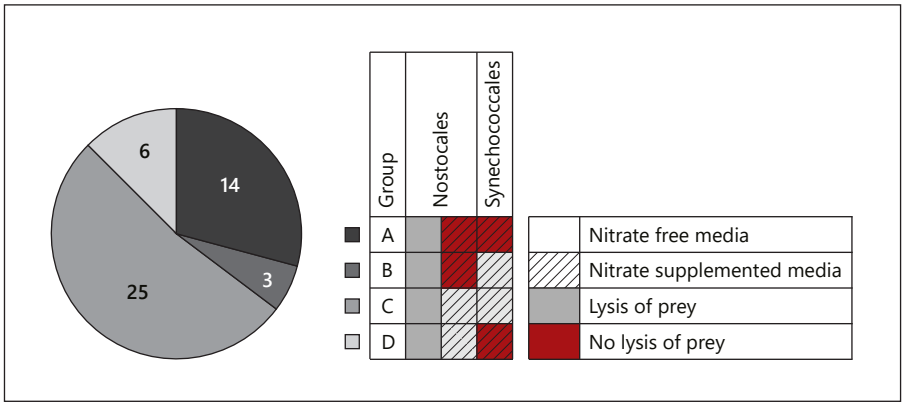

Fig. 5. Cluster of 48 environmental water isolates by their predatory behaviour. Isolates were clustered by their ability to lyse prey bacteria of the order Nostocales and Synechococcales taking into account the nitrate level of the medium. Group A: only *Anabaena* spp. on nitrate-free BG11 medium were lysed. Group B: nostocales and Synechococcales were lysed. The medium had no effect. Group C: only Nostocales were lysed. Group D: only *A. variabilis* on standard BG11 medium was not lysed.

Nostoc muscorum, and *Chlorogloeopsis fritschii*. The bacteria attach to the prey cell, penetrate the sheath, and in some cases infiltrate the cell. The authors suggest that the infiltration of the cell happens after the cell death of the prey bacterium. One strain is reported to preferably lyse the nitrogen fixing cells of *A. variabilis, termed* heterocysts, and the spore-like cells, called akinetes [Duda et al., 2009]. *Achromobacter denitrificans*, a betaproteobacterium (former *Alcaligenes denitrificans*) preys on *Microcystis* by direct cell-cell contact, but the lysing mechanism remains unclear [Pathmalal et al., 2000; Coenye et al., 2003].

Before taxonomic classification by 16 S analysis was possible, predatory bacteria of the genus *Lysobacter* (Gammaproteobacteria) were often falsely assigned to the genus *Myxococcus* [Christensen and Cook, 1978]. Shilo [1970] described a bacterium of the genus *Lysobacter* that lyses its prey by direct contact, that is, by attaching the tip of the predator's cell to the prey bacterium. *Lysobacter's* prey belong to the species *Leptolyngbya boryana*, *Oscillatoria prolifera*, *Arthrospira platensis*, *Arthrospira tenuis*, *Nostoc* sp., *Asterocapsa nidulans*, and *Cyanobacterium staniera* (names correspond to the current taxonomy). In case of heterocyst-forming species, only vegetative cells are lysed. The cell envelope of vegetative cells consists of an inner membrane, a periplasmic space, a peptidoglycan layer, and the outer membrane. Heterocysts are surrounded by an additional glycolipid layer (reviewed by Nicolaisen et al. [2009]). This extra feature could protect from predatory bacteria. However, heterocysts are terminally differentiated and do not reproduce any more. Therefore, the vegetative cells are not protected by the additional glycolipid layer of the heterocyst.

In the phylum Bacteroidetes, four predators of cyanobacteria are known. *Saprospira grandis* is a Gram-negative bacterium that forms spiral-shaped filaments of several cells and was isolated from marine habitat [Lewin, 1997]. It belongs to the class Saprospiria and catches prey by attachment to the prey's flagellum. Shi et al. [2006] isolated a *Saprospira* strain that preys on *Anabaena* spp. by moving as a bundle of cells. Many filaments of the predator surround the prey cells and lyse them. Predation by the closely related species *Saprospira albida* leads to colourless *Microcystis* cells, a distinctive sign of cell death of the prey [Ashton and Robarts, 1987]. *Flexibacter flexilis* of the order Cytophagales lyses *Oscillatoria williamsii*. It attaches to the sheaths of the cyanobacterial cell and excretes lysozyme. The prey cell lyses and the predator takes up the resulting compounds [Sallal, 1994]. The last two predators belong to the family Cytophagaceae. *Fibrella aestuarina* is likely to establish physical contact with its prey *N. muscorum* as treatment with the supernatant induced no lysis [Svercel et al., 2011]. Bacteria of the genus Cytophaga lyse several cyanobacterial strains. In their study, Rashidan and Bird [2001] isolated two Cytophaga strains from Brome Lake in Canada, both predating cyanobacteria. With direct cell-cell contact, strain 1 lysed only *A. flos-aquae*, whereas strain 2 lysed only *Synechococcus* sp. and *A. nidulans*. This indicates that bacteria belonging to the same genus and isolated from the same source can still have a different prey spectrum.

Occurrence of Bacterial Predators of Cyanobacteria in Common Freshwater Samples

To get an overview over the occurrence of bacterial predators of cyanobacteria in freshwater samples, we screened for predatory bacteria using the cyanobacterial strain *A. variabilis* PCC 7937 as a model prey. Forty-eight isolates containing lytic activity were obtained and clustered in four different groups, according to their ability to prey on either diazotrophic- or nitrate-grown *Anabaena*

cells, as well as on the unicellular cyanobacteria *Synechococcus elongatus* PCC 7942 and *Synechocystis* PCC 6803 on nitrate-supplemented medium (see Fig. 5). The detailed experimental procedure is provided in the supplemental material (for all online suppl. material, see www. karger.com/doi/10.1159/000516427).

The 14 isolates of group A were only able to prey on *A. variabilis* and *Anabaena* PCC 7120 on nitrate-free media, whereas no lysis occurred on nitrate-supplemented BG11 medium. They also did not lyse the tested non-diazotrophic unicellular strains *Synechococcus* and *Synechocystis*, grown on nitrate-supplemented media. Hence, these predators probably lyse the cyanobacteria as a source of combined nitrogen, which would explain why predation is supressed by high nitrate concentrations. In this case, the isolates would behave as facultative predators. Another possibility is that the high nitrate content in BG11 is, directly or indirectly, toxic for the predators. Normally, the nitrate level in surface water lies between 0 and 18 mg/L and does not naturally exceed over 4–9 mg/L [World Health, 2003]. Due to agricultural fertilizers, levels can rise up to 1,500 mg/L which was shown for groundwater in an agricultural area in India [Jacks and Sharma, 1983]. The standard BG11 medium contains 1,085 mg/L nitrate (1,495 mg/L $NaNO_3$), which is higher than most naturally occurring levels of nitrate and might be unfavourable for the predators. In nature, it is likely that filamentous cyanobacteria do form heterocysts at the low naturally occurring levels of nitrate.

The isolates in group B (3 isolates) did not lyse the non-heterocystous *A. variabilis* on nitrate-supplemented media but the heterocyst containing *A. variabilis* and *Anabaena* PCC7120 on nitrate-free media. The Synechococcales on nitrate-supplemented media were also lysed, which means the nitrate itself is not responsible for the lack of lysis. It is possible that the metabolic state of the nitrate-grown *Anabaena* makes them resistant to predation by the organisms in group B.

The isolates from group C showed a rather unspecific prey spectrum as they lysed all the tested cyanobacteria on all tested media. The predatory bacterium *B. cereus* (Firmicutes) has also a broad prey spectrum within the cyanobacteria, as mentioned above [Shunyu et al., 2006]. Obviously, there are certain predators with a broad prey spectrum. While group C seems unspecific, the members of group D (6 isolates) appear to be specific for the tested cyanobacteria of the order Nostocales, as the Synechococcales were not lysed. In the study of Rashidan and Bird [2001], one isolate of Cytophaga lysed only the tested filamentous cyanobacterium, and the second isolate, from the same source, only lysed the tested unicellular cyanobacteria. Hence, the prey spectrum of strains from the same genus and the same source can still be different. The isolates of groups C and D were both taken from the Schwarzenbachtalsperre in Forbach, Germany. It is possible that the predators of both groups belong to the same genus but have, as in the case of Cytophaga sp., a different prey spectrum.

The isolates were observed under the microscope in a random sample survey. All observed isolates contained bacteria. Some also contained fungi. Most isolates (31 isolates) showed lytic activity after filtration with a pore size of 0.45 μm. Ultramicrobacteria like *Kaistia* and *Bdellovibrios*/BALOs with the smallest size of 0.2 μm in width and 0.5 μm in length can pass a 0.45-μm filter [Rendulic et al., 2004; Duda et al., 2009]. In rare cases, they could theoretically also pass through the 0.22-μm filter. Even so, no isolate retained lytic activity after filtration through a 0.22-μm filter. This also excludes most cyanophages as source of lysis [Chen and Lu, 2002; Sullivan et al., 2005; Pope et al., 2007]. Some, however, like the cyanomyovirus AS-1 measure over 0.3 μm (90 nm head, 243 nm tail) [Sarma, 2012]. Therefore, microorganisms in this fraction (0.22–0.45 μm) can be bacteria or large myoviruses. Two isolates lost their lytic activity after 0.45 μm filtration and hence contain predators with a size between 1 and 0.45 μm. From the above-mentioned considerations, we deduce that these predators are likely to be bacteria. In 15 isolates, lytic activity was already lost after filtration through a 1-μm filter. These isolates probably consist of larger predators. These could be organisms such as *M. xanthus* which forms vegetative cells of 7 μm in length and 0.5 μm in width and spherical spores of 1.7 μm in diameter [Müller et al., 2012]. Both would rather not pass through a 1-μm filter. Another example, *S. grandis*, forms long filaments from 10 to 500 μm [Reichenbach, 2006]. Besides big predatory bacteria, those isolates can contain protozoa (1 μm to several mm) and fungi (>10 μm hyphae, >1 μm spores) [Singleton and Sainsbury, 2001; Yamamoto et al., 2012]. Because the lysis of *A. variabilis* on nitrate-free agar plates was not impaired when the antifungals nystatin and cycloheximide were added, fungi can largely be excluded as source of lysis. No correlation was detected between the prey-specific grouping of the predator and their size.

Conclusion

When it comes to predation of cyanobacteria, the literature provides a plethora of research articles about grazing and cyanophages and their impact on cyanobac-

terial blooms. Those systems are well studied. But the importance and occurrence of bacterial predators of cyanobacteria is still underestimated. As reviewed in this article, only few bacteria are known to prey on cyanobacteria. The published studies mainly focused on the presence of the predator but did not investigate the mechanisms of lysis or the prey spectrum in much detail. In our screening experiment, we found predators of different size and predation behaviour indicating the existence of a variety of bacterial predators of cyanobacteria.

Because of agricultural fertilization, high nitrate levels occur in natural systems and can promote bloom formation. We found indications that high nitrate levels impair bacterial predation. It needs to be investigated if the explosive growth of cyanobacteria and a loss of predatory activity could be a double-negative effect of high nitrate levels in freshwater systems.

In future, bacterial predation could be a new approach to control cyanobacterial blooms; however, intensive research efforts are required to pursue this aim.

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Author Contributions

Conceptualization: K.F.; writing-original draft preparation: A.B.; review and editing: A.B and K.F.

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